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Shrub cover and fire history predict seed bank composition in Great Basin shrublands

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A R T I C L E I N F O

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A B S T R A C T

Dormant seeds in the soil are an important contribution to the regenerative potential of an area. Understanding factors that affect seed bank dynamics in arid regions provides insight into how communities respond to disturbance and environmental change. We characterized seed banks in a Great Basin sagebrush steppe system, using field surveys and seed bank studies to compare 17 sites that differed in above-ground vegetation, fire history, and grazing use. We asked whether shrub cover, ground cover, climate, or disturbance history were predictive of seed densities, diversity, the presence of rare species, and similarity between above- and below-ground communities. Fire frequency and a coarse measure of grazing use were not highly predictive of seed bank dynamics, with the exception that sites that burned < 10 years ago had greater above-vs. below-ground similarity. Shrub cover predicted multiple below-ground characteristics: *Ericameria nauseosa* was associated with increased density of introduced species, *Chrysothamus viscidiflorus* was associated with increased densities of native annual species, and *Artemisia tridentata* was associated with increased richness of rare native species. Shrub cover estimates were predictive of seed bank composition, and suggest that areas dominated by *A. tridentata* would have the greatest restoration potential within their seed banks.

1. Introduction

Ungerminated seeds that persist in the soil are important components of plant communities that affect long-term species composition (Hopfensperger, 2007). While the seeds of some species exist in the seed bank for less than one year, forming a transient seed bank, seeds of other species may endure in the seed bank for greater than a year, and sometimes much longer, forming a persistent seed bank (Thompson and Grime, 1979). Persistent seed banks arise from dormancy mechanisms that prevent germination until appropriate dormancy-breaking conditions are met (Baskin and Baskin, 2014). Viable seeds may remain in the soil for some time after plants have disappeared from the above-ground community through successional processes, and there are many examples of plant communities where above-ground and below-ground composition are quite different (Hopfensperger, 2007; Kemp, 1989; Pekas and Schupp, 2013). The species composition of the seed bank, including the relative proportion and diversity of native and introduced species, strongly influences the successional trajectory of an area after disturbance (Hassan and West, 1986; Kemp, 1989; Levassor et al., 1990). Given this, the soil seed bank can act as both a snapshot of the past vegetation in an area and an indication of the regenerative potential of a site (Koniak and Everett, 1982; Osem et al., 2006a; Simpson et al., 1989).

Plants growing in arid systems and in areas with high environmental variability, such as the cold deserts of the Great Basin, often evolve high levels of seed dormancy, as this strategy can allow for species persistence during extended periods of reproductive failure during drought or unfavorable precipitation regimes (Facelli et al., 2005; Kinloch and Friedel, 2005). Thus, persistent seed banks are especially common in harsh and variable environments (Freas and Kemp, 1983; Jurado and Flores, 2005). Both biotic and abiotic factors can affect seed bank composition. For example, seed banks of Great Basin annuals fluctuate as a result of temporal variability in precipitation and productivity (Gutierrez et al., 2000; Young and Evans, 1975). Differences in dispersal ability, seed longevity, and granivory also impact seed bank composition (Chambers and MacMahon, 1994; Guo et al., 1998; Kemp, 1989). The presence of shrubs can contribute to the distribution of seeds within the seed bank (Guo et al., 1998; Li, 2008), and plant litter can trap seeds during dispersal (Chambers and MacMahon, 1994) and constrain the germination of seeds (Facelli and Pickett, 1991; Xiong and Nilsson, 1999). These processes result in highly transient seed banks in arid regions (Gul and Weber, 2001), with large site-to-site variation in seed bank composition despite similarities in above-ground vegetation (Guo et al., 1998; Kemp, 1989; Young and Evans, 1975).

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Disturbances such as fire and livestock grazing can also affect seed bank characteristics. In some areas, invasive annuals can dominate the seed bank and prevent establishment of native perennials after fire (Humphrey and Schupp, 2001), and grazing can have highly variable effects on similarity between the above-ground and below-ground community composition, depending on site history, productivity, and grazing timing and intensity (Bakker and de Vries, 1992; Kinloch and Friedel, 2005; Osem et al., 2006a, 2006b; Peco et al., 1998). The loss of seeds from the seed bank over time due to germination and extended periods without plant regeneration will limit the viable seed composition of the seed bank and, in disturbed sites, may lead to an increased proportion of introduced species (Bossuyt and Honnay, 2008; Esque et al., 2010).

The Great Basin desert of North America contains broad expanses of sagebrush steppe vegetation. Within this region, plant communities vary greatly in composition, from relatively intact systems (often at higher elevations) to highly degraded sites (West, 1999; Young et al., 1972). Some of the most degraded sites have lost a majority of their native plant communities, likely due to the combined effects of multiple disturbance factors such as legacy effects of heavy grazing, invasion by introduced annual grasses, and repeated fire (Knick et al., 2011; Miller et al., 2011). Other sites may have experienced fewer disturbance factors (i.e. heavy grazing pressure and some invasion, but no fire) or less frequent or intense disturbances, and thus may retain elements of their native structure, such as an intact shrub community but a degraded native understory community (West, 1999). Degradation of sagebrush shrublands affects ecosystem services and can result in loss of biodiversity and habitat for obligate sagebrush species. For example, degradation of sage-grouse brooding habitat has resulted in population reductions and range shifts, evidenced by abandonment of sites by sage-grouse that were once active leks and nesting grounds (Aldridge and Boyce, 2007; Knick et al., 2011).

Restoration opportunities vary on these different types of sites, and responses to treatments can vary greatly depending on the abundance of introduced and native seeds in the soil. Identifying easy-to-measure factors that are predictive of seed bank dynamics in an area are important for land management, as the success of management actions designed to increase diversity in degraded or invaded systems, such as tree removal, herbicides, or prescribed fire, can be positively affected by the existence of seed banks of desirable species, or negatively affected by abundant weed seeds (Bakker and Berendse, 1999; Meyer, 1994; Pywell et al., 2002; Smith et al., 2002). Here, we contrast the predictive power of easily-obtained but potentially coarse site characteristics (estimated local climate, fire history, permitted grazing animals) with on-site measurements of ground and vegetation cover, asking which factors are most predictive of seed bank composition. We characterized the seed bank and above-ground vegetation for a series of sagebrush steppe sites that vary in their fire history, grazing use, and current vegetation composition. Focusing on 17 sites located within two ecoregions in Northern Nevada that are of high-priority for sensitive wildlife, we address the following questions:

1) What is the relationship between site characteristics (shrub cover, ground cover, climate, fire history, and grazing use) and the density of introduced and native seeds in the seed bank?
2) Can site characteristics predict seed bank and above-ground diversity (measured by richness and evenness) and the presence of rare native species?
3) Can site characteristics predict similarity between seed banks and above-ground vegetation?

We predicted that, overall, site disturbance history would have the strongest influence on seed bank composition, and expected that the density of introduced species would increase and that species richness would decrease in areas with more recent fires and higher grazing allocation. Given that water is a limiting resource in many sagebrush dominated sites, we expected to see a positive relationship between precipitation and native seed density and richness in the seed bank. We also expected that shrub cover would be associated with seed bank composition, given the known relationships between shrub composition and disturbance history (Morris and Leger, 2016; Young and Evans, 1974). Specifically, we predicted that there would be a positive relationship between shrub cover of sagebrush (*Artemisia tridentata* Nutt.), a later seral species, and native richness, and that we would find more rare species in areas with greater sagebrush cover. We expected the opposite relationships to occur in areas with higher cover of rabbitbrush species (*Ericameria* nauseosa (Pall. ex Pursh) G.L. Nesom & Baird and *Chrysothamnus viscidiflorus* (Hook.) Nutt.), as these species are more abundant after disturbance (Miller et al., 2013). Finally, we predicted that below-ground species composition would be more similar to the above-ground composition in areas with higher levels of disturbance and lower precipitation.

