FINAL REPORT

Understanding and Combating the Fire-Enhancing Impact of Non-Native Annuals in Desert Scrub through the Tools of Population and Landscape Ecology

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This project examined the hypothesis that some of the now dominant and problematic non-native invasive annuals are able to spread into the areas between the shrubs by employing population strategies that sharply contrast with those of native species. This greatly increases the fuel load in the matrix, which has historically produced a natural firebreak between shrubs. Our particular aims were to: (1) gain an understanding of the landscape-scale population dynamics of fire promoting and fire retarding plant species; (2) test the hypothesis that once fire becomes important, naturally formed islands of fertility will break down and a negative feedback will enhance fire even further; (3) apply the results to aid management practices that will help restore the original environmental pattern of islands of fertility in a low-nutrient matrix and therefore prevent future wildfires; and (4) understand the effects of non-native invasive plant species on fire regimes. The results derived from this project's experimental and simulation modeling approaches facilitate a better understanding of the association between annual plants and desert shrubs with respect to key interactions and the development of spatial pattern that may influence fire risk. It also provides insights into the different role the exotic species *Schismus arabicus* plays in fire spread within the Mojave and Sonora Desert sites. This understanding is a first step in characterizing the interaction of fire and soil disturbance in changing the likelihood of future fire occurrences through the direct influence on the creosote shrub plant community.

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Keywords

Fire, desert Southwest, Mojave Desert, Sonoran Desert, exotic species, climate change, disturbance, SERD, field experiments, modeling, soil nutrients

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Abstract

Objectives: Biological invasion, the spread of non-native organisms, is occurring rapidly worldwide, and many desert areas currently show a dramatic increase in the arrival and spread of non-native invasive plant species. Among the detrimental effects are alterations in fire regimes and direct negative impacts on native plant species performance. Prior invasion, native annual plants were mostly restricted to nutrient-rich areas under desert shrubs and infrequently occurred within the open areas between shrubs. This project examined the hypothesis that some of the now dominant and problematic non-native invasive annuals are able to spread into the areas between the shrubs by employing population strategies that sharply contrast with those of native species. This greatly increases the fuel load in the matrix, which has historically produced a natural firebreak between shrubs. Our particular aims were to: (1) gain an understanding of the landscape-scale population dynamics of fire promoting and fire retarding plant species; (2) test the hypothesis that once fire becomes important, naturally formed islands of fertility will break down and a negative feedback will enhance fire even further; (3) apply the results to aid management practices that will help restore the original environmental pattern of islands of fertility in a low-nutrient matrix and therefore prevent future wildfires; and (4) understand the effects of non-native invasive plant species on fire regimes.

Technical Approach: This project explored an apparently novel population dynamics strategy of non-native invasive plant species in southwestern United States deserts, which is not used by native species. Field observational and controlled experimental studies in two contrasting desert sites (Mojave and Sonoran Desert) set up to parameterize detailed, landscape-scale, spatially-explicit population models. The major components of the approach were: experimental studies to obtain demographic data under different environmental conditions for several target species, both non-native invasive and native; characterization of spatial patterns of fertility using data from the experimental studies; development of landscape-scale, spatially-explicit simulation models of the spread of non-native invasive species (NIS) in matrix habitat, based on parameters obtained in the experimental studies; and simulation studies of fire spread and efficacy of different management strategies under varying climatic regimes, based on a ground-truthed version of the simulation models.

In the initial years of the project, permanent research sites were established in creosote bush communities in the Sonoran Desert (Barry M. Goldwater Range) and the Mojave Desert (Fort Irwin), spatially explicit density data was gathered for shrubs and herbaceous plants, and it has been explored how the spatial pattern of shrubs and native and non-native herbaceous plants can lead to desert wildfires. In the following years further investigations occurred through experimental studies as to whether these initial conclusions held and whether the underlying mechanisms for this could be elucidated. These experiments examined the combined effects of fire, disturbance, and precipitation amounts on the demographics of native and non-native invasive annual plants. Factorial experiments were conducted to determine the effects of fire, rainfall change, seed limitation, and disturbance on the populations of native and non-native desert annuals. Methods included burning individual shrubs, installing rain-out shelters and irrigating plots to mimic changing rainfall amount, experimentally disturbing soils, and adding seeds of already present NIS to the experimental sites. Spatial patterns of fertility and soil moisture availability were characterized using data from the experimental studies. Basic

landscape-scale, spatially explicit simulation models of the spread of NIS in matrix habitat have been developed based on initial parameters obtained in the experimental studies.

Results: Project data on annual and perennial plant densities and their spatial distributions suggest that different processes have the potential to promote fire in the two contrasting desert sites. In the Mojave the rise of NIS also occupying the areas between shrubs indeed has the potential to promote fire. In the Sonoran Desert native species also occupy the areas between shrubs and potentially provide enough fuel to carry wildfires. In addition, higher shrub densities and lesser shrub segregation in the Sonoran Desert might be the key factor for promoting wildfires, even in the absence of NIS. Population parameter studies in the Mojave and Sonoran Deserts are consistent with the hypothesis that one of the populations of the primary NIS in the study sites (*Schismus arabicus*) indeed uses strategy that has elements of source-sink dynamics in the Mojave Desert, but not in the Sonoran Desert. In the Mojave *Schismus* maintains high densities in the area between shrubs that seem to be supported by higher seed production under shrub canopies.

Responses of annual plants populations and communities to our treatments show that native species and NIS in both deserts react differently. As expected, annual biomass increased in both deserts with increasing rainfall; however, fire increased biomass only in the Sonoran and had little effect in the Mojave. Disturbance had strong increasing effects on biomass in both deserts. In the Mojave Desert disturbance and decreasing rainfall favored NIS, whereas burns did not cause a relative increase of NIS. In contrast, annual NIS in the Sonoran Desert did not become more abundant with fire, most likely due to a strong reaction of native species; rather, they increased with disturbance and drought. This suggests that the invasion processes differ between the deserts and that the impacts of fire are regionally quite different.

This project explored the dynamics of fire spread in a simple, fairly abstract, version of *FireGrid*, the simulation model developed for this project. The results are consistent with percolation theory from landscape ecology and suggest that catastrophic spread of fire will only occur if 60% or more of an area has enough fuel to burn. However, the potential for fire spread will be altered dramatically depending upon the flammability state of the creosote shrubs, which can help connect the landscape even when adequate fuel loads between shrubs are below 60% coverage. The latter will occur when creosote is in a high state of flammability. Under conditions when creosote is less prone to catch fire, it can actually act to slow fire spread under otherwise appropriate conditions. Another factor that can play a role in fire spread is the rate at which fire moves through the annual litter layer between shrubs. This can be lowered when the hydraulic status of the site is elevated or if plants are not evenly distributed at short distances. Under these circumstances fire only spreads under conditions of greater fuel loads than predicted by traditional percolation theory. There is also a large stochastic element to the process. Even if a fire can easily spread through the landscape, given the current fuel loads and potential of spread, there is still a great deal of variability in the degree of spread that occurs from a localized fire source depending on the local distribution of fuels. This makes prediction of fire spread in any one location less precise when considering individual events.

Benefits: The results derived from this project's experimental and simulation modeling approaches facilitate a better understanding of the association between annual plants and desert

shrubs with respect to key interactions and the development of spatial pattern that may influence fire risk. It also provides insights into the different role the exotic species *Schismus arabicus* plays in fire spread within the Mojave and Sonora Desert sites. This understanding is a first step in characterizing the interaction of fire and soil disturbance in changing the likelihood of future fire occurrences through the direct influence on the creosote shrub plant community.

1. Objective

Our project addressed directly two of the key research needs as laid out in the SERDP FY 2010 Statement of Need (Southwest ecological systems on Department of Defense lands: altered fire regimes and non-native invasive plants, issued November 6, 2008). Our results clearly improve our understanding of some of the non-native invasive plants that have significant impact on native ecological systems (SON 1) and improve our understanding of contemporary fire regimes and their interaction with non-native invasive plants (SON 2). SON 3 (predictive model of fire regimes under climate change) and SON 4 (development of management strategies) are not addressed conclusively within this project, however the advanced understanding of the role of non-native invasive species that have been gained through our combination of empirical and modeling approaches is building the base for such advancements and will inform future research implementations.

Using methods of empirical, experimental, and descriptive plant ecology, coupled with current methods of modeling spatially-explicit, ecological dynamics, we investigated the following specific questions:

- What allows some non-native species to maintain populations in matrix habitat that appears to exclude most native species?
- Does fire in the desert scrub ecosystem lead to a decrease in the environmental contrast between shrub islands and matrix habitat that will allow other plant species to invade (i.e., non-native species that are currently shrub restricted, e.g. *Bromus spp.)*?

Of the four originally posed broader objectives two have been fully addressed:

- To gain an understanding of the landscape-scale population dynamics of fire promoting and fire retarding plant species
- To test the hypothesis that once fire becomes important, naturally formed islands of fertility will break down and a negative feedback will enhance fire even further

The two additional broader objectives have been addressed partially and will inform further research:

- To apply the results to aid management practices that will help restore the original environmental pattern of islands of fertility in low-nutrient matrix and therefore prevent future wildfires
- To understand the effects of non-native plant species on fire regimes and their interdependence with future climate scenarios as predicted by current General Circulation Models.

2. Background

2.1: Altered fire regimes in the desert –biological invasion

Biological invasion, the spread of non-native organisms, is occurring rapidly worldwide and many desert areas currently show a dramatic increase in the arrival and spread of non-native invasive plant species (Kemp and Brooks 1998, Brooks 1999, Mack et al. 2000). At present, the deserts of the American Southwest seem to be particularly affected (Brooks 1998, Kemp and Brooks 1998). Historically plants have originated from the Old World and have consisted mostly of grasses (e.g., annual *Bromus* species, some perennial grasses (Beatley 1966, Hunter 1991)), but increasingly members of other plant families are invading many desert communities and can have strong impacts on the native flora and fauna. Among the detrimental effects are dramatic changes in fire regimes and direct negative impacts on native plant species. Invasive plant species tend to increase the amount of dry standing biomass, which in turn increases the fuel load leading to greater fire frequency and intensity (Rogers and Vint 1987). It has been recognized that fire regimes in desert scrubland were altered dramatically mostly due to the arrival of non-native plant species. While human impact might have decreased fire frequency in some of the vegetation types of the semi-arid and arid SW, desert scrub communities are affected by a clear increase in the incidence and scale of fire, chiefly due to fuel build-up by non-native grasses that is reinforced by certain aspects of global climate change (Brooks and Matchett 2006, Brooks and Minnich 2006). Since the native organisms of desert ecosystems are typically not adapted to frequent fires (Brooks and Esque 2002), large-scale changes in community composition and ecosystem functioning are the consequence (Gill and Burke 1999). While changes in vegetation pattern that cause increased fire frequencies have been amply documented, a mechanistic understanding of how non-native plants are changing desert communities and landscapes is still lacking. There are also a number of factors other than fire that act to alter the degree of invasion by exotic species that are not yet fully understood.

Desert surfaces are dominated by biogenic crust (Belnap 2008) that have strong interactions with vascular plants by affecting nutrient and water availability and by influencing seedling establishment (Belnap et al. 2001, Prasse and Bornkamm 2000). Human caused soil disturbance (whether due to direct human activity or livestock impact) will affect the integrity of these crusts and thereby strongly influence growth and establishment of vascular plants (Bolling and Walker 2000). Direct interaction effects of non-native species on native plants in deserts can also be strong. Even though direct negative effects of non-native herbaceous plants on shrubs have been shown experimentally (Holzapfel and Mahall 1999, DeFalco et al. 2006, Rodriguez-Buritica and Miriti 2009, and others), the strongest effects are expected among the herbaceous plants cohabiting the often dense sub-canopy of desert shrubs (Brooks 2000b, Tielbörger and Kadmon 2000). Coexistence of annual and other herbaceous plants in desert ecosystems depends on balanced life history trait trade-offs that have evolved in the native flora (Pake and Venable 1995, Venable 2007, Angert et al. 2009). An increase of highly competitive non-native species, with life history traits that differ from native species will potentially have detrimental effects on native species. In this respect it is important to understand whether non-native species evolved different life strategies in their new range compared to their old range. A large number of comparative studies (see review in Moloney et al. 2008) suggest that many species evolve novel evolutionary strategies when colonizing new ranges. It has been suggested that evolution

is a continuing process and the strength of interaction diminish over time as non-native species integrate into communities (Dietz and Edwards 2006, Moloney et al. 2008). As this question requires inter-continental, comparative approaches, we do not intend to include this in the current proposal but will seriously consider extending our work in this direction at later stages. The current study is designed to investigate the current ecological situation, keeping in mind that over evolutionary time the nature of the interaction may change.

2.2: Developing a mechanistic understanding of non-native plant fire interaction – towards a hypothesis

Shrub-dominated arid ecosystems are characterized by nutrient-enriched shrub sites that are surrounded by comparatively nutrient-poor inter-shrub areas. Shrubs provide "islands of fertility" in a "sea of infertility" through the accumulation of organic material and by locally increasing soil moisture, further facilitating biomass degradation (Garcia-Moya and McKell 1970, Schlesinger and Pilmanis 1998, Cross and Schlesinger 1999). Most native annual plants are restricted to shrub habitats (shrub islands) as they benefit from net facilitation provided by shrubs (Holzapfel and Mahall 1999) and their populations therefore either stay within the same shrub island or disperse to adjacent shrub islands. This strategy will reinforce the patchy distribution of nutrients in desert shrubland (Schlesinger and Pilmanis 1998). A few, usually small-statured, native annuals are restricted to inter-shrub sites (matrix habitat), but typically do not reach high densities nor build up large amount of biomass (e.g., in the Mojave Desert *Cryptantha, Pectocarya*). Some of the introduced, non-native annuals that already are (or are becoming) problematic invaders in these ecosystems appear to employ population strategies sharply contrasting with those of native species. For example, species such as *Schismus arabicus*, *Brassica tournefortii,* and *Pennisetum spp.* are able to inhabit both shrub and matrix habitat types and appear to use the fertile shrub sites as source populations that in most year send propagules into the lower productivity inter-shrub areas, thereby avoiding strong inter- and intra-specific competition.

One of the invasive species that has received increasing attention is the small grass *Schismus arabicus* (and in some regions its morphologically and ecologically very similar congener *S. barbatus*) that arrived in the New World in the early 1900's and started to become more dominant much later (Brooks, 2000). In the Mojave Desert it can form dense stands across the desert landscape, as it is able to spread into the areas between the shrubs (Brooks, 1999), a pattern that apparently is not found in other arid regions, including in its native range (Holzapfel, et al. 2006). In our current research on the potential importance of non-native annual plant species for fire risk in SW deserts we singled out the non-native grass *Schismus* as likely employing a different strategy than most other species, with productive source populations under shrub canopies and less productive, sink populations between shrubs. *Schismus* has been shown to have relatively low competitive abilities and, accordingly, tends to avoid low light conditions (Tielbörger and Kadmon, 2000; Abella et al., 2011). However, it is relatively drought resistant (Gutterman et al., 2010). We predict that the ability to maintain populations in unproductive sink habitats depends on the overall aridity of the region and therefore is found in the open only in the Mojave Desert, a relatively cool, high desert that is overall less arid than the lower and hotter Sonoran Desert and the overall more arid deserts of the Middle East (Goudie & Wilkinson, 1977; MacMahon & Wagner, 1985). One central hypothesis is therefore that *Schismus* is employing

population strategies in the Mojave that sharply contrast with those of native species and thereby can greatly increase the fuel load in the open areas between shrubs, which have historically produced a natural firebreak between shrubs.

Thus, it appears that annual plants follow two distinct strategies. The "traditional" strategy, which we call the "**source focus strategy**" where populations tend to remain in their focus habitat (shrub understory), and the new strategy, which appears to have been adopted by some non-native plants and we call the "**source-sink strategy**". The concept of the later strategy has been used and explored in population ecology for quite a while already (Shmida and Ellner 1984, Pulliam 1988) and has been demonstrated in an Old World desert system (Kadmon and Tielbörger 1999). In this respect it is intriguing that in the study by Kadmon and Tielbörger (1999) species were investigated that are either identical or similar to the Old-World species that are currently invading the North American deserts. If this is indeed a novel strategy realized chiefly by species non-native to the North American desertsand not by native species, this would be another indication for the hypothesis that invasion success by non-native species can be attributed to novel characteristics (Callaway and Aschehoug 2000, Verhoeven et al. 2009). The environmental consequences of this new strategy are that the formerly open inter-shrub areas are filling with plant biomass. This biomass, especially after the growing season, can greatly increase the fuel load in the matrix, which has historically produced a natural firebreak between shrubs. The system will therefore develop in a positive feedback loop, a type of regulation that is not rare in plant communities (Wilson and Agnew 1992) and that has been described as typical for grass invasions (D'Antonio and Vitousek 1992). Increased fire frequency, or even the novelty of fire in some desert ecosystems, can then result in redistribution of soil nutrients that potentially will result in the disappearance of distinct fertility islands. This could provide another feedback loop that would further the biomass load between shrubs, which in turn would increase the incidence of fire even more.

Here we describe a new approach to exploring this apparently novel strategy that could aid in developing landscape scale management protocols to mitigate the impacts of invasion into these systems. The study combines detailed field experiments that manipulate and monitor annual plant communities and spatial nutrient distributions. We utilized field observational and controlled experimental studies to parameterize a detailed, landscape-scale, spatially-explicit population model.

3. Site Selection and Setup

3.1: Team buildup and division of tasks and responsibility

At Rutgers University Newark we employed (1) a postdoctoral researcher in July 2010 (responsibilities: annual plant data, soil nutrient regime): Dr. Jennifer Schafer until July 2011, Dr. Marjolein Schat from Sept. 2011 to June 2014; (2) a full time field technician in September 2010 (Carolyn Haines: logistics, data management, field work) until Sept 2012; (3) a part-time research assistant in July 2010 (Hadas Parag, M.Sc.: soil seed bank, seed collection, plant surveys, field work).

At Iowa State University we employed (4) a postdoctoral researcher in August 2010 (Dr. Erika Mudrak: spatial pattern surveys, modeling) until Aug. 2013; (5) a Ph.D. track graduate student, in August 2010 (Andres Fuentes Ramirez: landscape and population modeling, fire ecology) until Nov. 2014.

3.2: Initial site selection

Starting in September 2009 we contacted Range Management personnel of various military installations in the Mojave and Sonoran Desert regions. After narrowing the search to two installations, Fort Irwin National Training Center in the Mojave and Barry M. Goldwater Range in the Sonora, we visited with range personnel in January and March 2010, and after extensive scouting trips we were able to select appropriate experimental sites in each desert (see Fig. 1). With assistance of the local range personnel (Richard Whittle, Environmental Science Management at Luke AFB, and David Housman and Ruth Sparks at Integrated Training Area Management -ITAM- program at Fort Irwin) we obtained the necessary site permits.

