SEED BANK COMPOSITION WITHIN TWO SAGEBRUSH COMMUNITIES:

A COMPARISON OF DROUGHT, MICROSITE, AND ABOVEGROUND

COMMUNITY EFFECTS

By

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ABSTRACT

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Allison M. Nunes

Soil seed banks are critical biodiversity repositories for many dryland plant communities. Understanding how environmental factors alter seed bank composition can provide valuable information on ecological processes within a community and be useful for creating land management strategies. Using the seedling emergence method, I characterized the seed bank of two adjacent dryland plant communities that vary in dominant sagebrush species, structure, and function. Specifically, within an *Artemisia arbuscula* dominated community and *Artemisia cana* dominated community, I assessed the influence of three environmental factors on each seed bank: experimentally imposed drought, shrub microsites (compared to interspaces), and aboveground vegetation. Within the *A. arbuscula* community, drought decreased seed species diversity, seed species evenness, and exotic forb seed density, and increased exotic grass seed density. Total seed density, native forb seed density, and seed species diversity was greater in shrub microsites compared to interspaces. Within the *A. cana* community, drought only decreased exotic forb seed density and there were no microsite effects. Bray-Curtis index showed low similarity ($<27\%$) between the seed bank and existing vegetation, and seed banks were comprised of over 50% exotic annual grass seeds. My study suggests that

seed banks of drylands similar to *A. arbuscula* dominated plant communities (with large expanses of bareground) may experience more drought induced impacts than adjacent sagebrush communities. Additionally, while native annual forb seeds may remain resilient during drought, changing climatic regimes could concurrently promote an increase in propagule pressure of invasive annual grasses such as *Ventenata dubia* (ventenata). My study also highlights the role of shrub canopies as beneficial microsites for seeds, especially in preserving seed bank diversity and native forb seed density within *A. arbuscula* dominated plant communities.

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INTRODUCTION

Soil seed banks are a critical component of ecological communities. As repositories of genetic diversity, they contribute to local population persistence, and provide a signature of past, present, and future characteristics of a community (Thompson, 2009). Soil seed banks (hereafter "seed banks") can also be used as a resource for restoration efforts or invasive species management, and may potentially contribute to range expansion (Bossuyt & Honnay, 2008; Gioria et al., 2014; Kildisheva et al., 2016; Kottler & Gedan, 2020). Similar to aboveground floristic composition, seed bank composition is influenced by a wide range of biotic and abiotic factors (Abella et al., 2013; Foronda et al., 2020; Gioria & Pyšek, 2015; Haight et al., 2019; Ooi, 2012), and understanding how these factors affect seed bank composition can provide valuable information to land managers. For example, if a plant community experiences a disturbance, such as a long-term drought, the seed bank may reflect reproductive responses by exhibiting a decrease or increase of viable seeds in the soil.

Plants species posess diverse life-history strategies to cope with disturbances and environmental variability to maintain populations within a community. For example, plant species with persistent seeds (seeds that remain viable for > 1 yr) typically grow quickly and produce copious amounts of small seeds that remain dormant in the soil until suitable germination conditions occur – annual forbs often follow this strategy (Baskin &

Baskin, 2014; DeMalach et al., 2021; Sternberg et al., 2003). In contrast, plant species

that form transient seeds (seeds that remain viable for < 1 yr in the soil) typically rely less

on seed survival, and instead have long life-spans to persist within a community – woody

plants, perennial forbs, and perennial grasses are often examples of species with these

traits (Adler et al., 2014; Aziz & Khan, 1996; O'Connor, 1991). Finally, exotic annual

grasses generally contribute large quantities of relatively large seeds to the seed bank that

do not exhibit facultative dormancy, and rely on individual germination and survival,

rather than growth and long-life spans (Adler et al., 2014; Metz et al., 2010). These

"resource-acquisitive" traits allow exotic annual grasses to quickly become dominant

(germinate and produce seed rain), especially in open areas following a disturbance, such

as fire or drought (LaForgia et al., 2020). In part due to contrasting life-history strategies

among species, many studies have found that the seed bank is dissimilar to the

aboveground plant community, both in species diversity and abundance. Hopfensperger

(2007) conducted a comprehensive review of over 100 studies comparing the seed bank

and corresponding vegetation and found that forests, wetlands, and grasslands exhibited

31%, 42%, and 54% similarity, respectively. Characterizing the species and plant

functional groups present within the seed bank can provide insight regarding how species

persist within a plant community. For instance, ecosystems with variable abiotic

conditions promote evolution of persistent seed banks, and seeds within these types of

communities often exhibit facultative dormancy to preserve genetic biodiversity (García & Zamora, 2003; Gremer & Venable, 2014; Pake & Venable, 1996; Thompson et al., 1998).

Drylands, which occupy 41% of the earth's land surface, are characterized by low and variable precipitation (Prăvălie, 2016). These heterogenous landscapes are dominated by shrubs or perennial grasses and patches of bare ground are often prevalent. Annual and perennial forbs, which constitute the majority of diversity in drylands, generally grow in interspaces between shrubs or perennial grasses. The spatial structure of shrubs prominently affects seed bank composition and distribution. Shrubs often play a strong nurse role in the community and create beneficial microsites for seeds, especially in areas with low productivity in interspaces (Barga & Leger, 2018; Chambers, 2000; Foronda et al., 2019; Guo et al., 1998). These favorable microsite conditions provide ample nutrient/water availability, and minimize soil erosion and albedo (Ochoa-Hueso et al., 2018). Shrubs also act as barriers, and seeds are redistributed from interspaces to beneath shrub canopies through wind and water runoff, depending on the height and thickness of vegetation or litter in the interspaces (Chambers & MacMahon, 1994). This accumulation of seeds beneath shrubs causes high spatial variation in seed banks, and has been found to contribute to higher seed densities and seed species richness beneath shrubs compared to interspaces (Li, 2008).

Disturbances such as drought, fire, and livestock grazing are examples of other environmental factors that alter seed bank composition (Barga & Leger, 2018; del Cacho et al., 2012; Funk et al., 2019). A growing body of research suggests that predicted increases in frequency and severity of droughts will negatively affect plant community dynamics within dryland ecosystems across North America (Bradford et al., 2020). Yet there is a paucity of studies that have directly tested the impacts of intensified drought on the seed banks of dryland ecosystems (del Cacho et al., 2012; Funk et al., 2019). Current research suggests that long-term severe droughts could have both direct and indirect negative effects on seed banks (Basto et al., 2018; Hoover et al., 2014; Stampfli & Zeiter, 2020). For instance, decreased precipitation could directly decrease seed production, leading to lower seed densities within the seed bank. Severe drought could also increase mortality or shift species composition in the aboveground plant community, leading to changes in seed bank species richness and diversity over time (Hoover et al., 2014; Stampfli & Zeiter, 2020). Furthermore, predicted decreases in soil moisture within drylands may directly decrease the longevity of existing seeds in the seed bank, particularly in areas where soil is exposed (Basto et al., 2018; Bradford et al., 2020).

The sagebrush steppe is the most extensive dryland ecosystem in North America (U.S. Fish & Wildlife Service, 2014). It spans across much of the western United States, although anthropogenic disturbances, particularly habitat fragmentation and exotic species invasion are currently major threats to the region. Like other drylands, the sagebrush steppe is precipitation-limited and it relies on winter precipitation to recharge the soil (Schlaepfer et al., 2012). Sagebrush steppe is also adapted to low-intensity fires, with infrequent fire return intervals (between 60-110 years; Whisenant, 1990). *Artemisia tridentata* (big sagebrush) is the dominant sagebrush species within the region and the majority of research has focused on this species. However, other sagebrush species are common in areas with differing abiotic conditions. Within the greater sagebrush steppe landscape, many directly adjacent plant communities vary in dominant sagebrush species, structure, and function. Furthermore, some sagebrush species also have distinct site characteristics related to them which create various conditions for seeds.

Two sagebrush species that inhabit areas that differ in structure and function are *Artemisia arbuscula* (low sagebrush) and *Artemisia cana* (silver sagebrush). *Artemisia arbuscula* is a low growing sagebrush species that occupies 11 million hectares across the western US. It often resides near forested areas, and grows on xeric, sterile clay soils with shallow water tables. The shallow water tables flood or saturate the soil during the winter/spring and as soil desiccates during the summer a hard veneer crust forms. Aside

from these edaphic features, *A. arbuscula* dominated plant communities are associated with low productivity and large extents of bare ground compared to other sagebrush communities (Francis, 2004). *Artemisia cana* is the second most abundant sagebrush species in North America distributed across 14 million hectares, and often resides on transitional wet-to-dryland sites, where soils dry by late summer (Connelly et al., 2004). However, the high productivity and proximity to high water tables inhibit the creation of veneer crusts. Since *A. cana* requires more moisture and a higher water table than most sagebrush species, it is also characteristically found in close proximity to the edge of ephemeral stream banks. *Artemisia cana* dominated plant communities are generally highly productive, with persistent litter and minimal exposed bare ground (potentially <3%) (Howard, 2002). Currently, there is scarce research on these two species of sagebrush and there has been no work investigating seed bank composition of their associated plant communities.