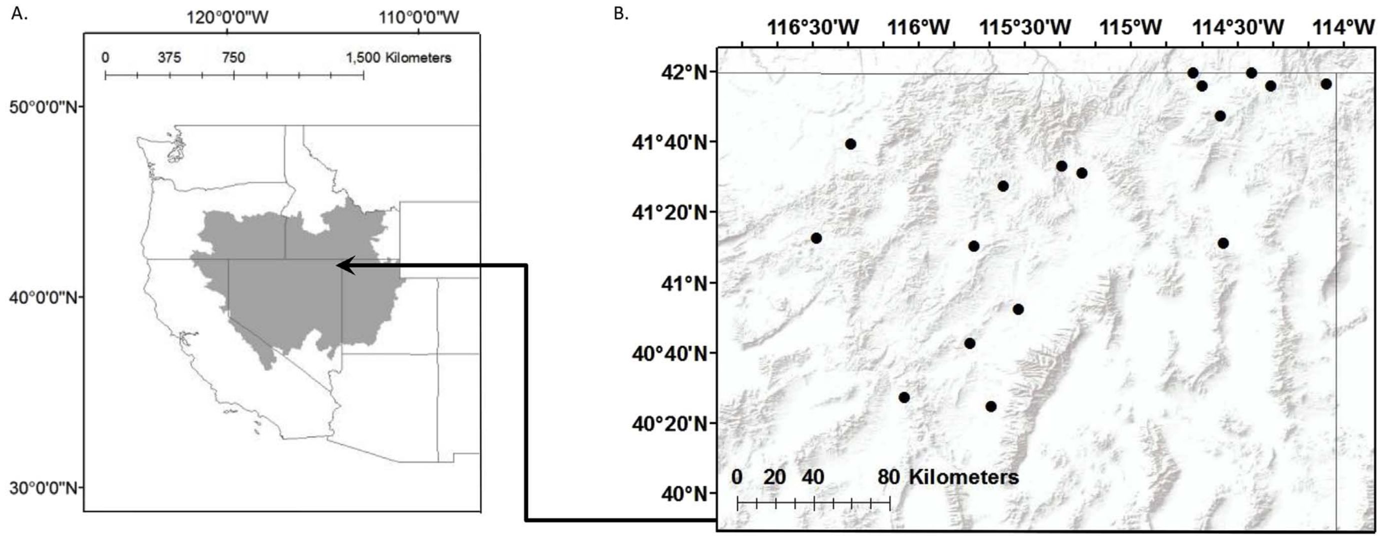


Fig. 1. Map of field sites showing (A) the western United States with the floristic Great Basin highlighted in gray and (B) north-eastern Nevada site locations within two sagebrush steppe dominated ecoregions, as designated by the U.S. Environmental Protection Agency (13M - Central Basin and Range, 80A - Northern Basin and Range).

Table 1
Schedule of seed bank treatments. Each treatment period lasted until seedling emergence tapered to nearly zero for at least two weeks. All watering occurred three times each week for 10 min using a watering system with overhead misters.

Date of Onset	Treatment Phase	Duration (weeks)	Treatment
15 October 2014	First	20	Watering
4 March 2015	Second	8	Stir Soil, Watering
27 April 2015	Third	8	Dry
1 July 2015	Fourth	5	Watering
4 August 2015	Fifth	11	Dry
20 October 2015	Sixth	3	Watering
10 November 2015	Seventh	10	Smoke Water
22 January 2016	Eighth	6	Gibberellic Acid

2. Materials and methods

2.1. Study site

Sites were selected within two sagebrush-dominated ecoregions located in north-eastern Nevada (Fig. 1), as designated by the Environmental Protection Agency (Level IV Ecoregions: Central Basin and Range - 13 M and Northern Basin and Range - 80A) (Omernik and Griffith, 2014). These ecoregions were selected based on their importance for sensitive wildlife habitat, and specific study sites were selected using a nesting habitat model for the greater sage-grouse (Gibson et al., 2016), a species of concern in the Great Basin. Study sites were selected randomly in areas of high nesting habitat quality within 6 km buffer around 17 current or historic sage-grouse leks. Sites were rejected if they were inaccessible, and a new site was generated. We used historic fire maps (1910–2013) and historic grazing animal use (permitted animal unit months, or AUMs) from the United States Bureau of Land Management to estimate site history. We tabulated the number of AUMs for the allotment surrounding each research site by subtracting the suspended AUMs from the permitted AUMs for each location (https://www.blm.gov/ras/- last accessed: 04March15). We quantified the fire history on our sites using both distance and temporal metrics to create four distinct fire categories. We noted whether fires occurred either on the site (hereafter, “on-site”) or within 1km of a site (“nearby”), and further noted whether the fire(s) were within 10 years (“recent”) or greater than 10 years from the sampling date (“past”). “Recent” and “past” fire designations were based on the estimates of long-term vegetation recovery in sagebrush, which can begin to return to pre-fire conditions > 10 years after a fire (Miller et al., 2013). Measures of fire “on” or “nearby” account for potential seed dispersal of introduced species from neighboring sites that have burned.

2.2. Vegetation and seed bank sampling

Plant surveys and seed bank sampling took place in June 2014, with the goal of sampling the seed bank at the point where most seeds had germinated for the season but before seeds of most species had fallen to the ground from that year's seed production. Each site was represented by one 4 ha plot, which was sampled using twenty randomly-placed 1 m^2 quadrats in a stratified random design, with five quadrats placed in each of the four quadrants of the plot. Within each quadrat, we assessed the percent cover of each species and collected four 128 cm^3 soil samples from the top 5 cm of soil in each quadrat, including the litter layer. These samples were bulked to represent the seed bank in that 1 m^2 location. We also assessed shrub cover across the plot using a point-intercept sampling method at 1 m intervals along five 25 m transects randomly located within each plot. We noted all living shrub species encountered along a transect, as well as dead shrubs that were still providing woody structure on the landscape, and we referred to the latter as standing dead.

