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Increased fire risk in Mojave and Sonoran shrublands due to exotic species and extreme rainfall events

Kirk A. Moloney,[1,†] Erika L. Mudrak,[1,2] Andres Fuentes-Ramirez,[1,3,4] Hadas Parag,[5]
Marjolein Schat,[5] and Claus Holzapfel[5]

[1]*Department of Ecology, Evolution and Organismal Biology, Iowa State University, 251 Bessey Hall, 2200 Osborne Dr, Ames, Iowa 50011 USA*
[2]*Cornell Statistical Consulting Unit, Cornell University, 244 Garden Avenue, Ithaca, New York 14850 USA*
[3]*Laboratorio de Biometría, Departamento de Ciencias Forestales, Universidad de La Frontera, Casilla 54-D, Temuco, Chile*
[4]*Instituto de Ecología y Biodiversidad (IEB), Santiago, Chile*
[5]*Department of Biological Sciences, Rutgers University, 195 University Avenue, Boyden Hall 408 (lab 435), Newark, New Jersey 07102 USA*

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Abstract. Historically, desert ecosystems in the southwestern United States have been characterized by low incidence of fire. However, widespread wildfires in these systems have been recently observed. Large areas of creosote bush (*Larrea tridentata*) scrub scattered in the Mojave and Sonoran deserts were impacted by wildfires in 2005, after a series of years with above-average precipitation. It has been hypothesized that exotic invasive grasses, for example, *Schismus arabicus*, are responsible as they are able to grow in the open and may produce sufficient biomass to carry fires during high-rainfall years. However, there has been little experimental evidence to support this hypothesis. We conducted a field experiment exploring the response of the annual plant community to increased rainfall in two creosote-dominated sites in the Sonoran and Mojave deserts by manipulating precipitation levels, fire history, soil disturbance, and exotic-annual-plant seed availability. We examined how these treatments impacted fuel loads (biomass) and species distributions as a function of distance from shrubs. We found that enhanced rainfall produces a general increase in biomass and density of annual plants. At the Sonoran site, rainfall tends to increase the density of exotic annuals. At the Mojave site, it is the opposite, where native annuals benefit more from higher rainfall. However, it is important to note that in the Mojave site, native annuals produce higher biomass under shrubs and exotic annuals produce higher biomass in the open in response to increased rainfall. The introduction of fire at both sites slightly increased biomass production as well. Soil disturbance and seed addition had only subtle effects. From our results, it is clear that increased rainfall in southwestern U.S. deserts is conducive to increasing biomass of annual plants, especially in the inter-shrub areas, which in turn can lead to enhanced fire risk. The potential to shift toward higher dominance by exotic annuals with fire at the Sonoran site could further enhance this risk. With several consecutive years of high rainfall, increased seed production by exotics would potentially amplify this effect.

Key words: climate change; creosote shrublands; exotic species; extreme events; fire; invasive species; *Larrea tridentata;* Mojave; precipitation; *Schismus arabicus;* Sonoran; Southwest Desert.

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† **E-mail:** kmoloney@iastate.edu

INTRODUCTION

Global climate change is considered to be one of the greatest environmental challenges faced by mankind (Vitousek 1992, IPPC et al. 2007). The primary driver is global warming due to the increasing presence of anthropogenically produced greenhouse gases in the atmosphere (Vitousek 1992). Potentially more important in an ecological context will be an increase in variability of the global climate in time and space (Schar et al. 2004, Jentsch et al. 2009). This is predicted to lead to more extreme weather events (Karl et al. 1995, Karl and Knight 1998, Easterling 2000, Easterling et al. 2000, Diffenbaugh et al. 2005). Less fully appreciated are the numerous cascading effects that will also occur due to global climate change, many of which include impacts on the biosphere (Parmesan 2006, Scholze et al. 2006, Thuiller et al. 2008, Jentsch et al. 2009). Species distributions are shifting toward more extreme latitudes and altitudes as temperatures increase, with more mobile species being able to respond more readily to shifting climatic patterns than less mobile species (Iverson and Prasad 1998, Kelly and Goulden 2008, Thuiller et al. 2008). The timing of biological events is also changing, with earlier flowering, breeding seasons, and arrival of migrant birds and butterflies (Parmesan and Yohe 2003, Schwartz et al. 2006). These changes may also cause irreversible shifts in the functioning of ecosystems.

One of the most striking examples of cascading effects produced by climate change is the increased occurrence of severe wildfires globally (Piñol et al. 1998, Moritz et al. 2012). In North America, the prevalence of record setting fires in natural ecosystems has been well publicized over the last several decades (Westerling et al. 2006). Currently, we are seeing an increase in frequency and severity of fires across the western United States. Several studies have linked these fires to the historical suppression of fire, leading to higher accumulation of fuels (Hurteau et al. 2014, Coen et al. 2018). Moreover, fire exclusion can interact with other phenomena, such as the widespread mortality of trees due to the attack of bark beetles, the occurrence of extreme drought events, and higher summer temperatures (Allen et al. 2010, Berner et al. 2017). As a result, massive and destructive wildfires can occur more frequently. The drought conditions and high temperatures leading to these wildfire outbreaks are thought to be directly related to climate change (Allen et al. 2010). Other areas of the globe, including non-fire-adapted ecosystems, are also being increasingly influenced by wildfires due to factors related to climate change and human disturbances (e.g., introduction of exotic invasive plant species; D’Antonio and Vitousek 1992, Brooks and Matchett 2006, Parks et al. 2015).

Perhaps least well understood with respect to fire risk are systems that have historically been less prone to fire but are now are being increasingly impacted (Brooks and Matchett 2006). For example, arid and semiarid desert ecosystems, such as creosote bush (*Larrea tridentata* (DC.) Cov.) scrub in the desert southwest of the United States, are becoming more susceptible to fire (D’Antonio and Vitousek 1992, Brooks and Matchett 2006, Brooks and Chambers 2011, Fuentes-Ramirez et al. 2016). One reason for this is the presence of exotic species that grow in dense populations in areas where there is only sparse growth by native species (Brooks et al. 2004, Brooks and Matchett 2006, Fuentes-Ramirez et al. 2016). Fuel loads increase due to the presence of exotics, particularly during wet climate cycles. This has led to an increasing prevalence of wildfire in areas with little or no historical occurrence of these types of events (Parks et al. 2015). Compared to forest or grassland ecosystems, fire impacts have been less studied in arid and semiarid deserts by ecologists, and the mechanisms by which the plant community responds to fire still remain unclear (but see Rao and Allen 2010, Rao et al. 2011, Martin et al. 2012), further exacerbating our limited understanding of the potential for increased fire risk, especially under scenarios of climate change.

As stated above, the historical lack of fire in creosote shrublands has been ascribed to the fact that most native annuals grow under-canopy of the dominant shrubs, with not enough biomass (fuel) occurring between shrubs to carry fire. It is further argued that this has changed with the invasion of the system by exotic annual plants, such as *Schismus arabicus* Ness, *Brassica tournefortii* Gouan, and *Bromus rubens* L., which are able to grow in the open inter-shrub areas and produce a continuous layer of fine fuels between the shrubs that can carry fire (Brooks and Matchett 2006, Fuentes-Ramirez et al. 2016). Fire risk is further intensified during years of heavy rainfall when exotic species can rapidly proliferate over vast areas (Hereford et al. 2006, Rao et al. 2010). A clear example of this occurs in the Sonoran and Mojave deserts, where the invasive grasses *S. arabicus* and *B. rubens* establish at high densities after elevated rainfall (Brooks and Matchett 2006, Schafer et al. 2012). Strong evidence for the relationship between high rainfall and increased fire risk, due to fine fuel production by exotic invasive species, is provided by the well-documented, widespread outbreak of fires in 2005, following three years of historically high rainfall levels in the Sonoran and Mojave deserts (Brooks and Matchett 2006, Esque et al. 2013).

The scenario for increasing fire risk in creosote shrublands was developed primarily through observational studies in the Mojave Desert and has been assumed to be similar in the creosote shrublands of the Sonoran Desert. However, preliminary evidence suggests that increasing fire risk in the Sonoran Desert under extreme rainfall may also be driven by native species, which more readily grow in the open (Schafer et al. 2012). Why the Sonoran native species grow more in the open is still unknown but could be associated with the fact that creosote shrubs are smaller than in the Mojave (Mudrak et al. 2014), exerting less influence on the distribution of annuals due to a lesser nutrient island effect. Also, the existence of summer monsoonal rains in the Sonoran Desert serves to moderate the impact of drought, allowing native annuals to grow more in the open inter-shrub areas.