Given the importance of seeds banks and their role in ecological processes within dryland communities, it is critical to understand how seed banks might respond to changing environmental factors. Since severe drought, shrub microsites, and aboveground vegetation can all influence the seed bank, the goal of my research was to examine the effects of these three environmental factors within two dryland plant communities.

Specifically, I addressed four research questions within an *A. arbuscula* dominated community and an adjacent (~ 60 m apart) *A. cana* dominated community:

1. Does a severe 3 year drought affect seed bank composition and seed density?

2. Does microsite (i.e., shrub microsite or interspace microsite) affect seed bank composition and seed density?

3. Is there a difference in the direction and magnitude of response to drought and microsite between the two sagebrush communities?

4. How similar is aboveground and belowground (seed bank) species composition at the two vegetation types?

METHODS

Study Area

I utilized two adjacent study sites (~60 m apart) on land managed by Bureau of Land Management near Gerber Reservoir, Oregon (42°184 N, 121°015 W). The sites are located near the western-most edge of the sagebrush steppe ecosystem, within the Great Basin region (Figure 1 & Figure 2). Mean annual precipitation is 406 mm and mean annual temperature is 8°C, with the majority of precipitation arriving as snow or rain during the winter months (Western Regional Climate Center, Station ID: 3250F1DC). Both sites are surrounded by a *Pinus ponderosa* (Ponderosa pine) forested area and located within a grazing exclosure where grazing has been excluded for 27 years. There are no signs of recent anthropogenic disturbance and the absence of large fires can be confirmed back to at least 1985 (*MTBS Fire Viewer*).

Figure 1. The extent of the sagebrush steppe ecosystem in the western US and my study site in Oregon.

Figure 2. Map of my study site, with 10 plots on north side of the ephemeral stream (AA site) and 10 plots on the south side of the stream (AC site; Kaczynski, 2016).

The two sites are characterized as semi-arid sagebrush steppe, dominated by *A. arbuscula* (AA site; Figure 3) or *A. cana* (AC site; Figure 4). There are no other co-dominant shrub species present at either site. An invasive annual grass, *Ventenata dubia* (ventenata), is increasingly common at both sites, but more prominent at the AA site, whereas *V. dubia* and *Bromus japonicus* (Japanese brome) are both abundant at the AC site. Common native perennial bunchgrasses at the AA site are *Festuca idahoensis* (Idaho fescue), *Elymus elymoides* (squirreltail), and *Danthonia californica* (California oatgrass). Common forbs include *Packera cana* (woolly groudsel), *Erigeron bloomeri* (scabland fleabane), *Sedum stenopetalum* (wormleaf stonecrop), and *Eriogonum sphaerocephalum* (rock buckwheat). At the AC site, common native perennial bunchgrasses include *F. idahoensis*, *Poa secunda* (sandberg bluegrass), and *E. elymoides*. Common forbs include *Perideridia oregana* (Oregon yampah), *Achillea millefolium* (common yarrow), *Epilobium brachycarpum* (tall annual willowherb), and *Collomia grandiflora* (grand collomia).

Figure 3. Example of a drought plot within the *Artemisia arbuscula* dominated community (AA site) site in May 2019.

Figure 4. Example of a drought plot within the *Artemisia cana* dominated community (AC site) site in May 2019.

Experimental Design

In July 2016, Dr. Kerry Byrne selected ten areas at each site with similar species composition and established ten 4.0 m^2 plots with at least one sagebrush individual rooted near the center of each plot. Treatments were randomly assigned (drought or unmanipulated control) to plots (n=5 for each treatment at each site). She constructed rain-out (drought) shelters for the drought treatment following the standardized protocol of the International Drought Experiment (IDE; Knapp et al., 2015). Each shelter passively excluded 41% of incoming precipitation to simulate a 1-in-100 year drought, based on 100 years of precipitation records for this area. The shorter side of the shelters were ~1.2 m and the taller sides were ~2.0 m, allowing the shelters to be at least 0.75 m above maximum vegetation height. The roofs were made of 15 cm wide strips of corrugated polycarbonate (Dynaglas brand), which transmits greater than 90% PAR. The corrugated strips channeled precipitation to a rain gutter that lead water away from the plots. The shelters extended an additional 0.5 m beyond the plot in each direction to help reduce the amount of rain flowing horizontally into the plots from the outside. Shelter sides were open to maximize air movement and minimize potential influence of temperature and relative humidity. The shelters were left up year-round since July 2016.

Precipitation Data

To interpret my experiment within the historical 50 year precipitation record (1970-2020), I compiled annual precipitation records using a local weather station (Western Regional Climate Center, Station ID: 3250F1DC) from 1986-2020 and PRISM (PRISM Climate Group, 2021) for 1970-1985, when reliable local precipitation data were not available. I then calculated the normalized precipitation value using the equation, $X_n=(X_i-\mu)/\sigma$, where X_n is the normalized precipitation value, X_i is the value for the year i, and μ and σ are the mean and standard deviation of the historical 50 year precipitation data set. I compared these values to the 10th (extreme drought) and 15th (moderate drought) percentiles of the historical data set (Knapp et al., 2015).

Seed Bank Sampling

In mid-May 2019, before any seed set occurred, I collected soil cores in each plot both beneath sagebrush canopies (shrub microsites) and in adjacent interspaces at least 10 cm from the edge of sagebrush canopy (interspace microsites) to account for potential differences in seed storage (Coffin & Lauenroth, 1989). I collected and composited two cores (each 5 cm diameter x 5 cm depth) on the east and west side of sagebrush plants, for a total of 36 composited samples at the AA site: 18 shrub microsite and 19 interspace microsite; and 38 composited samples at the AC site: 20 shrub microsite and 18 interspace microsite. The number of samples varied based on the number of sagebrush individuals present within each plot.

I air dried samples and stored them for five months at room temperature before beginning a seed bank emergence study in October 2019. I transferred the samples to trays and spread each sample 1 cm deep over potting soil. I randomly placed each tray and two control trays (without seeds) in the glasshouse at Humboldt State University where they were subject to natural background temperature variation and grow lights for 16 hours daily (1500-0500). I watered once daily to maintain moist soil conditions. I identified, recorded, and removed each seedling that emerged, or transplanted it to a separate container until it was identifiable.

After 4 months, and no new seedling emergence for more than 14 days, I scraped the top 0.5 cm of soil to promote germination of smaller buried seeds. I left the trays in the glasshouse for a total of 8 months, to account for two growing seasons and allow ample time for seeds to germinate.

To check for remaining ungerminated seeds, I used the floatation method with a small subset (four) of sample trays following Malone (1967). I soaked remaining organic matter and seeds in a solution of 1000 ppm gibberellic acid for 8 hours, then spread it thinly across the glasshouse tray and placed it back under growing conditions for three weeks. Due to the lack of additional seedlings in this subset of samples, I did not use this method for the remaining seed trays.

Aboveground Cover

In July 2018, I measured aboveground plant species composition within a 1.0 m^2 subplot of each 4.0 m^2 plot by ocular estimation of percentage canopy cover for each species present using canopy classes (Daubenmire, 1959). I used the midpoint of each cover class to convert to species-specific percentage cover, and divided plants into different functional groups on the basis of growth form: exotic annual grasses, perennial grasses, annual forbs, perennial forbs, sagebrush, and other shrubs (including a few tree seedlings).

Data Analysis

I described patterns of seed bank community structure by means of Shannon-Weiner diversity index (H') and Pielou evenness index (J). I divided seed bank data into the following plant functional groups: total seeds, exotic forb seeds, native forb seeds, and exotic annual grass seeds. I excluded other functional groups from my analyses due to low (<5%) and inconsistent abundance among plots. In most cases (7/10 plots AA site, and 9/10 plots AC site), I collected the same number of soil samples (four) per plot. In cases where I collected fewer samples, I accounted for the unequal soil volume by multiplying the number of seeds for each response variable in the sampled volume of soil by 4/X, where X is the number of samples collected in that plot prior to data analysis. This method may over- or underestimate the number of seeds per plot, but it allows for direct comparison between treatments and sites.

To compare the magnitude (how large of an effect) and direction (negative or positive) of responses to drought between sites, I calculated effect size values using the log response ratio, $\ln(R_i) = (X_{it}/X_{ic})$, where X_{it} represents a response variable in each treatment plot t, and X_{ic} is the mean of the response variable i in the control plots c. R is a unitless measure of the proportional change in the response variable relative to controls and provides a comparable value for both the direction (negative or positive) and magnitude of responses to drought. I calculated R_i for the following response variables: native forb seed density, exotic forb seed density, exotic annual grass seed density, seed bank diversity and seed bank evenness.

I also calculated R_i using paired interspace and shrub microsite samples in each plot. In this analysis, R_i represents the magnitude and direction of the response variable in shrub microsites relative to interspace microsites. Due to natural spatial variation in the seed bank, some replicates, particularly those in interspaces, had 0 seeds. In these cases, I added 0.01 to the data before calculating the log response ratio. I reported mean log response ratios and 95% confidence intervals, along with bootstrapped confidence intervals when data were not parametric (Nakagawa & Cuthill, 2007) using the boot package (Canty & Ripley, 2012). I considered effects to be significant when the confidence intervals did not overlap 0 (Di Stefano, 2004; Nakagawa & Cuthill, 2007).