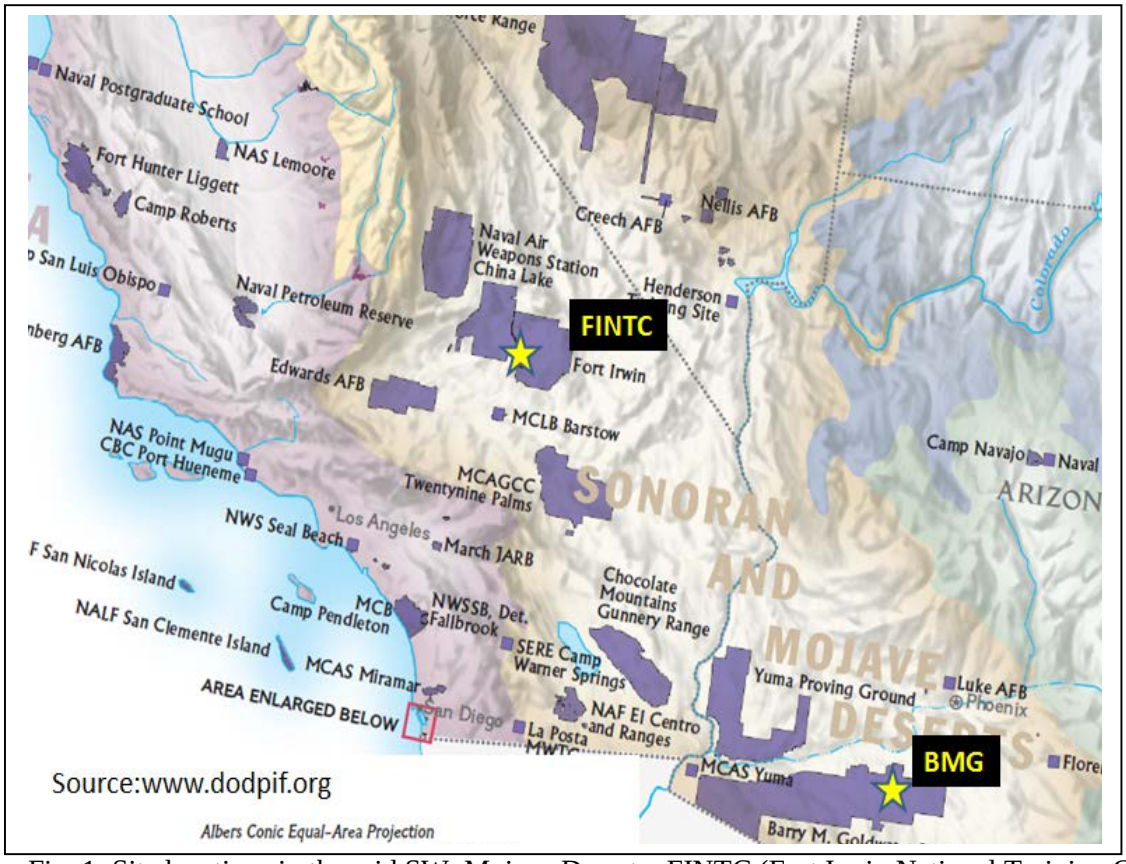
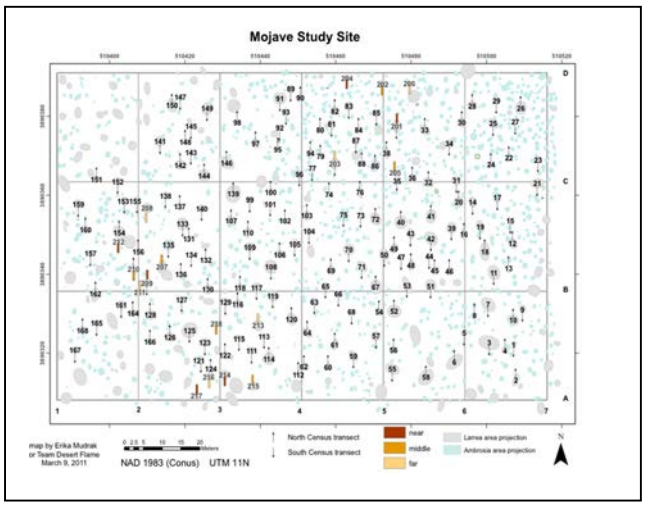


Fig. 1: Site locations in the arid SW: Mojave Desert – FINTC (Fort Irwin National Training Center); Sonoran Desert – BMG (Barry M. Goldwater Range)

3.3: Site setup

In September 2010, we established one 83 m x 130 m experimental macroplot, situated in flats and open Creosote bush bajadas, within each of the Mojave and Sonoran sites. We selected this habitat as it is representative of a large proportion of both deserts and also constitute most of the fire prone fire ranges on military installations in the arid Southwest. The vegetation of this habitat is characterized by a low diversity of desert shrubs and a high diversity of desert annuals (both native and non-native). Very few perennial herbaceous and graminoid species are present in this habitat and these were therefore not selected as target species for our study (note that one invasive perennial species of concern, bufflegrass (*Pennisetum ciliare*), grows in the selected habitat, but restricted to roadsides in the Lower Sonoran Desert (in contrast to the Arizona Sonoran Desert uplands, Tellman 2002).



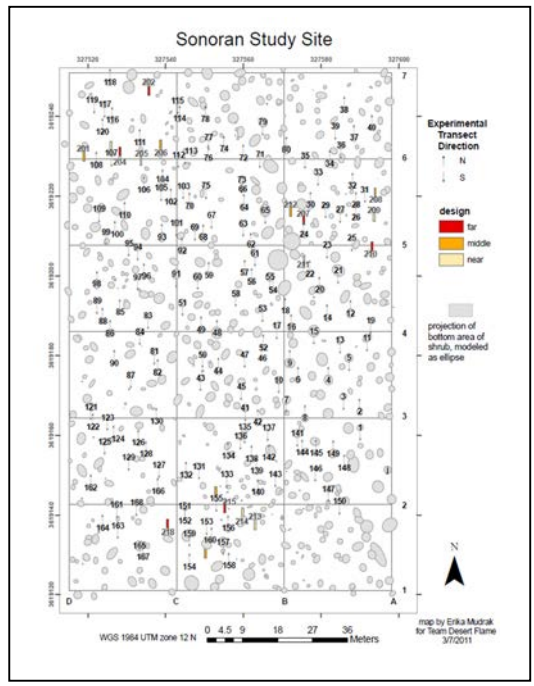


Fig. 2: Site maps. Shown are all shrubs on the site and their relative sizes. Colored transects are soil sample transects.

Within each macroplot, we selected, marked and georeferenced focal *Larrea* individuals (n = 168 per site) that were at least 170 cm away from other *Larrea* individuals (canopy edge to canopy edge, see site maps Fig. 2). These were the individuals to be used for subsequent experimental treatments. Under each of the 168 shrubs, we established two transects beginning under the canopy and extending north (N) or south (S) into the open area among shrubs (Fig. 3A). In the Mojave site, some *Ambrosia* shrubs were closer than 170 cm to the focal shrubs, but transects were established to avoid the influence of *Ambrosia*. Plots (800 cm^2) were established along each transect in four microhabitats: under the canopy (UC), at the canopy drip line (CD), in the open inter-shrub area near the focal shrub (ON), and in the open inter-shrub area far from the focal shrub (OF) (Fig.3A). The mean extent of the canopy drip line in the transect direction was estimated visually, and to accommodate the UC and CD plots, focal shrubs had a minimum canopy radius of 35 cm in the transect direction.

The mean extent of the canopy drip line in the transect direction was estimated visually, and to accommodate the UC and CD plots, focal shrubs had a minimum canopy radius of 35 cm in the transect direction.
Each plot was divided into two 20 x 20 cm subplots: one for monitoring recruitment and survival of annual species (using non-destructive methods) and one for assessing soil nutrient availability (Fig. 3B).

On average, our focal *Larrea* individuals were smaller in the Sonoran site than in the Mojave site; thus, the ends of the transects under the canopy were 0-10 cm and 5-35 cm away from basal *Larrea* stems in the Sonoran and Mojave sites, respectively.

Under the canopy, the two transects were separated by 10-25 cm, depending on the canopy size along the east-west axis of the shrub, and the distance between transects increased with distance from the canopy. All transects extend 150 cm from the canopy dripline into the inter-shrub area, and we measured the distance from the OF plot to the nearest neighboring

shrub. The distance from the CD plot to the UC plot varied depending on the canopy size in the transect direction along the N-S axis of the shrub.

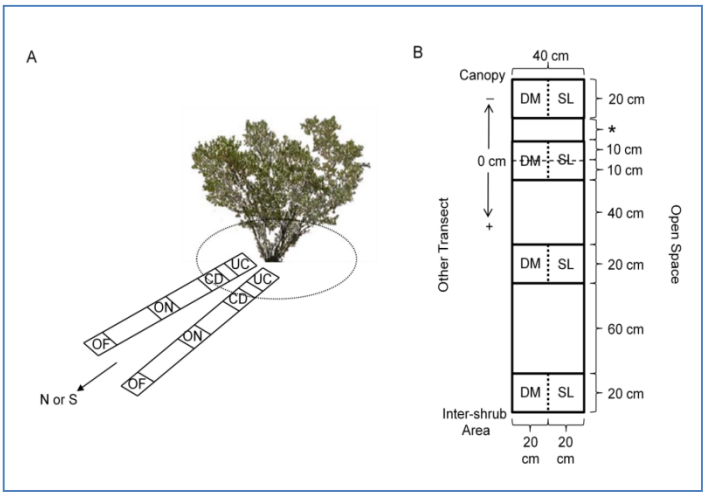


Fig. 3: Set up of experimental transects at *Larrea* shrubs. (A) Shrub diagram with transects, plots, and a dotted line indicating the location of the *Larrea* canopy drip line. UC = Under Canopy; CD = Canopy Drip line; ON = Open Near shrub; OF = Open Far from shrub. (B) Transect diagram with plot sizes and distances between plots within a transect. DM = demography plot (always toward the other transect); SL = soil plot (always away from the other transect); * indicates that this distance is variable and depends on the size of the shrub. The mid-point 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.

In both areas we selected and established, in addition to the experimental plots, a previously burned wildfire area that will allow us to gather additional, comparative data. The *Sonoran Burn Site* was selected in January 2011 at BMG, from areas listed in a GIS file obtained from Luke Air Force Base that contained information on fires occurring within BMG during the summer of 2005, prior to July 6. An 83 m x 130 m macroplot was established within the site, which was located within 2.5 km of the Sonora macroplot. *Larrea* individuals were selected, marked, georeferenced and classified as alive, dead, or stumps (14 for each category).

The *Mojave Burn Site* was selected in March 2011 from a list obtained from California Forest Resources Assessment Program (FRAP). We chose the "Opal Fire", on BLM land, with an alarm date of May 29, 2005. The fire was contained the same day it was discovered and was started by an unknown cause, burning 131 acres. Since this burned site was relatively far from the Mojave main site (25 km), we split the original 83 x 130 grid into two 83 x 65 grids, one within the burned area and one just north of the fire line boundary, thus serving as a control. As in the experimental plots, 20x20 cm quadrats along transects representing the microhabitats were established at the burned sites in both deserts and all shrubs have been georeferenced and measured at a later date (for coordinates of sites see Table 1).

Table 1: UTM Coordinates of boundaries, rounded to the outside meter.

Site	**Datum**	**West Bdry (UTM)**	**East Bdry (UTM)**	**SouthBdry (UTM)**	**North Bdry (UTM)**
Mojave Main	NAD83 11N	510386	510517	3890308	3890391
Mojave Burn	NAD83 11N	485889	486014	3882173	3882400
Sonoran Main	WGS84 12N	327515	327598	3619121	3619251
Sonoran Burn	WGS84 12N	325880	325963	3611592	3611723

3.4: Selection of target species and seed collection

Botanical survey and target species selection: Species lists were compiled for the two macroplots and an 'electronic field guide' to the seedlings of all species was assembled based on photos taken in the field and the greenhouse (seed bank experiment). Project personnel were trained based on this in the field and the greenhouse. We are currently working on a version of this guide that can be shared with personnel of the respective installations. We selected 10 species as target species for which demographic data have been collected.

Seed collection

Seeds of three non-native species (*Bromus madritensis rubens*, *Schismus arabicus* and *Brassica tournefortii*) were collected in various locations in the Mojave and Sonoran Deserts during March-April 2010 (seeds are not from our experimental sites, because at the time the seeds were collected locations for the core sites were not yet determined, Table 2). Seeds were cleaned, quantities calculated, and germinability tested at the Rutgers Newark lab. Decision of which seed 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 site.

Table 2: Seed collection sites

species	Collection ID#	desert	place	detailed location	coordinates
Bromus	10-04-19-006	Mojave	15 miles NE of Mojave, CA	Pine Tree Canyon Rd at Rte 14 (Aerospace Hwy)	N35 13.928 W118 02.812
Brassica	10-03-25-001	Sonoran	Coachella, CA	Ramon Rd.	N37 25.191 W122.0506
Schismus	10-04-20-015	Sonoran	Morongo Valley, CA	Big Morongo Canyon Preserve	N34 02.866 W116 34.032
	10-04-22-023	Sonoran	Anza Borrego, CA	Yaqui campsite	N33 08.195 W116 22.761
	10-03-01-001B	Sonoran	Anza Borrego, CA	Borrego Springs	

Seed cleaning methods, quantities and methods for future seed addition are described in Table 3. The relationship between seed weight and seed number for each species was determined by counting 100 seeds and weighing them (repeated for several samples). Germination of all seed sources was tested by placing seeds on moist filter paper in Petri dishes (seed source locations are listed in Table 2).

Seed addition to our experimental plots

Brassica tournefortii and *Schismus arabicus* were added in BMG, the Sonoran site, and *Bromus m. rubens* were added at Fort Irwin, the Mojave site, in September 2011 before the onset of the winter rainy season. It was decided not to add *Schismus* at Fort Irwin since natural seed densities (as seen in the first hydrological season) are very high, even before addition, and additions would not significantly increase plant densities. Seeds were added by scattering on the ground in September 2011. The number of germinable seeds needed to produce 20 plants each of *Brassica* and *Bromus* and 40 of *Schismus* were added (note that the double amount of *Schismus* was added since this plant tends to be smaller than the first two species and typically occurs at higher densities). For future field application, seeds for treatment subplots were packed in the lab in single portions (one portion per plot) – *Bromus* and *Brassica* seeds were counted; *Schismus* seeds were weighed (Table 2).

Table 3: Seed collection and cleaning methods

	Bromus	*Schismus*	*Brassica*
number of seeds in the collection	19,145	59,288	80,269
Cleaning method	Separated from the spike, and quality judged by stiffness of the grain.	Seeds were cleaned by releasing them from the husks by applying moderate pressure, then separated from the husks and sand by passing them through sieves.	Seeds were cleaned when collecting – collected pods were crumbled in a paper bag and separated from the seeds. Further cleaning by removing remaining fragments of pods was done manually in the lab.
germination rate (%)	98	39.8	93.3
Number of germinable seeds to be added to plot	20	40	20
number of seeds needed to have that number of germinable seeds	20	101	21
100-weight (weight of 100 seeds, g)	0.1893	0.0074	0.1265
weight per plot (g)		0.0075	
portion-packing method	counted	weighed	counted
packed in	paper envelopes	Eppendorf tubes	Eppendorf tubes
site seeds are added at	**Mojave**	**Sonoran**	**Sonoran**

4. Pre-treatment Site Characterization

4.1: Climate

Methods

One climate station (WeatherHawk Inc.) has been installed at each of the two sites in the fall of 2010 and operated until spring of 2014 (in fact they remain active to date at the sites under the supervision of the installation's administration). Hourly weather data that include rainfall have been constantly recorded and relayed per satellite. Based on this the timing of monitoring trips to the sites had been determined and the monitoring results have been related to ambient rainfall and other climatic factors.

Results

Fig. 4 shows the precipitation amount in comparison to the long-term annual means at the two sites. Based on this graph it is clear that most growing seasons were relative dry in both the Mojave (winters 2011/12 and 2012/13) and in the Sonoran deserts (winters 2011/12 and 2012/13 and summer 2011).

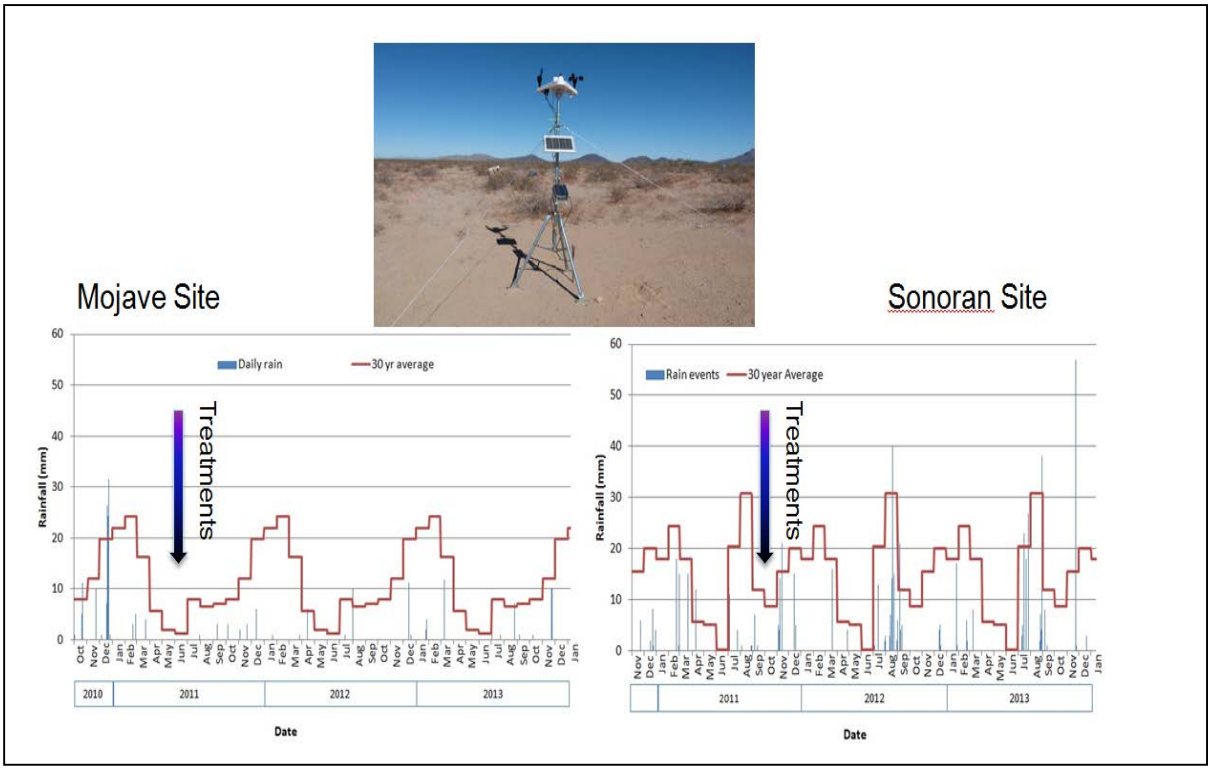


Fig. 4: Precipitation events at the two sites (blue spikes) and long–term averages (red solid line) during the investigation period. The vignette shows the climate station in the Sonoran Site (WeatherHawk, Logan, UT)

4.2: Present disturbance regime and soil crusts

Methods

In June and September 2011 we collected data to characterize the frequency of natural disturbance present on the study quadrats and the extent and thickness of soil crust. Since we established the quadrats in the fall of 2010 and chose mostly undisturbed sites, we were able to quantify new soil disturbances (mostly due to rodent and reptile burrowing activities). Soil crust extent was estimated and soil crust thickness measured destructively on reference sites outside of the permanent plots.

Results

The incidence of natural soil disturbance did not differ between the two desert sites, however extent of soil crust and thickness of soil crust was clearly higher in the Sonoran Desert as compared to the Mojave Desert site (Table 4).

Table 4: Initial characterization of disturbance regime and soil crusts

	Natural disturbance (avg.% of quadrats)	Extent of soil crust (avg. % of quadrats)	Soil crust thickness (avg., mm)
Mojave Desert Site			
Under shrub canopy	9	43	2.1
Open	3	10	1.2
Sonoran Desert Site			
Under shrub canopy	10	85	3.5
Open	7	60	1.4

Fig. 5: Seed bank characterization set-up at the greenhouse. Soil samples are spread shallowly in trays, watered and emerging seedlings are identified and counted.

4.3: Seed bank characterization

Methods

Soil seed bank samples were collected from the north and south sides of 10 shrubs at each site before the winter rains (collection dates vary from late September to November). Sampling was conducted for the same four microhabitats used for population monitoring (see above: 10 shrubs x 2 sides x 4 microhabitats = 80 samples per site). The samples were spread over vermiculite in flats and irrigated in the greenhouse of Rutgers University Newark (Fig. 5). During four 3-4 weeks watering cycles (starting October-November the year of collection, and January, April, and September-October of the following year) emergent seedlings were identified, counted and removed. An identification catalog of seedlings has been developed based on seedlings observed in the field and emerging from the seed bank samples.

Results

Focusing on the distribution of invasive and native plants germinating from seeds in the seed bank, rather than in annual plant production in any given year, will enable us to estimate the potential fuel buildup and fire risk in high rainfall years, rather than patterns that may vary with annual precipitation. The seed bank represents the net fecundity during previous years (Guo et al. 1999), and may provide an accurate representation of potential fuel loads during high rainfall years (Esque et al. 2010).

Fig. 6, based on our results from the Mojave site, is an example showing density of non-native plants comparison between census data in the field site and germination in seed bank samples. Similar correlation between these data sets and the gradient of distance from the shrub recurred in burned sites and in the Sonoran Desert (in preparation).