There is clearly a need to examine more thoroughly the cause and effect relationships among invasive exotic species, native species, and climate factors in the Mojave and Sonoran deserts to better understand the risks of future catastrophic fires in these systems. Toward that end, we designed a field experiment examining the causal relationships linking fire, extreme rainfall events, soil disturbance, and seed limitation to the growth of exotic and native annual plants. We hypothesized that (1) increased rainfall leads to a buildup of fine fuels in the inter-shrub area, dominated by exotic annuals in the Mojave Desert and a higher proportion of native annuals in the Sonoran Desert; (2) the occurrence of fire and disturbance enhances the patterns produced by increased rainfall; and (3) seed limitation for exotic invasive species in the Sonoran Desert is partially responsible for the higher abundance of native species in the inter-shrub areas.

In two desert sites, one each in the Mojave and Sonoran deserts, we combined a suite of experimental small-scale burns with water availability manipulations (irrigation and rainout shelters) and soil surface disturbance treatments to examine their impacts on the distribution and abundance of both native and exotic annual plant species. Although the two sites were chosen to represent two ends of a spectrum, going from a northern Mojave site with little or no summer rains to a Sonoran site impacted by summer monsoonal rains, we cannot make any direct comparisons due to lack of replication within deserts, which was a limitation imposed by logistical and funding agency constraints.

The study at both sites was done in a spatial context, recognizing that the distribution of annual plants in these deserts is greatly influenced by the presence of creosote shrubs, which are widely spaced and produce a significant nutrient island effect (Mudrak et al. 2014). We were particularly interested in exploring potential feedbacks between fire and the distribution and abundance of exotic annual plants, as an earlier study has shown that soil nutrients become less concentrated under shrubs over time after a fire event, potentially leading to further dominance by exotic annuals at the expense of the native species (Fuentes-Ramirez et al. 2015). This could in turn lead to increased fire risk going forward.

METHODS

Experimental plots

Our experiment was conducted in two *L. tridentata* (DC.) Cov.-dominated shrublands located in the Sonoran and Mojave deserts. The Sonoran Desert site was characterized by summer and winter rainy seasons, whereas the Mojave site has only a winter rainfall season. WeatherHawk 232 climate stations were installed at each of the sites in the fall of 2010 and operated until spring of 2014 and recorded hourly weather data, including rainfall. The Sonoran Desert site

(32.697° N, 112.839° W) was located on a flat area (Holocene lower bajada) within the eastern section of the Barry M. Goldwater Range at an elevation of 322 m, approximately 30 km south of Gila Bend, Arizona. *Larrea tridentata* (hereafter referred to as *Larrea*) is the single dominant perennial shrub at this site. The Mojave study site (35.156° N, 116.885° W) was located within the Fort Irwin National Training Center, California, USA, at an elevation of 865 m on a southeast-facing Holocene upper bajada with a 7.5% grade. Unlike the Sonoran site, *Larrea* and *Ambrosia dumosa* (A. Gray) Payne (referred to as *Ambrosia*) were codominant shrubs in the Mojave site. However, our experiment focuses on the impact of *Larrea*, as *Ambrosia* is much smaller in comparison (mean basal area 0.53 m^2 vs. 3.47 m^2 for *Larrea*) and makes up only about one-tenth of the total canopy volume of *Larrea* in the study area (Mudrak et al. 2014).

Experimental plots were constructed at each of the two sites in September 2010. Each plot was 83 × 130 m in size. Within each plot, all *Larrea* shrubs were georeferenced and quantified by size (see Mudrak et al. 2014 for methods used). We will use the metric *Larrea*-stem-volume to characterize the size of individual shrubs. *Larrea*-stem-volume was calculated using values measured for height (H), stem area (S), and area of the canopy top (T) for each shrub as $V_{\mathrm{shrub}} = H/3\ (S + T + (S \times T)^{0.5})$. S and T were determined as in Mudrak et al. (2014; S and T are equivalent to A_{base} and A_{top} in the referenced paper).

Within each site, 168 *Larrea* individuals were selected to serve as focal shrubs for the experiment. Selection of shrubs was stratified spatially by choosing 24 shrubs at random within each of seven equal area strips arrayed along the long axis of the plot to control for spatial variability. Two transects were run in parallel from the base of each shrub. The two transects were separated horizontally in the E–W direction by 10–25 cm, depending upon shrub size. Half of the transect pairs were run to the south of the shrub and half to the north. Four 20 × 20 cm experimental units (i.e., microplots) were located along each transect to characterize different microhabitats (referred to as the "habitat treatment") associated with the fertility island effect produced by shrubs in semiarid environments (Garcia-Moya and McKell 1970, Schlesinger et al. 1996, Mudrak et al. 2014, Fuentes-Ramirez et al. 2015). Moisture and nutrient availability are strongly impacted by shrubs in these semiarid systems, affecting the distribution of other plant species. The four habitat treatments included in the experiment were the under-canopy (UC) habitat; the canopy drip-line (CD) habitat; open, near-to-shrub (ON) habitat; and open, far-from-shrub (OF) habitat. The microplots representing the UC habitat were placed 0–10 cm away from basal *Larrea* stems in the Sonoran site and 5–35 cm in the Mojave site. The UC microplots were used to characterize environmental conditions directly under the shrub. The location of the UC microplots varied based on the overall geometry of the shrub and reflects the fact that shrubs were generally larger at the Mojave site (Mudrak et al. 2014). Canopy dripline microplots were placed at a position along the transect that was visually determined to be at the edge of the shrub canopy, representing the transition between shaded locations under the influence of the canopy and locations fully in the open. The centers of the ON and OF microplots were located 60 and 140 cm from the canopy dripline, respectively (Fig. 1). The OF microplots were located such that they represent sites least under the influence of neighboring shrubs, given the average spacing of shrubs. Total transect length ranged from 184 to 308 cm (mean = 221 cm) in the Mojave site and 180 to 266 cm (mean = 206 cm) in the Sonoran site, due to the variability in shrub size influencing the placement of the UC microplots.

Pretreatment site characterization

Site conditions were characterized during 2010 in anticipation of introducing experimental manipulations in 2011. Soil nutrient distributions as a function of shrub size and distance from shrub at both sites were modeled as reported in Mudrak et al. (2014). All of the microplots were censused for number of emergent seedlings by species during 4–12 November 2010 in the Mojave and 21–24 January 2011 in the Sonoran. The Sonoran census was conducted later due to later arrival of winter rains. A second census counting all surviving plants was conducted in the microplots from 17 March to 4 April 2011. Complete census results can be found in Schafer et al. (2012). We will provide a reanalysis of a subset of the data corresponding to the

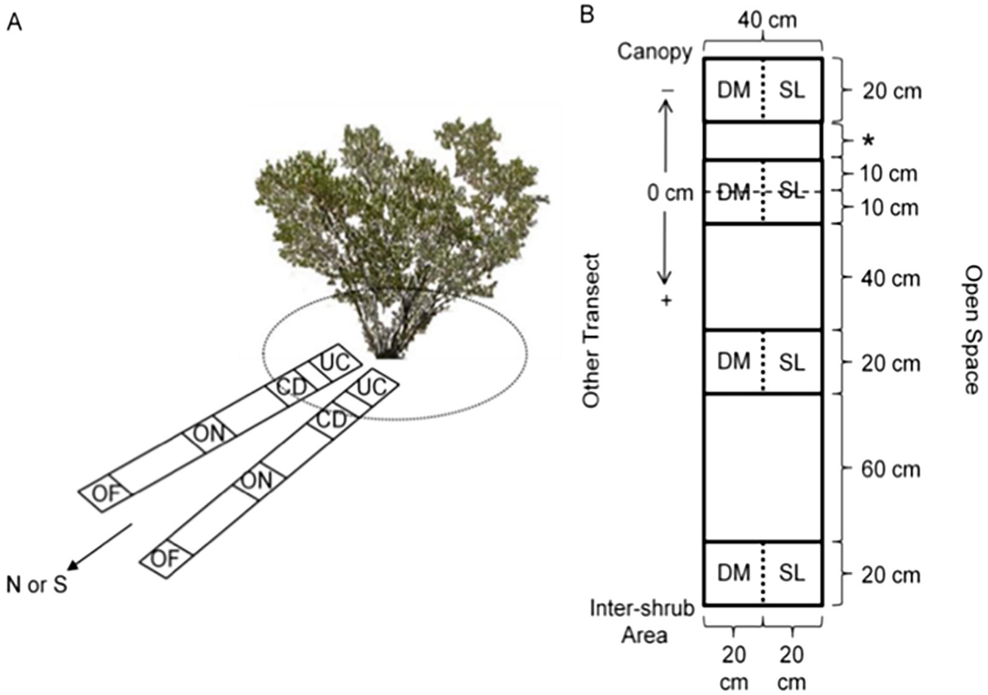

Fig. 1. *Larrea* experimental transects. (A) Shrub diagram with transects, microplots, and a dotted line indicating the location of the *Larrea* canopy dripline. UC, under-canopy; CD, canopy dripline; ON, open, near-to-shrub; and OF, open, far-from-shrub habitats. (B) Transect diagram with plot sizes and distances between plots within a transect. DM, demography microplot (always oriented toward the other transect); SL, soil collection microplot (always oriented away from the other transect); * indicates that this distance is variable and depends on the size of the shrub. The midpoint of the CD plot is considered to be at 0 cm, such that each transect ends 150 cm into the inter-shrub area and a possible location for the UC plot is −20 to −40 cm.

microplots used in the experiment described below to provide a more direct comparison with the results of the experiment.