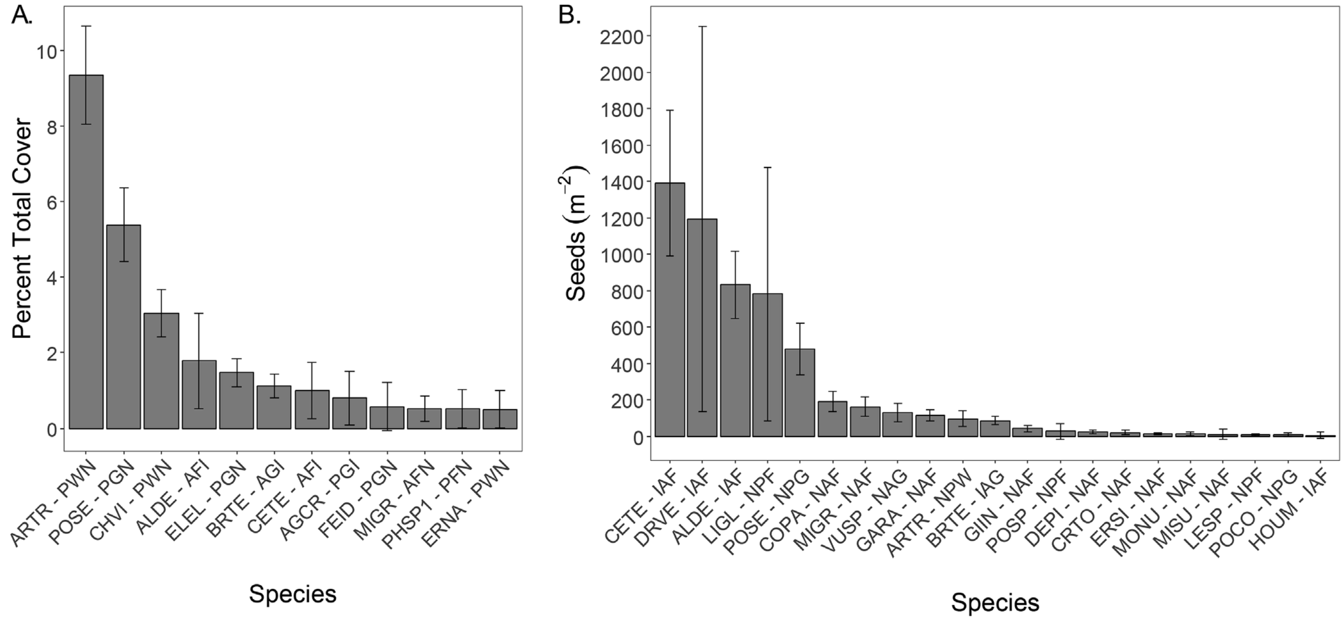
2.3. Quantifying the seed bank

We assessed the seed bank using our standard lab method (Espeland et al., 2010). Seed bank samples were processed in the greenhouse at the University of Nevada, Reno starting in October 2014. Samples were sieved through a ½ cm screen to remove large rocks. Tables and trays (Garland - Mini Seed Tray 6.5″L X 4″W X 2″H) were prepared such that they allowed for wicking of moisture in and out of the soil samples (Espeland et al., 2010), and a 118.3 cm^3 portion of each soil sample was used in each tray. In order to promote an even distribution of the samples from each plot across the greenhouse area, trays were arranged in four blocks using a stratified random design, with each block having an equal number of samples from each plot and all blocks placed along the same greenhouse table in an east-west orientation. The location assignment on the table for blocks, and trays within blocks, were randomized every two weeks throughout the experiment.

The experimental design consisted of eight treatments, with each treatment period lasting until seedling emergence tapered to nearly zero for at least two weeks (Table 1), with samples checked for emergence once or more per week. The greenhouse temperature was constrained to highs and lows consistent with ambient weather, with high temperatures ranging between 16 and 21 °C and low temperatures allowed to fluctuate with ambient conditions, but held to a minimum of 2 Cº. Alternating wet and dry treatments began in October 2014, and the experiment lasted ~16 months, ending in January 2016. At the beginning of the seventh treatment period in November 2015, we applied 3 ml of a 5% liquid smoke solution (pH 3, Lazy Kettle Brand Hickory Liquid Smoke) prepared using methods outlined in Doherty and Cohn (2000) followed by normal watering, to trigger germination by any species that break dormancy in response to fire cues. The final treatment included the application of gibberellic acid (GA), a plant hormone that can trigger emergence in dormant seeds. We applied 3 ml of GA solution (10 mg/L - Super-Grow SG-GA3 20) to each tray and provided normal watering thereafter. As seedlings emerged from the trays, we cataloged each distinct morphotype, and raised representative individuals to maturity for identification. We were unable to identify a small portion of both the above- and below-ground plants, equivalent to less than 1% of individuals, and these plants were excluded from our analyses. Nineteen morphotypes were identified to genus, and were analyzed as a single species at each site. We also identified two species within the seed bank that were riparian obligate species (*Veronica anagallis-aquatica* L. and *Myosurus apetalus* C. Gay). Because these species were only represented by a few seeds and would not normally grow in our focal habitats, we excluded them from our analyses.

2.4. Data analysis

We analyzed our data using generalized linear models (GLMs) in program R (R Development Core Team, 2016) in a two-step process. First, we asked how well different types of environmental characteristics predicted above- and below-ground characteristics, running separate models for each set of characters. Second, if multiple best models were identified for a particular response variable, we used an iterative model averaging process that included all environmental characteristics to determine which were the most predictive. Categories of environmental characteristics were: shrub cover, ground cover, climate, and disturbance (see Supplemental Table 1 for characteristics of model variables, including range of values). The predictor variables for the shrub cover model included the fraction of shrub cover of the three most dominant shrubs on our sites: *A. tridentata*, *C. viscidiflorus*, and *E. nauseosa*. The predictor variables for the ground cover model included the fraction of different types of ground cover at our sites based on our quadrat sampling, including: standing dead, bare ground, litter, and rock. The predictor variables for the climate model included annual measures of precipitation (mm), minimum temperature (°C), and maximum temperature (°C) at the sites based on 64 year averages



N = native, I = introduced, A = annual, P = perennial, F = forb, G = grass, W = woody

Fig. 2. Mean composition of species composing ≥0.5% of (A) total above-ground cover or (B) seed bank density, averaged across all sites. Error bars show standard error across sites. Acronyms are: AGCR - *Agropyron cristatum*, ALDE - *Alyssum desertorum*, ARTR - *Artemisia tridentata*, BRTE - *Bromus tectorum*, CETE - *Ceratocephala testiculata*, CHVI - *Chrysothamnus viscidiflorus*, COPA - *Collinsia parviflora*, CRTO - *Cryptantha torreyana*, DEPI - *Descurainia pinnata*, DRVE - *Draba verna*, ELEL - *Elymus elymoides*, ERNA - *Ericameria nauseosa*, ERSI - *Eriastrum signatum*, FEID - *Festuca idahoensis*, GARA - *Gayophytum ramosissimum*, GIIN - *Gilia inconspicua*, HOUM - *Holosteum umbellatum*, LESP - *Lesquerella* sp., LIGL - *Lithophragma glabrum*, MIGR - *Microsteris gracilis*, MISU - *Mimulus suksdorfii*, MONU - *Monolepis nuttalianus*, PHSP1 - *Phlox* sp., POCO - *Poa compressa*, POSE - *Poa secunda*, POSP - *Potentilla* sp., VUSP - *Vulpia* sp.

derived using PRISM data from 1950 to 2014 (Daly et al., 2008). Lastly, the predictor variables for the disturbance model included permitted AUMs, number of recent fires nearby, number of past fires nearby, number of recent fires on site, and number of past fires on site. We performed a Pearson's correlation analysis among all predictor variables to confirm that they were not highly correlated ($R < \pm 0.7$). We also used plots of residual versus fitted values to check for trends within the residuals for each of the models. We ran preliminary analyses to determine whether the block factor in our greenhouse experimental design was predictive of seed bank composition, and found that it did not have a significant effect; this factor was not included in final models.

When analyzing our GLMs, we selected the best model using Akaike's information criterion (AIC) scores, with better models possessing lower AIC scores and models < 2 from the best model considered to be comparable to the best model. When we identified multiple best models for a particular response variable, the second step was to analyze the GLMs using multi-model inference using the *MuMIn* package for program R (Barton, 2016). For this step, we generated a set of candidate models using the *dredge* function. In order to reduce the chance of overfitting our models, based on our sample of 17 sites and 15 predictor variables, we limited candidate models to contain no more than three terms from the global set of predictor variables from all of the aforementioned models. We then performed model averaging across all candidate models in order to obtain estimates of the regression coefficients for each variable averaged across all models and weighted by the corrected AIC scores for those models. We calculated model averages using two approaches: the zero average (ZA) approach and the natural average (NA) approach. For the ZA approach, parameter estimates of zero are used for predictor variables that are excluded from a particular model when performing model averaging (Burnham and Anderson, 2002). For the NA approach, parameter estimates are averaged exclusively for models containing that particular predictor (Burnham and Anderson, 2002). The ZA approach is best for comparing the relative importance of different parameters, while the NA approach is best for determining the importance of an individual parameter (Burnham and Anderson, 2002; Grueber et al., 2011). We also report estimates of parameter importance (IMP) for each of the predictor variables, calculated based on the proportion of highly predictive models containing the focal parameter: higher IMP values can result when a parameter is included in more models and/or is included in highly predictive models. For model selection, we present the groups of environmental characteristics that produced the best models, as well as the individual significance of factors in those models. We also present results of model averaging for response variables with multiple best models. When there were significant relationships, we present the results of linear regressions for a select group of factors and responses. We report effect sizes, standard errors, and p-values for all best models based on model selection, and effect sizes for both ZA and NA approaches for model averaging results (see Supplemental Materials).