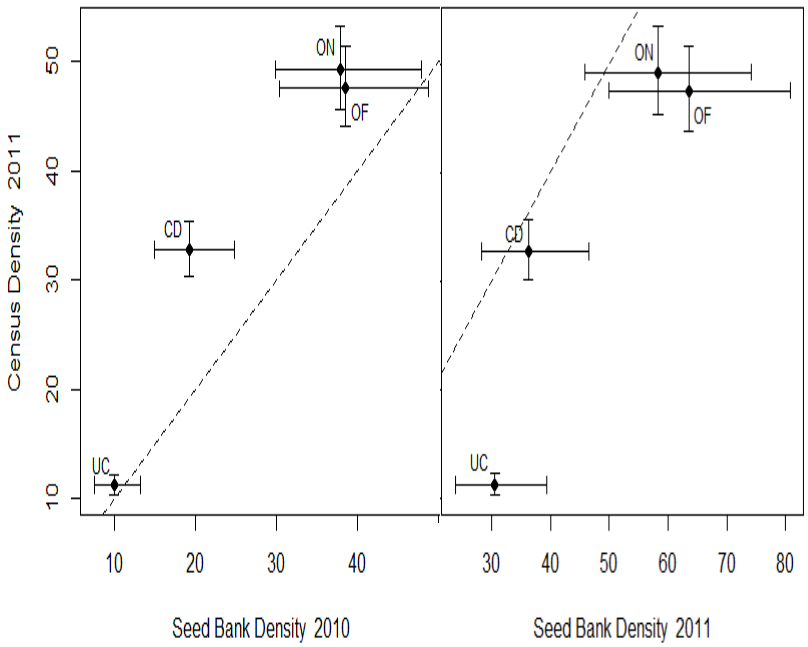


Fig. 6: Relationship between seed bank density and aboveground abundance during an average rainfall year for invasive species in an unburned Mojave Desert site at different distances from shrub centers: under canopy (UC), canopy drip line (CD), open near canopy (ON) and far from canopy OF). Dotted line is x=y. Bars represent 95 percent confidence intervals obtained from a generalized linear mixed model analysis.

4.4: Soil nutrient distribution

Methods

The spatial distribution of soil nutrients was measured along transects running from the sub-canopy of a shrub (N and S side) into the open areas between shrubs. To asses soil fertility we used ion exchange resin membranes that exhibit surface characteristics and nutrient sorption phenomena that closely resemble plant root surfaces. These membranes, which have been tested successfully in the Mojave Desert (Drohana et al. 2005), have been buried in the soil in the main rooting horizon to assess nutrient supply rates by continuously adsorbing charged ionic species (e.g., NO_3^-, N, P, S, Al, Fe, Mg, Cu, Zn, B). Plant Root Simulator (PRS) Probes (by Western Ag Innovation) have been used, which after exposure have been harvested and sent for analysis to the manufacturer. Budgeted were 188 samples (376 probes; half anion and half cation) for the initial sampling at each site. Ten or eleven probe pairs (one anion, one cation) were placed in transects starting at the base of 18 shrubs for a total of 180 samples in the Sonoran and 186 samples in the Mojave. Two samples were used as blanks. These samples were kept out of the field, but rinsed in the same way as the samples that were in the field. Minimum probe spacing will be 20cm, as this is our quadrat size. The decline of nutrients was modeled with distance from focal shrubs using hierarchical mixed models that included the effects of transect direction and shrub canopy size.

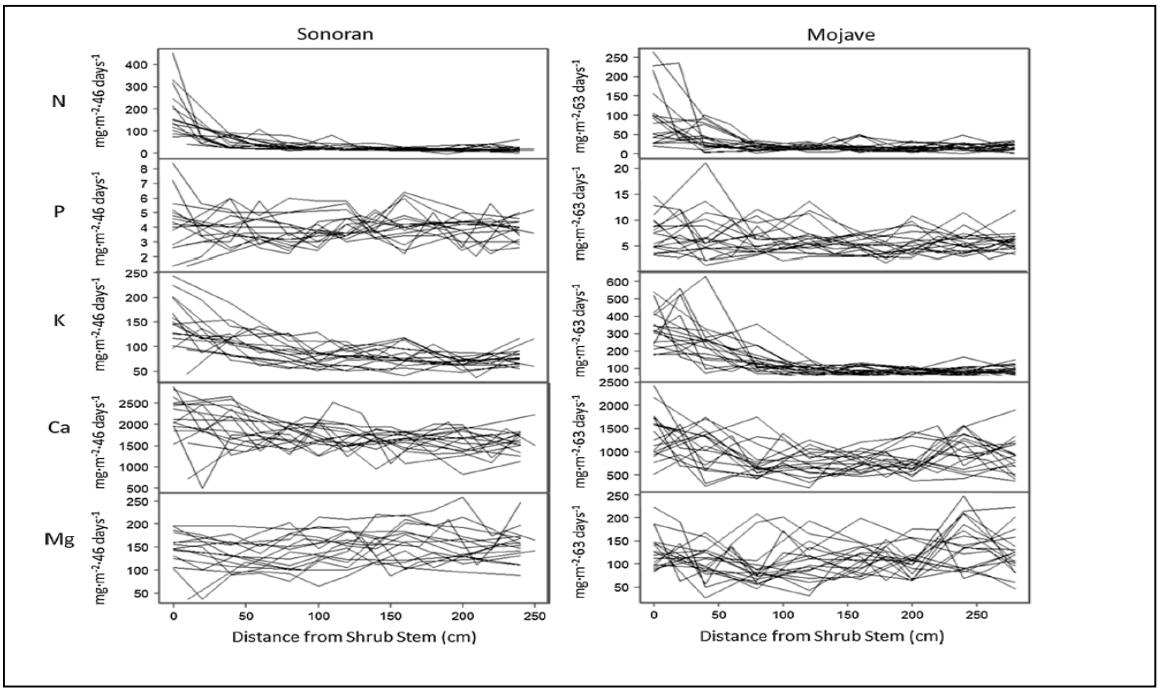


Fig.7: Nutrient concentrations obtained from PRS-probes plotted against distance from shrub stems. Lines connect samples from the same transects. Note scale differences for nutrient concentrations, which are reported in mg m^{-2} burial $period^{-1}$

Results

Of the nutrients considered, nitrogen and potassium had the strongest response to distance from focal shrubs (Fig.7). In the Sonora, both depended on canopy size and had different patterns to the north versus the south. In the Mojave, potassium depended on size and direction, but nitrogen only on canopy size. The fitted model equations and the location and canopy size of all *Larrea* shrubs within the macroplots were used to estimate nutrient concentrations at 20 cm resolution. This produced maps showing nutrient "hotspots" centered on *Larrea*. The models predicted up to 60 % of the variation in nutrient availability the following growing season. Our models efficiently used a moderate number of sample locations to predict nutrient concentrations over a large area, given easily measured values of shrub size and location. This method can be applied to many systems with patchily distributed resources focused around major structural landscape features.

4.5: Soil water distribution and microclimate

Methods

On adjacent transects soil water content was monitored constantly with soil water and temperature sensors (Decagon Devices, Inc.) in four microsites along four shrub transects per desert site (Fig. 8). We had initially proposed to assess soil water content with gravimetrical methodology but realized that repetitive, destructive sampling would be detrimental for the integrity of the long-term experimental site. The sensors were deployed in September and October 2011 and continued to collect data until January 2014.

Results

Wetting and drying cycles have been well documented by the soil water sensors. As shown in Fig. 9, it was also apparent that areas between shrubs (e.g., the habitats OF – far from canopy and to lesser extent UN – near canopy) received larger amounts of rainfall compared to areas beneath shrubs. As this was evident also during periods when shrubs and associated annual plants were not active and uptake of water is therefore unlikely, this seems to indicate that passive interception of rainfall by shrub canopies is important in our systems. This emphasizes the leading role of increased nutrient availability under shrubs rather than potential effects on soil water availability on the increased annual plant biomass under shrub.

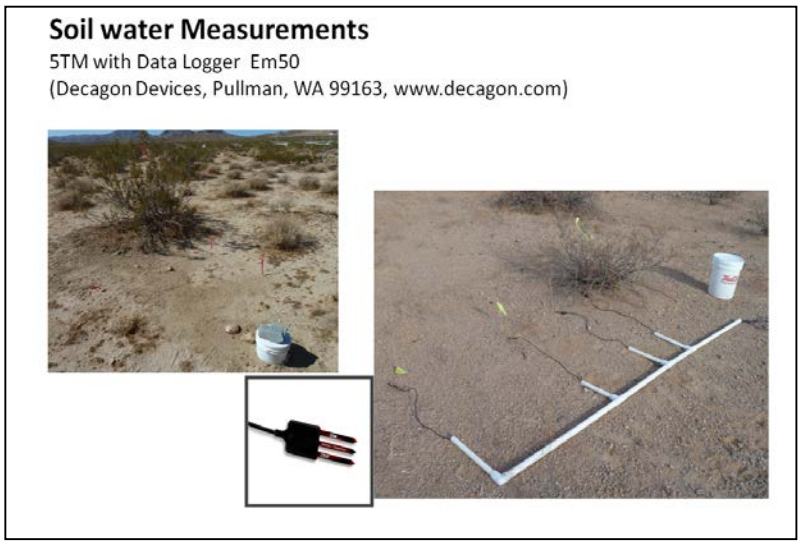


Fig. 8: Field setup of soil-water and temperature sensors. The sensors were connected to the data logger via cables below-ground, which were encased in PVC tubes to avoid UV and damage by digging rodents.

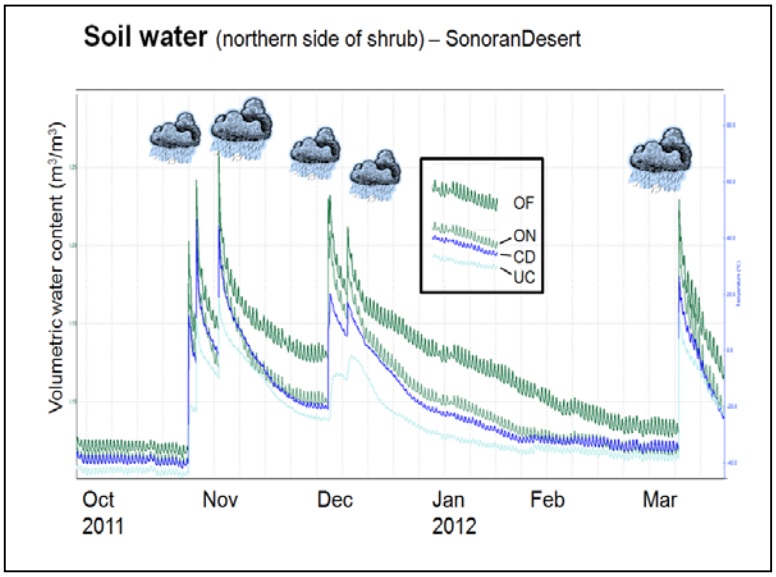


Fig. 9: Examples of soil moisture data obtained in the field. Five naturally occurring rainfall amounts show the water recharge of the soil in the four microhabitats associated with shrubs. Note that the areas between shrub show stronger recharge than the sub-canopy microhabitats.

4.6 Annual plant populations in association with shrubs

Methods

After sufficient rainfall occurred in the Mojave Desert, initial plant density counts were completed during November 4-12, 2010 and due to a later commencement of rainfall we conducted a similar count at the Sonoran site on January 21-24, 2011. All emerging seedlings were enumerated by species or by morpho-type, the latter for cases where species identification was not possible (a number of species are very similar in appearance at the seedling stage, necessitating the use of morpho-types in categorization). Seedlings were identified to genus and species when possible. Some seedlings were marked with colored toothpicks so that specific individuals could be revisited later. Unknowns were photographed and described. Counts of plants at the reproducing stage were conducted at both sites from March 17 to April 4, 2011.

These very time-consuming counts were conducted on 1344, 20 cm x 20 cm permanent quadrats at each site. In addition, seed production was quantified for 8 dominant, native and non-native, plant species. Thus by mid-April, the pre-treatment survey, which serves as a control for the experimental treatments, was completed at both sites.

Results

The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran Deserts was detailed in (Schafer et al. 2012). In both deserts, annual plant abundances were highest on the north side of *Larrea* and in open areas (Fig. 10). Native annuals in the Mojave were most abundant near the edge of the shrub canopy, whereas native annuals in the Sonoran were most abundant in open areas. The effects of *Larrea* fertility islands on annual plant abundances were not consistent between the two deserts we studied. This study emphasizes the importance of research on native and non-native annuals in multiple regions before generalizations can be made about the effects of *Larrea* on annual plant abundances in desert scrub ecosystems.

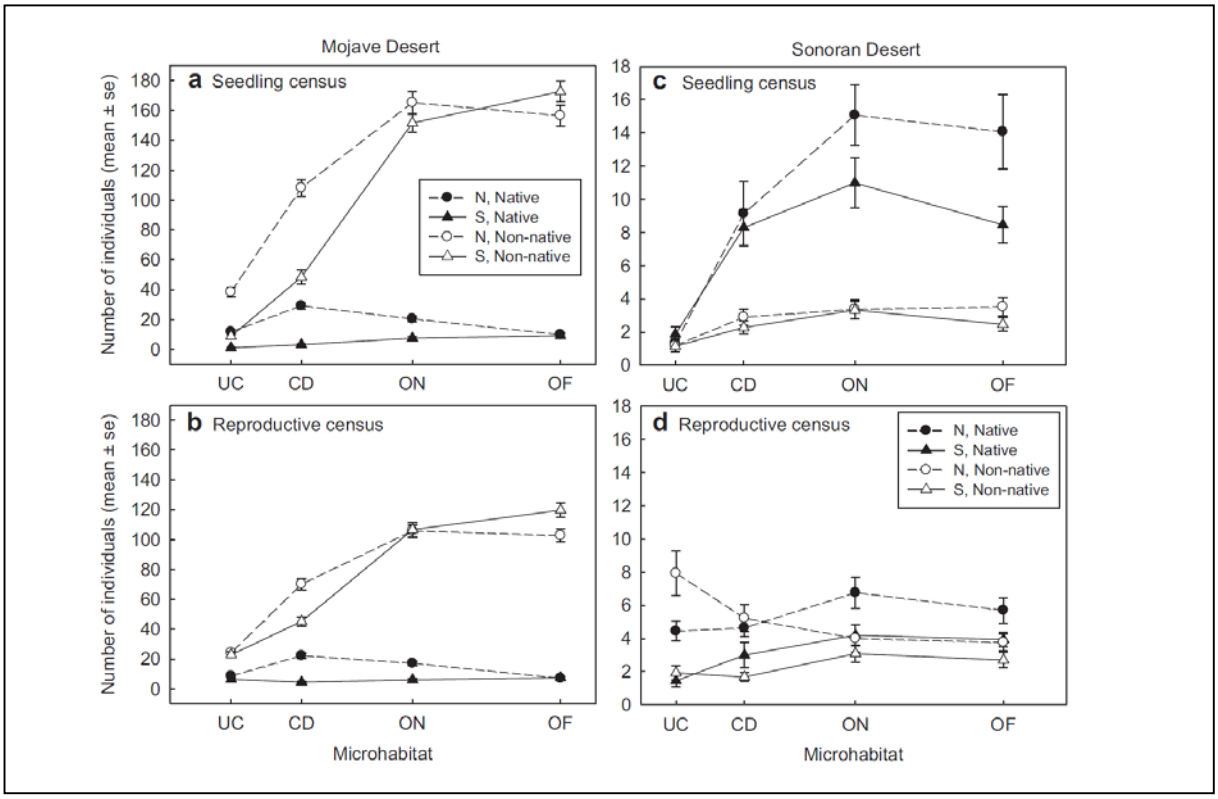


Fig. 10: Native and non-native plant abundance in different microhabitats associated with *Larrea* shrubs. Mean (_1 se) number of native and non-native individuals in each microhabitat and direction (summed across equivalent microhabitats of the two transects associated with each shrub) for the seedling (a) and reproductive (b) censuses in the Mojave Desert and the seedling (c) and reproductive (d) censuses in the Sonoran Desert. The x-axis is scaled according to the distance between plots with the *Larrea* stem at zero. Note the differences in the scale of the y-axis between deserts.

Our results from population counts are also consistent with the hypothesis that *Schismus* populations use a source-sink strategy in the Mojave Desert, but not in the Sonoran Desert. Likewise, another non-native species (*Erodium cicutarium*) and many native annuals do not seem to employ the source-sink strategy. This is demonstrated in Fig. 11, which shows plant densities in comparison to per-capita seed production along a shrub sub-canopy to open gradient (Microhabitats: UC=under canopy, CD=canopy edge, ON=open near canopy, OF=open far from canopy). As indicated by the difference between density and seed output (with density much higher than seed production as a sign for populations sinks), it follows that open habitats appear to be sinks and sub-canopy habitats act as sources for *Schismus* in the Mojave Desert.

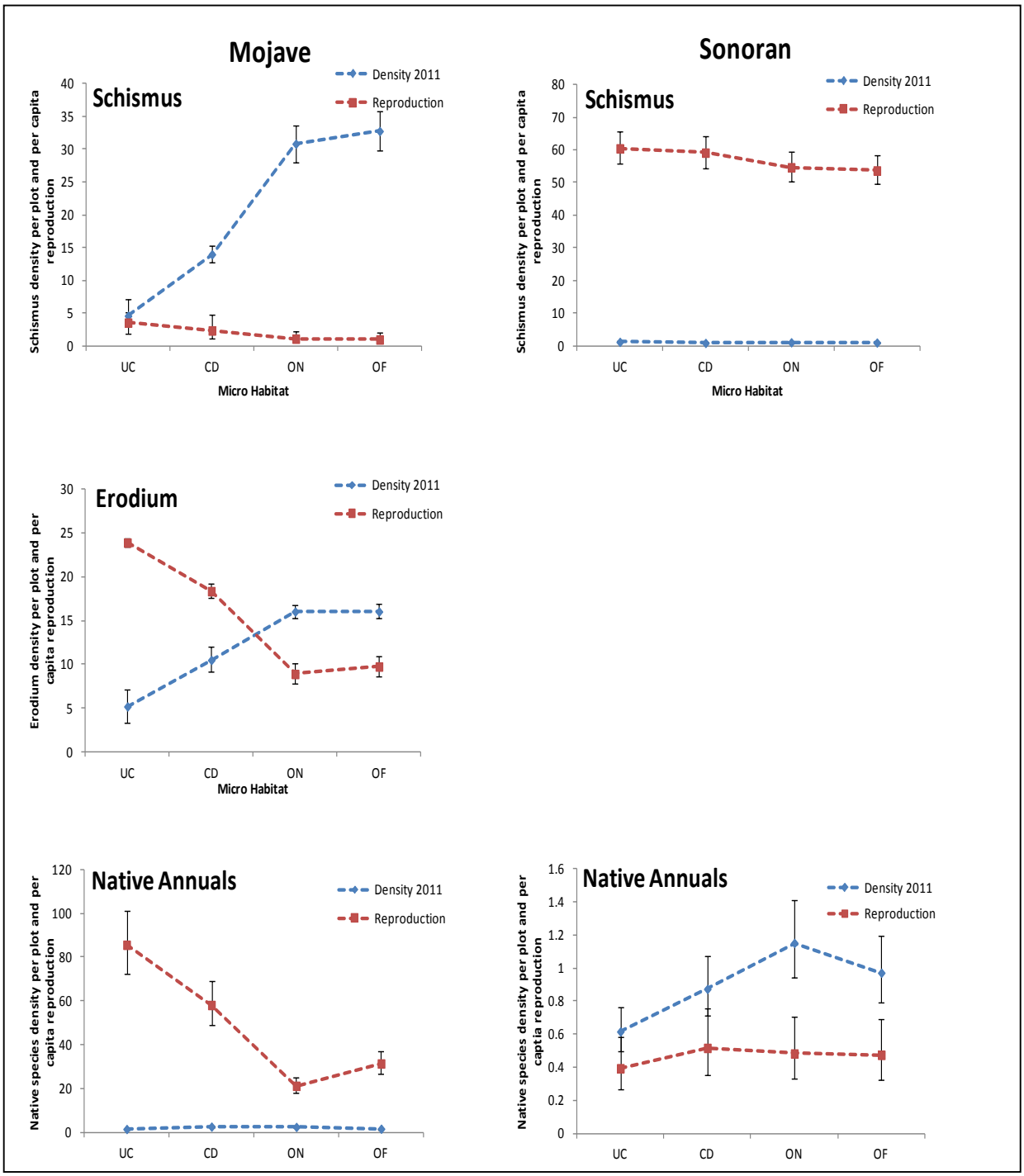


Fig. 11: Plant densities and per capita reproduction along sub-canopy to open gradients in the Mojave (left column) and Sonoran Desert (right column).