Experimental design

Manipulation of microplots involved five different treatments, applied in a split-plot, factorial design: (1) *Fire*—burned (B) vs. unburned (UB); (2) *Turbation*—turbated (T) vs. unturbated (UT); (3) *Precipitation*—drought (D), ambient (A) and excess (E) precipitation levels; (4) *Seed limitation*—seed addition (Sd) and no seed addition (USd); and (5) *Transect direction*—north (N) and south (S). All treatments were applied at the level of the shrub in a factorial design, except for turbation. In the case of turbation, microplots along one of the two transects for each shrub were turbated and the microplots along the second transect were unturbated (treatment methods described below). The complete experimental design consisted of 168 shrubs (2 fire × 3 precipitation × 2 seed limitation × 2 transect directions × 7 replicates; see Appendix S1 for a map of treatments at both experimental sites) and 1344 microplots (168 shrubs × 2 transects × 4 microplots). However, we eliminated several treatments from the design before introducing treatments due to logistical constraints. Collection of the pretreatment data proved to be extremely time-consuming and impractical when all 1344 microplots were included. We eliminated several of the treatment combinations involving the S-facing transect treatment. For south-facing (S) transects, we dropped the drought (D) and excess (E) precipitation treatments involving burned (B) shrubs (224 microplots) and the D precipitation treatment for UB shrubs (112 microplots), resulting in 1008 microplots at each site in the final experiment. The decision to drop treatments from the S-facing transects was based on the analysis of pretreatment data, which showed conclusively that there were more annuals growing on the north side of shrubs due to increased shading (Schafer et al. 2012), coupled with the added effort involved in implementing the B, D, and E treatments (see *Fire treatment* and *Precipitation treatment* sections).

Fire treatment.—In June 2011, 56 of the focal *Larrea* shrubs were burned at the Mojave Desert site, 42 with N-facing transects and 14 with S-facing transects. Shrubs for the burn treatment were chosen at random from the 168 focal shrubs, with the restriction that they could not be closer than 4 m to other treatment shrubs to avoid impacting them by the effects of fire. Shrubs and dry annual vegetation under shrub canopies and along the transects were ignited with Fusee flares, and the fire was allowed to finish uninterrupted. Fusees (Orion Safety Products, Easton, Maryland, USA) are easily controllable, ignite at 191°C, burn as hot as 1600°C, and can be used to ignite plant material that is relatively moist. Unlike drip torches, only minimal amounts of residue from Fusees come in contact with the soil surface. Fifty-six shrubs were burned at the Sonoran site in late September 2011 using the same protocol.

The fire treatment we imposed had an impact on individual shrubs and the immediate area surrounding the shrub but may differ in impact from natural wildfires that affect a broader area. This has implications on the distribution of nutrients and moisture after fire.

Turbation treatment.—Soil disturbances were produced by breaking up any soil surface crusts present and turning and mixing soil up to a depth of 10 cm using a hand trowel. This was done to determine whether the presence of biological crusts has an impact on patterns of plant recruitment.

Precipitation treatment.—The three levels of the precipitation treatment were randomly assigned to shrubs using the reduced experimental design. This resulted in 28, 56, and 42 shrubs with the D, A, and E precipitation treatments, respectively. The transects for the shrubs receiving the D treatment were covered by rainout shelters that were erected to intercept 50% of incoming precipitation, using a design adapted from Yahdjian and Sala (2002; Fig. 2). Shrubs with the A treatment had no modification. Water was added to the transects of the E treatment shrubs by controlled hand irrigation and was equivalent to 25 mm of rain in the Mojave Desert site and 12.5 mm in the Sonoran site, where larger amounts could not be used due to higher runoff. Water was applied during the winter growing season, approximately once a month, starting at the end of December and was last applied 2–4 weeks prior to peak vegetation and flowering, resulting in three applications per winter growing season in the Mojave Desert site, and two in the Sonoran Desert site. Overall, the amount of water available in the E treatment was 191% of the long-term, average annual rainfall and 426% (2012) and 334% (2013) of ambient precipitation in the Mojave Desert site and an increase of 133% in the long-term average and 139% (2012) and 160% (2013) in ambient precipitation in the Sonoran Desert site. The intent of the E treatment was to mimic years with extreme amounts of rainfall.

Although the local microplots directly received the adjusted amounts of precipitation in the three treatments, the amount of rain received in the surrounding site remained at ambient levels. This may influence the overall impact of our precipitation treatments relative to the impact of changes in precipitation at the scale of the landscape.

Seed limitation treatment.—Seeds of potentially seed-limited, but already present, exotic, invasive species were added to half the shrubs. *Brassica tournefortii* and *S. arabicus* were added in the Sonoran site, and *B. rubens* was added at the Mojave site in September 2011, before the onset of the winter rainy season. We decided not to add *Schismus* at the Mojave site since natural seed densities were very high, even before addition, and additions would not significantly increase plant densities. Seeds were added by scattering on the ground. We added the number of germinable seeds needed to produce 20 plants each of *Brassica* and *Bromus* and 40 of *Schismus.* We added twice the amount of *Schismus* as it tends to be smaller than the first two species and typically occurs at high densities. The seeds of the three exotic species were collected in various locations in the Mojave and Sonoran deserts during March–April 2010. Seeds were not collected at our experimental sites, as the sites were not yet determined at the time. Seeds were cleaned, quantities calculated, and germinability tested at the Rutgers Newark Lab. Decision of which seed

Fig. 2. Completed rainout shelter at the Fort Irwin study site.

sources to use was made according to the number of seeds available for the species, best germination rates, and collection sites similar or close to the experimental sites.

Data collection

After introducing the above-mentioned treatments at the end of the growing season in 2011, vegetation data were collected during the two following growing seasons (2012 and 2013). The densities of all annual plant species and total annual plant cover values were determined in each microplot during peak development in March 2012 and March/April 2013 for the Mojave Desert site and February 2012/March 2013 for the Sonoran Desert site. Cover was visually estimated.

We determined aboveground peak biomass of the entire plant community separately for each desert site in each microplot for each census. This was done nondestructively from measures of percent aerial cover (*cov*) and height (*h*) in cm, using regressions of these quantities against dry biomass (*bio* in g/100 cm^2). Regressions were developed in an analysis of plants harvested from similar microplots in adjacent areas at each site during each year of the study (Appendix S3).

Ambient precipitation at the Mojave site was well below long-term averages (Table 1), resulting in extremely low levels of biomass and density during our study. In contrast, rainfall at the Sonoran site was slightly above average, at least as compared to a nearby reference weather station in Gila Bend, Arizona, USA (Table 2). We selected the year with the most biomass production at each site for experimental analysis and analyzed each site separately (Table 2): that is, 2013 for the Mojave Desert site and 2012 for the Sonoran Desert site.

Statistical analysis

Response variables that were analyzed pre- and post-treatment included (1) total biomass, (2) total density (density of all annual plants), (3) *Schismus* density, and (4) proportion of native plants (i.e., native density/total density). For

Table 1. Monthly precipitation data collected from on-site weather stations at the BMG Sonoran study site and the Fort Irwin Mojave study site, along with long-term averages from nearby weather stations.

	Precipitation					
	Site (mm)				Reference station, average	
Month	2010	2011	2012	2013	Inches	mm
BMG Sonoran site†						
January		25	0	18	0.61	15
February		35	0	9	0.62	16
March		15	16	5	0.61	15
April		12	4	0	0.21	5
May		0	0	0	0.13	3
June		0	0	0	0.05	1
July		15	19	68	0.73	19
August		3	88	53	0.99	25
September		8	33	9	0.51	13
October		0	0	0	0.38	10
November	6	44	0	59	0.5	13
December	19	20	10	3	0.68	17
Total	25	177	170	224	6.02	153
Fort Irwin Mojave site‡						
January		0	1	9	0.72	18
February		8	0	0	0.59	15
March		4	1	11	0.61	15
April		0	7	0	0.21	5
May		0	0	0	0.08	2
June		0	0	0	0.12	3
July		1	1	3	0.27	7
August		0	10	7	0.31	8
September	0	3	0	1	0.26	7
October	17	3	0	1	0.27	7
November	10	5	0	29	0.37	9
December	109	6	12	0	0.51	13
Total	136	30	32	61	4.32	110

Note: Long-term data were obtained from the Western Regional Climate Center website (https://wrcc.dri.edu) on 14 September 2017.