I used the Bray-Curtis similarity index to make within- and between- treatment and site comparisons of species present in the seed bank and aboveground vegetation. Prior to calculation, I converted belowground (seed bank) species composition to relative

density and aboveground species composition data to relative cover. I conducted all

community analyses using the vegan package (Oksanen et al., 2020) in R (R Core team,

2021) and created figures with ggplot2 (Wickham, 2016).

RESULTS

Precipitation Manipulations

Annual water year precipitation (Oct-Sep) during the 3-year experiment (2016-2019) was approximately 493, 378, and 376 mm, respectively. Since I collected the soil samples in May 2019, the 2019 value excludes 68 mm of precipitation that was received after I collected to soil samples (Jun-Sep 2019;
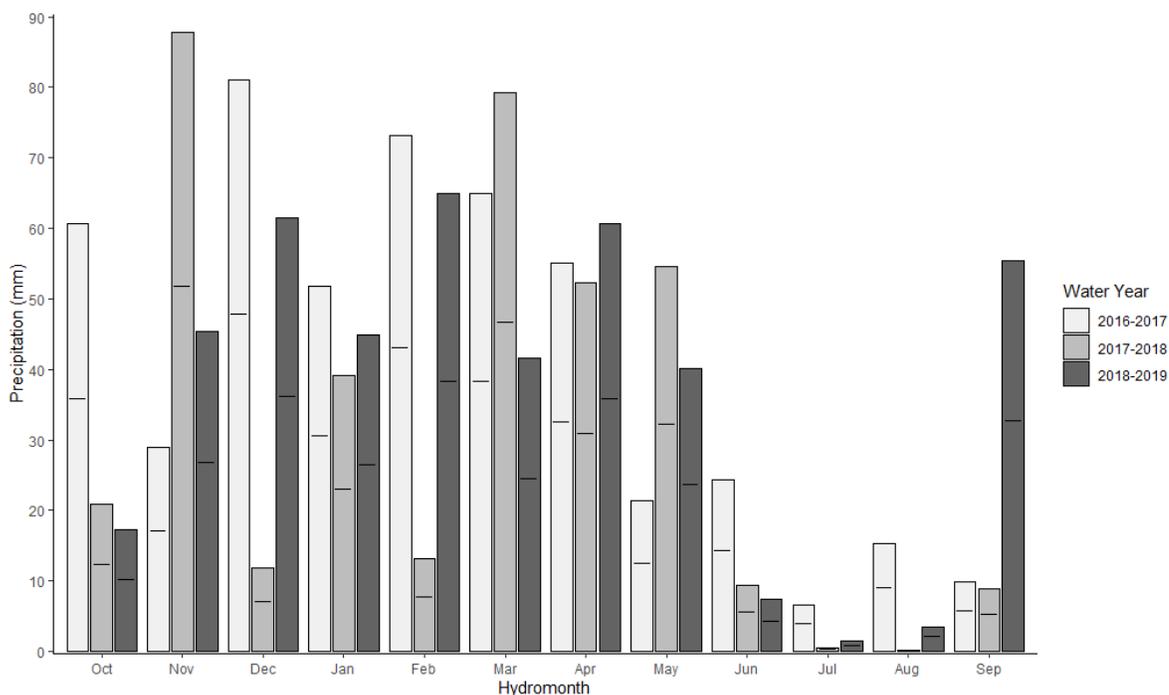
Figure 5). Interpreted within the historical probability distribution of the 50-year annual precipitation record, extreme dry years and extreme wet years (<10th percentile and >90th percentile) had normalized precipitation values of -1.16, and 1.11, respectively. Moderately dry years (15th percentile) had a normalized precipitation value of -1.00. The

normalized precipitation values for 2016-17, 2017-18, and 2018-19 were: 0.98, 0.08, and

0.07, indicating that the control plots were not under extremely dry or extremely wet

conditions during the project. Assuming 41% interception by the rainfall shelters, the

drought plots received approximately 291, 223, and 222 mm of precipitation. The

normalized precipitation values beneath the drought shelters were: -0.61, -1.14, and -

1.15, indicating that the drought plots were under moderately dry conditions during the

second year and third year of the experiment.
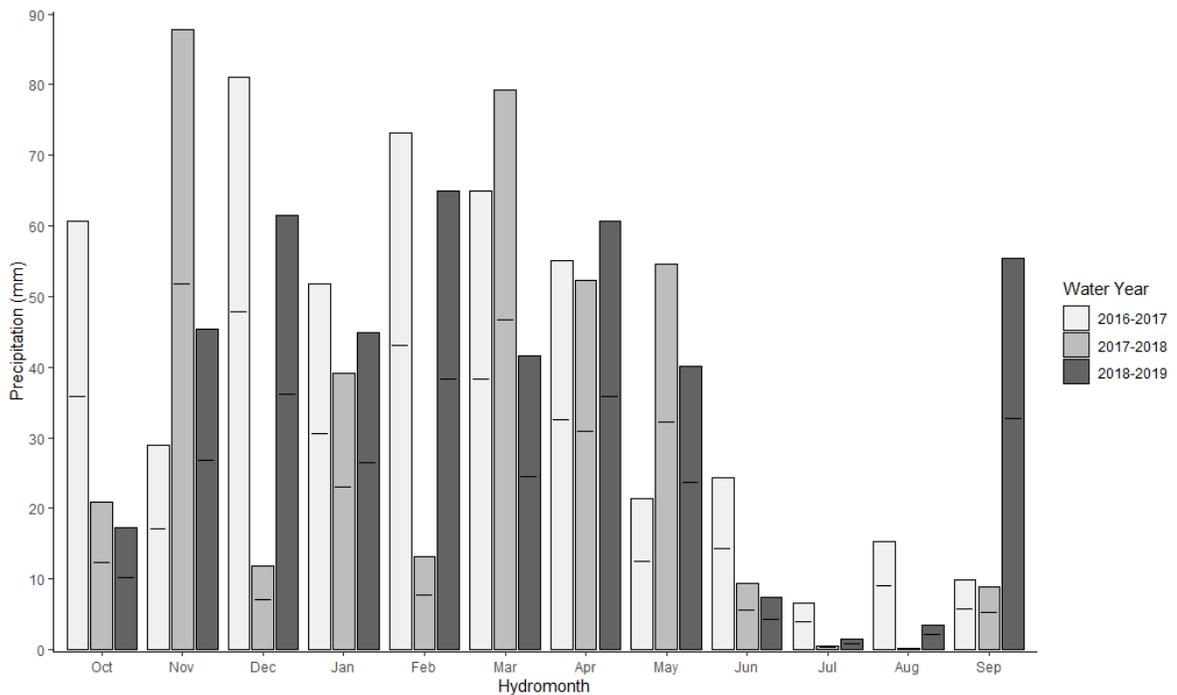
Figure 5. Monthly precipitation received during each water year throughout the experiment. Solid black horizontal lines represent 41% reduction in precipitation for each month.

Seed Bank

A total of 341 individual seeds and 10 species germinated from the AA site. Half (5) of the species were only present in the seed bank and not in aboveground vegetation (Table 1). The majority of seedlings were exotic annual grasses (58%) and annual forbs (41%). Of the exotic grasses, 99% were *V. dubia*, and 1% were *B. japonicus*.

A total of 501 individual seeds and 19 species germinated at the AC site. Nine of the species were only present in the seed bank and not in aboveground vegetation (Table 2). Similar to the AA site, the majority were exotic annual grasses (55%) and annual forbs (40%). Of the exotic grasses, 67% were *V. dubia*, and 33% were *B. japonicus*. For both sites, the most abundant species that emerged were *V. dubia* and *Draba verna* (exotic forb).

Table 1. AA site: list of species, their functional group, and their corresponding presence. Presence of species was either "S" present in only the seed bank, or "S/A" present in the seed bank and aboveground plant community, or "A" present only aboveground.

Functional Group & Species	Presence
Exotic annual forb	
Draba verna	S/A
Exotic annual grass	
Bromus japonicus	S/A
Ventenata dubia	S/A
Native annual forb	
Asteraceae sp.	A
Blepharipappus scaber	A
Collinsia parviflora	S/A
Crepis sp.	A
Gnaphalium palustre	S
Montia linearis	S
Navarretia intertexta	A
Polygonum sp.	A
Trifolium sp.	S

Functional Group & Species	Presence
Veronica peregrina	S
Native annual grass	
Bromus carinatus	S
Native perennial forb	
Allium acuminatum	A
Eremogone congesta	A
Erigeron bloomeri	A
Lomatium sp.	A
Nothocalais troximoides	A
Packera cana	A
Perideridia oregana	A
Phlox hoodii	A
Sedum stenopetalum	S/A
Trifolium macrocephalum	A
Native perennial grass	
Danthonia californica	A
Elymus elymoides	A
Festuca idahoensis	A
Shrubs and Trees	
Artemisia arbuscula	A
Eriogonum sphaerocephalum	A
Pinus ponderosa	A

Table 2. AC site: list of species, their functional group, and their corresponding presence. Presence of species was either "S" present in only the seed bank, or "S/A" present in the seed bank and aboveground plant community, or "A" present only aboveground.