4.7 Shrub-size distribution

Methods

In September 2010, one 83m x 130m macroplot was established in each of the Sonoran and Mojave sites. Between November 2010 and January 2011, all *Larrea* shrubs within both macroplots were georeferenced using a submeter Trimble Geo-XT 2003 GPS unit. A "shrub" was defined to be the collection of stems with overlapping canopies located on a single soil mound. Differential correction to location and elevation data was applied, using the nearest base provider. This resulted in a spatial accuracy of 30–50 cm. All UTM coordinates were transformed prior to analysis so that the origin of each macroplot (i.e., (x, y) = (0, 0)) was located at the southwest (SW) corner. We measured shrub geometry using a modification of methods outlined in McAuliffe et al. (2007). Each shrub was visually assessed to determine the long axis, which determined all "length" measurements, and the perpendicular axis was used for "width" measurements (Fig. 12). For each shrub was measured to the nearest cm: height (H) of the tallest living stem, length (D1) and width (D2) of the canopy top (defined by live stems in the upper 1/3 of the canopy), length (B1) and width (B2) of the canopy base (defined by living and dead branches in the lower 1/3 of the canopy, Abase), and length (S1) and width (S2) of the area of stems emerging from the soil surface (Astem, Fig. 12).

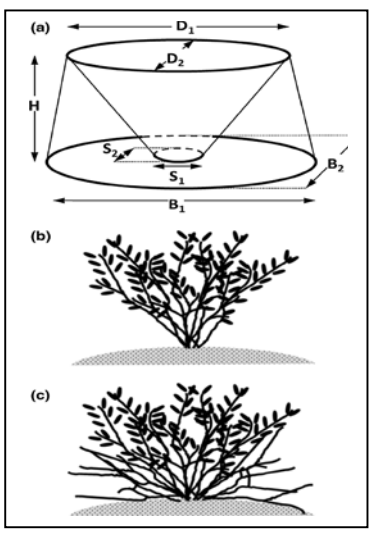


Fig. 12: a. Measurements used to determine size of shrub canopy. b. *Larrea* with an inverted cone shape. c. *Larrea* with a hemispherical shape. Figure modified from McAuliffe et al. 2007

Results

In the Sonora the average canopy base of 713 mapped shrubs (Fig. 12A) was 2.05 m^2, and the average stembase (Astem) was 0.26 m^2 (Fig. 13). In the Mojave, the shrub canopies were much larger, as the average Abase of 303 mapped shrubs was 3.47 m^2 and average Astem was 0.77 m^2 (Fig. 12B, See Mudrak et al. 2014).

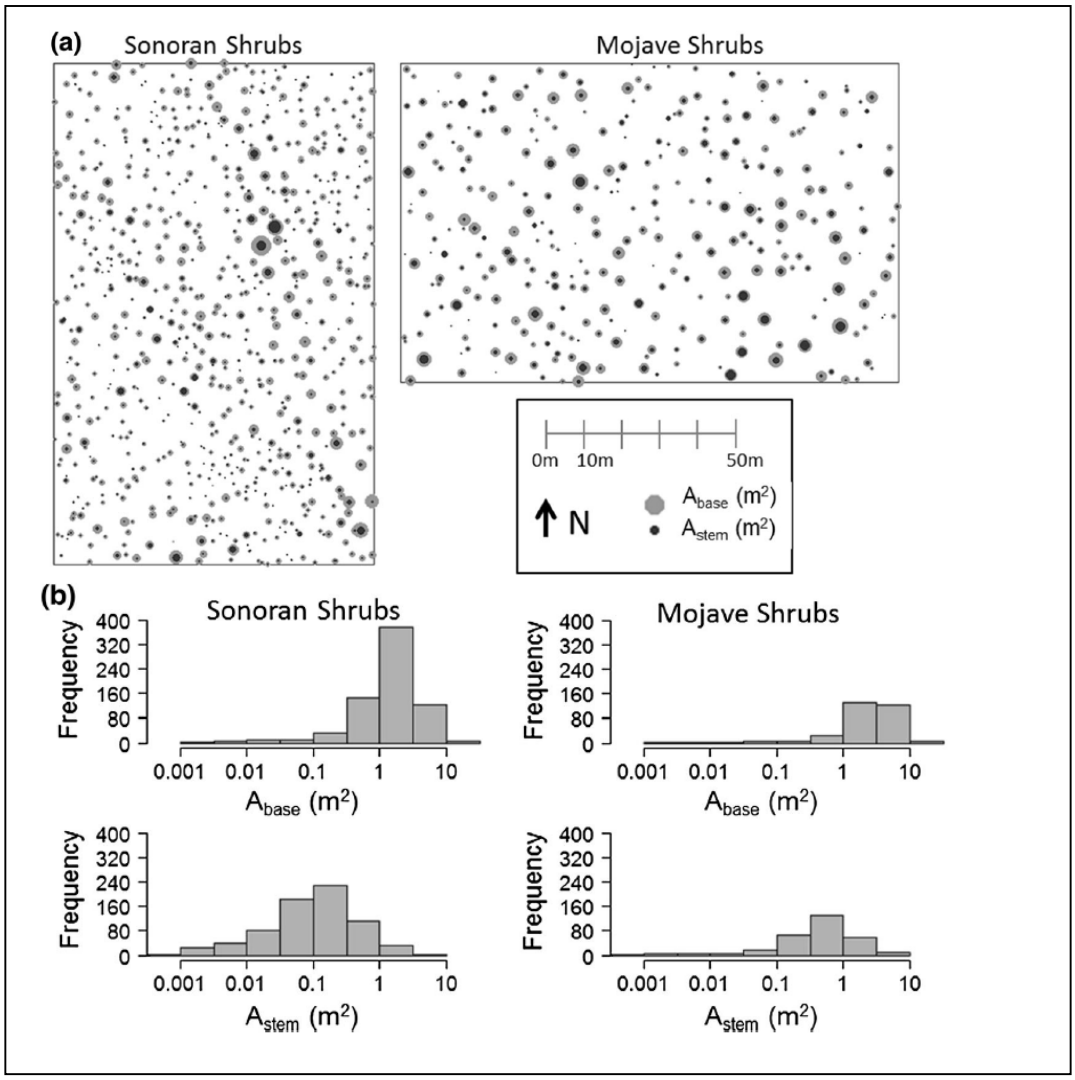


Fig 13: Distribution and size of *Larrea tridentata* in the two core sites. A. Maps of Larrea in the Sonoran and Mojave macroplots. Circular representation of canopy base (Abase, light gray) and Stem base (Astem, dark gray) are shown to scale. B. Histograms showing distributions of aforementioned parameters of shrub sizes for each study site.

4.8: Discussion of Pre-treatment Site Characterization

<u>Conclusions</u>

Larrea seems to have overall negative effects on the abundance of annual plants, regardless of provenance, unlike the desert shrub *Ambrosia dumosa*, which has facilitative effects on annuals (Holzapfel and Mahall, 1999); this difference could be related to the fact that *Larrea* is allelopathic and *A. dumosa* is not (Mahall and Callaway, 1992). Negative and positive effects of

shrubs can occur at the same time (e.g. Callaway, 1994; Facelli and Temby, 2002; Holmgren et al., 1997; Holzapfel and Mahall, 1999), and the balance of positive versus negative effects of *Larrea* appears to depend on environmental factors that vary with respect to direction. In addition, the importance of facilitative versus competitive effects of shrubs depends on the intensity of abiotic stress (Bertness and Callaway, 1994), and our results suggest that the intensity of abiotic stress under *Larrea* varies during the winter growing season in the Mojave and Sonoran Deserts. Differences in abiotic stress over the growing season may be related to size-specific interactions (Morris and Wood, 1989) or changes in resource availability. Furthermore, differences among site factors such as rainfall, soil characteristics, and species composition either within or among deserts likely influences interactions between *Larrea* and annual plants. Further knowledge of the effects of *Larrea*, which is a dominant species throughout the southwestern United States, on abundance of native and non-native annuals is necessary to gain a better understanding of the dynamics of species interactions in desert scrub ecosystems.

The demonstrated difference between *Schismus* density and seed output indicates a higher ratio of seeds accumulating in seed banks of potential sink populations (open areas) as compared to sources (shrub sub-canopy). Such differentiation of habitats into sources (sub-populations in high-quality habitats that produce excess offspring) and sinks (sub-populations in lower-quality habitats that need an external propagule supply in order to persist) is expected to be quite common in meta-populations in spatially and temporally varying environments (Pulliam, 1988). It has been postulated that sub-populations in sink habitats are not persistent in isolation, either due to biotic interactions such as strong interspecific competition (Amarasekare, 2003) or spatially differentiated herbivory (Berry et al., 2008), or due to low abiotic habitat quality (Kadmon and Shmida, 1990). It is interesting to note that in temporally varying environments source and sink populations may switch roles and thereby both contribute to species persistence and coexistence (Hanski, 2009). As much as source-sink population dynamics have been discussed theoretically and have become an established pillar in basic population theory, empirical tests for it are still relatively rare (see reviews in Diffendorfer, 1998; Gundersen et al., 2001). In particular, clear experimental work is needed to relate theory to populations in the field. Moreover, the few experimental studies that exist show that such source-sink dynamics are dependent on the systems at hand and evidence of dispersal-mediated population persistence has either been confirmed (Gunderson et al. 2001, Berry et al., 2008) or is lacking (e.g., Kunin 1998, Kadmon and Tielbörger 1999).

5. Effects of Experimental Treatments

5.1 Site Treatments

The factorial treatment design that combines disturbance treatments (disturbed and undisturbed, direction of transect (north and south), fire regime (burned vs. unburned, rainfall/hydrology treatments (ambient, elevated, drought) and invasive plant seed addition (seeded vs. not seeded) is shown in Fig. 14.

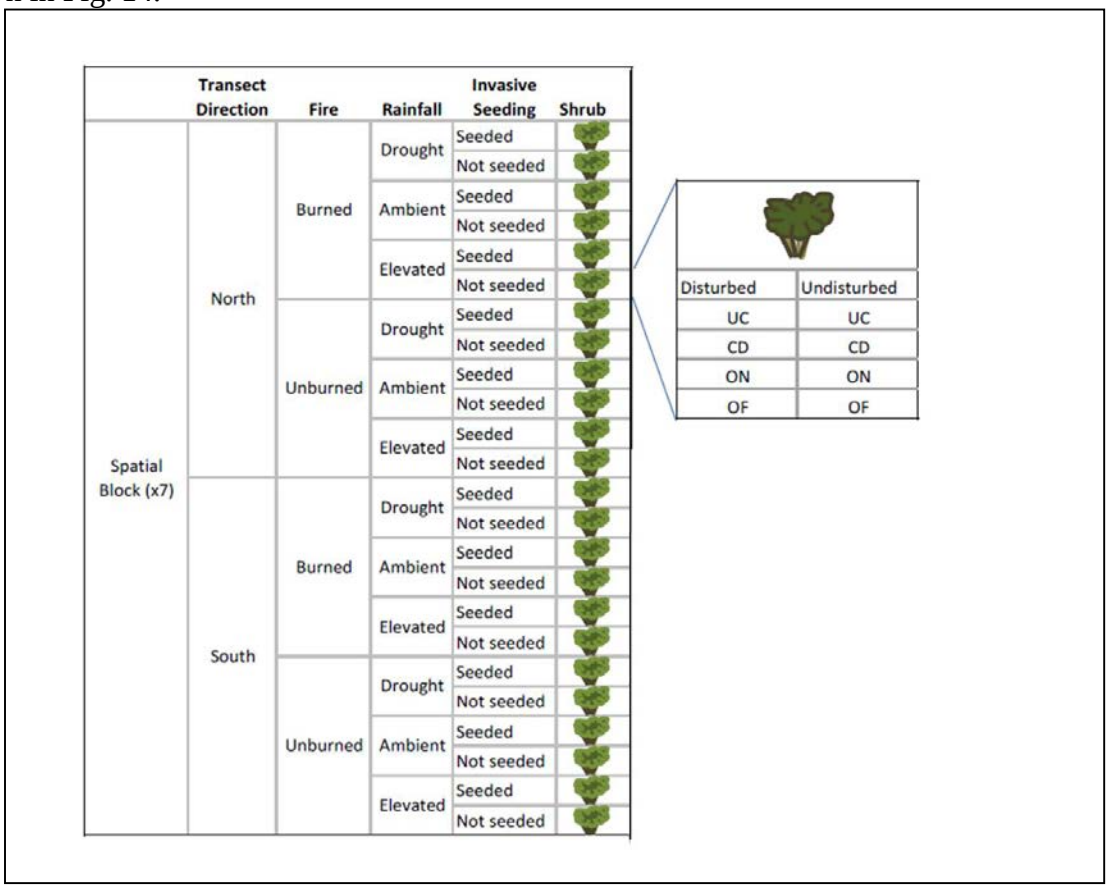


Fig. 14: Full treatment regime. Note that each shrub has an undisturbed (control) and a disturbed transect. Undisturbed and disturbed quadrats in the four microhabitats (UC=under canopy, CD=canopy drip-line, ON=open near shrub, OF=open far from shrub) are fully nested into the overall factorial experimental design. Each treatment combination is replicated seven times. .

<u>Controlled Burn Treatment</u>

In June 2011 *Larrea* shrubs were burned in the Mojave Desert site. 56 individual shrubs were selected on the basis of minimum distance from other treatment shrubs to avoid accidental fire spread in general and to other experimental units in particular (Fig. 15). T he burn was conducted by a crew from the Fort Irwin Fire Department (Fig. 16). Shrubs and the dry annual vegetation under shrub canopies were ignited with Fusee flares and the fire was allowed to finish uninterrupted. Such flares are commonly used in forestry, firefighting, wildland fire suppression and in the ignition of controlled burns. Fusees are easily controllable, ignite at 375 °F (191°C) and burn as hot as 3,000 °F (1,600°C) and therefore can be used to ignite plant material that is

relatively moist. Unlike drip torches, only minimal amounts of residue come in contact with the soil surface. This is important for our experiments. Great care was taken that the fire did not spread to adjacent shrubs. The fire crew had a water truck on standby and 2 of the fire crew carried back sprayers at all times. A similar burn has been conducted in late September 2011 at the Sonoran site (in this location we were allowed to conduct the burn ourselves, and were accompanied by installation personnel).

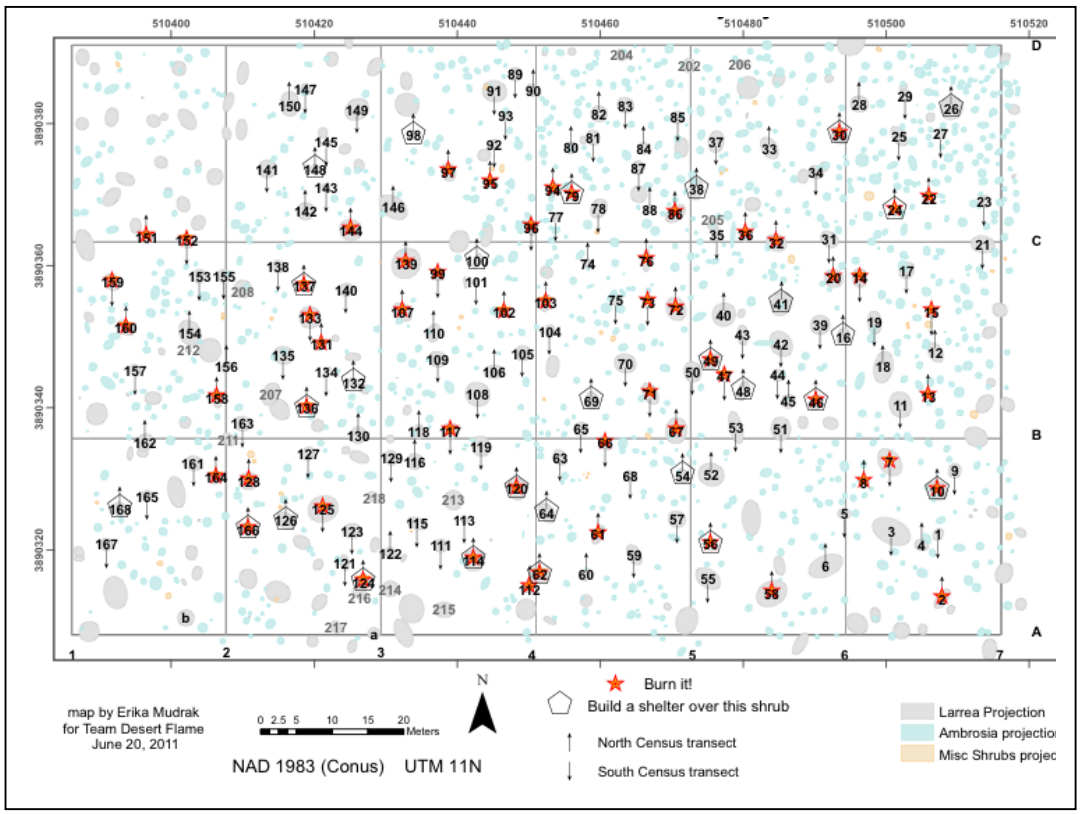


Fig.15. The spatial arrangements of burned shrubs in the Mojave desert site together with the distribution of rain-out shelters.

Fig. 16: Images from Mojave controlled burn in June 2011. Left photo shows use of Fusee to ignite fire. Right photo shows a *Larrea* shrub in mid-burn.

Installation of Rain-out shelters

For the drought treatment rainout shelters were erected that intercept 50% of the precipitation. They are similar to the ones described by Yahdjan and Sala (2002), but have been modified by E. Mudrak and A. Fuentes- Ramirez to fit the size our *Larrea* shrub plots. These permanently fixed rainout shelters utilize strips of plastic (greenhouse-grade product with no UV absorbance to ensure that the plants underneath get a full spectrum of natural light) to intercept a given amount of rainfall. The shelters were constructed of frames of metal tubing with a height of 1.5 to 2 meter. These frames are covered with equally spaced strips of plastic. The roofs are angled and drain to gutters at the down-slope edge of the roof. Gutters leading to collecting vessels drain the water and allow for measuring amounts of water intercepted by the roof, as well as provide a source of water for irrigating the elevated-rainfall treatment shrubs. In June of 2011 28 of these shelters were erected at the Mojave Desert site (Fig. 17B). 28 shelters were built in the Sonoran Desert site in September of the same year.

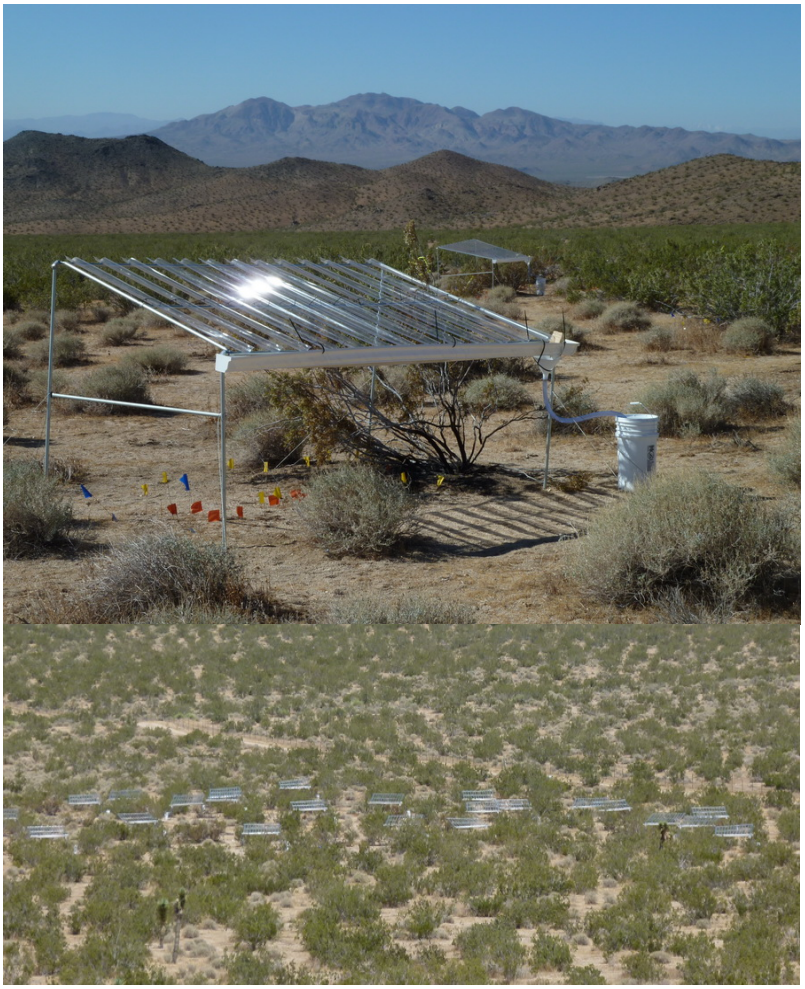


Fig. 17 Rainout shelters. A. Upper image shows a completed shelter in the foreground. B. Lower image shows the distribution of several completed shelters within the macroplot at the Fort Irwin site of the Mojave Desert.