† Reference station in Gila Bend, Arizona, USA. Averaged from 1 December 1892 to 19 June 2014.

‡ Reference station in Barstow, California, USA. Averaged from 1 January 1903 to 31 March 1980.

pretreatment analysis, data were collected in 2011 before treatments were applied. These provided a baseline for the relationships in the system, although there was a great deal of year-to-year variability in plant density and total biomass due to between-year differences in rainfall and temperature. Pretreatment analyses for this same system have been reported elsewhere (Schafer et al. 2012), although those analyses were structured quite differently, using all 1344 microplots at each site. We present a brief reanalysis here, structuring the data the same way as in the analysis of the current experiment for a more direct comparison of pre- and post-experiment results; that is, we used only the 1008-microplot subset from each site, although for the pretreatment analysis we averaged the values of the pair of microplots in the same microhabitats located in the two transects. This was done to avoid pseudo-replication within a shrub. The two transects were analyzed separately for the experiment as they represented the two levels of the turbation treatment.

All analyses were conducted in R (R Core Team 2017). Analysis of density data and proportion of native plants was conducted using the *glmer* function from the *lme4* package (Bates et al. 2015), using a Poisson error model for density and a binomial error model for proportion native. Analysis of biomass data was conducted using the *lme* function.

Biomass pretreatment data were analyzed using a Hurdle model, due to zero-inflated data in 2011, especially at the Sonoran site (Table 2). This was not done in the analysis of the experimental data, as we only analyzed the experiment in years that had relatively few observations of zero biomass. The first step in the Hurdle model was to estimate the probability that microplots had zero measured biomass. The second step was to only include microplots with biomass greater than zero in a mixed-model regression analysis.

Zero-inflated data were not a problem for the density variables as many of the microplots recorded with zero biomass had plants in them, just in low numbers. Also, density data were modeled as a Poisson process, which does allow inclusion of zero values. The analysis of the proportion native plants was modeled as a binomial process (i.e., observed individuals were either native or exotic) weighted by the number of observations in the sample; observed values of zero density were therefore not included in the analysis.

We conducted a mixed-model analysis for the pretreatment data with habitat (*mh*) and transect direction (*dir*) as fixed effects, *Larrea* shrub volume (*lsv*) as a cofactor, and shrub (*shID*) as a random effect, that is, *glmer*(density ~ *mh* × *dir* + *lsv* + (1|*shID*), family = poisson) for density,

Table 2. Least-squares means estimates for biomass in grams for 20 × 20 cm microplots in the four habitats of the Sonoran and Mojave deserts for the three census years 2011, 2012, and 2013.

	UC			CD			ON			OF		
Site and year	Prob non-zero	Mean	95% CI	Prob non-zero	Mean	95% CI	Prob non-zero	Mean	95% CI	Prob non-zero	Mean	95% CI
Mojave												
2011	0.92	4.17	3.81–4.58	0.94	3.50	3.19–3.84	0.92	2.1	1.89–2.34	0.86	1.64	1.47–1.85
2012	0.07	0.03	0.02–0.05	0.12	0.04	0.03–0.06	0.19	0.02	0.02–0.03	0.23	0.02	0.02–0.03
2013	0.47	1.20	1.70–2.35	0.7	1.92	1.70–2.20	0.84	1.30	1.19–1.43	0.83	1.00	0.90–1.11
Sonora												
2011	0.1	0.15	0.11–0.21	0.06	0.231	0.11–0.64	0.1	0.15	0.11–0.21	0.08	0.15	0.08–0.29
2012	0.98	2.45	2.20–2.75	0.97	1.93	1.72–2.18	0.95	1.23	1.08–1.42	0.93	1.23	1.06–1.43
2013	0.96	1.08	0.99–1.19	0.98	1.01	0.92–1.11	0.99	0.76	0.69–0.83	0.95	0.72	0.64–0.90

Notes: Mean biomass values were estimated using a Hurdle model as described in the *Methods* section. Separate analyses were conducted for each habitat without consideration of the underlying experimental design. These results are not presented for hypothesis testing, but to illustrate the year-to-year variability in biomass values characterizing these study sites. Prob non-zero is the probability that a microplot will have non-zero biomass. Mean is the mean biomass for microplots containing biomass. 95% CI is the 95% confidence interval for the estimated mean. Microhabitat designations are the under-canopy (UC) habitat, the canopy dripline (CD) habitat, open, near-to-shrub (ON) habitat, and open, far-from-shrub (OF) habitat.

glmer(propNative ~ *mh* × *dir* + *stem_vol* + (1|*shID*), weights = totalDensity, family = binomial) for proportion native plants, and *lmer*(biomass ~ *mh* × *dir* + *lsv* + (1|*shID*)) for biomass.

Analyses similar to those of the pretreatment data were conducted for the experimental results, although the model structure was more complex due to the unbalanced, nested factorial treatment design as described above (*trans:shID* is a nesting factor of transect within shrub, and *mh:trans:shID* is microplot nested within transect, which is nested within shrub). Fixed effects included (1) habitat (*mh*), (2) fire treatment (*fire*), (3) precipitation treatment (*precip*), (4) turbation treatment (*turb*), and (5) seed treatment (*seed*), with *lsv* as a covariate. The full model analyzed included all interactions among the first four treatments, with seed only entering as a main effect, that is,

$$\begin{aligned} &lmer(\text{biomass} \sim mh \times fire \times precip \times turb + \\ &\quad seed + lsv + (1|shID) + (1|trans:shID)) \end{aligned}$$

and

$$\begin{aligned} &glmer(\text{density} \sim mh \times fire \times precip \times turb \\ &\quad + seed + lsv + (1|shID) + (1|trans:shID) \\ &\quad + (1|mh:trans:shID), \text{family} = \text{poisson}) \end{aligned}$$

After analysis of the full model, we reduced the model by sequentially removing higher-order interactions that did not contribute to model significance. This was assessed using the R ANOVA function and *F*-tests to determine whether there was a significant difference between models with or without the interaction being removed. Terms were removed if there was no significant difference between models with and without the term. This same approach was applied to main effects that were no longer involved in an interaction term remaining in the model. Model reduction stopped once terms could not be removed without creating a difference in model significance.

After model reduction, we used *lsmeans* analysis in R to determine whether there were significant pairwise treatment differences in the reduced models (Lenth 2016).

RESULTS

Pretreatment

Plant densities and total biomass were much lower at the Sonoran site in 2011 than at the Mojave site (Table 2; Schafer et al. 2012). In fact, only total density could be analyzed for the Sonoran site due to the low numbers of plants.

In the Mojave site, a majority of the plants were invasive species (primarily *Schismus*) within all microhabitats (Fig. 3). The interaction between transect direction and habitat was significant for all analyses conducted on pretreatment data (Figs. 3, 4). Total density at the

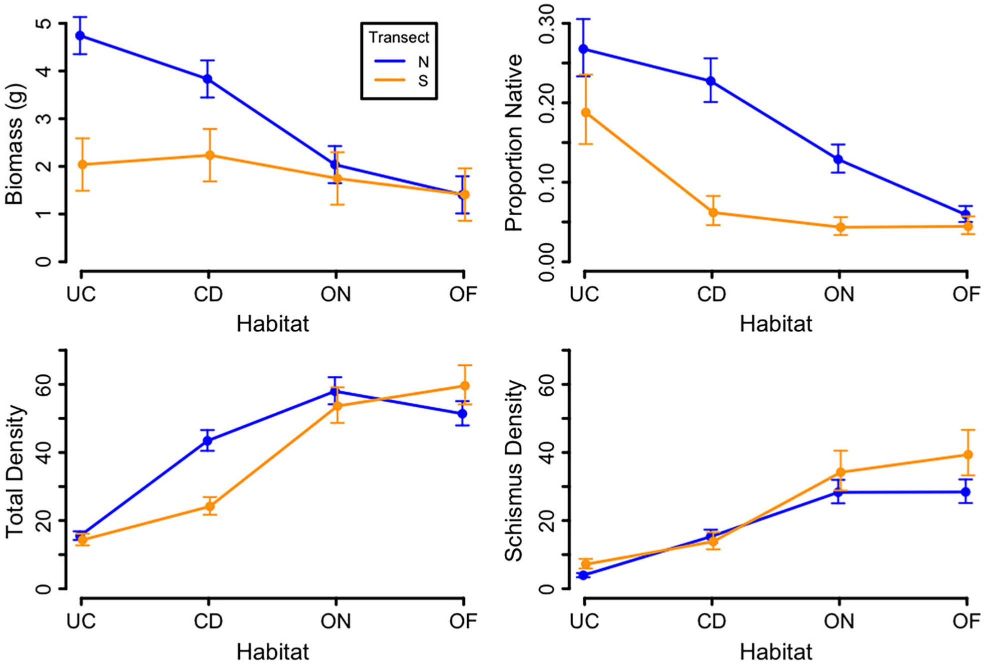

Fig. 3. Pretreatment least-squares means estimates for direction × habitat for the Mojave Desert experimental site in 2011. Data values are based on mixed-model analysis results with error bars representing 95% confidence intervals of the estimates. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section. Proportion native and density means and confidence intervals were back-transformed to the original scales before plotting the figure.