Functional Group & Species	Presence
Exotic annual forb	
Draba verna	S/A
Exotic annual grass	
Bromus japonicus	S/A
Ventenata dubia	S/A
Native annual forb	

Functional Group & Species	Presence
Acmispon americanus	A
Asteraceae sp.	A
Collinsia parviflora	S/A
Collomia grandiflora	S/A
Epilobium brachycarpum	S/A
Erythranthe guttata	S
Eriophyllum lanatum	A
Gilia sp.	S/A
Gnaphalium palustre	S
Montia linearis	S/A
Navarretia intertexta	S
Polemoniaceae sp.	A
Polygonum sp.	A
Rorippa curvisiliqua	S
Trifolium sp.	S
Other forb sp.	A
Veronica peregrina	S
Native annual grass	
Bromus carinatus	S
Perennial forb	
Achillea millefolium	S/A
Delphinium sp.	A
Lithophragma sp.	A
Lomatium sp.	A
Perideridia oregana	A
Trifolium macrocephalum	A
Verbascum thapsus	S
Native perennial grass	
Carex sp.	A
Elymus elymoides	A
Festuca idahoensis	A
Poa bulbosa	A
Poa secunda	A
Shrub or Tree	

Functional Group & Species	Presence
Artemisia arbuscula	A
Artemisia cana	S/A
Other shrub sp.	S

Drought Effects

At the AA site, drought consistently reduced exotic forb seed density, seed

diversity, and seed evenness, and increased exotic annual grass seed density, but did not

affect total seed density or native forb seed density (Figure 6). At the AC site, drought

consistently reduced exotic forb seed density, but did not affect exotic annual grass seed

density, native forb seed density, total seed density, seed diversity, or seed evenness

(Figure 6).
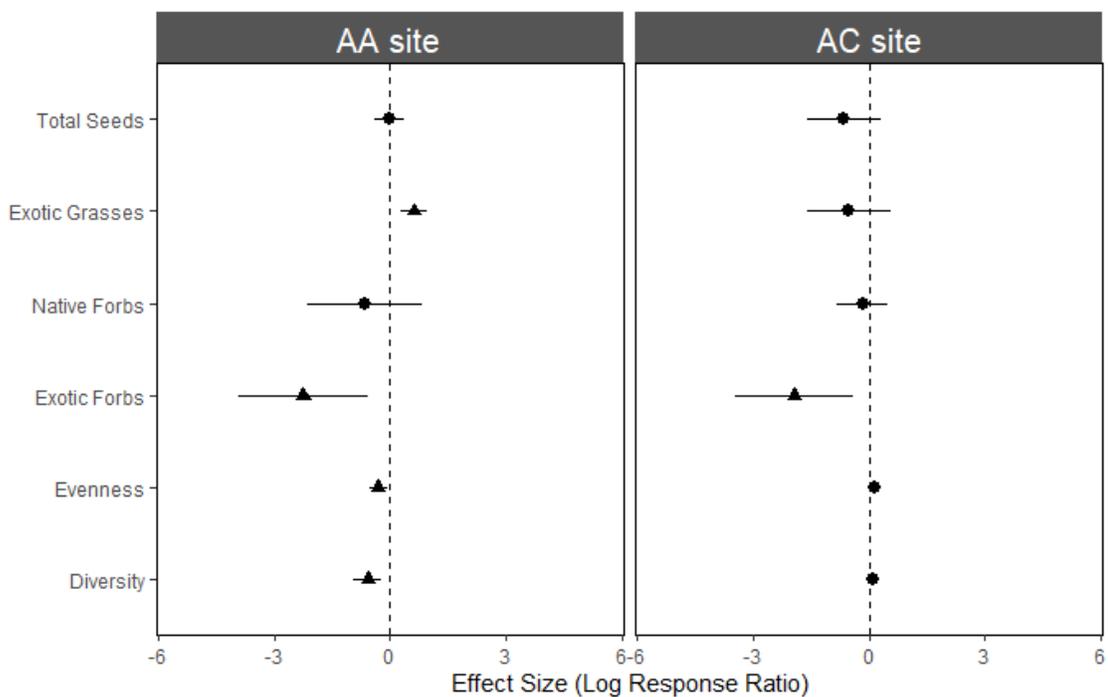
Figure 6. Responses to drought (Ln response ratio ± 95% confidence interval) of seed density (total seeds, exotic annual grasses, native forbs, exotic forbs), seed bank species evenness, and seed bank species diversity. Triangles denote effect sizes with confidence intervals that do not overlap with zero, while circles denote effect sizes with confidence intervals that overlap zero. Confidence intervals that do not overlap 0 indicate a significant positive or negative effect.

Microsite Effects

At the AA site, shrub microsites had consistently greater native forb seed density, total seed density, and seed diversity compared to interspaces, but microsite did not affect exotic forb or annual grass seeds, nor seed evenness (Figure 7). In contrast, microsite differences did not affect any of the response variables at the AC site (Figure 7).
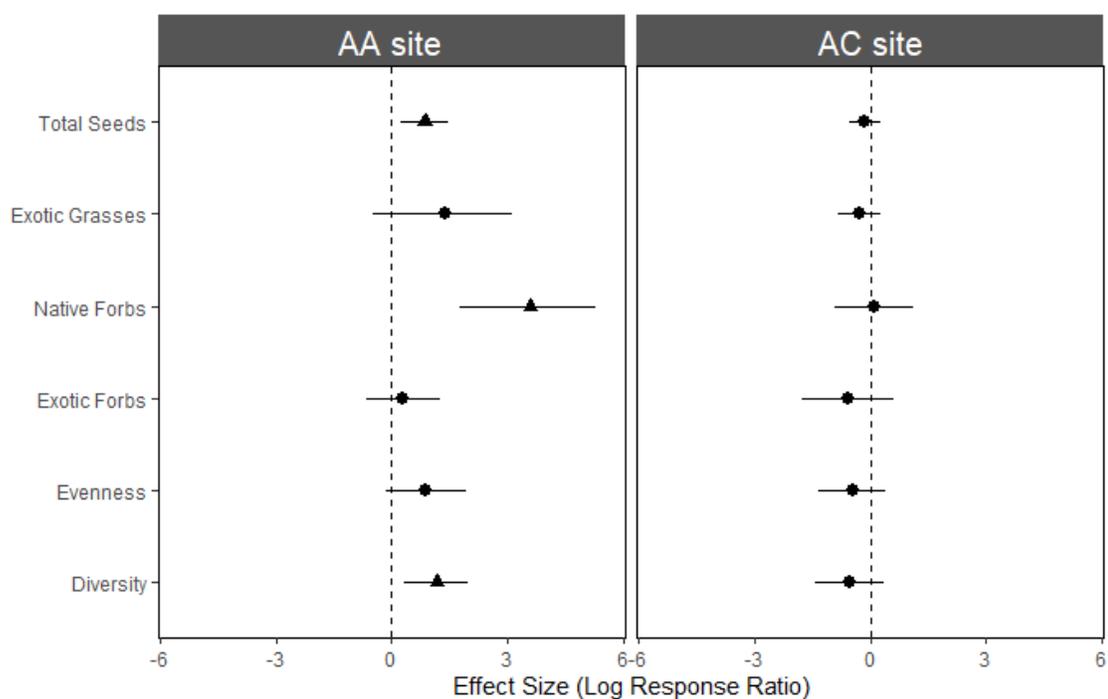
Figure 7. Responses to shrub microsites compared to interspace microsites (Ln response ratio ± 95% confidence interval) of seed density (total seeds, exotic annual grasses, native forbs, exotic forbs), seed bank species evenness, and seed bank species diversity. Triangles denote effect sizes with confidence intervals that do not overlap with zero, while circles denote effect sizes with confidence intervals that do overlap zero. Confidence intervals that don't overlap 0 indicate a significant positive or negative effect.