We tabulated seed bank densities for each site by species status, noting whether each species was annual, perennial, native or introduced (USDA NRCS, 2017). We averaged seed densities across all 20 samples taken from a site for use as a response variable in our GLMs. We calculated species richness by counting the number of species observed within the seed bank samples from each site, and species evenness for both native and introduced species from the average values for either seed density or percent cover for species across all samples for a site. Evenness was calculated as follows:

$$\left(\left(\sum_{i=1}^{S}(P(i)*\ln P(i))\right)*-1\right)\Big/\ln(S)$$

Here, S is the total number of species and $P(i)$ is the proportion of species i within the sample.

To determine the presence of rare species, we summed the number of unique native species found at each of our seventeen sites, calculating this number separately for above- and below-ground species composition. We designated a species as “rare” if it only occurred at one of our sites; forty-five species in the above-ground community and fifteen species in the below-ground community received this distinction. Species richness, species evenness, and the number of rare plants on a site were used as response variables in our GLMs, for both above- and below-ground communities.

Finally, we calculated two measures of similarity between the above- and below-ground species composition at our sites for use as response variables in our GLMs. First, we calculated the Bray-Curtis (Sorensen) similarity index (Gardener, 2014) for the presence/absence of species, with higher values indicating that the above- and below-ground communities are more similar. Next, we calculated the Bray-Curtis dissimilarity index (Gardener, 2014) for the density of species, with higher values indicating that the above- and below-ground communities are more different from each other. Standardized effect sizes for our models were obtained using the *QuantPsyc* package in program R (Fletcher, 2012).

3. Results

3.1. Above-ground and seed bank composition

In total, we identified 126 species in the above-ground community and 62 species in the seed bank (Supplement 1, Supplemental Table 2). Overall, 27 species were found in both the above-ground and below-ground communities across all sites. These included 19 native species (10 annuals and 9 perennials) and 8 introduced species (6 annuals and 2 perennials) (Supplemental Figure 1); note that these species were not necessarily found in both the above- and below-ground communities at all sites (Supplemental Table 2). Species found in both the above- and below-ground communities made up 12.7–41.7% of the cover in the above-ground community and 54.2–99% of the contents of the seed bank. Across sites, the mean total percent cover was 5.8–42.0% native species and 0.3–26.8% introduced species (Fig. 2A, Supplemental Figure 2). Below-ground, 53.3–85.7% of the 62 species identified in the seed bank were native, and invasive species made up between 20 and 96.7% of the density of seeds in the seed bank across all sites (Fig. 2B, Supplemental Figure 3).

3.2. What is the relationship between site characteristics (shrub cover, ground cover, climate, fire history, and grazing use) and the density of introduced and native seeds in the seed bank?

Contrary to our prediction, disturbance history was not the best predictor of seed bank density. Rather, shrub cover was the best predictor of the seed density of both native and introduced species (Table 2A). Introduced species density was higher when there was increased cover of *E. nauseosa* ($P = 0.008$), and seed bank densities of native annual species were higher in areas with more cover of *C.*

Table 2

Model results for generalized linear models and model averaging assessing the relationships between (A) seed density, (B) diversity, (C) rarity, and (D) above-vs. below-ground similarity and environmental characteristics. The relationship column shows the specific relationships between the response and the model variables. For response variables with multiple best models, the AIC values and model averaging results for the natural average (NA) are provided in their own column.

A. Seed Density (m^{-2})						
			Best Model			Relationship
Native Annual			Shrub Cover			↑ CHVI**
Native Perennial			Shrub Cover			↑ ERNA^{t}
Introduced			Shrub Cover			↑ ERNA**
B. Diversity						
			Model Selection			Model Averaging (NA)
	Community	Native/ Introduced	Best Model(s)	AIC	Relationship	Relationship
Richness	Above-ground	Native	Shrub Cover	121.17	↑ARTR*, ↑CHVI*	↑ Fire Near > 10 Years**,
			Climate	121.33		↓ Maximum Temp.**
		Introduced	Ground Cover		↓ Standing Dead**, ↓ Rock**	
	Below-Ground	Native	Disturbance	85.56	↑ Fire Near < 10 years^{t}	↑ ARTR^{t},
			Shrub Cover	86.18	↑ ERNA^{t}	↑ Fire Near < 10 Years^{t}, ↓ Fire On > 10 Years^{t}
		Introduced	Shrub Cover	63.34		↑ ERNA***,
			Disturbance	64.99	↓ Fire Near > 10 Years^{t}	↓ Fire Near > 10 Years***
Evenness	Above-Ground	Native	Shrub Cover		↓ARTR^{t}	
		Introduced	Climate		↑ Precipitation**, ↑ Maximum Temp.**	
	Below-Ground	Native	Ground Cover		↑ Rock*, ↑ Bare Ground^{t}	
		Introduced	Shrub Cover	9.44	↓ ERNA*	↓ ERNA*,
			Disturbance	10.67	↓ Fire On > 10 Years^{t}	↓Fire On > 10 Years*
C. Rarity						
			Best Model			Relationship
Above-Ground			Shrub Cover			↑ CHVI*
Below-Ground			Shrub Cover			↑ ARTR**
D. Above vs. Below-Ground						
			Best Model			Relationship
Similarity - Presence			Ground Cover			↑ Litter*, ↑ Bare Ground*
Similarity - Density			Disturbance			↓ Fire On < 10 Years*

ARTR = *A. tridentata*, CHVI = *C. viscidiflorus*, ERNA = *E. nauseosa*.

t = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

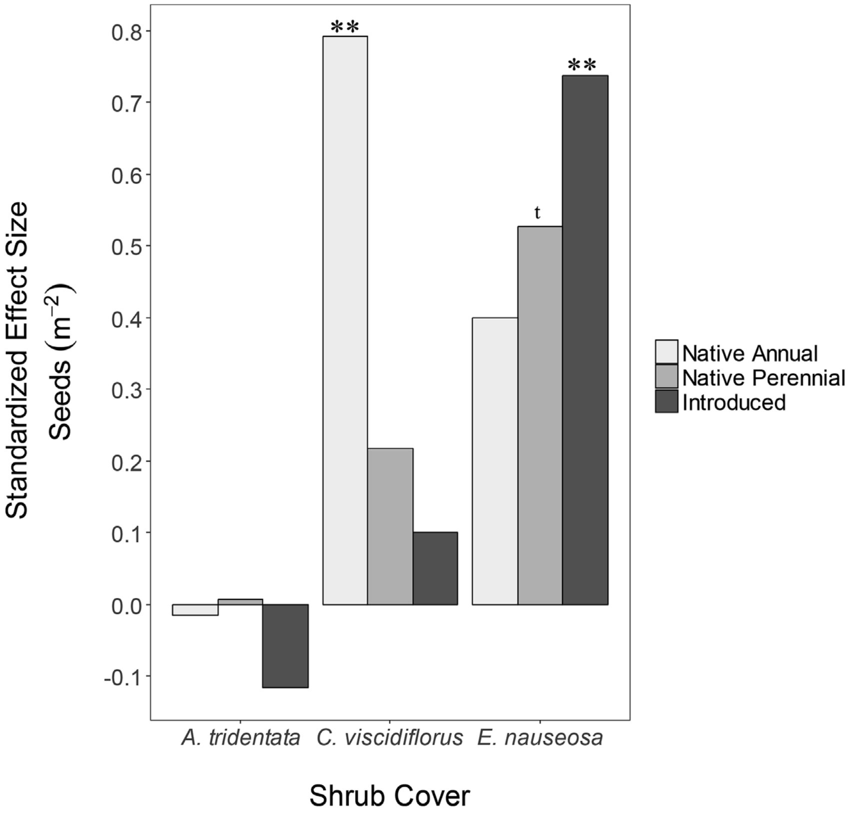


Fig. 3. The relationship between shrub cover of three dominant shrub species and soil seed bank densities (seeds m^{-2}) of native annual, native perennial, and introduced species. Values have been converted to standardized effect sizes for ease of comparison. Significance is indicated, with ** = $P < 0.01$, t = $P < 0.10$.

viscidiflorus ($P = 0.004$) (Fig. 3, Supplemental Tables 3A and 3C). Density of native perennial species in the seed bank exhibited a positive relationship with shrub cover of *E. nauseosa* ($P = 0.087$), but though this was the best predictor identified with model selection, this factor was not significant (Fig. 3, Supplemental Table 3B).