Sonoran site was significantly higher on the north side of shrubs than on the south for all comparisons within habitats, perhaps due to a shading effect to the north by the shrubs (Fig. 4). The pattern was not as clear for the Mojave site as the differences between transects were not consistent across habitats or among response variables (Fig. 3). For biomass, the values near to the shrub (UC and CD) were higher for the north transect, but away from the shrub (ON and OF), there was no difference in density. With respect to total density, only the canopy dripline (CD) exhibited higher values to the north. Proportion native plant density was higher in all microhabitats to the north, with the exception of OF.

In the Mojave site, biomass declined with distance from the shrub, especially to the north, whereas density increased, perhaps indicating a decreasing trend in self-thinning with distance from the shrub, as a result of less biomass production producing fewer competitive interactions. Density levels at the Sonoran site were too

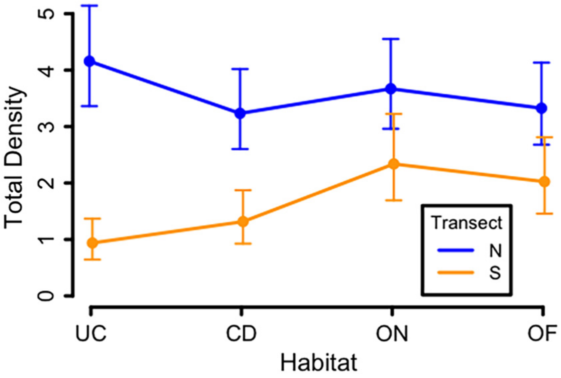

Fig. 4. Pretreatment least-squares means estimates for total density at the Sonoran Desert experimental site in 2011. Data values are based on mixed-model analysis results with error bars representing 95% confidence intervals of the estimates. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section. Density means and confidence intervals were back-transformed to the original scales before plotting the figure.

low to show any observable trend with distance from shrub.

Annual plant biomass

In both the Mojave and Sonoran experiments, there was a significant effect of precipitation on the biomass response (Table 3). In both sites, the greatest biomass production was seen in the water addition treatment (E), as expected (Fig. 5; Appendix S2: II.2.2.4 and II.2.1.2). This effect was the greatest in the Mojave site where the increase in biomass was as high as 5× the biomass at the canopy dripline habitat as compared to the ambient rain (A) and drought (D) treatments. Although we expected a priori that the ambient rain treatment (A) would yield higher biomass levels than the drought treatment (D), we observed the opposite with significantly lower *lsmeans* values for the A treatment in both desert sites (Fig. 5; Appendix S2: II.2.2.4 and II.2.1.2). Whether this was due to an environmental effect of the rainout shelters is not clear but represents a possibility.

In the Sonoran Desert site, the precipitation effects were independent of all other treatments (Appendix S2: II.2.2.4). However, in the Mojave site there was a significant interaction with habitat. For the rain addition treatment (E), the highest biomass values were observed at the canopy dripline (CD) where biomass was significantly greater than in all other habitats (Appendix S2: II.2.1.2.1). In contrast, there were no significant differences among habitats within the ambient rain or drought treatment, with the exception of slightly lower values in the undercanopy (UC) within the drought treatment.

In the Sonoran Desert site, biomass levels were the lowest in the habitats away from shrubs (ON and OF) and generally increased in value in the vicinity of shrubs (UC and CD; Fig. 5). The nature of this increase, however, was influenced by significant two-way interactions between habitat and the fire and turbation treatments. The turbation treatment only influenced the biomass response in the under-canopy (UC) habitat, where there was a significant increase in biomass with turbation. Burning a shrub had a broader impact, significantly increasing the amount of biomass produced in both shrub influenced habitats (UC and CD). There was also a significant

Table 3. Final reduced models for response variables with highest-order interactions involving each independent treatment factor remaining in the model after eliminating interactions that did not contribute to model significance.

Response variable	Mojave Desert 2013	Sonoran Desert 2012
Biomass†	Habitat × Precipitation Fire	Habitat × Fire Habitat × Turbation Precipitation Seed
Total Density‡	Habitat × Precipitation§ × Fire Precipitation§ × Fire × Turbation Habitat × Turbation Shrub_volume	Habitat × Fire Habitat × Precipitation Habitat × Turbation Seed
Schismus Density‡	Habitat × Precipitation§ × Fire Precipitation§ × Fire × Turbation Habitat × Turbation Seed	Habitat × Precipitation Turbation Seed
Proportion Native¶	Habitat × Precipitation§ Precipitation§ × Turbation Fire Shrub_volume	Habitat × Precipitation Habitat × Fire Habitat × Turbation Precipitation × Turbation Turbation × Fire Seed Shrub_volume

† *lmer* analysis with the following nested, random factors: (1|*larrea_id*) + (1|*transSide:larrea_id*).

‡ *glmer* analysis with *family* = *poisson* and the following nested, random factors: (1|*larrea_id*) + (1|*transSide:larrea_id*) + (1|*mh:transSide:larrea_id*).

§ Precipitation treatments in the Mojave 2013 analysis did not include D as there were too many empty plots due to the prevailing drought conditions.

¶ *glmer* analysis with *family* = *binomial* and the following nested, random factors: (1|*larrea_id*) + (1|*transSide:larrea_id*) + (1|*mh:transSide:larrea_id*).

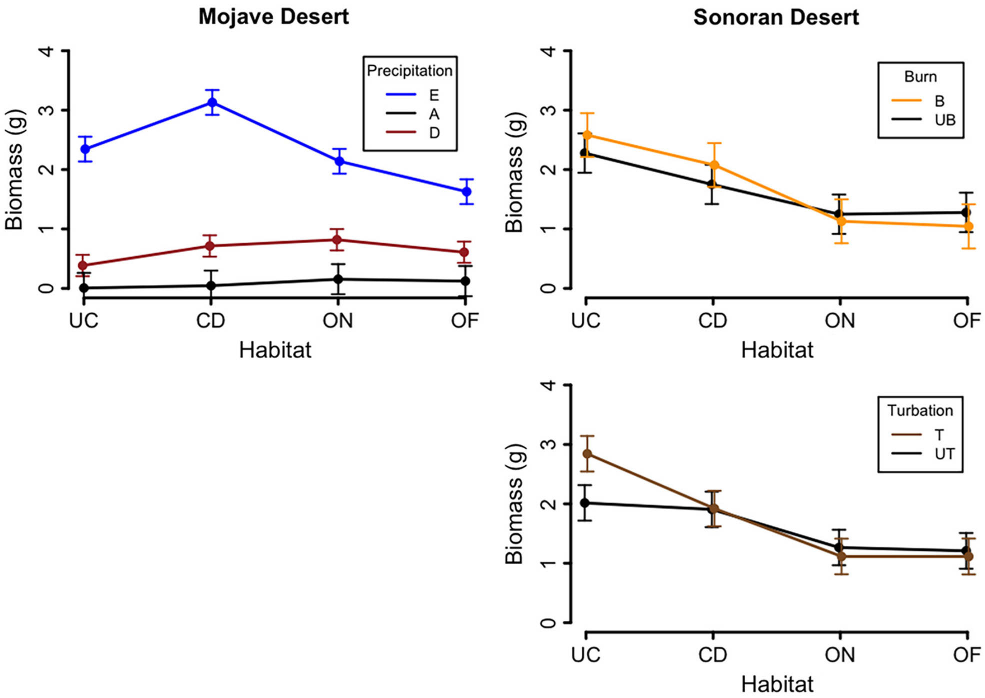

Fig. 5. Significant experimental results for biomass involving an interaction with habitat. Error bars indicate 95% confidence intervals. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section.

increase in biomass produced by burning in the Mojave site, but this was independent of all other treatments (Appendix S2: II.2.1.3).