In both macroplots water was added to 28 plots so that 28 plots received ambient, 28 half ambient, and 28 double ambient rainfall.

5.2 Treatment effects on annual plant populations

Methods

For all permanent quadrats complete counts of annual plant populations together with estimations of biomass production were conducted and seed production for selected, dominant species was determined during the rainy seasons of 2012 and 2013. Even though a large number of response variables have been explored, two major, integrative ones are presented here: annual biomass and alieness (percent non-natives in the annual plant community). Biomass was estimated from vegetative cover and average height of vegetation. Correlations calculated separately for each desert and year based on collection of plant material from just outside our study grid to estimate biomass for each plot were used. Biomass correlation samples were collected over a range of plot covers and heights, materials were air dried and weighed in the lab. Proportion of non-native species was calculated based on plant density. The number of

individuals of each species present was counted, the data for non-native species and all species were added and then the proportion of non-native species was calculated.

Results

Fire effects: experimental fire significantly increased ($p<0.001$) annual pant biomass in both deserts, however this increase was stronger in the Sonoran Desert compared to the Mojave Desert (Fig. 18, fire x desert interaction effect, $p<0.01$). The fire effects were not different among different microhabitats along the sub-canopy-to-open transects. Fire increased the percentage of non-native species in the annual community ($p< 0.01$, Fig. 19) in the Sonoran desert. This increase was not found in the Mojave Desert (fire x desert interaction, $p<0.001$).

Disturbance effects: Overall, disturbance is increasing annual biomass and alieness for the communities (Fig. 20 and 21, biomass $p<0.05$; alieness $p >0.001$); and both deserts and all microhabitats react similarly to disturbance in this respect (no significant interactions).

Effects of watering treatment: As expected, irrigation increased annual biomass and drought treatments decreased it (Fig. 22, $p<0.001$). This was similar for both deserts and all microhabitats (no significant water treatment and desert or microhabitat interactions). It was surprising that drought treatments increased the percentage of non-natives in the annual communities in both deserts (Fig. 23, $p<0.05$). This was likely due to the greater role the invasive grass *Schismus* played in experimentally droughted areas. In contrast, experimental increase of water availability did not change the proportion of non-native species significantly.

The short-term responses of annual plants populations and communities to our treatments show that native and non-native species in both deserts react differentially. As expected annual biomass increased in both deserts with increasing rainfall, however fire increased biomass only in the Sonoran and showed little effect in the Sonoran Desert. Disturbance had strong increasing effects on biomass in both deserts. In the Mojave Desert disturbance and decreasing rainfall favored non-native species, while burns did not cause a relative increase of non-natives. In contrast, non-native annuals in the Sonoran Desert did become more abundant with fire, but did not increase with disturbance and drought. This demonstrates that the invasion processes differ in both deserts and that the impacts of fire can be regionally very different.

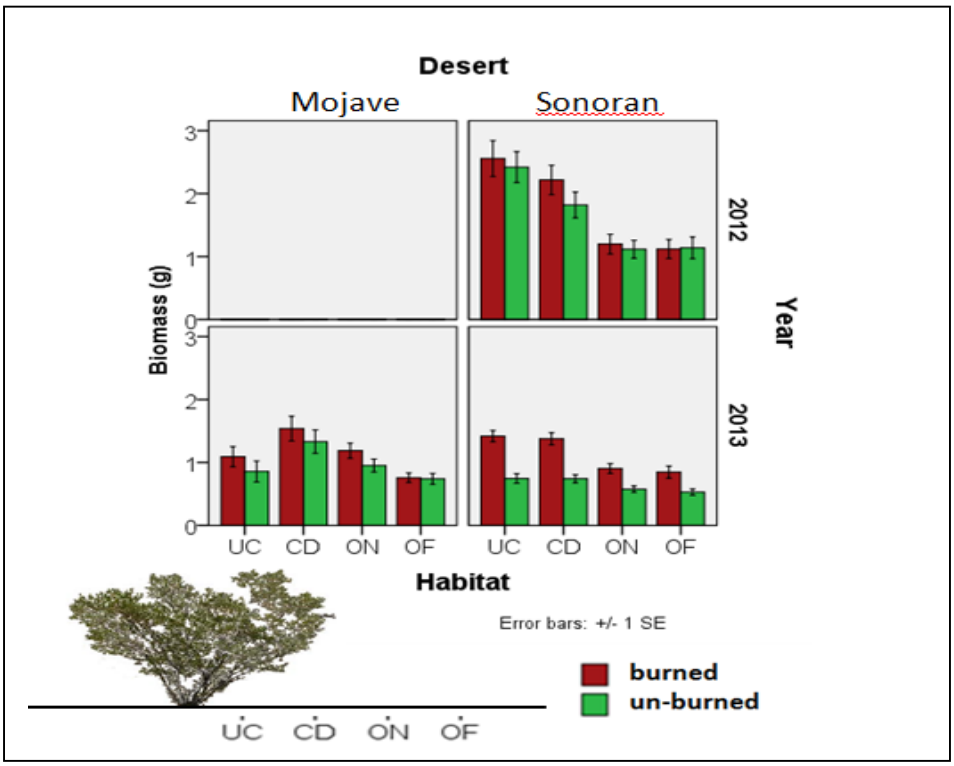


Fig. 18: Effect of fire treatment on annual plant biomass. Shown are results for the two desert sites in the years 2012 and 2013 broken down by habitats (UC=under canopy, CD=canopy edge, ON=open near canopy, OF=open far from canopy). ANOVA *p* values: fire effect <0.001, fire x desert <0.01, fire x habitat >0.05, fire x desert x habitat <0.05. Due to very low rainfall amounts during the winter of 2011/12analysis was possible for 2012.

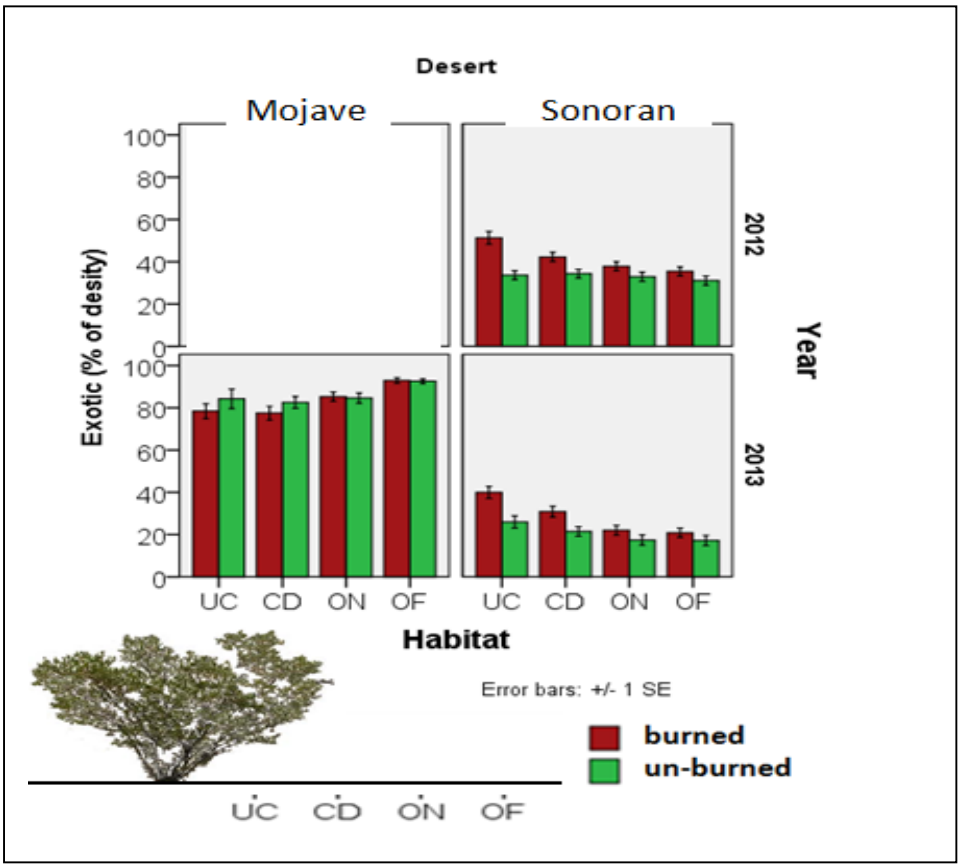


Fig. 19: Effect of fire treatments on alieness (=percent invasives in annual community), for full legend see Fig. 18:. ANOVA *p* values: fire effect <0.01, fire x desert <0.001, fire x habitat >0.05, fire x desert x habitat <0.05.

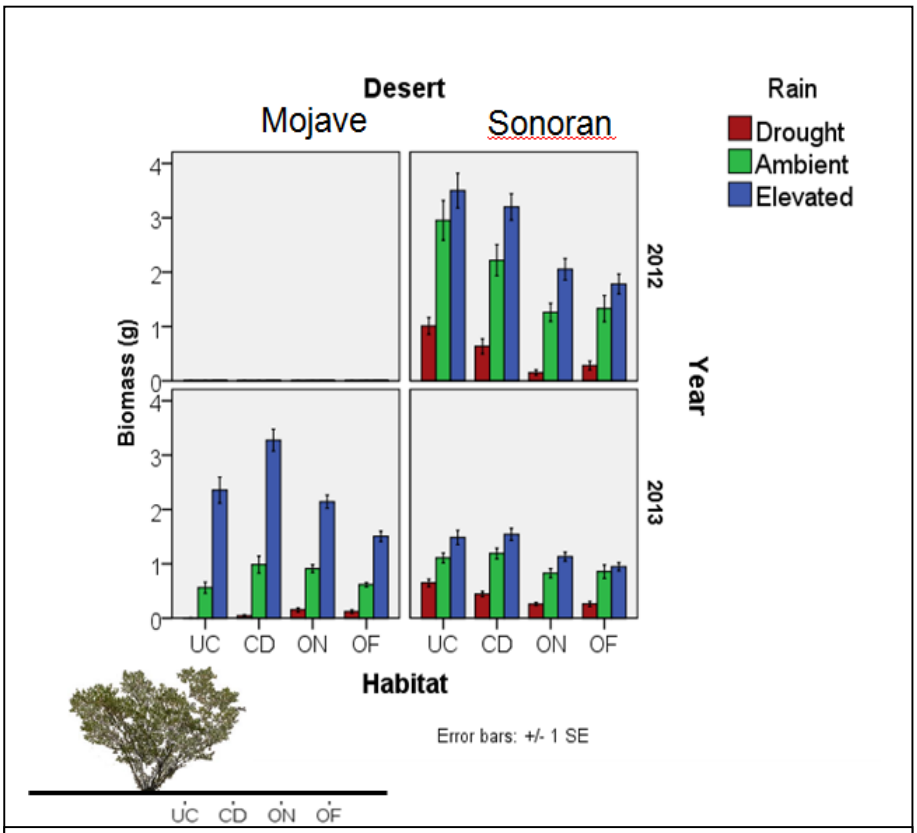


Fig. 20: Effect of hydrology treatments on annual plant biomass, for full legend see Fig. 18. ANOVA *p* values: hydrology effect <0.01, hydrology x desert >0.05, hydrology x habitat >0.05, hydrology x desert x habitat <0.05.

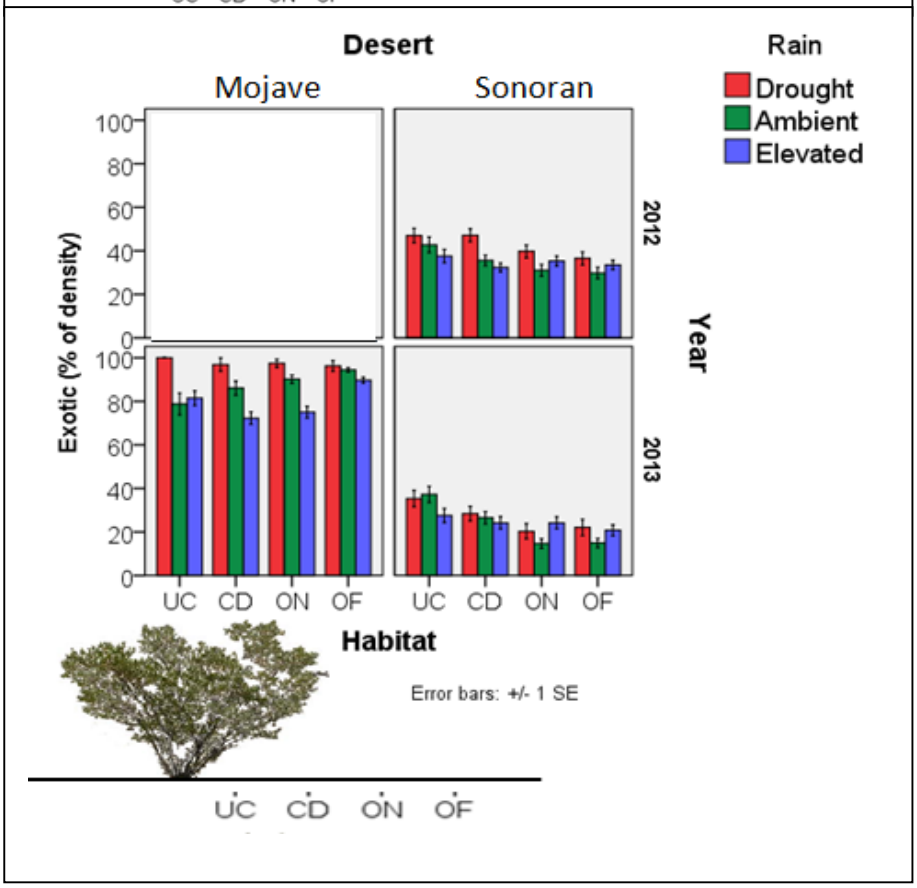


Fig. 21: Effect of hydrology treatments on alieness (=percent invasives in annual community), for full legend see Fig. 18. ANOVA *p* values: hydrology effect <0.05, hydrology x desert >0.05, hydrology x habitat >0.05, hydrology x desert x habitat >0.05.

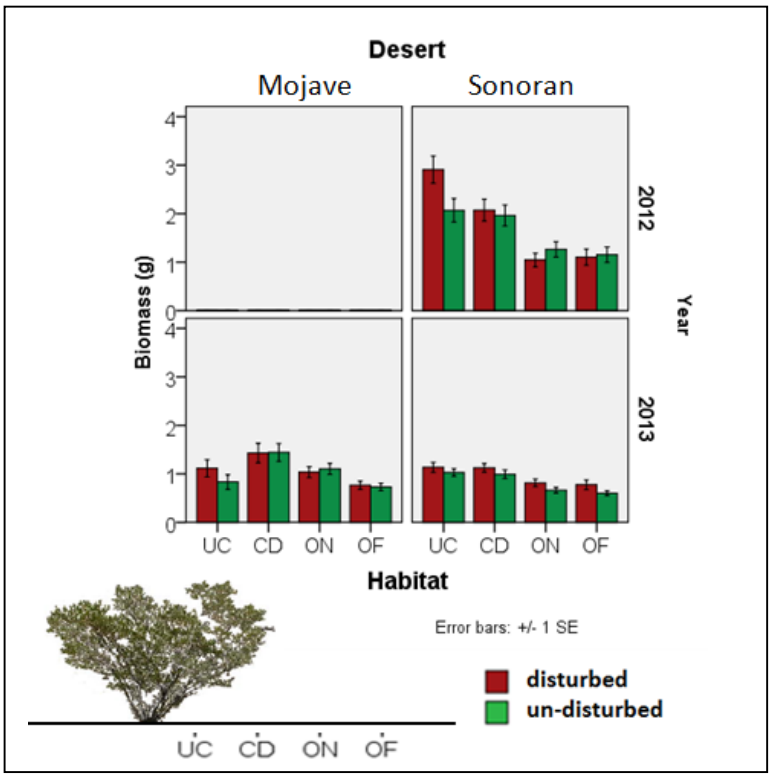


Fig. 22: Effect of soil disturbance treatments on annual plant biomass, for full legend see Fig. 18. ANOVA *p* values: disturbance effect <0.05, disturbance x desert >0.05, disturbance x habitat >0.05, disturbance x desert x habitat >0.05.

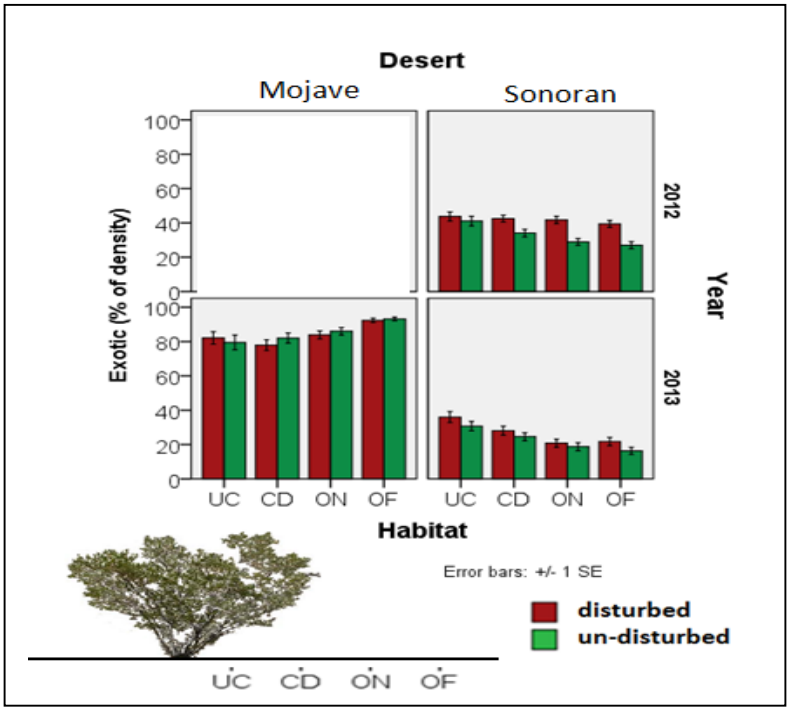


Fig. 23: Effect of soil disturbance treatments on alieness (=percent invasives in annual community), for full legend see Fig. 18. ANOVA *p* values: disturbance effect <0.001, disturbance x desert >0.05, disturbance x habitat >0.05, disturbance x desert x habitat >0.05.

5.3 Quantification of treatment effects on soil crusts and differentiation of physical and biotic soil crusts

Methods

Resistance of soil crust (biogenic and physical) was measured in 2012 and 2013 using a soil penetrometer.

Results

These measurements indicated that soil crust was reduced by physical soil disturbance (Fig. 24) in both desert sites. Experimental fire did not significantly change soil crusts in either desert (data not shown). In the Sonoran sites where coverage of cryptogamic crust ranged from 0 to 30% a clear negative correlation with the density of the dominant invasive grass (*Schismus arabicus*) was found, suggesting potential antagonistic interactions between the invasive grass and the crust. Experimental treatments had no measurable effect on the presence of the biogenic crust.

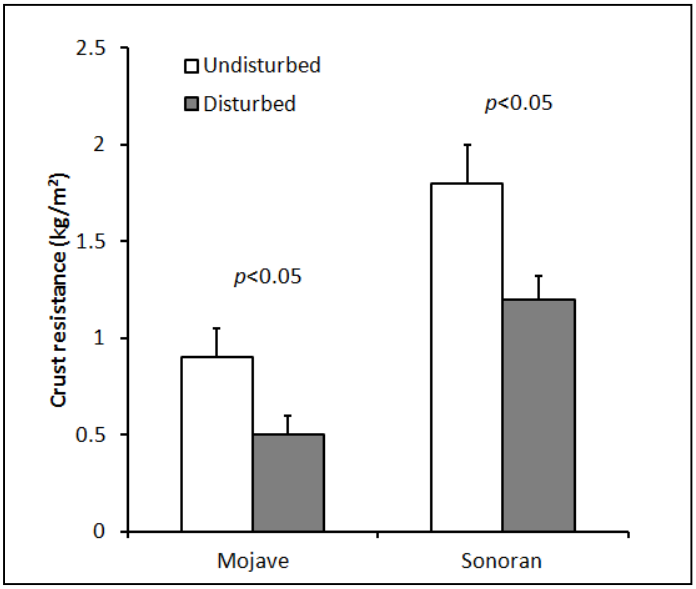


Fig. 24: The effect of experimental disturbance on soil crust resistance. Crust resistance (kg/m^2) is shown as effected by total winter rainfall (mm). Blue bullets are from undisturbed soil, green bullets are measurements form disturbed soil crust.