3.3. Can site characteristics predict seed bank and above-ground diversity (richness and evenness) and the presence of rare native species?

3.3.1. Above-ground richness

Shrub cover was one of the two best predictors of above-ground native species richness (Table 2B), with the richness of native species increasing with increasing shrub cover of *A. tridentata* ($P = 0.041$) and *C. viscidiflorus* ($P = 0.047$) (Supplemental Figure 4A, Supplemental Fig. 5A and 5B). The predictive ability of the climate model was comparable to that of the shrub model, but none of the climate variables were significantly associated with above-ground native species richness. Model averaging found that above-ground native species richness increased when there was fire nearby > 10 years ago (natural average, NA: $P = 0.009$, zero average, ZA: $P = 0.190$), and decreased as maximum temperatures increased (NA: $P = 0.003$, ZA: $P = 0.116$) (Supplemental Table 4). The above-ground richness of introduced species was best predicted by ground cover (Table 2B), increasing with decreasing amounts of standing dead ($P = 0.0097$) and rock ($P = 0.005$) on a site (Supplemental Figure 4B, Supplemental Fig. 5C and 5D).

3.3.2. Below-ground richness

Below-ground native species richness was best predicted by disturbance history and shrub cover (Table 2B). Native species richness in the seed bank increased when there was fire nearby < 10 years ago ($P = 0.070$). Shrub cover was a comparable predictor of below-ground richness of native species, with increased below-ground richness in communities with greater cover of *E. nauseosa*, but this variable was not individually significant ($P = 0.076$). Model averaging identified that the following characteristics were most predictive of seed bank richness: the richness of native species in the seed bank increased with increasing cover of *A. tridentata* (NA: $P = 0.085$, ZA: $P = 0.515$), increased when there was fire nearby < 10 years ago (NA: $P = 0.053$, ZA: $P = 0.421$), and decreased when there was fire on a site > 10 years ago (NA: $P = 0.090$, ZA: $P = 0.540$) (Supplemental Table 5A). Again, shrub cover and disturbance history were comparable to each other in their ability to predict the richness of introduced species in the seed bank (Table 2B). Model averaging found that below-ground richness of introduced species increased with increasing shrub cover of *E. nauseosa* (NA: $P = 0.0004$, ZA: $P = 0.007$) and decreased when fires had not occurred nearby for > 10 years (NA: $P = 0.0003$, ZA: $P = 0.004$) (Supplemental Table 5B).

3.3.3. Above-ground evenness

Shrub cover best predicted above-ground native species evenness (Table 2B), with species evenness decreasing with increasing cover of *A. tridentata* ($P = 0.063$) (Supplemental Figure 6A, 7A, Supplemental Table 6A). In areas with lower native species evenness, the species composition and abundances varied from site-to-site, however, *P. secunda*, a common native perennial grass, and two perennial *Phlox* species (*P. hoodii* and *P. longifolia*) were dominant species at several of the sites. These plots also contained high densities of other perennial forb species, including *Leptodactylon pungens* (Torr.) Torr. ex Nutt., *Viola beckwithii* Torr. & A. Gray, and the grasses *E. elymoides* and *Hesperostipa comata* (Trin. & Rupr.) Barkworth. Climate best predicted above-ground introduced species evenness (Table 2B), with evenness increasing with increasing precipitation ($P = 0.001$) and maximum temperature ($P = 0.009$) (Supplemental Figure 6B, 7B, Supplemental Table 6B).

3.3.4. Below-ground evenness

Ground cover best predicted below-ground native species evenness (Table 2B), with evenness increasing with increasing rocky ground cover ($P = 0.022$) (Supplemental Figure 6C, Supplemental Table 6C). Shrub cover and disturbance history were comparable predictors of below-ground evenness of introduced species (Table 2B), and evenness was found to decrease with increasing cover of *E. nauseosa* (NA: $P = 0.041$, ZA: $P = 0.334$) and when fire was on a site $>$ 10 years ago (NA: $P = 0.021$, ZA: $P = 0.266$) (Supplemental Table 5C).

3.3.5. Rare plants above- and below-ground

Shrub cover was the best predictor of both the above- and below-ground presence of rare plants (Table 2C). Above-ground, the presence of rare species increased with increasing cover of *C. viscidiflorus* ($P = 0.031$) (Fig. 4A and B, Supplemental Table 3D). Below-ground, the presence of rare species increased with increasing shrub cover of *A. tridentata* ($P = 0.007$) (Fig. 4A and C, Supplemental Table 3E).

3.4. Can site characteristics predict similarity between seed banks and above-ground vegetation?

Ground cover was the best predictor of the similarity between the presence of above- and below-ground plant species (Table 2D). Sites possessing a higher degree of similarity were those with higher cover of bare ground ($P = 0.043$) and more litter cover ($P = 0.018$) (Fig. 5A, Supplemental Table 7A). This similarity was mostly due to the presence of introduced species, such as *A. desertorum, C. testiculata*, *B. tectorum*, and *A. spicatum*; however, native species, such as *C. parviflora* and *P. secunda*, also contributed to the observed similarities. Disturbance history was the best predictor of the dissimilarity between the density of species above- and below-ground (Table 2D). Sites experiencing fire $<$ 10 years ago possessed a higher degree of similarity ($P = 0.017$) (Fig. 5B, Supplemental Table 7B). These similarities were predominantly due to their low above- and below-ground species richness. The most similar communities were characterized by the presence of the introduced species *B. tectorum, A. desertorum,* and *C. testiculata*, although *P. secunda* also contributed to the similarity in these communities, and *C. parviflora, M. gracilis*, and *A. tridentata* were also partially responsible for these results.

4. Discussion

Seed banks can provide insight into the environmental factors that shape plant communities and, ultimately, help predict how sites can respond to disturbance and environmental change (Simpson et al., 1989). In deserts, where environmental conditions can vary greatly from year-to-year, seed banks can be important part of bet-hedging strategies that ultimately shape above-ground species composition (Gremer et al., 2016; Venable, 2007). Our study aimed to identify characteristics that are predictive of the seed bank composition within areas of high wildlife habitat value in the Great Basin, assisting our predictions of how particular types of habitat may respond to environmental change and restoration efforts. We found that shrub cover was most predictive of seed bank composition. Of ten responses related to below-ground factors, shrub cover was predictive of seven factors, including seed densities and richness of native and introduced species, evenness of introduced species, and the presence of rare species. Fire history was the next most predictive factor, and was comparable to shrub composition in the ability to predict three below-ground responses (native and introduced richness, introduced evenness), and fire history was the main predictor of similarity between above- and below-ground composition. Climate factors were associated with several above-ground, but no below-ground responses, and AUMs were not predictive of any of our response variables.