Seed addition only had a significant effect in the Sonoran Desert site, where there was a slight increase in biomass production with the addition of exotic seed (Appendix S2: II.2.2.5). Movement of added seed out of the microplots, since seeds were simply scattered on the soil surface, may have played a role in the low significance of this treatment.

Total density

The distribution patterns for total annual density with respect to habitat were quite different from the biomass patterns (Fig. 6). In the Sonoran Desert site, total density was the same in all habitats with the exception of the under-canopy habitat, which had significantly lower total densities when compared to some of the other habitats in some treatment combinations (Fig. 6; Appendix S2: II.3.2). There were also significant two-way interactions between habitat and three of the other treatments: precipitation, fire, and turbation (Table 3). The interaction between precipitation and habitat was due to a decrease in density in the under-canopy (UC) habitat under increased precipitation (treatment E). Density also decreased in the UC treatment when the site was burned but was unaffected by the fire treatment in other habitats (Appendix S2: II.3.2.2). Turbation acted to increase density, but again only under the shrub canopy (UC). There was a slight increase in total density when seeds were added.

The total density response was much more complex in the Mojave Desert site, even though we only included the ambient and elevated precipitation treatments in the analysis, due to few annuals growing in the drought treatment (Fig. 6; Appendix S2: II.3.1). Habitat was involved in a three-way interaction with the precipitation and fire treatments and a two-way interaction with turbation. The general pattern across habitats was for the lowest total density values to be found under shrub canopies (UC), with significant

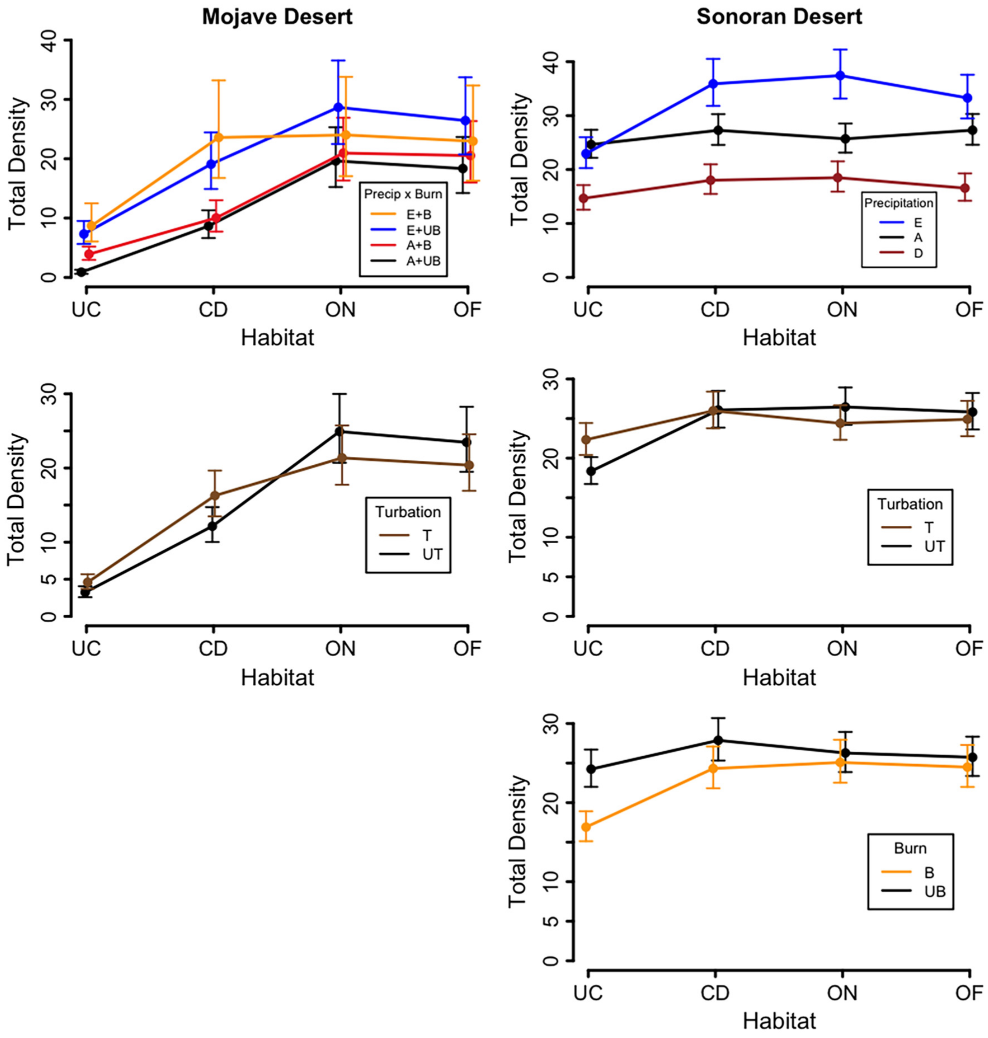

Fig. 6. Significant experimental results for total density involving an interaction with habitat. Error bars indicate 95% confidence intervals. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section. Density means and confidence intervals were back-transformed to the original scales before plotting the figure.

increases at the canopy dripline (CD), and a continuing increase with distance away from shrubs (ON and OF). Total density levels did not differ between the two habitats in the open (Fig. 6). The same pattern across habitats was seen in the two-way interaction with turbation. In two cases, total density levels at the canopy dripline did not differ from habitats away from shrubs, that is, when plots were turbated (two-way interaction; Appendix S2: II.3.1.4.1) or when there was increased precipitation in burned plots (E+B; Appendix S2: II.3.1.2.1).

In the three-way interaction involving precipitation, fire, and habitat treatments, total densities were higher with increased moisture (E>A), except for the OF+B treatment combination where total densities were not affected by precipitation (Appendix S2: II.3.1.2). Total density was also greater in elevated compared to ambient rain treatments under all combinations of the turbation and fire treatments. The three-way interaction involving precipitation, fire, and turbation treatments also revealed that there was no effect of the fire treatment except under conditions of ambient precipitation (A) with no turbation (N; Appendix S2: II.3.1.3). In this case, there was an increase in total density when burned. Turbation only had a significant effect in the ambient precipitation (A), UB treatment, where total density increased.

Schismus *density*

The density of *Schismus* in the Sonoran Desert site varied among habitats, but how this was expressed depended upon the precipitation treatment, as there was a significant two-way interaction between these two factors (Fig. 7; Appendix S2: II.4.2). Within each precipitation treatment, the lowest density differed significantly from the habitat with the highest density. In the case of the enhanced precipitation treatment (E), under-canopy (UC) was the lowest density habitat and differed significantly from the density in all the other habitats. The lowest *Schismus* density in the ambient precipitation treatment was in the habitat farthest from shrubs (OF), and in the drought treatment, it was in the open habitat near shrubs (ON).

Precipitation effects on *Schismus* density in the Sonoran Desert site were not significantly different within the under-canopy habitat (Appendix S2: II.4.2.2.1). Within the habitats away from shrubs, *Schismus* density was significantly higher with elevated rainfall than under either ambient rainfall or drought treatment conditions. Within the canopy dripline habitat, *Schismus* had the highest density in the elevated precipitation treatment, but only when compared to the ambient precipitation treatment. *Schismus* density increased slightly in turbated sites (Appendix S2: II.4.2.3) and in sites with added seed compared to control (Appendix S2: II.4.2.4).