5.4: Discussion of Effects of Experimental Treatment

The lack of crust in our Mojave Desert site warrants the question on how typical this situation is in the current landscape across the deserts that were studied in this project. The current vegetation pattern with discrete shrub-formed islands of fertility might be the consequence of past grazing pressure. The landscape prior to livestock grazing might have been quite different (e.g., more of a grassland) and formation of biogenic soil crusts could have been main cause for this. Biological soil crust (BSC) are often not restricted to such islands of fertility and can potentially cover up to 70% of shrub interspaces in deserts (Friedmann & Galun 1974, Belnap 1994). While some studies did not show that BSC contribute to nutrient buildup between shrubs (e.g. Thompson et al. 2005), recent research by Williams and coworkers (Williams et al. 2010, 2012, 2013) provided strong evidence that especially lichens and mosses within BSC can provide

added focus of nutrient supply between shrubs that can facilitate the colonization by vascular plants as well. That raises the question whether landscapes with well-developed BSC are typically characterized by a less patchy nutrient distribution with less discrete islands of fertility. Such regions would allow colonization of forbs and grasses between shrubs. BSCs are easily impacted by physical force (off-road vehicles, grazing, etc.), and are therefore highly sensitive to land use changes (Belnap 1995). Grazing, either by high densities of wild ungulates or by livestock is known to be a highly disruptive to BSC (Brotherson et al. 1983). It is reasonable to assume that cryptogamic crusts were more abundant before livestock grazing was introduced to the arid SW in the 18th century.

Even though there appears to be no early report on soil crusts per se, the detailed analysis of early sources describing Californian vegetation by Minnich (2008) allows to deduct some trends. Minnich (2008) notes accounts of early Spanish explorers at the end of 1700s indicating that some desert areas appear to have had a higher abundance of bunchgrasses than is found today. Intensifying grazing by domestic livestock (cattle, horse, sheep) from this the Spanish period on to a peak around the gold rushes (1849) appeared to have eliminated these grasses in favor of less palatable desert shrubs. It is to note that feral ungulates might also have played an important role in this (burros, wild horses). Fremont (1945) reported large flocks of wild horses among other native ungulates. It its therefore very possible that the patchy vegetation in the shrublands of the Mojave and Lower Sonoran Desert is at least in part the result of heavy grazing. It is intriguing to note that some authors stress (notably Martin 2005) that the region of the arid SW has been under heavy grazing pressure in the Pleistocene, at least until the native megafauna disappeared due to factors that are discussed (overkill, climate change). Could it be that a desert landscape with discrete shrubs and accompanying islands of fertility and with restricted cryptogamic crusts is at least partly a natural steady state? A stable steady state that replaced former grasslands with strongly developed crusts that could exist only under low grazing pressure?

That intense grazing is responsible for the shrub/island of fertility pattern has been discussed recently. Allington and Valone (2010, 2011) published studies that indicate that islands of fertility caused by the patchy distribution of shrubs may be indeed the consequence of grazing. By comparing desert site in the desert of Arizona inside and outside of grazing exclosures they demonstrate that fro nitrogen and soil carbon islands of fertility are reduced when grazing is excluded. Besides direct destruction of BSC Allington and Valone (2011) discuss the removal of biomass and soil compaction (with the consequence of decreased water infiltration and increased runoff).

6. Model Development, Validation and Experiments

6.1 Modeling Philosophy

We have developed *FireGrid*, a model for fire simulation in desert shrubland landscapes, in parallel with the field and experimental studies detailed in this report. The primary objective for developing the model was to characterize fire spread as a function of fuel loads based on our understanding of the ecological relationships of the creosote shrubland system. This will aid in developing a better understanding of the conditions that are necessary for the occurrence of high probability "catastrophic" wildfires. We also wanted to tie our work to current ecological theory, as this provides a broader context within the study of fire ecology, linking to the current ecological theory of fire dynamics.

The understanding of the dynamics of fire in an ecological context is well developed for systems that have been historically more impacted by fire and there have been a large number of fire dynamic models developed for these systems (cf., Sullivan 2009). In contrast, there has been little work done on fire dynamics and fire modeling in desert shrubland systems, primarily because fire in these systems has been historically unimportant until more recently (Brooks 2002). A good example of the disconnect in knowledge between the general field of fire ecology and fire dynamics in desert shrublands can be seen in a U. S. Forest Service technical report, characterizing a range of fuel load models based on vegetation type (Anderson 1982). The report is comprehensive and covers a broad range of conditions where fire plays a role. However, it does not cover the conditions of generally low fuel loads that occur in the open areas between bushes in creosote shrublands. This is also true for other aspects of fire ecology, where creosote shrublands fall outside the range of conditions generally considered. *FireGrid* represents a model designed to fill the gap in knowledge by linking the general field of fire ecology to the situation occurring in a system that has historically not been impacted by fire, but which may be more prone to fire as exotic species become established and more extreme rainfall years are experienced.

Our modeling philosophy for the development of *FireGrid* has been to "begin simple and then add complexity". There are a number of reasons for this. First, this allows us to link model results to well-established theory that has been developed by landscape ecologists beginning in the 1980's and 90's. The approach derives originally from percolation theory, which was adapted by ecologists from statistical physics for the study of the spread of organisms through landscapes (Gardner et al. 1987, 1989). A second reason for starting simple is that this allows us to understand more fully how various ecological factors affect fire spread in the landscapes we are studying. If we begin with a complex model with many factors, it is extremely difficult to isolate the causative factors. However, if we add complexity one element at a time, in a logical, well-thought-out sequence, we can determine more precisely how different ecological elements impact fire spread. This will lead to a better understanding of how fire spreads in low fuel load systems and how it might be controlled.

The percolation models used to study animal movement characterize the landscape as comprised of individual cells in a grid. Cells are in two potential states, either suitable for animal occupancy or not suitable. Animal movement is dictated by habitat availability and most animals, with the exception of those that can fly, require reasonably continuous, suitable habitat to be able to move across a landscape. The restriction on movement imposed by fragmented landscapes has been of great interest in the field of conservation biology and has been studied

using these simple cell-based, so-called cellular automata (CA) models. One example of the importance of fragmentation to animal movement is represented by the SLOSS (single large or several small) debate, which centers on judging how movement needs to be considered in constructing conservation habitat. The central issue is still being explored empirically (e.g., Hoyle and Harborne 2005) and the theory has advanced to add more ecological reality to what began as pure theoretical explorations (see Kingsland 2002 for a good overview of the development of the issue). There have also been recent studies demonstrating the relevance of more abstract CA models to findings obtained from more complex, less general fire models (Zinck and Grimm 2009).

Clearly, there is a striking similarity between the issue of fire spread in the creosote shrubland system, where the distribution of the fuel bed is normally quite fragmented, and the movement of animals within a fragmented landscape. It seems natural to leverage the findings of the approach used in studying the impact of fragmented landscapes on animal movement to examine fire spread in creosote shrublands.

As with animal movement, fire can only spread through a landscape if there is fuel available to burn. The spatial distribution of sufficient fuel loads to carry fire can determine how fire spreads through the landscape. Highly abstract CA based models have been used to explore fire spread, much like the models that were developed to examine animal movement (Niessen and Blumen 1986, Ohtsuki and Keyes 1986, Cox and Durrett 1988, Drossel and Schwabl 1992, Zinck and Grimm 2008). However, we have extended this approach to consider more complex landscapes, where there is an extremely heterogeneous fuel bed, with a large proportion of the landscape generally having extremely low fuel loads. Most of the development of fire modeling using the CA approach has been in systems with well-developed fuel beds and the models have been used to examine the pattern of fire spread or examine fire return times, taking into account stand regrowth. In our system, the process is very different. Most years, there is not a sufficient amount of fuel to carry a fire. The goal instead is to determine the threshold conditions that can lead to catastrophic spread, since under most environmental conditions fuel loads are too low to carry fire. Increased rainfall can lead to increased fuel loads, particularly in the inter-shrub area. What is important to determine is the interplay between extreme rainfall events, establishment of annuals in the inter-shrub area and fire risk. *FireGrid* was designed to explore these linkages.

6.2 The *FireGrid* Blueprint: Basic Model Structure

The model was initially envisioned as being developed from sub-models interacting as shown in Fig. 25. The landscape provides the spatial template within which the model operates. The primary dynamics occur in three vegetation layers, two of which are made up of annual herbs and grasses, as described below. These can be affected by environmental conditions, which in the context of this study involve water availability and soil disturbance. Vegetation and the environment interact to produce a distribution of fuel (litter) that can act to spread fire through the landscape. Fire, in turn, can produce changes in the environment, alter fuel loads (litter), and impact the three vegetation layers.

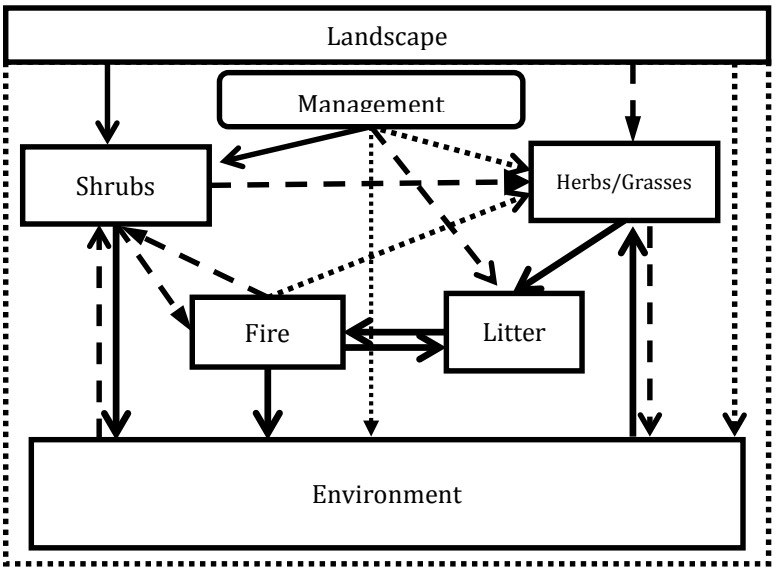


Fig. 25: Basic model structure as envisioned prior to model development.

We began model development with a very simple model, based on a grid of cells, which did not include all of the compartments shown in Fig. 25. Each cell represents a 0.20 m x 0.20 m area of land, which is the scale of our field samples and experimental units. This allows us to match our experimental findings precisely to the model structure. Most of the simulation experiments were conducted on an 80m x 40m landscape, which is approximately the same dimension as our experimental sites. Since we have a precise map of all of the shrubs at this scale for both our study sites, our simulation experiments can be conducted using the observed shrub distributions in examining fire spread.

The vegetation in the model consists of three distinct components: (i) shrubs; (ii) annual plants growing in the open with no influence on their distribution due to shrubs; and (iii) annuals growing under the shrub canopies. The reason for using this three-layer structure is based on our understanding of the basic ecology of interspecific interactions in this system. We have found that the shrubs have little influence on the abundance and demography of annuals growing in the open (20 cm or so outside *Larrea* canopy drip-lines). Plants within the matrix exhibit virtually no spatial structure and can be modeled using appropriate frequency distribution models to characterize their abundance and spatial locations. In contrast to annuals growing in the open, annuals growing closer than 20 cm to the drip line of shrubs are influenced by the environment of the shrubs, which impact nutrient availability and soil moisture. The under-canopy annuals are generally larger and more densely distributed than plants growing in the open.

Larrea shrubs in this system change little in stature from year-to-year, as their growth rates are extremely slow. There is also negligible recruitment of new shrubs into the community over a period of 10 years or more. Because of these characteristics, shrubs in this system can be treated as a static landscape element influencing the distribution and demography of the annual plants, which dominate these systems, at least in the absence of fire. We are, however, interested in exploring the impact fire can have on the community by eliminating shrubs when fire is able to spread. An examination of this is one goal of the simulation modeling studies.

In the simplest models, we examine fire spread through the landscape by randomly setting cells to a state that allows them to burn. The idea behind this approach is that we want to understand how fire will spread through a patchy landscape where the only vegetation we

consider is annual plants growing in the open. This forms the basis for understanding how shrubs and under-canopy annuals modify fire spread during high fire risk years.

6.3 Linking to Percolation Theory

The first model experiments we conducted set a foundation for linking our approach to a well-established theory of landscape ecology, which is based on two components (i) neutral landscapes and (ii) percolation theory. In a classic paper, Gardner et al. (1987) introduced the concept of **neutral landscapes** to the field of landscape ecology, where neutral landscapes were defined to be areas characterized by a grid of cells that were in two habitat states: unsuitable versus suitable. In the case of *FireGrid*, this corresponds to the states of flammable versus non-flammable. A neutral landscape is one in which there is no structure to the distribution of the two states, i.e., their locations are randomly distributed with no exogenous or endogenous processes structuring the distribution. This produces a family of models that are determined by the parameter p_{land}, the probability that a site is in one of two possible states, in our case flammable as opposed to non-flammable. By definition, the alternative state, non-flammable, occurs with the probability 1- p_{land}. A neutral landscape is constructed by randomly setting each cell in the landscape to one of the two possible states with probability p_{land}; all other cells are then set to the alternative state (Fig. 26).

Percolation in a landscape context, which is technically referred to as site-percolation, is defined to occur when there is at least one path that spans from one side of the landscape to the opposing side through connecting landscape elements or cells. Originally, landscape ecologists were interested in this as it could be used to study the likelihood that organisms could traverse fragmented landscapes made up of habitable and non-habitable sites (Gardner et al. 1989). In our analogous case, we are interested in determining the likelihood that fire can spread or move through a landscape.

Typically, when percolation theory is applied to landscapes, the 4-neighbor rule is used whereby connections occur between two adjacent cells having an edge in common in one of the four cardinal directions (i.e., E, W, N, S). Other definitions of spread can be used, e.g., 8-neighbors comprising cells immediately adjacent to a central cell. The choice of the neighborhood spread rule impacts the probability of spread in a predictable fashion, with spread being easier with an 8-neighbor rule than a 4-neighbor rule (Malarz and Galam 2005).

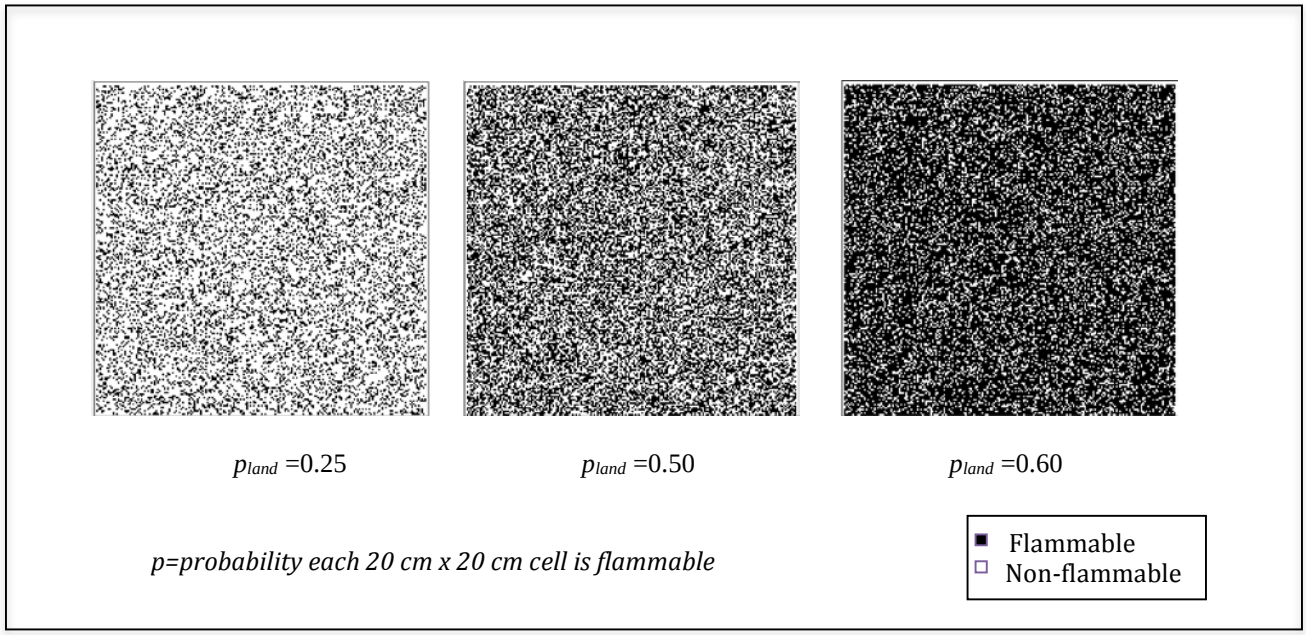


Fig. 26: Neutral landscapes for different values of *p*, the probability that a cell is flammable.

For an infinite landscape employing the 4-neighbor rule there is a critical threshold (p_{crit}) above which the probability of site-percolation asymptotically approaches a value of one (Milne 1991), below this threshold percolation does not occur. For a grid using the 4-neighbor rule, $p_{crit}\approx 0.5928$. In contrast, the percolation threshold for the 8-neighbor rule is $p_{crit}\approx 0.407$ (Malarz and Galam 2005). Although this theoretical result is interesting, it only holds exactly for an infinite landscape. For finite landscapes, a high probability of percolation may occur at a narrow range of values below p_{crit} and the point at which there is 100% probability of percolation is somewhat above p_{crit}. We explored these issues in the simplest version of *FireGrid* using a model that only considered fire spread through a matrix that was composed of cells that were flammable and non-flammable. We used the 4-neighbor rule in all of our simulations, acknowledging that use of the 8-neighbor rule would make fire spread easier if no other changes were made to the model. However, the threshold behavior of the model would be the same independent of the neighbor rule employed; catastrophic spread would just occur at lower levels of fuel load. However, the dynamics can be adjusted to account for this difference through other aspects of the model, once the rate of fire spread is calibrated to field conditions based on experimental evidence. The bottom line is that the broad scale behavior of the model does not depend upon the choice of the neighbor rule.

Percolation analysis is conducted by first setting cells within the landscape to a flammable or non-flammable state depending upon the model being employed. Once the landscape is constructed, all flammable cells along the southern edge of the landscape are ignited and fire is allowed to spread across the landscape following the fire spread rules currently being used, i.e., 4-neighbor rule in our case. Once fire spread is complete, the northern boundary is inspected to determine if any cells burned. If at least one cell at the northern boundary burned, the landscape percolated with respect to fire.

Experiments on a simple binary landscape

Changing Landscape size. We varied the size of the landscape to examine the impact this had on fire spread as a percolation process. Essentially we explored the conditions under which there was a high probability that there was at least one path through which fire could traverse a landscape from the southern edge to the northern edge as a function of landscape size. The expectation is that an infinitely sized landscape would convert from zero percolation probability to always percolating at a threshold value of $p_{crit}\approx 0.5928$ or above, i.e, for landscapes where 59.28% of the cells or more are flammable the landscape percolates and at lower values it does not. For landscapes of finite size, the expectation is that the probability of percolation is not a threshold process, but instead varies in value across a range of flammability values. Although this has been studied before, it provided a test of the performance of our fire model and confirmation that it produced consistent results with the relevant theory.

We set the allometry of our landscapes based upon the geometry of our study sites. The size used in most analyses was 80 m x 40 m, with 80 m oriented in the E-W dimension. We also set cell size to 0.20 m x 0.20 m, which was the scale of all of our observations in the field. As a result, the baseline landscape was 400 cells x 200 cells. Our exploration of landscape scale on the percolation process varied landscape size by powers of two, starting at 200 cells x 100 cells and stopping at 12,800 cells x 6,400 cells, the maximum size allowed by the architecture of our computer. For each landscape scale, we conducted a series of simulations for a range of flammability parameter values spanning from no observed cases of percolation to always percolating, based on 100 replicates at each value of p_{land} for each landscape. We varied p_{land} in increments of 0.002, which provided a fine enough mesh to provide an accurate estimate of the percolation probability for each value of p_{land} for each landscape.

We analyzed the resulting data in R using an incidence function approach, since our dependent variable consisted of a binomial response: percolates (scored as 1) or does not percolate (scored as 0). Instead of using the parameter value of p_{land} set in running each replicate as the independent predictor variable, we calculated the actual proportion of flammable cells in the landscape using the formula

$$p_{obs} = \frac{flammable}{flammable + non-flammable} \ ,$$

which provided a more fine-grained analysis of the relationship between p_{land} and the likelihood of percolation. The data were analyzed using binomial regression, which is appropriate for analyzing binary data as in the case here. The R model statement used in the analysis was *model<-glm(perc~*p_{obs}*, binomial)*, as discussed in Crawley (Crawley 2007).
The results of this analysis are shown Fig. 27.