Seed Bank and Aboveground Comparison

At the AA site, exotic annual grasses contributed 58% of total seedling emergence, annual forbs accounted for 41%, perennial forbs 0.5%, perennial grasses 0.3%, shrubs 0%, and no sagebrush individual germinated (
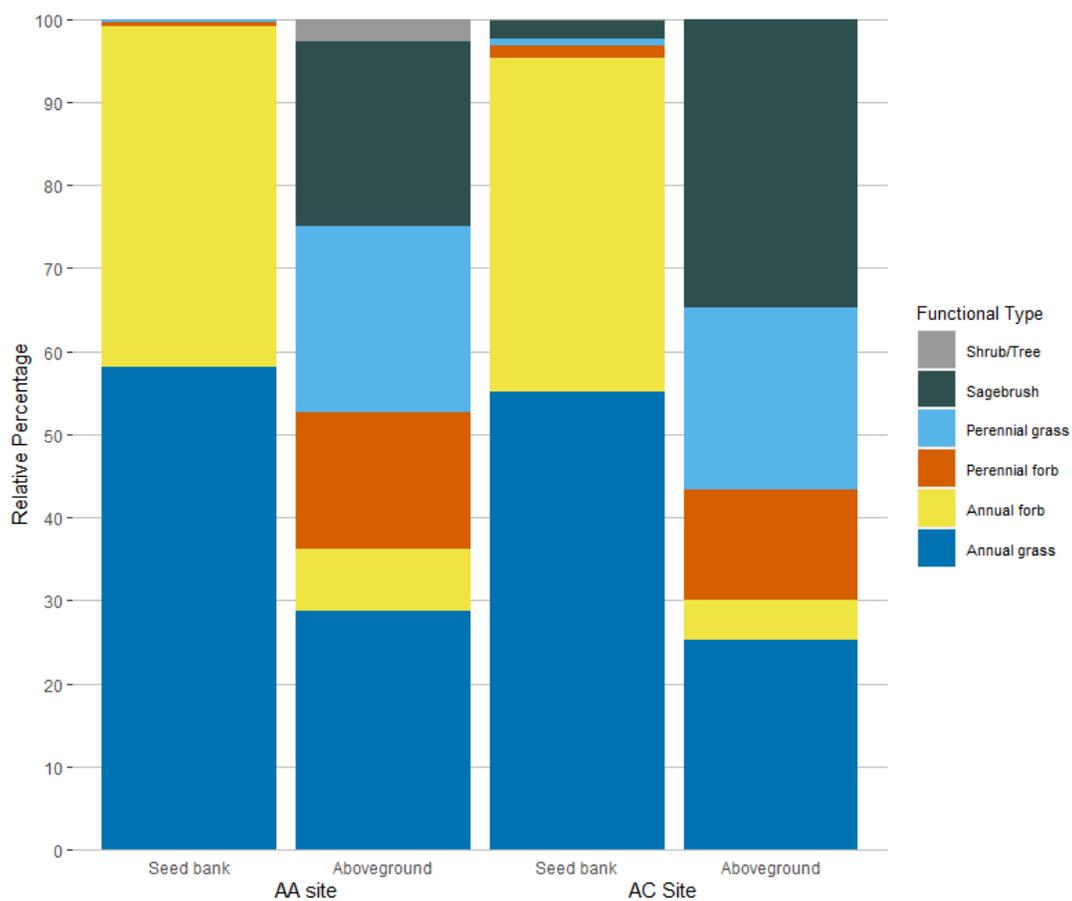
Figure 8). In contrast, the aboveground relative cover was comprised of 29% exotic annual grasses, 8% annual forbs, 16% perennial forbs, 22% perennial grasses, shrubs 3%, sagebrush 22% (
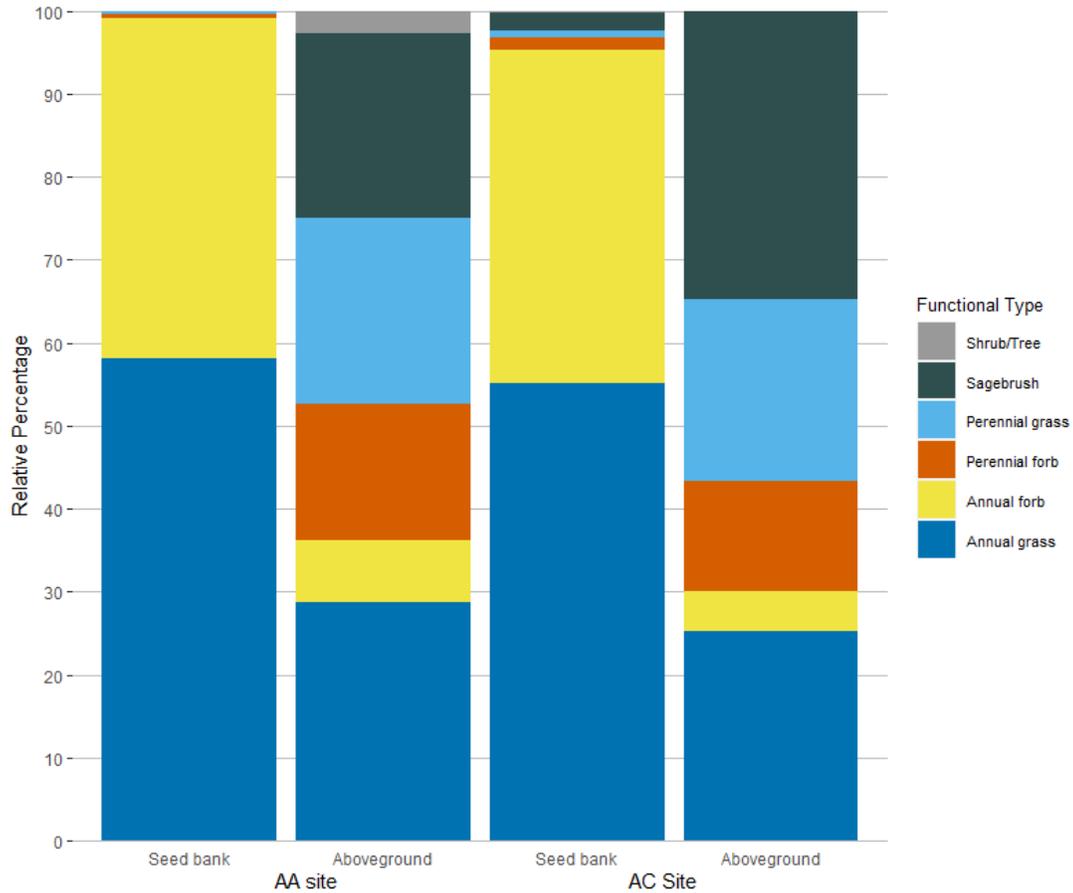
Figure 8). There were 5 species found only in the seed bank and 22 found only

aboveground. 5 species were found both in the seed bank and aboveground (Table 1). Of

the 5 species found only in the seed bank, 4 were native annual forbs (Table 1).