Shrubs are indicators of past disturbance and foundation species that can affect the successional trajectory of a community (Bechtold and Inouye, 2007; Holthuijzen and Veblen, 2015; Prevéy et al., 2010). For example, shrubs can influence the establishment and distribution of plant species through mechanisms such as increasing resource availability (Bechtold and Inouye, 2007) and affecting seed dispersal (Guo et al., 1998). In our study, native annual seed densities were higher in areas with greater cover of *C. viscidiflorus*, introduced seed densities and richness were higher and introduced evenness was lower when there was greater cover of *E. nauseosa*, and there were more rare species in seed banks of sites with greater cover of *A. tridentata*, consistent with other work demonstrating that this later-seral species is associated with reduced invasion and higher diversity of native plants (Prevéy et al., 2010). Both *C. viscidiflorus* and *E. nauseosa* are found in areas that have experienced disturbance in the past (Miller et al., 2013; Scheinost et al., 2010; Tilley and St. John, 2012), and both annual and introduced species are known to perform well in disturbed areas in this region (Beatley, 1969; Young et al., 1972). Differences in seed bank composition between areas containing different early-seral shrubs (*C. viscidiflora* and *E. nauseosa*) indicate potential differences in the ecology of these shrub species. One possibility is that these shrubs may have different preferences for soil type, differ in response to past disturbance, or differ in other environmental conditions that also affect understory communities. Another possibility is that the environmental requirements and disturbance responses for these shrubs are the same, but that the shrub species differ in the types of microsite conditions they provide for understory species (Donovan and Ehleringer, 1994; Gholami et al., 2018; Paterno et al., 2016). Future work could differentiate the role that these species play, as either indicators of past change or engineers of understory and seed bank dynamics.

Although the cover of *A. tridentata* and *C. viscidiflorus* was not highly correlated ($R^2 = 0.029$), sites with higher native species richness typically contained some proportion of both of these shrub types. This may indicate that the site has either experienced patchy disturbance in the past or may be recovering from disturbance. Moderate levels of disturbance are thought to create more niches for supporting a higher diversity of species (Connell, 1978; Hobbs and Huenneke, 1992). Sites with higher cover of *A. tridentata* typically contained more above-ground native perennial species, likely indicating that they have not experienced recent disturbance and have reached a later successional stage, one which might not possess as many micro-site types for supporting diverse communities (Hobbs and Huenneke, 1992). The relationships we found between shrub cover and the richness of rare species also support the idea that areas experiencing a moderate level of disturbance would have more niches to support a broader range of above-ground species; whereas areas dominated by late seral species, like *A. tridentata*, may have supported a broader range of species over time and contain a multitude of species within their seed banks in a state of dormancy.

In addition to our on-the ground measurements, we incorporated coarse measures of fire history, climate, and grazing use into our modeling, as this information is broadly available for researchers as well as land managers for use in decision-making. Our research indicated that while some of these measures were predictive of seed bank dynamics, AUM permits, in particular, were not predictive of above- or below-ground responses, possibly because they are not good indicators of land use at finer scales. Grazing pressure by livestock is difficult to quantify without on-the-ground measurements (Landsberg and Crowley, 2004), and estimating the effects of grazing using permitted AUMs is challenging, because it does not take into consideration many important factors, such as dietary preferences of the animals (West, 1999), movements through space, densities across the allotment, historic use, or and the amount of time spent in an area (Pringle and Landsberg, 2004). These important factors likely explain the wide variation in results of studies on grazing and seed banks in arid systems (Bakker and de Vries, 1992; Kinloch and Friedel, 2005; Osem et al., 2006a; Peco et al., 1998). Measuring seed banks within areas of long-term, controlled grazing experiments would be an excellent way to understand these potential interactions.

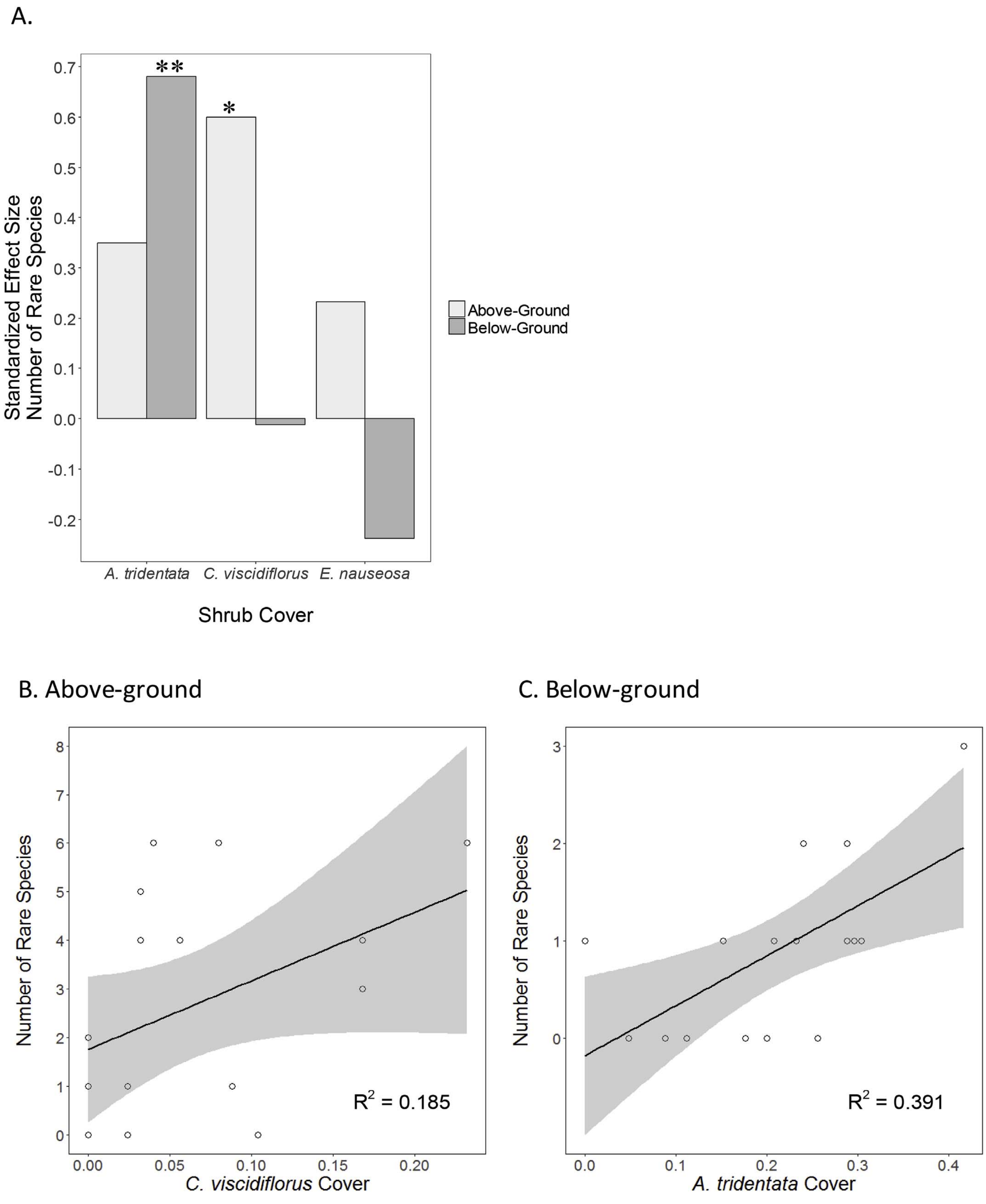


Fig. 4. Relationships between A) shrub cover of the three dominant shrubs and the number of rare species above- and below-ground, (B) *C. viscidiflorus* cover and the number of above-ground rare species, and (C) *A. tridentata* cover and the number of below-ground rare species. Significance is indicated as * $= P < 0.05$, ** $= P < 0.01$, and R^2 values are for the linear trendline for the single regression between number of rare species and shrub cover.