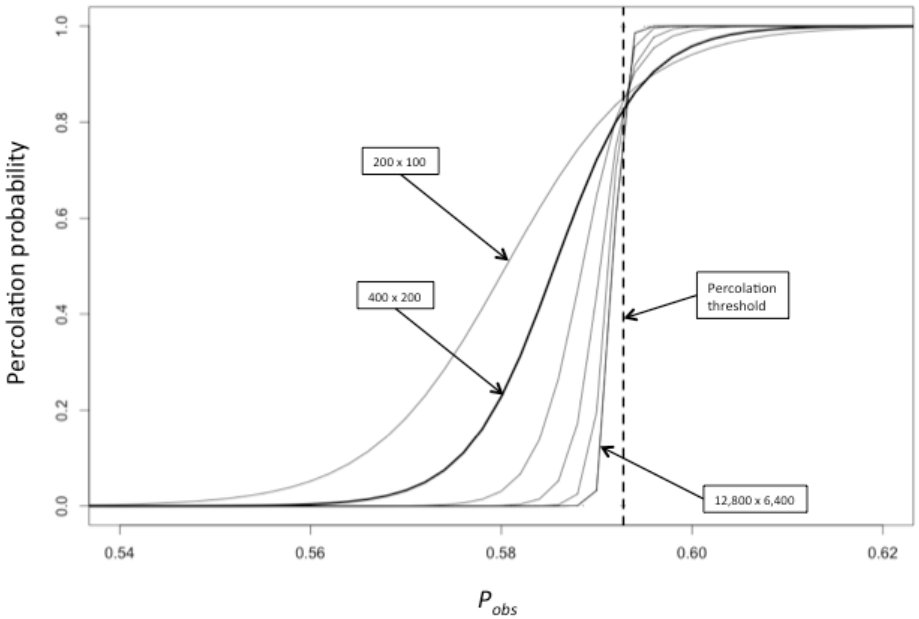


Fig. 27: Percolation probability as a function of p_{land}, the proportion of the landscape set to a flammable state. Landscape scales change by a power of two ranging from 200 cells x 100 cells to 12,800 cells x 6,400 cells. The landscape scale of 400 cells x 200 cells is indicated by a bold line, since it is a reference the landscape scale used in a majority of the simulations employed in the other analyses of this project.

The percolation probability curve for the largest landscape approaches a step function going from 0.00 probability to a probability of 1.00 over a very narrow range of scales. In fact, there were no observed percolation events in landscapes with a p_{land} of 0.588 or below and all landscapes percolated at $p_{land} \geq 0.594$, matching the expectations of $p_{crit} \approx 0.5928$ for an infinite landscape. As the size of the landscape was reduced, the percolation probability curve broadens with a significantly greater chance of percolation at lower flammability values and a slower approach to a probability of 1.00 at higher flammability values (Fig. 27). One interesting observation from Fig. 30 is that there appears to be an intersection point for all of the percolation probability curves that is at a value close to the percolation threshold.

Changing the probability of spread. Percolation theory, at least in ecology, has treated spread as a process that always occurs between available sites that are in contact. However, even though fire is occurring in a specific location, it may not spread to adjacent sites with 100% certainty, factors such as humidity, wind direction or uneven local distribution of fuel may alter the likelihood that fire moves from one location to another. We conducted a series of experiments to examine the effect of altering the probability of fire moving from a burning cell to an adjacent flammable cell to determine how this would impact the probability of percolation. These experiments were all conducted on a 400 cell x 200 cell landscape. Cells in the landscape were set to flammable or non-flammable based on the parameter p_{land} and the 4-neighbor rule was used, as before.

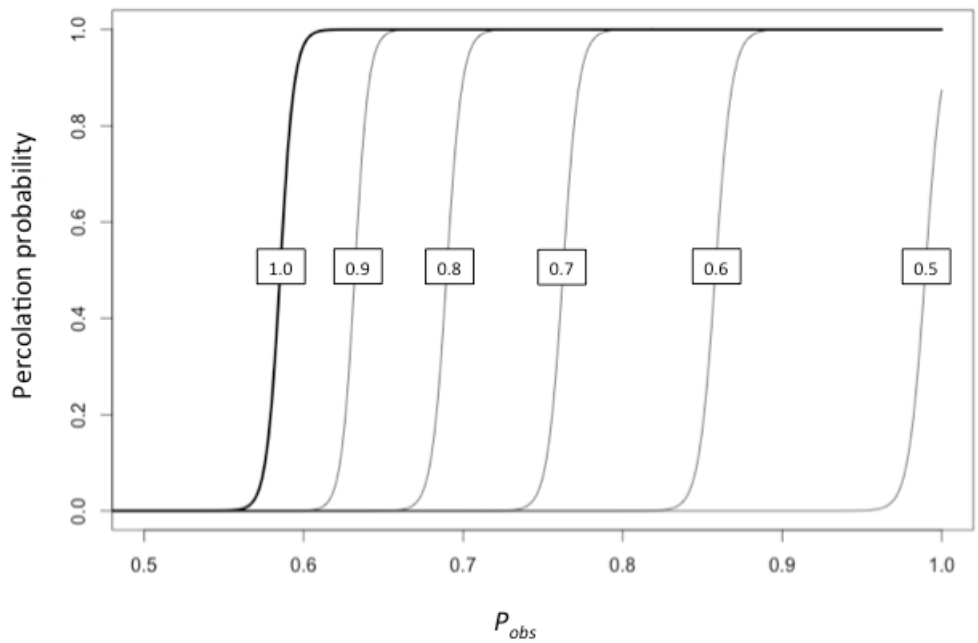


Fig. 28: Effect of altering p_{spread} on the percolation probability of a binary landscape. p_{spread} values are indicated by boxes overlaying the percolation curves. All simulations were conducted using a grid of 400 cells x 200 cells.

However, in this case the model dynamics were altered by setting a second probability parameter p_{spread} to values between 0.5 and 1.0 in increments of 0.1 to determine how the percolation probabilities were changed for a range of values for p_{land}. As the spread probability decreases, the percolation curves shift to the right. For all values of p_{spread}>0.5 in Fig. 31 the percolation probability reaches a value of 1.00 at some value of p_{land}. However, for p_{spread} of 0.5, the percolation probability never reaches a value of 1.00, even when all of the cells in the landscape are flammable. This makes sense as the effective probability across the landscape falls below the percolation threshold.

General conclusions of the percolation analysis

Percolation analysis on a very simple binary landscape provides a general understanding of the key characteristics that must exist if a fire is to spread across a landscape. At least 60% of the landscape must have high enough fuel loads to carry a fire, provided that fuel is randomly distributed across the landscape (i.e., there is no significant spatial autocorrelation in the distribution of fuel). The proportion of the landscape needing enough fuel to spread fire increases dramatically if factors limit the ignition possibility from location to location, as can be seen in the shift to the right of the percolation curve in Fig. 28. Factors limiting fire spread even

when enough fuel is available to allow percolation would be anything that lowers the ignition potential of available materials, e.g., increased humidity, locally uneven spread of fuels, plant materials with higher ignition points, etc.

In the following sections we build in more complexity to the basic model of fuel distributions, taking into account some of the key ecological components structuring the Mojave and Sonoran creosote shrublands. However, before adding in more detail, we first need to examine how fire spreads from a localized ignition point, as this provides a more realistic view of how fire naturally spreads. The percolation analysis is somewhat artificial as it examines the process of spread when all of the sites along a single boundary of a map are set on fire simultaneously.

6.4 Fire spread from a single ignition point

In the following simulation experiment, we examined how fire spreads within a landscape when there is a single, randomly chosen ignition point. We first examined this using the simple binary landscapes considered in the percolation analysis. Once we characterized how this relationship worked, we added more realism to the model and explored how this could affect fire spread.

The method of assessing fire spread from a single ignition point differs from percolation analysis. Instead of determining whether a fire can spread from one edge of the landscape to the opposite edge, we determined the proportion of the landscape that burns (λ) as determined by the ratio of the number of cells that burn (b) divided by the proportion of the landscape that can potentially burn (p_{obs}, as in the percolation analysis): $\lambda = \frac{b}{p_{obs}}$. Each landscape effectively has its own value of p_{obs}, even though we set a value for p_{land} as before. This occurs because the flammability state of each cell in the landscape is set at random.

In order to fully explore the ability of fire to spread within the simple binary landscape, we systematically varied p_{land} and p_{spread}. The p_{land} values ranged from 0.50 to 0.988 in increments of 0.002 and p_{spread} varied from 0.5 to 1.0 in increments of 0.1. We ran 100 simulations for each pair of parameters, resulting in 125,100 simulations, and determined values for the proportion of the landscape that was flammable (p_{obs}) and the proportion of the flammable landscape that actually burned (λ). For p_{spread}=1.0, we were looking at the situation where fire spreads to any adjacent cell that is flammable, whereas for p_{spread}=0.5 there was only a 50% chance of fire spreading to adjacent cells that were flammable.

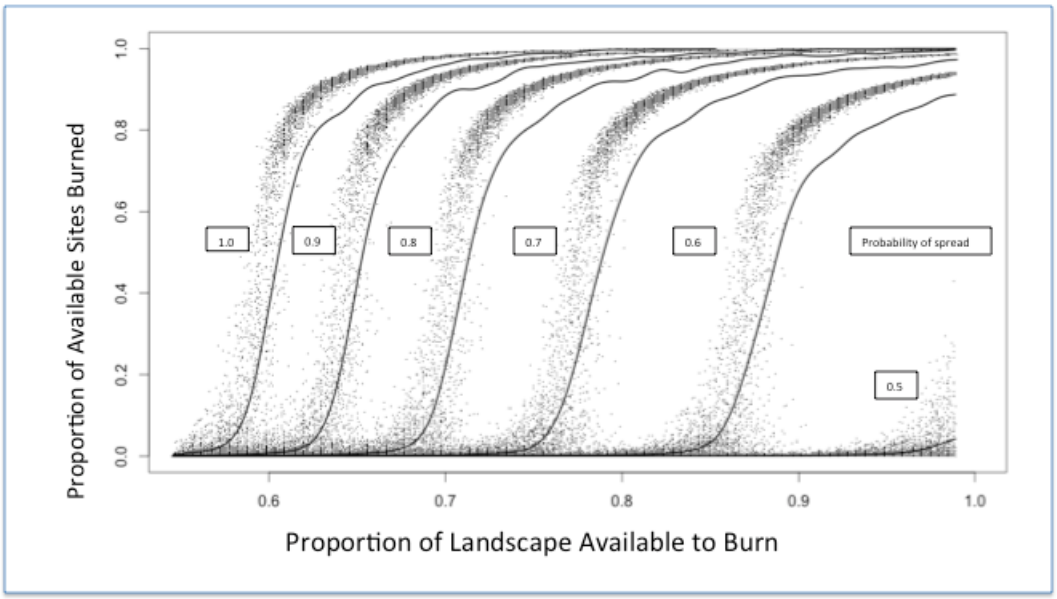


Fig. 29: Fire spread through a landscape with varying proportions of flammable cells and differing degrees of probability of spread from one flammable cell to another one (see text for more detail). Solid lines associated with each cloud of points are smoothed splines fit to the data for one value of probability of spread.

Focusing on landscapes where p_{spread}=1.0 (leftmost cloud of points and curve in Fig. 29), we obtained an understanding as to how well connected landscapes are with respect to fire spread. At values below p_{crit} (i.e., p_{obs}<0.59), less than 50% of the cells that could burn actually burn. At levels of p_{obs}>0.65 most of the flammable cells actually burn, which is not surprising given the percolation results. However, there is a very major caveat to this general observation. The curve associated with the results for p_{spread}=1.0 falls below the cloud of points for the same relationship. This is due to the fact that there are a large number of simulations for which the fire spreads little, if at all. This occurs when a fire is initiated at a point that is not well connected to other flammable cells, i.e., the fire starts in an isolated cluster of flammable cells. This is even true for landscapes with high values of p_{obs}, representing situations with a majority of cells that are flammable. As we lower the probability of spread, we see that the curves fall even further below the cloud of points indicating that there is an increase in the number of simulations where fire does not spread.

General conclusions

When we examine the potential for fire spread from a single ignition point in the simple binary model, we find that the process is highly stochastic. Catastrophic spread can occur over a range of conditions, but whether or not it does is highly stochastic. Even though conditions appear to be ripe for extensive fire spread, i.e., high values of p_{obs} and p_{spread}, it is not guaranteed to occur if a random site is ignited. Local conditions, such as neighborhood connectivity, will determine the likelihood of spread through a majority of the system.

6.5 Adding realism: plant (fuel) density

Background

The basic binary model was clearly unrealistic, although it provided a null case to test against models where more realism was added. One aspect of the model that can be modified is to more clearly depict the distribution of fuel loads in the field, which may be highly variable on a fine scale (i.e., 20 cm x 20 cm). There are three layers of fuel that need to be considered: (i) fine fuels in the matrix, made up primarily of annual herbs and grasses; (ii) more robust growth by annual plants growing under and in the vicinity of the canopies of *Larrea* shrubs; and (iii) live and dead woody material associated with *Larrea* shrubs. The fine fuels in the matrix are necessary for fire to spread from shrub to shrub and historically have been quite sparse, which is why these systems have historically been free of fire. However, fire risk has increased with the introduction of exotic annual forbs and grasses that can grow in the open more readily than native species.

The motivation for adding a consideration of species distributions into the matrix was that the distribution of species within the matrix is very patchy. There can be locations with a high density of plants in close proximity to locations with few, if any plants. The nature of this pattern will clearly change depending upon rainfall patterns, but this will only be considered at a future stage of model development, once the experimental treatments have been fully analyzed and their implications understood.

The basic binary model was modified to allow us to set the density of individual species in each cell using a frequency distribution as determined for individual species. There are a number of frequency distributions that could be used, e.g., Poisson, binomial, negative binomial, gamma, geometric and normal. In many cases, it has been shown that the negative binomial distribution provides a good fit for the distribution of species abundance data (Chen et al. 2008).

One of the key exotic species in the two systems we are studying that may lead to fire spread is *Schismus arabicus*. It does so by growing in the open, which is not characteristic of most native species. As a consequence, we began adding realism to our simulation model by replacing the binary representation of fuel loads (flammable vs non-flammable) with a more detailed characterization of the distribution of *Schismus* as a fuel within the matrix. We are using data collected in 2011 at the Mojave site, as this was a relatively normal rainfall year with the highest species abundances occurring within unmanipulated plots.

We examined the frequency distribution of *Schismus* in open sites (OF microhabitat) to determine the best model for characterizing the distribution of *Schismus* in the matrix. The best fit to the data was provided by a negative binomial model (Fig. 30), when compared to other candidate distribution models (e.g., Poisson and geometric). This resulted in parameter estimates of $r=2.04$ and $p=0.05$ for the negative binomial distribution (cf., Lindén and Mäntyniemi 2011). We used the results of this analysis to produced simulated landscapes with the abundance of *Schismus* set at random in individual cells, using a negative binomial distribution. We then analyzed the resulting simulated landscape using the same protocol used in analyzing the field data (Fig. 30). The fit resulted in the same parameter values being estimated as those that were observed in the field data, verifying that the negative binomial routine used in producing the distribution in the model accurately replicated the field distribution.

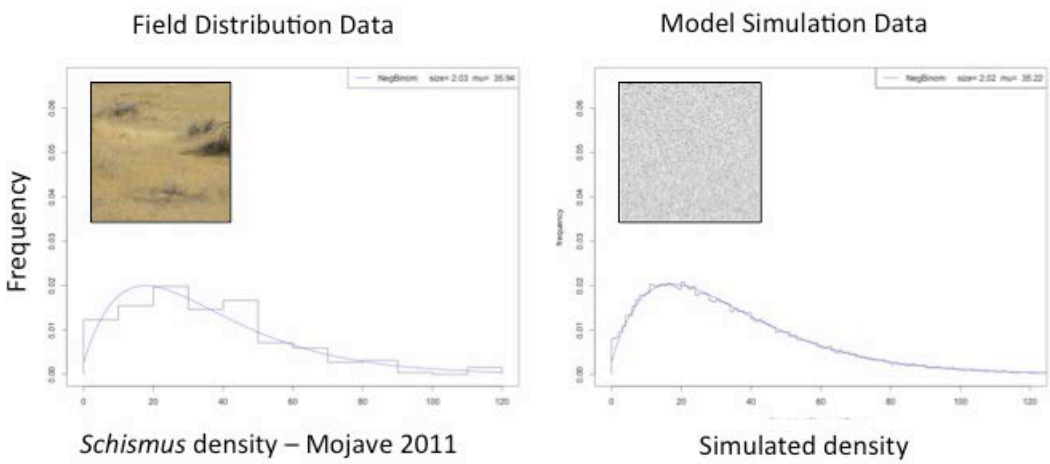


Fig. 30: Comparison of the frequency distribution of abundance data for *Schismus* (left panel) in the field with data simulated in FireGrid (right panel).

Simulations

We ran a series of simulations setting the abundance of *Schismus* within cells using the negative binomial distribution as described above. In these simulations, fuel loads f were set such that any cell with an abundance of d or more plants was capable of burning, i.e., if $f<d$ in a cell, it was not flammable, and if $f \geq d$ it was. This approach assumed that there was a minimum fuel load below which fire could not carry.

In conducting a simulation experiment to compare to the earlier study using the simple binomial landscape, we produced replicate, random landscapes with the same underlying distribution of *Schismus* as described above. By changing values of d we produced an *ad hoc* protocol for examining how fire spread changes with different fuel loads, distributed with an underlying negative binomial distribution.

In the model simulations discussed here, we varied the probability of fire spread by changing two basic parameters: (i) p_{spread} and (ii) d. The values of p_{spread} ranged from 0.5 to 1.0 in increments of 0.1 as in the binomial landscape experiment. The density threshold d was varied from a value of one (almost all cells are flammable) to a value of 28. This produced an effective range of p_{land} spanning from 1.0 to 0.5, as in the experiments for the binomial landscape. The results are shown in Fig. 31, where the observed values for simulations with *Schismus* in the matrix are overlain on the results from the simpler, binomial landscape as shown in Fig. 33.

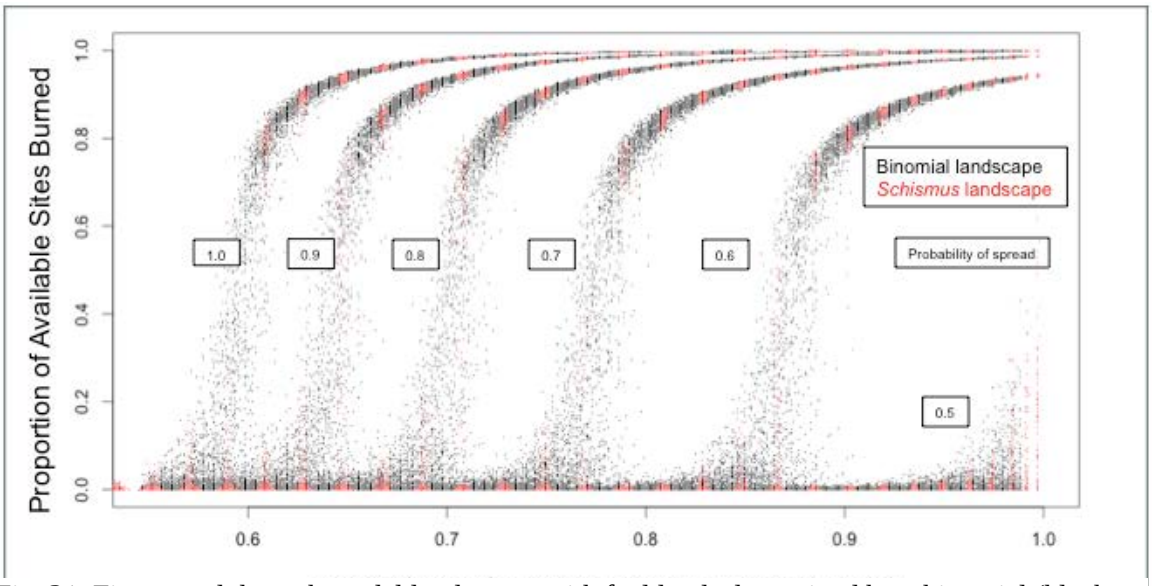


Fig. 31. Fire spread through model landscapes with fuel loads determined by a binomial (black dots) or negative binomial (red dots, i.e., *Schismus*) disturbed fuel bed.