     At the AC site, exotic annual grasses contributed 55% to seed bank functional

group composition, annual forbs accounted for 40%, perennial forbs 1%, perennial

grasses 1%, shrubs 0.3%, and one sagebrush individual germinated, 0.2% (
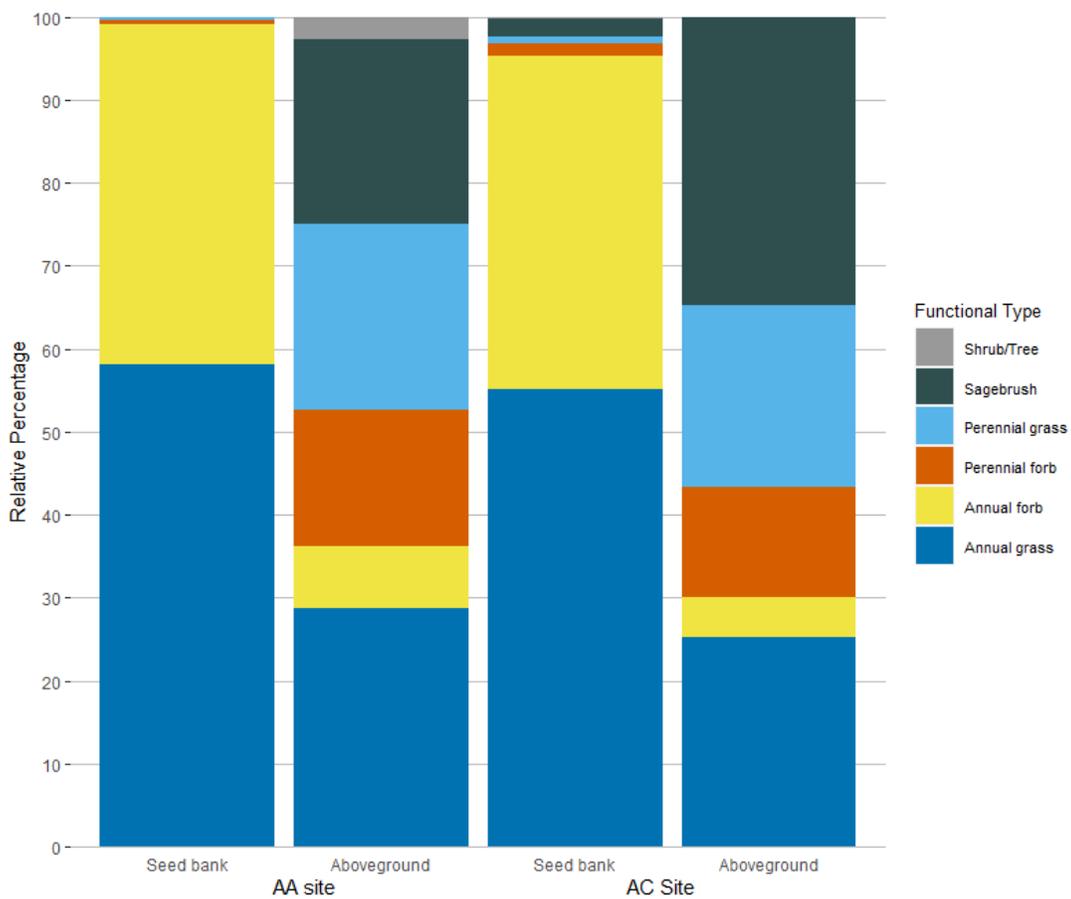
Figure 8). Aboveground functional group relative cover was comprised of: 25% exotic annual grasses, 5% annual forbs, 13% perennial forbs, 22% perennial grasses, shrubs 0%, sagebrush 35% (
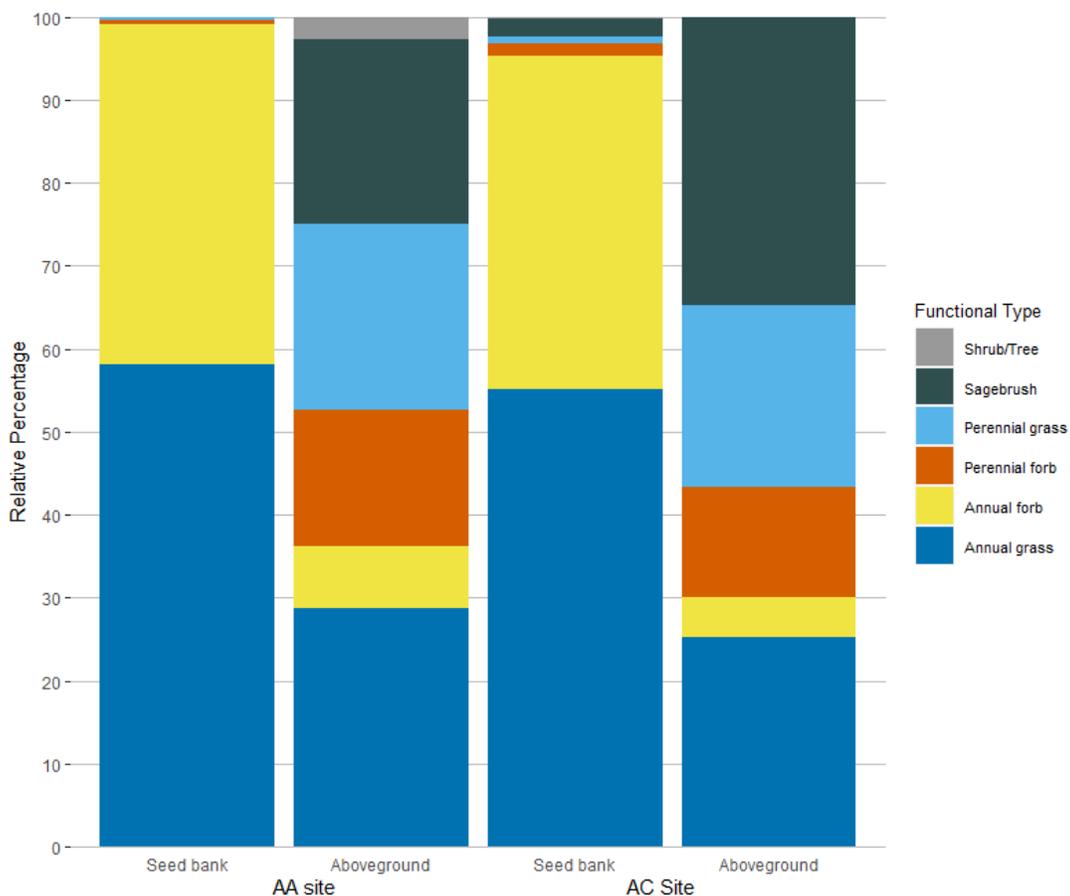
Figure 8). There were 10 species found only in the seed bank and 17 found only aboveground. 10 species were found both in the seed bank and aboveground (Table 2). Of the 10 species found in the seed bank 7 were native annual forbs (Table 2).

The Bray-Curtis similarity analysis showed that among plots within drought and control treatments at the AA site, relative species seed density compared to relative species cover was 27% and 25% similar (respectively; Table 3a), relative seed density was 73% and 69% similar (Table 3b), and aboveground cover was 67% and 40% similar (Table 3c). For within site treatments at the AC site: relative species seed density compared to relative species cover for drought and control plots was 26% and 18%

similar (respectively; Table 3a), relative seed density was 53% and 62% similar (Table

3b), and aboveground cover was 61% and 38% similar (Table 3c). For between site

comparisons of drought and control plots, AA site relative seed density was 44% and

66% similar to the AC site (Table 3b), and relative species cover at the AA site was 17%

and 22% similar to the AC site (Table 3c).

Table 3. Average Bray-Curtis similarity percentages (with SDs) for drought and control plots between and within sites. Seed x Cover (a) represents percentage similarity comparing relative seed density and relative aboveground plant cover within each site. Seed x Seed (b) and Cover x Cover (c)represent percentage similarity for the seed bank and aboveground cover; both within-site similarity between plots at the same-site (values in bold) and between-site similarity (values in italics).

Site by comparison	AA site		AC site	
	Drought	Control	Drought	Control
(a)Seed x Cover				
AA site	**27 (0.2)**	**25 (5)**		
AC site			**26 (2)**	**18 (1)**
(b)Seed x Seed				
AA site	**73 (7)**	**69 (3)**		
AC site	*44 (5)*	*66 (5)*	**53 (12)**	**62 (4)**
(c)Cover x Cover				
AA site	**67 (7)**	**40 (4)**		
AC site	*17 (2)*	*22 (4)*	**61 (6)**	**38 (5)**
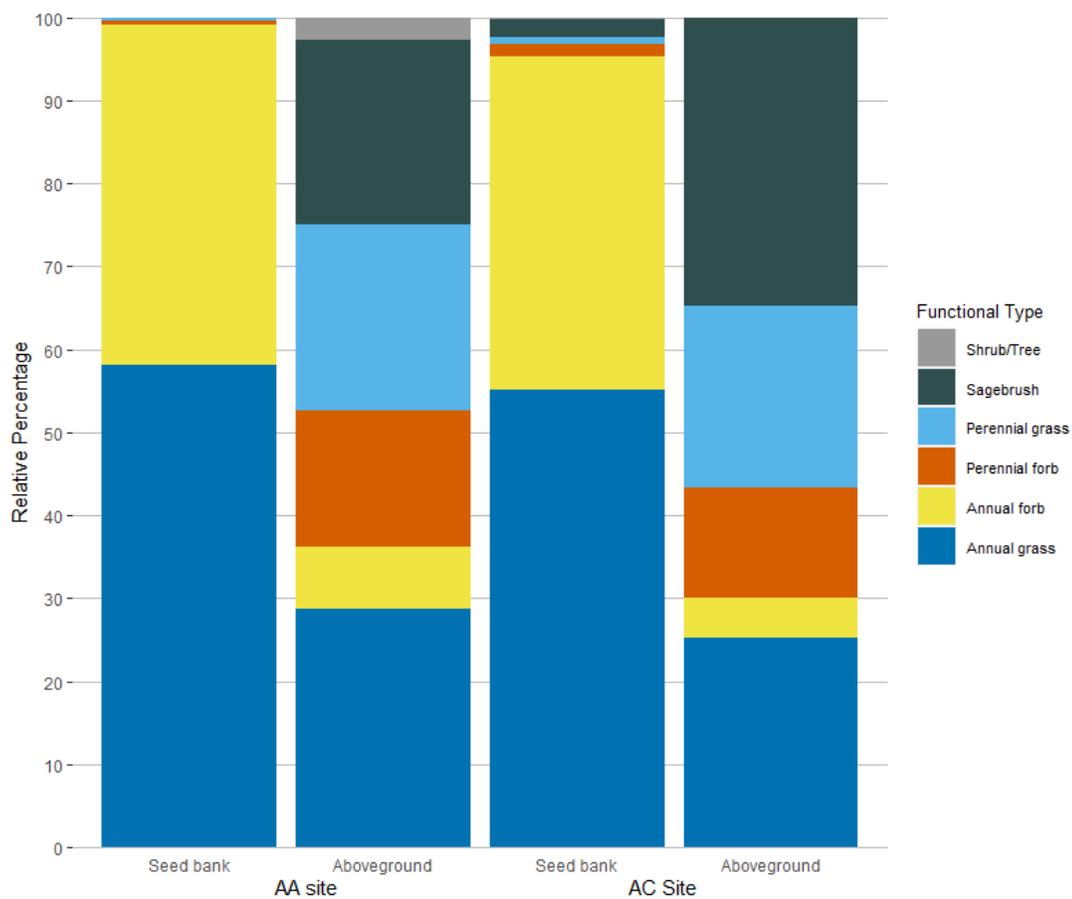
Figure 8. Relative seed density within the seed bank compared to relative aboveground plant community cover congregated by plant functional groups at both sites. Functional groups are stacked in the same order for each bar.

DISCUSSION

Seed banks are a crucial component of plant communities, and understanding seed bank responses to environmental factors provides insight into past, present, and future plant community dynamics. As anthropogenic disturbances such as climate change and exotic species invasion stress aboveground plant communities and their associated seed banks in novel ways, it is more important than ever to understand how seed banks may respond to these perturbations. My study found that the effects of drought and vegetation structure (shrub cover) will differ among plant associations, even at sites within close proximity to each other. This work highlights the idiosyncratic nature of plant community responses to anthropogenic climate change and the challenges associated with predicting those responses.