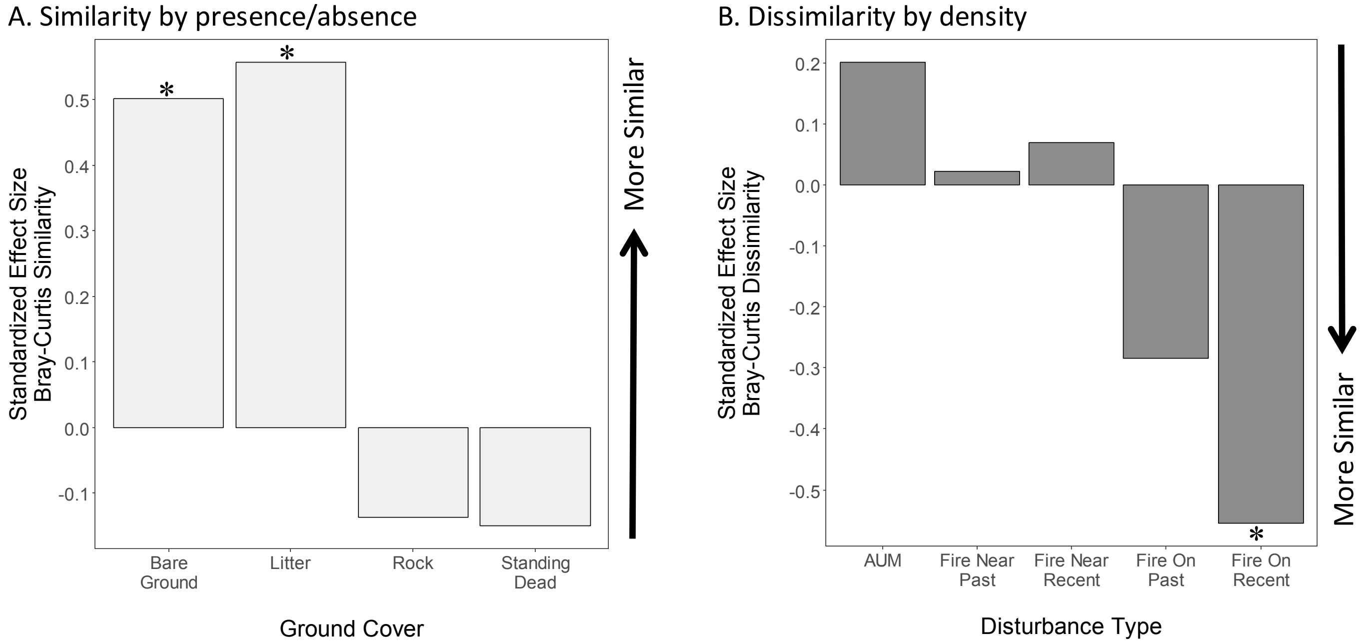


Fig. 5. Above- and below-ground similarity in community composition as predicted by (A) ground cover and (B) disturbance history. In (A), values are standardized Brays-Curtis similarity indices based on presence/absence of species in the above- and below-ground communities, with higher numbers indicating greater similarity. In (B), values are Brays-Curtis dissimilarity indices based on species densities, with lower numbers indicating greater similarity. Significance is indicated as * = $P < 0.05$.

Similarly, estimating site fire history from public records is challenging, considering that fire frequency from mapped perimeters does not account for other important aspects of fire, such as fire intensity and the rate of spread (Brooks et al., 2004; Miller et al., 2013). Despite the coarseness of our fire estimate, this factor was associated with some response variables, including above-ground richness of native species and below-ground richness and evenness of introduced species. Fire frequency was also the best predictor of the similarity between the relative densities of species contained in the above- and below-ground communities. This pattern was primarily due to high densities of introduced species, which tend to dominate the seed bank after fires (Humphrey and Schupp, 2001; Knapp, 1996). Finally, while climate means were predictive of some above-ground characteristics (including richness of native species and evenness of introduced species), they were not associated with any below-ground characters. While abiotic factors clearly affect seed production, more fine-scaled information (like previous year's precipitation) may be more predictive than averages across years. Further, our sites were purposely selected within two ecoregions that have similar climatic conditions (Supplement Table 1), but increasing sampling across sites with a wider range of abiotic conditions could lead to stronger climate/seed bank relationships.

Ground cover is known to vary across sagebrush communities, and different types of ground cover can differentially influence seed dispersal and seedling recruitment (Chambers, 2000; Facelli and Pickett, 1991; Xiong and Nilsson, 1999). The loss of woody species and increased cover by water-impermeable surfaces may also create suitable conditions for highly opportunistic introduced species to dominate in an area, as a result of higher availability of water in particular microsites (Prevéy et al., 2010). Other research has shown that rocks may act as obstacles to seeds landing or dispersing through an area, accumulating seeds along their edges and/or facilitating burial in the crevices between rocks, but that they may not provide suitable sites for seedling survival (Chambers, 2000). In our study, we found that bare ground and litter were strong predictors of the similarity in the presence of species in the above- and below-ground communities, with sites with less bare ground and more litter showing high similarities coupled with low species richness. We also found that ground cover predicted below-ground evenness of native species and above-ground richness of introduced species. Sites with higher amounts of rocky ground cover typically contained low to moderate densities of native species within their seed banks; these seeds may have remained dormant due to suboptimal conditions for germination. Areas with high amounts of rock and standing dead were typically dominated by one or two introduced species, *B. tectorum* and/or *C. testiculata*. Although fire is a common cause of shrub death, we also observed standing dead shrubs on unburned plots during field surveys, likely due to other factors such as resource limitation, erosion, or senescence. Because increases in resource availability, even over short periods, can increase invasion success (Davis and Pelsor, 2001), these competitive introduced species may have benefited from water resources made available as a result of both shrub death and a more concentrated delivery of moisture by runoff from rocky ground cover.

Overall, our results indicate that field surveys of shrub and ground cover may be useful tools for predicting seed bank characteristics in areas of sagebrush steppe. Acquiring these data is fairly straightforward, and can potentially provide insight regarding the long term disturbance history of an area and the relative abundance of native and introduced species. These findings support other research showing that plants act as strong indicators of the effects of land use on rangeland biodiversity (Landsberg and Crowley, 2004). Further work should be done to explore these patterns and to distinguish what differences in the ecology between *C. viscidiflorus* and *E. nauseosa* are affecting seed bank composition, with the hope of being able to disentangle their contrasting relationships to the seed bank dynamics of native and introduced species.

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Author contributions

SCB and EAL designed the experiment, interpreted the data analyses, wrote the manuscript, and edited the manuscript. SCB also collected and analyzed the data.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2018.03.004.

References

Aldridge, C.L., Boyce, M.S., 2007. Linking occurrence and fitness to persistence: habitat-based approach for endangered Greater Sage-Grouse. Ecol. Appl. 17, 508–526.

Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends Ecol. Evol. 14, 63–68. http://dx.doi.org/10.1016/S0169-5347(98)01544-4.

Bakker, J.P., de Vries, Y., 1992. Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. J. Veg. Sci. 3, 247–252.

Barton, K., 2016. In: MuMIn: Multi-model Inference, . https://cran.r-project.org/package=MuMIn, v. 1.15.6.

Baskin, C.C., Baskin, J.M., 2014. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination, Second. ed. Academic Press, San Diego. http://dx.doi.org/10.1016/b978-0-12-416677-6.00004-4.

Beatley, J.C., 1969. Biomass of desert winter annual plant populations in southern Nevada. Oikos 20, 261–273.

Bechtold, H.A., Inouye, R.S., 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. J. Arid Environ. 71, 122–132. http://dx.doi.org/10.1016/j.jaridenv.2007.02.004.

Bossuyt, B., Honnay, O., 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities. J. Veg. Sci. 19, 875–884. http://dx.doi.org/10.3170/2008-8-18462.

Brooks, M.L., D'antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., Ditomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. Bioscience 54, 677–688.

Burnham, K., Anderson, D., 2002. Model Selection and Multi-model Inference: a Practical Information-theoretic Approach. Springer, New York. http://dx.doi.org/10.1007/b97636.

Chambers, J.C., 2000. Seed movements and seedling fates in distrubed sagebrush steppe ecosystems: implications for restoration. Ecol. Appl. 10, 1400–1413. http://dx.doi.org/10.2307/2641294.

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Systemat. 25, 263–292. http://dx.doi.org/10.1146/annurev.es.25.110194.001403.

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science (80-.) 199, 1302–1310.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28, 2031–2064. http://dx.doi.org/10.1002/joc.1688.

Davis, M.A., Pelsor, M., 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecol. Lett. 4, 421–428.

Doherty, L.C., Cohn, M.A., 2000. Seed dormancy in red rice (Oryza sativa). XI. Commercial liquid smoke elicits germination. Seed Sci. Res. 10, 415–421.