It is clear from this result that the addition of more detail has not changed model behavior, which makes sense given the simple model of fire spread currently being employed. Also, the proportion of the landscape available to burn changes on a coarser scale for the *Schismus* landscape, since we can only alter flammability by changing *d* by integer values.

Adding a more realistic model of fuel load distributions as we have done here has not altered the basic behavior of fire spread. On reflection, this is not very surprising since in both the binomial model and this more realistic model, the distribution of fuels is random. We have simply changed from a coarse grained characterization of fuel loads (flammable vs. non-flammable) to one that contains more detail. However, the simple rule for fire spread has not changed. In both cases there is a threshold above which fire can occur. One of the next developments would be to alter the model of fire spread to account for density in individual cells. The likelihood of fire spread will be based on the levels of fuel load in adjacent cells. Fire spread would be an increasing function of density, given that a burning cell with a higher fuel load will be more likely to set adjacent cells on fire and cells with high fuel loads will be more likely to catch fire. This could be further modified to allow for a decrease in fire spread at extremely high densities if this is actually observed in experimental studies. A reason for this might be a decrease in oxygen availability through a smothering effect.

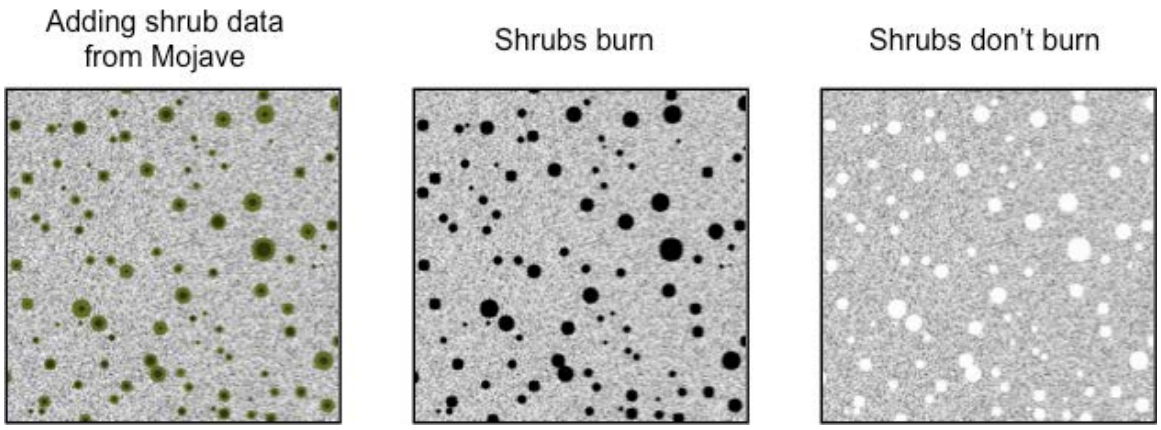


Fig. 32: Adding shrubs to the simulation model with *Schismus* in the matrix. Shrub locations are the same as observed at the Mojave study site and can impact fire spread as either burning upon contact with fire, or not burning. *Schismus* densities are indicated in gray scale with lower densities being represented by lighter shades of gray. Shrubs shaded black always burn, whereas those shaded white never burn.

6.6 Adding realism: *Larrea*

One of the key elements missing from the simpler model developed up to this point is the occurrence of shrubs in the landscape. The presence of shrubs can potentially alter fire dynamics in a number of ways. Shrubs may easily burn and potentially help spread fire under conditions when fuel loads are low. Or, if they don't burn very easily (i.e., are hard to ignite) then they may slow the spread of fire. The rate at which shrubs catch fire may be a function of hydrological status, such that they can range somewhere between the extreme conditions of always igniting to conditions of never igniting. In order to explore the effect of shrubs on fire spread, we added a shrub layer to the model, based on the shrub distributions observed at our Mojave study site. We mapped all of the shrubs in the study site by determining the location of the center of the shrub and then measure its size in terms of canopy profile. We then included the locations in the model that were under the influence of shrub canopies (Fig. 32).

In our first simple experiments examining the impact of shrubs on fire spread, we contrasted three different situations: (i) no shrubs present; (ii) shrubs present that always burn when a cell adjacent to the shrub catches fire; and (iii) shrubs present, but never burn. The background matrix in this experiment was set using *Schismus* as in the previous experiment. For this experiment we altered *d*, as in the previous experiment for each of the three shrub layer scenarios described above. In this case, we held p_{spread} fixed at a value of 1.0, since our expectation was that altering p_{spread} would simply act to shift the fire spread values to the right as in Fig. 33. One hundred replicate simulations were run for each of the three scenarios for each value of *d*.

The impact of introducing shrubs and altering the probability that they burn can be seen in Fig. 33. When shrubs can burn, fire spreads more effectively than in the same model without shrubs.

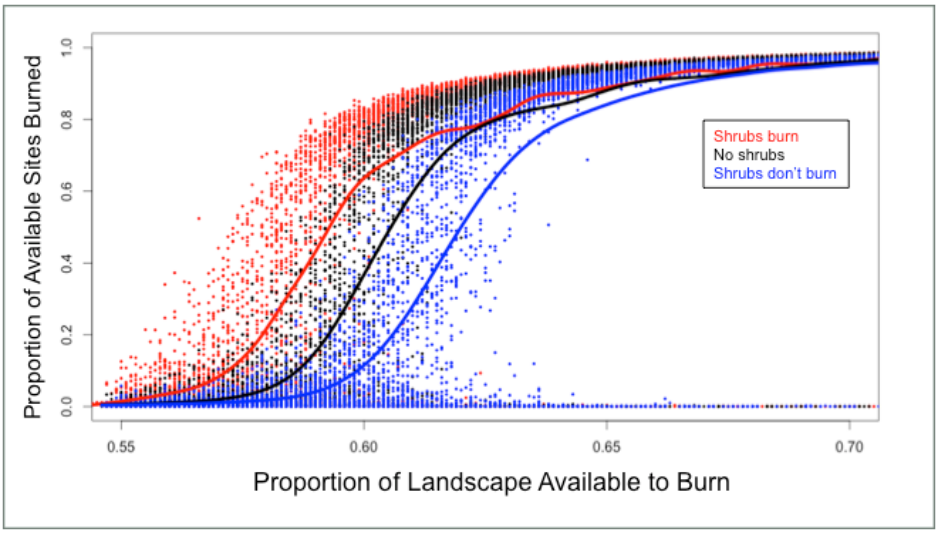


Fig. 33 Impact of shrubs on fire spread for a model with *Schismus* in the matrix.

Since individual shrubs occupy several contiguous cells, fire could more easily spread through areas that would generally not burn if they were occupied by matrix plants (*Schismus* in this case), since some cells in the matrix would have fuel loads below the threshold. In contrast, shrubs that don't burn effectively act as a firebreak and slow the spread of fire. In reality, shrubs will generally vary in the probability of catching fire and in how much of the shrub burns, depending on factors such as their current hydrological status or branch density. What these model experiments do is indicate a range over which fire behavior might be modified by the shrub layer. In reality, the observed relationships will fall somewhere in the middle.

Summary

These results indicate that the primary factor controlling fire spread is the distribution of annual plants in the matrix. However, fire spread can be further modified by the current flammability status of creosote bushes, increasing the risk of catastrophic fires under conditions of high creosote flammability and lowering it when creosote flammability is low, independent of the distribution of annuals in the open. The overall risk of catastrophic fire therefore represents a complex interaction between the availability of fuel in the open and the current hydrological status of the creosote community.

7. Conclusions and Implications for Future Research/Implementation

As predicted, our empirical data indicate that fire in the desert scrub ecosystem can lead to a decrease in the environmental contrast between shrub islands and matrix habitat. Because of this "melting" of distinct islands of fertility due to plant litter fed fire, annual plant species are increasingly able to invade areas between shrubs, which in the past only supported very little plant growth. In particular one non-native invasive species (NIS), *Schismus arabicus* appears to be well adapted to benefit from slight increases of nutrient availability in the matrix between shrubs after a fire. We were able to identify differences in the population dynamics among different microhabitats that indicate that this species is supporting sink populations in the shrub interstices supported by more fecund source sub-populations under canopies, although the impact of this differs between the two desert sites. The ability of *Schismus* to grow in the open is significant as it might help explain fuel buildup in sub-habitats that formerly were not fire prone leading to a connected landscape through which catastrophic fires can spread, at least during years of high rainfall. These findings address the two leading objectives of the research since it (1) significantly adds to our understanding of at least one major NIS species in American deserts and confirms (2) that natural islands of fertility indeed are prone to breakdown through the interaction of invasion and changed fire regimes.

Results from our experimental study on annual and perennial plant densities and their spatial distributions suggest that different processes have the potential to promote fire in the two contrasting desert sites. In the Mojave the rise of NIS occupying the areas between shrubs indeed has the potential to promote fire. In the Sonoran Desert native species also occupy the areas between shrubs and potentially provide enough fuel to carry wildfires. In addition, higher shrub densities and lesser shrub segregation in the Sonoran Desert might be the key factor for promoting wildfires, even in the absence of NIS. Population studies in the Mojave and Sonoran Deserts are consistent with the hypothesis that one of the populations of the primary NIS in the study sites (*Schismus arabicus*) indeed uses a source-sink strategy that has elements of source-sink dynamics in the Mojave Desert, but not in the Sonoran Desert. In the Mojave *Schismus* maintains high densities in the area between shrubs that seem to be supported by higher seed production under shrub canopies.

Responses of annual plants populations and communities to our treatments show that native species and NIS in both deserts react differentially. As expected, annual biomass increased in both deserts with increasing rainfall; however, fire increased biomass only in the Sonoran and showed little effect in the Mojave. Disturbance had strong increasing effects on biomass in both deserts. In the Mojave Desert disturbance and decreasing rainfall favored NIS, whereas burns did not cause a relative increase of NIS. In contrast, annual NIS in the Sonoran Desert did not become more abundant with fire, most likely due to a strong reaction of native species; rather, they increased with disturbance and drought. This suggests that the invasion processes differ in both deserts and that the impacts of fire are regionally quite different.

The modeling work done in parallel with the experiments, demonstrated that catastrophic spread of fire will only occur if 60% or more of an area has enough fuel to burn. However, the potential for fire spread will be altered dramatically depending upon the flammability state of the creosote shrubs, which can help connect the landscape even under lower fuel loads between shrubs. The

latter will occur when creosote is in a high state of flammability. Under conditions when creosote is less prone to catch fire, it can actually act to slow fire spread under otherwise appropriate conditions. Another factor that can play a role in fire spread is the rate at which fire moves through the annual litter layer between shrubs. This can be lowered when the hydraulic status of the site is elevated or if plants are not evenly distributed at short distances. Under these circumstances fire only spreads under conditions of greater fuel loads than predicted by traditional percolation theory. There is also a large stochastic element to the process. Even if a fire can easily spread through the landscape, given the current fuel loads and potential of spread, there is still a great deal of variability in the degree of spread that occurs from a localized fire source depending on the local distribution of fuels. This makes prediction of fire spread in any one location less precise when considering individual events.

Future work

In the future, a broad scale validation of shrub-annual distribution patterns across the Mojave and Sonoran Deserts, as observed in our two sites, should be explored. This could be done to test whether the detailed, fine-scale, multiyear results obtained for our two core sites (Fort Irwin/Mojave, BMG/Sonoran) are representative of a broader desert region. This will also act to allow the community-dynamics, fire model of RC-1721 to scale from the local to the regional scale and thereby make it more appropriate for exploring a broad range of conditions in the hot deserts of the arid SW. It would also serve as a mechanism for examining how universal the differences we found between the Mojave and Sonora site are when comparing more sites in the two deserts than were examined under the work reported here. We have begun conducting burn experiments with different fuel types from our study sites to develop a more nuanced understanding of fire spread, which we plan to integrate into the model (unpublished analyses).

Now that we have analyzed the experimental data, the basic version of *FireGrid* could be expanded by adding greater realism, allowing it to be used to explore the impact non-native species have on fire spread under variable environmental conditions through a series of simulation experiments. A component that should be added is a more precise model of fire spread incorporating results from experiments examining the flammability characteristics of key species from creosote shrubland sites, in particular *Larrea*, *Schismus* and a range of native species. Further work could also explore, in more detail, the impact of interactions between *Larrea* and annual species, both native and exotic, within the influence of creosote canopies, to determine how this impacts the potential for fire spread through the system. At this stage, we did not know the precise densities required for fire spread, although we are conducting burn experiments to determine this more accurately for several different species. Once we fully analyze the data from the experiments, as well as the field data, we will be able to alter the distributions of *Schismus,* and other key species, based on changing conditions of rainfall, soil turbation and seed input.

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Appendices

A. Supporting Data:

The following table gives an overview of the generated data sets and the type of data collected. As of now, the data are still located on local data servers but can be made available upon request and can be achieved publicly once further analyses are being made (e.g., on the Ecological Society of America Data Registry [http://data.esa.org/esa/] or any other data bank favored by SERDP).

		Sonoran				Mojave			
type of data	**site**	**2010**	**2011**	**2012**	**2013**	**2010**	**2011**	**2012**	**2013**
Plot set up - plot # assignment	Main	September & November				October			
	Burn		March				June		
Plot set up - Distance from plot to stem	Main	January					January		
	Burn		March			October	June		
Ambrosia Fertility islands mapped	Main						January		
Shrub Locations	Main	November	January				January		
	Burn		March					March	
Litter Measurements	Main	January					January		
	Burn		March			October			
Shrub Size	Main	November	January	March - 10 burned shrubs from each water treatment, September all burned shrubs remeasured			January	March - 10 burned shrubs from each water treatment	March - all burned shrubs were remeasured
	Burn							March	
Shelters built	Main		October				June		
Experimental burns	Main		October 4				June 20&21		
Seeding and turbating treatments applied	Main		September & October	September: Reseeded Brassica, returbated a few shrubs			October	September: Reseeded Bromus, returbated a few shrubs	
Water addition treatments	Main			Jan 3-4, Jan 28-31	Jan 13-15, Feb 18 - 21		Dec 29-31	Jan. 1, Jan 23-27, Feb 20-22	Jan 7-10, Feb 13-15, March 11-13
Soil nutrients from soil samples	Main		Collected October 7 received data from amherst March 22				Collected June - sent in with Sonoran samples received data March 22		
Seedbank samples	Winter Main	November - many unknowns	September	September		November (also censused growing seedlings), many unknowns	October	September	
Seedbank sample mass	Winter Main					Weighed Dec 12 after 3 germination pushes			
Reference photos	Main			February 27	March 22			March 26	March 29
Crust data	Winter Main			February - did not measure	March - 63/126 shrubs			March - all shrubs	March - 63/126 shrubs
	Winter Burn			February	March - 12/42			March	March - 17/28 burned; 9/14 unburned
	Summer main			September - measured all drought and ambient shrubs	September - measured all drought and ambient shrubs				
	Summer burn			September - data on 9/42 shrubs	September - data on all shrubs				
Soil moisture temp probes	Winter Main		Placed October 7 downloaded each trip out, last reading 13 January 2014		In September 2013 a few would not download		Placed October 12 downloaded data each trip last reading 7 January 2014	September - 2/4 transects had wires chewed through (W2-UC, W4UC, CD)	
Weather data	Winter Main	started	11/20/2010	ended	1/13/2014	started	9/29/2010	ended	1/7/2014
	Winter Burn								
	Summer main	Weather data year round continuous				Weather data year round continuous			
	Summer burn								

Seedbank samples	Winter Main	November - many unknowns	September	September		November (also censused growing seedlings), many unknowns	October	September	
Seedbank sample mass	Winter Main					Weighed Dec 12 after 3 germination pushes			
Reference photos	Main			February 27	March 22			March 26	March 29
Crust data	Winter Main			February - did not measure	March - 63/126 shrubs			March - all shrubs	March - 63/126 shrubs
	Winter Burn			February	March - 12/42			March	March - 17/28 burned; 9/14 unburned
	Summer main			September - measured all drought and ambient shrubs	September - measured all drought and ambient shrubs				
	Summer burn			September - data on 9/42 shrubs	September - data on all shrubs				
Soil moisture temp probes	Winter Main		Placed October 7 downloaded each trip out, last reading 13 January 2014		In September 2013 a few would not download		Placed October 12 downloaded data each trip last reading 7 January 2014	September - 2/4 transects had wires chewed through (W2-UC, W4UC, CD)	
Weather data	Winter Main	started	11/20/2010	ended	1/13/2014	started	9/29/2010	ended	1/7/2014
	Winter Burn								
	Summer main	Weather data year round continuous				Weather data year round continuous			
	Summer burn								

B. Scientific/Technical Publications:

1. Articles in peer-reviewed journals

Fuentes-Ramirez A., Schafer J.L., Mudrak E., Schat M., Parag H.A. ,Holzapfel C. &, Moloney K.A.. in review. Short and long term impacts of fire on soil nutrients in *Larrea tridentata* shrublands in the Mojave Desert, USA. Plant and Soil.

Fuentes-Ramirez A., Mudrak E., Caragea P., Holzapfel C. & Moloney K.A. 2015. Assessing the impact of fire on the spatial distribution of *Larrea tridentata* in the Sonoran Desert, USA. Oecologia. DOI 10.1007/s00442-014-3214-1

Mudrak E.L., Schafer J.L., Fuentes-Ramirez A., Holzapfel C. & Moloney K.A. 2014. Predictive modeling of spatial patterns of soil nutrients related to fertility islands. Landscape Ecology 29:491-505.

Schafer J.L., Mudrak E.L., Haines C.E., Parag H.A., Moloney K.A. & Holzapfel C. 2012. The association of native and non-native annual plants with *Larrea tridentata* (creosote bush) in the Mojave and Sonoran Deserts. Journal of Arid Environments 87:129-135.

A series of at least 6 further publications are in various stages of submission

2. Conference or symposium abstracts

2014 - Ecological Society of America, Annual Meeting, Sacramento, CA.
- "Short and long term impacts of fire on soil nutrients in *Larrea tridentata* (creosote bush) shrublands in the Mojave Desert" (Fuentes-Ramirez, A. et al.)
-"Physical geometry of enhanced fire risk in creosote shrublands invaded by exotic annuals" (Moloney, K. et al.)

2014 - Evenari Symposium, Sde Boqer, Israel (invited keynote):
- "Novel plant communities in arid lands: the role of climate change and annual plant invasion" (Holzapfel, C.)

2013 - Ecological Society of America, Annual Meeting, Minneapolis, MN.
- "Invasion by non-native annuals in the Mojave and Sonoran Desert: the role of fire, disturbance, and precipitation" (Schat, M. et al.)
- "Influence of soil disturbance, seed pressure, aridity, and burn history on community structure of winter annuals in North American deserts" (Schat, M. et al.)
-"The ability of high resolution aerial imagery to determine shrub location and size in creosote flats of the Sonoran and Mojave Deserts" (Kudrak, E. et al.)

2012 - Ecological Society of America, Annual Meeting, Portland, OR.
-"Invasive non-native annuals use novel source-sink strategies in North American deserts" (Schat, M. et al.)

- "Predictive modeling of spatial patterns of soil nutrients associated with fertility islands in the Mojave and Sonoran deserts" (Mudrak, E. et al.)

2012 - International Symposium on Invasive Plants and Global Change, Urumqi, China. June 14-17 (Session Keynote).
- "Novel plant communities in arid lands: the role of climate change and invasion" (Holzapfel, C.).

2011 - Partners in Environmental Technology - Technical Symposium & Workshop. Meeting DoD's Environmental Challenges, Washington, D.C.
-"Understanding the fire-enhancing impact of non-native annuals in deserts: the role of spatial patterns" (with Holzapfel, C & Moloney, K. et al.)

2011 - Ecological Society of America, Annual Meeting, Austin, TX
- "Spatial patterns in the distribution of creosote (*Larrea tridentata*) and burrobush (*Ambrosia dumosa*) in the Mojave and Sonoran deserts: A template for fire risk" (Mudrak, E.L. et al.)
- "Patterns of annual plant seedling recruitment differ between creosote dominated sites in the Mojave and Sonoran deserts" (Schafer, J.L. et al.)

2010 - Partners in Environmental Technology - Technical Symposium & Workshop. Meeting DoD's Environmental Challenges, Washington, D.C
-"Understanding and Combating the Fire-Enhancing Impact of Non-Native Annuals in Desert Scrub through the Tools of Population and Landscape Ecology" (Holzapfel, C. & Moloney, K. et al.)