Drought and The Seed Bank

The seed bank within the AA site experienced multiple drought induced effects, while the AC site only experienced one negative effect from drought (Figure 6). One explanation for these dissimilarities in seed bank responses is the contrasting structure and function between both sites caused differences in available resources for seeds. The AA site has a more heterogenous structure than the AC site, along with lower productivity, smaller dominant shrubs, and greater expanses of bare ground. The AA site also has greater clay content in the soil, an edaphic feature that specifically affects seed longevity (Baskin & Baskin, 2014). These distinct features at the AA site lead to lower

albedo, more extreme soil temperatures, greater soil aridity, and lower nutrient cycling; all of which affect seed production and seed viability (Baskin & Baskin, 2014; Egley, 1998). Furthermore, the contrasting seed traits among functional groups led to some species' seeds being affected by variable environmental conditions, while other plant functional groups were unaffected. For instance, drought did not affect native forb seeds at either site (**Error! Reference source not found.**). One possible explanation for the lack of drought response is that the annual forb seeds in these two plant communities possess persistent seeds, and were able to remain dormant during the 3 year drought (i.e. seed viability was unaffected by increasing soil aridity and temperatures). Indeed, 7 native annuals from my study did not emerge until after one month of ambient watering conditions in the glasshouse, providing further evidence that the species may have specialized bet-hedging strategies to remain dormant during until conditions are optimal to emerge. While some literature suggests that increases in drought frequency and severity will surpass seed viability thresholds (Ooi, 2012; Reed et al., 2012), recent literature suggests these thresholds are highly dependent on species and region (Gioria et al., 2020; Yi et al., 2019). In line with this, my results demonstrated that drought conditions did not affect seed longevity of native annual forbs within my two sites, perhaps due to species-specific adaptations or regional-specific adaptations. Regardless, native annual forb seeds exhibited resistance to a 3 year drought at both sites.

In contrast to drought having no effect on native forb seeds, drought had a relatively large negative effect on exotic forb seeds at both sites (Figure 6). However, this

decrease in exotic forbs was mainly attributed to *D. verna*, a winter annual with miniscule seeds (generally < 0.6 mm). While it's life-history traits differ from native species, it is notably an annual with small and coatless seeds that likely experienced a decrease in seed viability with slight increases in soil temperatures caused by drought (Saatkamp et al., 2013). Many smaller seeded species without vigorous bet-hedging strategies also have higher seedling mortality rates, but make up for this expected net loss of viable seeds by producing large quantities of seeds (Saatkamp et al., 2013). Although based on only one species, this result may suggest that exotic forb species that produce copious amounts of small uncoated seeds are not well-adapted drought conditions and exotic forb seeds are more sensitive to changes in temperature and precipitation than native forb seeds.

Perennial species were poorly represented in the seed bank at both sites. No perennial grasses emerged during the study, and only 3 perennial forb species emerged, which represented a small percentage of both seed banks (AA site: *Sedum stenopetalum* 0.5%, and AC site: *Achillea millefolium* and *Verbascum thapsus*, 1.2%;
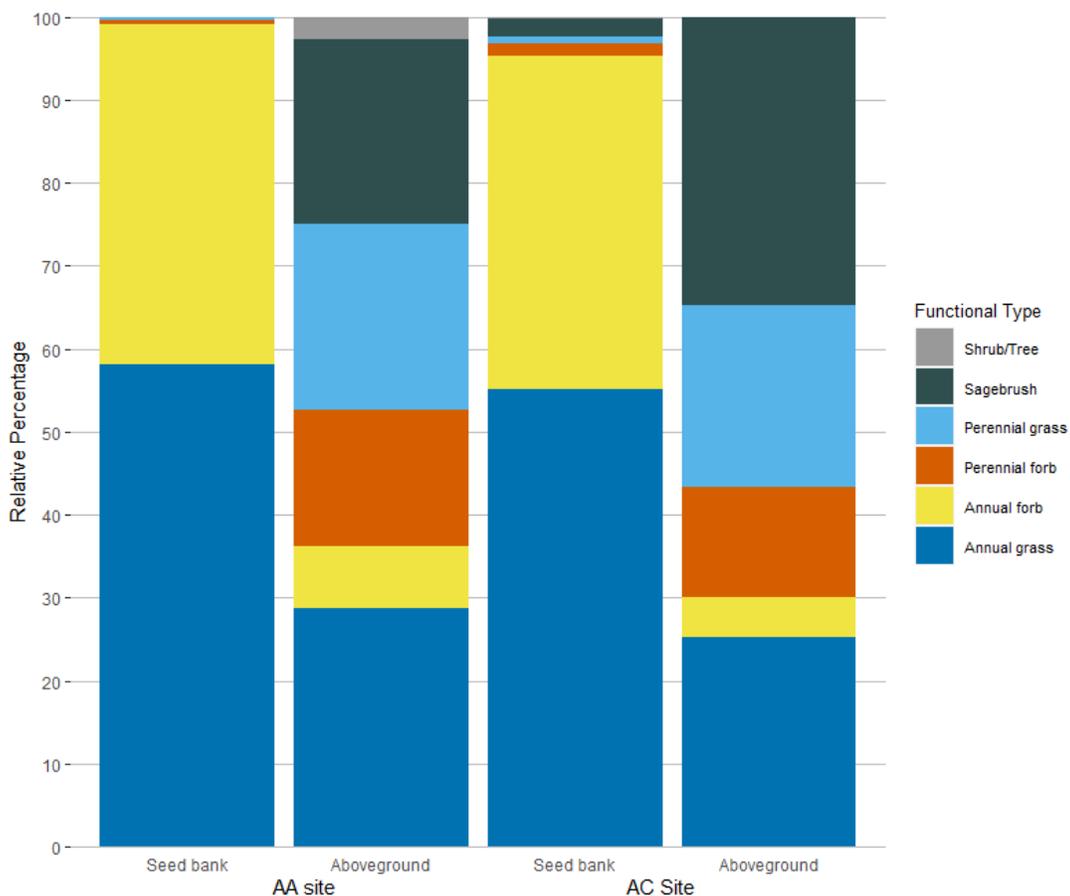
Figure 8; Table 1; Table 2). Anecdotally, the three perennial forbs that emerged were

only found in control plots. Other studies indicate that drought stress may exacerbate seed

deficiency by limiting flowering and reducing seed production of perennials (Clair et al.,

2009; Dietrich & Smith, 2016; Stampfli & Zeiter, 2020). For example, after prolonged

drought periods seeds of perennial grasses can be poorly represented compared to annuals

(Gutiérrez et al., 2000; O'Connor, 1991; Schwinning & Sala, 2004). Furthermore, poor

edaphic conditions caused by drought could increase the rate of mechanical decay and

cause high seed mortality, especially for transient seeds in which seed viability is already

vulnerable (Kiss et al., 2018; Thompson et al., 1998). If the duration of intense drought

increases in the future, my study provides some evidence that perennials could be negatively affected by experiencing decreased seed production or increased seed mortality.

Exotic annual grass seeds, particularly *V. dubia*, were positively affected by severe drought at the AA site (Figure 6). Previous research indicates that *V. dubia's* resource-acquisitive strategies and extremely shallow root system (between 1 and 5 cm) allow it to take advantage of early fall precipitation moisture near the soil surface of clay dominated and otherwise moisture limited systems, making timing and intensity of precipitation events less important (Bansal et al., 2014). Like other invasive grasses, *V. dubia* also has relatively large seeds, which can remain near the soil surface and rapidly germinate during sporadic precipitation events (Saatkamp et al., 2013). Since the design of the rain shelters decreases the size of each rainfall event by ~41%, this potentially hydrated the top surface of soil even during minor rainfall events, and allowed *V. dubia* seeds to germinate during early season precipitation. This vigorous seed trait of rapid germination was also observed in the glasshouse, where the majority of *V. dubia* seeds in the study emerged within the first few weeks of ambient watering conditions. Because many native annual plants take a more resource-conservative approach, and their smaller seeds remain dormant within the soil during unfavorable conditions (e.g. drought or sporadic precipitation events), it's also possible that this allowed for more niche space for *V. dubia* to take advantage of (Chambers et al., 2007). Over time, these contrasting reproductive strategies between native forbs and exotic annual grasses may create a

higher proportion of exotic seeds in the seed bank than native seeds (Borokini et al., 2020; Chambers et al., 2007). In sum, these results suggest that community invasibility at the AA site increased during drought disturbance, and *V. dubia* is taking advantage of open areas during drought, along with early rainfall events that saturate the surface soil layers for brief periods of time, to queue germination, grow in its life cycle, and contribute more seeds to the seed bank.

Seed bank species diversity and evenness were negatively affected by drought at the AA site (Figure 6). Since Shannon diversity (H') and Pileou evenness (J) account for both species richness and abundance, this minor negative effect was likely due to a *few* species' seeds being absent from drought plots (3/10 species: *V. peregrina*, *S. stenopetalum,* and *B. japonicus*), along with a large increase in the proportion of exotic annual grasses in the seed bank within drought plots. The exotic annual forb species *D. verna* was also dominant in the seed bank, but decreased in proportion in the drought plots. While my results showed that drought only had a minor effect on seed bank evenness and diversity, it's possible that over time, drought could continue to decrease evenness and diversity within the seed bank through the increase in the proportion of exotic grasses.