In the Mojave site, we again omitted the rain shelter precipitation treatment (D) from analysis due to very few plants occurring in these treatments. As with the total density response variable, the model for the Mojave site was more complex for the *Schismus* response variable than

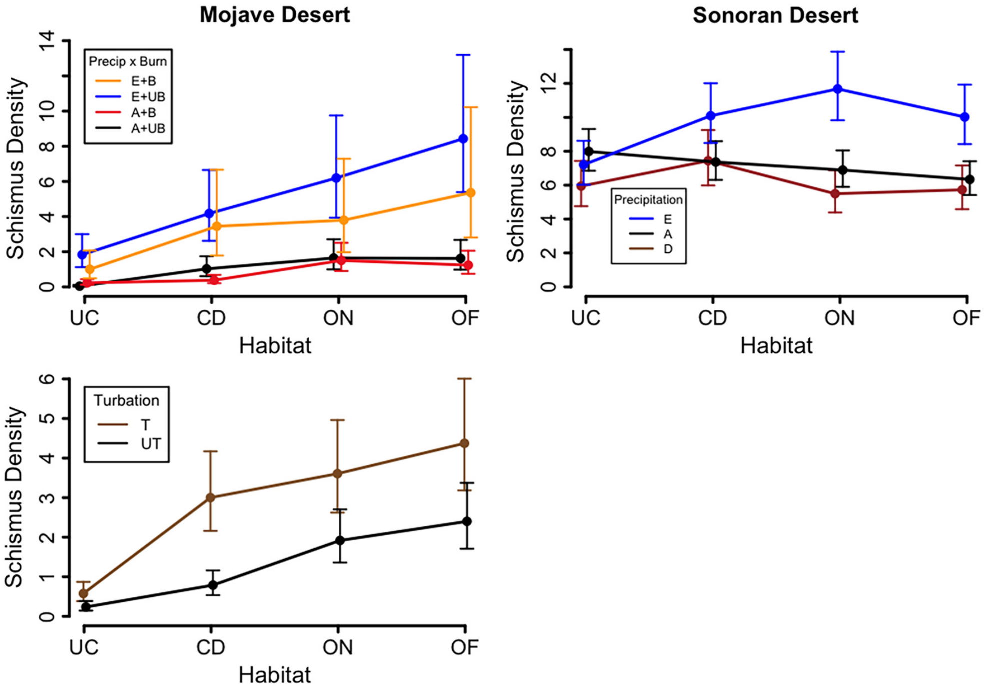

Fig. 7. Significant experimental results for *Schismus* density involving an interaction with habitat. Error bars indicate 95% confidence intervals. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section. Density means and confidence intervals were back-transformed to the original scales before plotting the figure.

for the Sonoran site. There were two significant three-way interactions, that is, habitat × precipitation × fire and turbation × precipitation × fire; one two-way interaction, that is, habitat × turbation; and a significant seed addition effect (Table 3).

The general response by *Schismus* in the habitat comparisons in the Mojave site was to increase in density along the transect from under-canopy to the areas away from shrubs (UC to OF; Fig. 7), although the significance in the pairwise comparisons between habitats varied depending upon the treatment combinations considered, for example, in the two-way interaction with turbation, UC<CD=ON=OF for turbated plots (Appendix S2: II.4.1.4), whereas UC<CD<ON=OF in unturbated plots. Similar differences in relationships were also seen for the three-way, habitat × precipitation × fire interaction, where the density for *Schismus* was always UC<CD<ON<OF in absolute magnitude within each treatment combination, but the significance of the differences varied among treatment combinations (Appendix S2: II.4.1.2). In pairwise comparisons, *Schismus* density in under-canopy habitats always differed significantly from at least one habitat at a higher density.

The precipitation treatment was consistent across all treatment combinations in the Mojave site, with E>A (Fig. 7; Appendix S2: II.4.1.2). In examining the three-way, turbation × precipitation × fire interaction, we found that turbation significantly increased *Schismus* density within the ambient (A) precipitation treatment but had no effect in the elevated (E) treatment (Appendix S2: II.4.1.3). Although the fire treatment remained as a significant factor in two interaction terms (Table 3), pairwise comparisons between burned and UB were always non-significant (Appendix S2: II.4.1.2 and II.4.1.3). However, burning does influence the response to other treatments; for example, the effect of burning on the response to precipitation tended to depress *Schismus* densities in burned plots.

Proportion native density

The proportion of annual plants made up of native species, as measured by density, was on average higher at the Sonoran site than at the Mojave site (Fig. 8). The impact of precipitation on the balance between native and invasive species was also quite different between the two desert sites. In the Mojave site, increased rainfall (E) resulted in a higher proportion of native species in all habitats other than directly under-canopy (UC). In the Sonoran site, the proportion of native plants observed under drought and enhanced rainfall conditions did not differ significantly in any habitat but was significantly higher than the proportions observed under ambient rainfall conditions for all habitats, with the exception of the sites farthest from the canopy (OF) where there were no significant differences among precipitation levels (Appendix S2: II.5.2.2.2).

In the Mojave site, the only significant interaction impacting the ratio of native to invasive species, other than the one between habitat and precipitation, was between precipitation and turbation (Table 3). There was a higher proportion of native plants under ambient rainfall conditions (A) with turbation, but no effect of turbation under enhanced rainfall conditions (E; Appendix S2: II.5.1.3). There was also a slight, but significant decrease in native species in response to fire (Appendix S2: II.5.1.4).

The impacts of the other treatment factors—turbation, fire, and seed addition—on the proportion of native plants in the community were more complex at the Sonoran site than at the Mojave site in that they were involved in more interactions (Table 3). Overall, there were more native individuals in UB and unturbated sites across all habitats (Fig. 8).

DISCUSSION

The causal relationships among fire, extreme rainfall events, soil disturbance, and seed limitation by exotics on the growth of exotic and native annual plants at the Mojave Desert and Sonoran Desert sites are complex, and no single overwhelming causal factor was evident in our experimental study. As can be predicted in arid systems, precipitation had a key influence on annuals, native and exotic alike, but the effects of precipitation were significantly modified by the other experimental factors as well. As a consequence, predicting the impacts of climate change on fire risk due to enhanced biomass production by annuals will require a nuanced view incorporating the findings of this and other studies

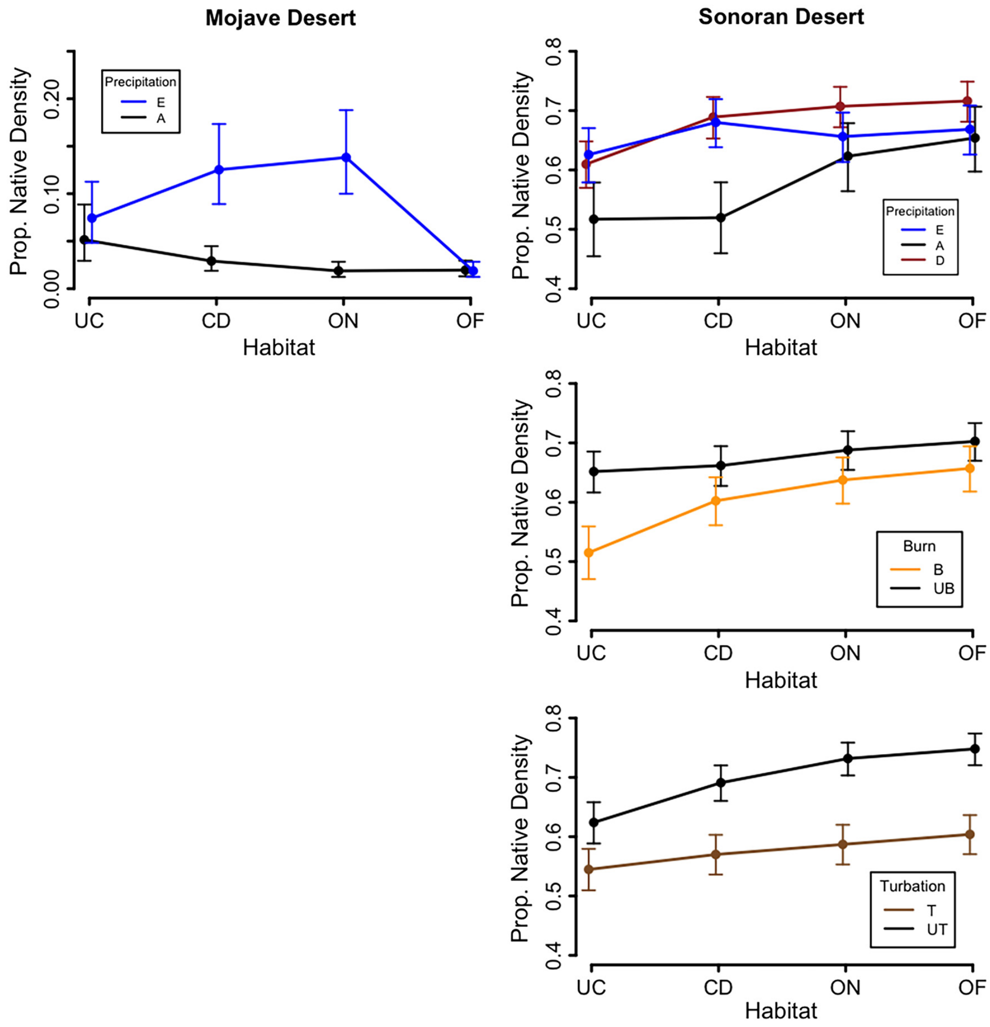

Fig. 8. Significant experimental results for proportion native annual plants involving an interaction with habitat. Error bars indicate 95% confidence intervals. Treatment levels indicated in the legend and along the *x*-axis are defined in the *Methods* section. Means and confidence intervals were back-transformed to the original scale from the *lsmeans* analysis before plotting the figure.

designed to tease apart these complex relationships. In the following, we will discuss our understanding of the importance of each of the main treatment factors in light of the results presented above.