Microsite and The Seed Bank

At the AA site, shrub microsites had a strong positive effect on native forb seed density compared to interspace microsites, and a relatively small positive effect on total seed density and diversity (Figure 7). The large positive effect of shrubs on native forbs is congruent with other studies which found that shrub microsites create conditions that can help prolong seed longevity (Caballero et al., 2008; Funk et al., 2019; Olano et al., 2005). These results also highlight the role of shrubs as crucial reservoirs for seed density and diversity within many dryland communities (Busso & Bonvissuto, 2009; Caballero et al., 2008; Foronda et al., 2019).

In contrast, shrub microsites had no effect on seed bank composition at the AC site (Figure 7). One possible explanation for the divergent role of shrubs within the two sites is the contrasting interspace conditions. The AA site contains large expanses of bare ground and extremely low productivity between shrub patches, while the AC site has relatively high productivity and greater quantities of litter in interspaces. Thus, the interspaces at the AA site are subject to more extreme soil temperatures, lower nutrient cycling, and lower water availability for seeds; all which exacerbate the need for refuge beneath shrubs at this site. Additionally, other studies indicate that shrubs can harbor more seed-bearing individuals beneath or near them, which also may have contributed more seeds to the seed bank at the AA site (Caballero et al., 2008; Foronda et al., 2019; Soliveres & Eldridge, 2014). While shrub microsites remain an important refuge for seeds at the AA site, they may become even more important during long duration

droughts as environmental conditions in the interspaces become more extreme than conditions beneath shrub canopies. While I could not test for the interaction between drought and micrositedue to low sample size, another study within a patchy shrubland ecosystem found that the importance of shrub microsites as a refuge for seeds was magnified during severe drought conditions (Funk et al., 2019).

Aboveground Composition and The Seed Bank

In line with previous studies carried out in sagebrush steppe communities, my results demonstrate that the seed bank and established vegetation contrast both in species composition and plant growth forms (Figure 8; Martyn et al., 2016; Pekas & Schupp, 2013). Martyn et al. (2016) also found less than 27% similarity between the seed bank and aboveground community and identified that the high volume of annual species in the seed bank drove this low similarity percentage. The divergent life-history strategies of annual and perennial plants make this dissimilarity finding not entirely unexpected. Annual plants may contribute more to the seed bank since they grow rapidly, produce large quantities of seeds, and often have long-lived seeds. It's also plausible that some seeds in my study were seed rain from years before the drought experiment began, and germinated (broke dormancy) under the ambient glasshouse conditions. In contrast, perennials and species like sagebrush contribute fewer seeds annually and those seeds are more short-lived. This dissimilarity result is also an artifact of the different methods I

used to calculate relative abundance for the aboveground and belowground data (relative

cover for aboveground data; relative density of seeds in belowground data).

Strikingly, over 50% of both seed banks were comprised of exotic annual grasses,

followed by ~40% native forbs (
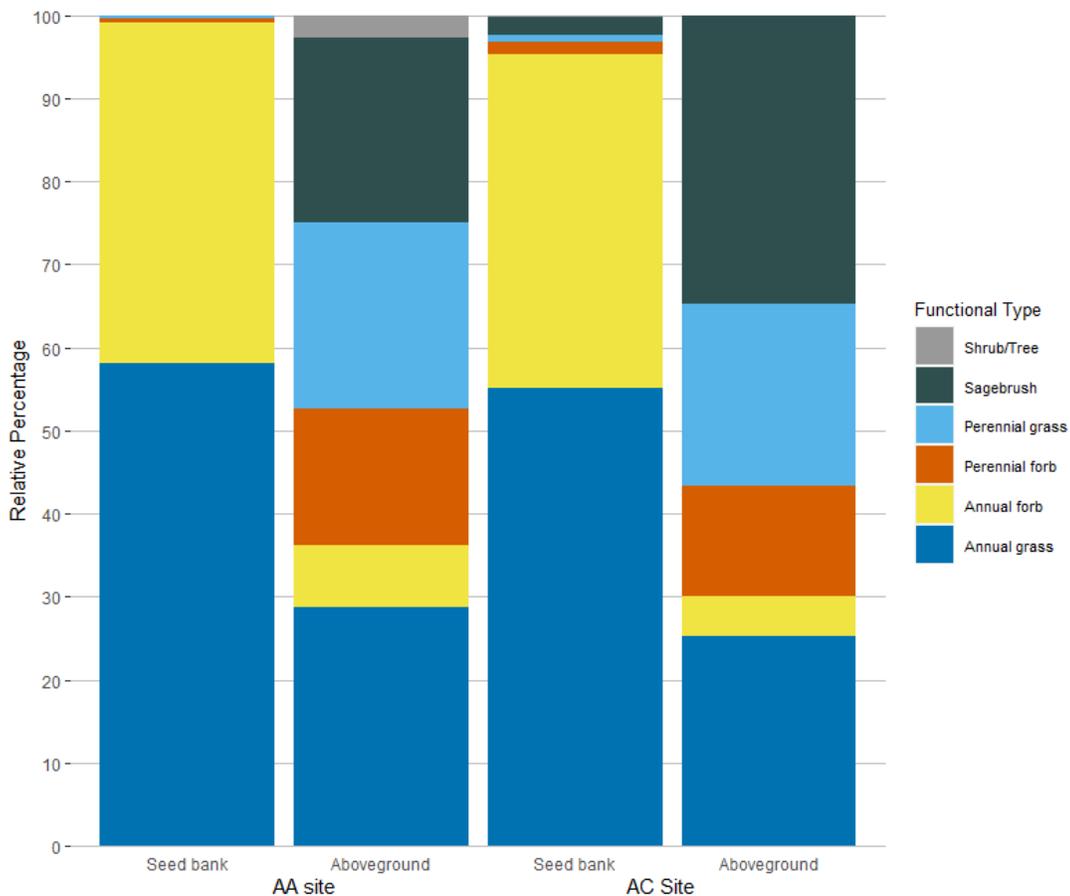
Figure 8). This result could be in-part due to the readily germinable traits of exotic

grasses, and the seedling emergence method favoring this trait. However, this still

indicates that both sites are disturbed and contain large proportions of annual grass seeds.

Other studies within sagebrush steppe have also found that at disturbed sites, invasive

grasses (primarily *Bromus tectorum*) can make up the majority of the seed bank

(Diamond et al., 2012; Humphrey & Schupp, 2001; Knapp, 1996). However, the

prevalence of exotic grasses can still vary year to year (Haight et al., 2019; Hassan &

West, 1986; Humphrey & Schupp, 2001). While the aboveground community remains an

important factor that influences seed bank composition, it's clear that characterizing the

seed bank and quantifying its dissimilarity to the aboveground community can aid in:

identifying how species are represented within a community (whether in the seed bank,

aboveground, or both), anticipating non-native species invasion, and predicting

successional trajectories of a community.

CONCLUSIONS

Overall, my study revealed that the impacts of environmental factors on seed bank composition will differ among plant associations even within close proximity to each other. In particular, changing climatic regimes and heterogenous structure (i.e. shrub presence) may greatly alter seed bank composition in plant communities similar to *A. arbuscula* dominated communities, with large expanses of bareground and relatively poor edaphic conditions (i.e. high clay content and low soil moisture availability). My study also indicated that species with persistent seeds may be able to "wait out" unfavourable conditions, at least for several years. However, changing climatic regimes may concurrently promote the spread of opportunistic species, such as *V. dubia*, and the increased propagule pressure of *V. dubia* as illustrated by my drought study may pose a potential risk to the aboveground community in the future. In sagebrush drylands, exotic grass invasion is a prevailing factor that induces fire return intervals beyond historical fire frequency and severity (as much as every 3-5 years, compared to historically: 60-100 years; Knick et al., 2005; Whisenant, 1990). Sagebrush shrubs are not well-adapted to high intensity fires, and these anomalous fire regimes have already led to elimination of sagebrush in plant communities across the western US (Knick & Rotenberry, 1997). Moreover, sagebrush seeds are extremely short-lived and the removal of seed-bearing individuals from a community may pose an additional threat to recovery after disturbance (Shriver et al., 2019), particularly large-scale disturbances such as high intensity fire. Although patches of bareground have historically kept fire from spreading, *V. dubia*

invasion may facilitate the spread of fires as flames are carried by continuous fuels between shrub patches and to neighboring forested areas. When small scale disturbances occur, the seed bank can be an important tool for regeneration. However, if *V. dubia* leads to larger fires, the distance to seed sources will also increase and it may create a positive feedback cycle (i.e. drought leading to increased *V. dubia* invasion, novel fire return intervals, and lack of regeneration from the native seed bank).

Given that the seed bank is a critical resource for dryland plant communities and can reflect responses to environmental factors, these results may aid land managers in maintaining biodiversity, anticipating non-native species invasion, and forecasting disturbance recovery. These findings may also help decipher what types of plant communities may need further attention based on distinct structural features or environmental influences, although future research should be conducted to test for direct correlations between site characteristics and seed bank characteristics.

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