Precipitation effects

As expected, the greatest impact on annual plant species in our experiment was produced by differences in levels of precipitation. High levels of precipitation led to a general increase in biomass production and higher densities of plants. In the Mojave site, higher levels of precipitation also favored native species over invasives. This is in contrast to studies from the Mojave suggesting that exotics, notably red bromes, are favored by increases in precipitation (De Falco et al. 2003, Salo 2004). However, invasive plants still make up more than approximately 75% of the total density of annual plants in the Mojave site, indicating that invasive species play a very significant role. In contrast, we found that enhanced precipitation at the Sonoran site generally favored invasives. This may be due to the lower abundance of exotics currently at the Sonoran site than observed in the Mojave site and suggests that invasive species will increase during periods of high rainfall. The difference in these two systems may also reflect a longer invasion history by annual plant species, *S. arabicus* in particular, in the Mojave site. In contrast to the functionally more arid Sonoran Desert, where the most important invaders tend to be perennial grasses (Brooks and Chambers 2011), a larger proportion of invasive annual plants historically first arrived in the more mesic region of California with Mediterranean-type climate (Axelrod 1973, Jackson 1985, Minnich 2008) and potentially spread from there during periods of favorable rainfall (Salo 2004).

The precipitation effects increasing annual biomass production were found to be highest under shrubs in the Mojave site, potentially demonstrating the effects of nutrient limitation in the open away from shrubs, due to the well-known nutrient island effect (Garcia-Moya and McKell 1970, Charley and West 1975, Schlesinger and Pilmanis 1998, Cross and Schlesinger 1999, Reynolds et al. 1999, Mudrak et al. 2014). Growth by annuals may be enhanced under shrubs, where there is higher nutrient availability, particularly when water is less limiting. However, we found that there was no direct indication of a nutrient island effect interacting with increased precipitation at the Sonoran site. Biomass production was higher with increased precipitation, but the magnitude of the effect was similar across all habitats. Shrubs at the Sonoran site are one-third smaller than in the Mojave site, and their influence on nutrients does not extend as far from shrub bases (Mudrak et al. 2014), potentially lessening the nutrient island effect. Another factor influencing the differential effect of rainfall on biomass distribution between the two sites is the higher density of invasive annuals in the Mojave site, coupled with a greater density response to precipitation by invasives at the Sonoran site. The latter is due to the increase in density of *S. arabicus* with enhanced rainfall at the Sonoran site, which would have a greater influence on biomass distribution than in the Mojave site and may explain, in part, the lack of an interaction between increased rainfall and habitat position in biomass production. In sum, for the Sonoran site, native annuals produce higher biomass under shrubs and exotic annuals produce higher biomass in the open in response to increased rainfall.

Fire effects

There was a slight increase in biomass production in response to controlled fires at both sites, although the effect at the Sonoran site was confined to the under-canopy (UC) and canopy dripline (CD) habitats. In contrast, fire effects on density were minimal with only a slight increase in overall density in the under-canopy (UC) treatment in response to fire. The only significant impact on *Schismus* density produced by fire occurred in the Mojave site under ambient rain conditions. In this case, *Schismus* density declined in response to fire in the under-canopy (UC) and canopy dripline (CD) habitats, indicating perhaps that the release of nutrients under-canopy gives a competitive edge to native species. This is reflected in a small increase in the proportion of native annual species in response to fire in the Mojave site, across all habitats. In contrast, the proportion of native species at the Sonoran site decreases significantly in all but the farthest open (OF) habitat in response to fire, therefore giving exotics a competitive advantage.

Disturbance effects

The effects of turbation were subtle, with minimal effects on biomass production, having only an impact at the Sonoran site in the under-canopy (UC) habitat, where turbation slightly increased biomass production. Density increased with turbation at both sites, but only in the under-canopy (UC) and canopy dripline (CD) habitats, with the latter occurring only in the Mojave site. The density of *Schismus* was increased by turbation across all treatments at the Sonoran site. In the Mojave site, turbation also increased *Schismus* density, but only under ambient precipitation conditions, not when precipitation was enhanced. This effect was seen across all habitats. Interestingly, the impact of turbation on the proportion of native annuals in the community went in opposite directions between the two sites. The proportion of native annuals increased in response to turbation at the Mojave site, but decreased at the Sonoran site. In general, we had expected that soil disturbance would favor exotic species over natives (Lozon and MacIsaac 1997, Buckley et al. 2007). The most significant effect of disturbance in arid areas is the destruction of microbiotic soil crusts (Faist et al. 2017), which in hot deserts has been shown to impede annual plant recruitment (Prasse and Bornkamm 2000, Belnap et al. 2001). The Sonoran Desert site showed stronger biological and physical soil crust development in comparison with the Mojave Desert site (unpublished data), and the observed contrasting response of exotic vs. native annuals might be due to this fact.

Exotic seed addition

The seed addition treatment was assessed only as a main effect to explore the potential role played by seed limitation in the response of exotic plants to the other treatments. This treatment also differed between the two sites as we added a different mix of seeds, as explained in the *Methods* section: *B. tournefortii* and *S. arabicus* at the Sonoran site, and *B. rubens* in the Mojave site. Addition of exotic seed had a more general impact at the Sonoran site, which currently has fewer invasive plants present than the Mojave site. Biomass, total density, and *Schismus* density all increased with exotic seed addition in the Sonoran site. There was also a decrease in the proportion of native annuals in the Sonoran site community.

There was generally no impact of exotic seed addition to the response variables in the Mojave site. The only significant effect was a marginal increase in *Schismus* density with the addition of exotic seed. This result is a bit odd as there was no *Schismus* seed added to the site, and the result is subtle and may represent a statistical anomaly. Seed limitation seems to play a role in the Sonoran Desert site, but not in the Mojave site, at least for those species whose seeds were introduced. Seed limitation is often cited as a factor that delays invasion by exotic plants (Rouget and Richardson 2003). Our results suggest that perhaps the Mojave site is nearer to an end state in the invasion process, relative to the Sonoran site, at least for the species we introduced in the seed addition treatment.

CONCLUSIONS

Climate models predict that the desert Southwest will become hotter and drier over the coming decades (Cayan et al. 2010, Woodhouse et al. 2010). However, there are also predictions that the same area will be impacted by more extreme rainfall events (Diffenbaugh et al. 2005, Wang and Zhang 2008). It is extreme rainfall events that pose the greatest risk for catastrophic fires in the creosote shrublands of the Southwest. With enhanced rainfall, there is a general increase in biomass in these systems, due to the response of annual plants to increased rain availability, as our experimental results have shown. At the Sonoran site, which has fewer exotic, invasive annuals, rainfall also acts to increase the abundance of the invasive species. The opposite appears to be the case in the Mojave site, where native annuals benefit more from higher rainfall. This may be due to the saturation of that system in terms of the proportion of exotic annuals already in place.

The most important aspect of extreme rainfall events in this area, in terms of fire spread, would be the increased production of fine fuels in the open area between shrubs. If the fine fuels reach levels high enough to carry fire between shrubs, then the risk of large-scale fires increases dramatically. An earlier study has shown that although *S. arabicus* does not burn hot enough to catch creosote on fire, it can carry fire to the understories of shrubs and ignite the annual plants that occur there (Fuentes-Ramirez et al. 2016). With higher rainfall, biomass due to native annuals growing under shrubs increases, producing more fuels that can ignite and increase the probability that the creosote bush itself will burn. One year of increased rainfall may not be enough to tip the balance, but if one high-rainfall year is followed by a second year, increased seed production during the first year could give rise to explosive biomass production during a second year of increased rain, further increasing fuel loads and fire risk. This seems to be the situation that led to the historically bad fire season in the desert Southwest during 2005 (Brooks and Minnich 2006). There were two years of increased rainfall, and very large fires occurred in creosote shrublands across the Sonoran and Mojave deserts (Western Regional Climate Center, https://wrcc.dri.edu).

In the aftermath of a fire, nutrient distributions will shift over time, becoming less concentrated as the nutrient island effect fades away, due to the absence of living creosote bushes (Fuentes-Ramirez et al. 2015). This change may permanently alter the structure of the creosote shrubland system, as the more open, less concentrated nutrient landscape would be an ideal situation for the increase in the abundance of invasive annual species, especially the grass *S. arabicus*. This may represent an irreversible change in this system, as creosote is slow to establish, grows slowly, and may take centuries to return to the same state as we find it in these systems today (Abella 2010). To avoid this scenario, it will be important to take additional steps in the management of these systems during high-rainfall years to decrease fire risk, for example, increase the level of public awareness of fire risk and institute policies to prevent fire spread in particularly risk-prone areas through the use of firebreaks and other suitable management techniques.

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