Donovan, L.A., Ehleringer, J.R., 1994. Water stress and use of summer precipitation in a Great Basin shrub community. Funct. Ecol. 8, 289–297. http://dx.doi.org/10.2307/2389821.

Espeland, E.K., Perkins, L.B., Leger, E.A., 2010. Comparison of seed bank estimation techniques using six weed species in two soil types. Rangel. Ecol. Manag. 63, 243–247 doi: 10.21.

Esque, T.C., Young, J.A., Tracy, C.R., 2010. Short-term effects of experimental fires on a Mojave Desert seed bank. J. Arid Environ. 74, 1302–1308. http://dx.doi.org/10.1016/j.jaridenv.2010.04.011.

Facelli, J.M., Chesson, P., Barnes, N., Facelli, J.M., Barnes, N., 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86, 2998–3006.

Facelli, J.M., Pickett, S.T.A., 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57, 1–32.

Fletcher, T.D., 2012. QuantPsyc: Quantitative Psychology Tools. https://CRAN.R-project.org/package=QuantPsyc, v. 1.5.

Freas, K.E., Kemp, P.R., 1983. Some relationships between environmental reliability and seed dormancy in desert annual plants. J. Ecol. 71, 211–217. http://dx.doi.org/10.2307/2259973.

Gardener, M., 2014. Similarity and cluster analysis. In: Community Ecology (Ed.), Analytical Methods Using R and Excel. Pelagic Publishing, Exeter, UK, pp. 366–418.

Gholami, S., Saadat, L., Sayad, E., 2018. Different microhabitats have contrasting effects on the spatial distribution of tree regeneration density and diversity. J. Arid Environ. 148, 1–5. http://dx.doi.org/10.1016/j.jaridenv.2017.10.008.

Gibson, D., Blomberg, E.J., Atamian, M.T., Sedinger, J.S., 2016. Nesting habitat selection influences nest and early offspring survival in Greater Sage-Grouse. Condor 118, 689–702. http://dx.doi.org/10.1650/CONDOR-16-62.1.

Gremer, J.R., Kimball, S., Venable, D.L., Pannell, J., 2016. Within-and among-year germination in Sonoran Desert winter annuals: bet hedging and predictive germination in a variable environment. Ecol. Lett. 19, 1209–1218. http://dx.doi.org/10.1111/ele.12655.

Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711. http://dx.doi.org/10.1111/j.1420-9101.2010.02210.x.

Gul, B., Weber, D., 2001. Seed bank dynamics in a Great Basin salt playa. J. Arid Environ. 49, 785–794. https://doi.org/10.1006/jare.2001.0826.

Guo, Q., Rundel, P.W., Goodall, D.W., 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. J. Arid Environ. 38, 465–478. http://dx.doi.org/10.1006/jare.1997.0353.

Gutierrez, J., Arancio, G., Jaksic, F., 2000. Variation in vegetation and seed bank in a Chilean semiarid community affected by ENSO 1997. J. Veg. Sci. 11, 641–648. http://dx.doi.org/10.2307/3236571.

Hassan, M.A., West, N.E., 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology 67, 269–272.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6, 324–337.

Holthuijzen, M.F., Veblen, K.E., 2015. Grass-shrub associations over a precipitation gradient and their implications for restoration in the Great Basin, USA. PLoS One 10, 1–19. http://dx.doi.org/10.1371/journal.pone.0143170.

Hopfensperger, K., 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116, 1438–1448.

Humphrey, L., Schupp, E., 2001. Seed banks of Bromus tectorum-dominated communities in the Great Basin. West. North Am. Nat. 61, 85–92.

Jurado, E., Flores, J., 2005. Is seed dormancy under environmental control or bound to plant traits? J. Veg. Sci. 16, 559–564. http://dx.doi.org/10.1658/1100-9233(2005)16[559:ISDUEC]2.0.CO;2.

Kemp, P., 1989. Seed banks and vegetation processes in deserts. In: Leck, M., Parker, V., Simpson, R. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 257–282.

Kinloch, J.E., Friedel, M.H., 2005. Soil seed reserves in arid grazing lands of central Australia. Part 1: seed bank and vegetation dynamics. J. Arid Environ. 60, 133–161. http://dx.doi.org/10.1016/j.jaridenv.2004.03.005.

Knapp, P.A., 1996. Cheatgrass (Bromus tectorum L) dominance in the Great Basin Desert: history, persistence, and influences to human activities. Global Environ. Change 6, 37–52.

Knick, S.T., Hanser, S.E., Miller, R.F., Pyke, D.A., Wisdom, M.J., Finn, S.P., Rinkes, E.T., Henny, C.J., 2011. Ecological influence and pathways of land use in sagebrush. In: Knick, S., Connelly, J. (Eds.), Greater Sage Grouse: Ecology of a Landscape Species and its Habitats - Studies in Avian Biology. University of California Press, Berkeley, CA, pp. 203–251.

Koniak, S., Everett, R.L., 1982. Seed reserves in soils of successional stages of pinyon woodlands. Am. Midl. Nat. 108, 295–303.

Landsberg, J., Crowley, G., 2004. Monitoring rangeland biodiversity: plants as indicators. Austral Ecol. 29, 59–77. http://dx.doi.org/10.1111/j.1442-9993.2004.01357.x.

Levassor, C., Ortega, M., Peco, B., Ortega, M., 1990. Seed bank dynamics of mediterranean patures subjected to mechanical disturbance. J. Veg. Sci. 1, 339–344.

Li, F.R., 2008. Presence of shrubs influences the spatial pattern of soil seed banks in desert herbaceous vegetation. J. Veg. Sci. 19, 537–548. http://dx.doi.org/10.3170/2008-8-18404.

Meyer, S.E., 1994. Germination and establishment ecology of Big Sagebrush: implications for community restoration. In: Monsen, S., Kitchen, S. (Eds.), Proceedings - Ecology and Management of Annual Rangelands: General Technical Report INT-313. USDA Forest Service Intermountain Research Station, Ogden, UT, pp. 244–251.

Miller, R.F., Chambers, J.C., Pyke, D. a, Pierson, F.B., Williams, C.J., 2013. A Review of Fire Effects on Vegetation and Soils in the Great Basin Region : Response and Ecological Site Characteristics. General Technical Report RMRS-GTR-308. doi:Gen Tech Rep RMRS–GTR-308.

Miller, R.F., Knick, S., Pyke, D., Meinke, C., Hanser, S., Wisdom, M., Hild, A., 2011. Characteristics of sagebrush habitats and limitations to long-term conservation. In: Knick, S., Connelly, J.W. (Eds.), Greater Sage-grouse: Ecology and Conservation of a Landscape Species and its Habitats - Studies in Avian Biology. University of California Press, Berkeley, CA, pp. 145–185.

Morris, L.R., Leger, E.A., 2016. Secondary succession in the sagebrush semidesert 66 years after fire in the Great Basin, USA. Nat. Area J. 36, 187–193. http://dx.doi.org/10.

3375/043.036.0211.

Omernik, J., Griffith, G., 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environ. Manag. 54, 1249–1266.

Osem, Y., Perevolotsky, A., Kigel, J., 2006a. Similarity between seed bank and vegetation in a semi-arid annual plant community: the role of productivity and grazing. J. Veg. Sci. 17, 29–36. http://dx.doi.org/10.1111/j.1654-1103.2006.tb02420.x.

Osem, Y., Perevolotsky, A., Kigel, J., Pugnaire, F., 2006b. Size traits and site conditions determine changes in seed bank structure caused by grazing exclusion in semiarid annual plant communities. Ecography 29, 11–20. http://dx.doi.org/10.1111/j.2006.0906-7590.04283.x.

Paterno, G.B., Siqueira Filho, J.A., Ganade, G., 2016. Species-specific facilitation, ontogenetic shifts and consequences for plant community succession. J. Veg. Sci. 27, 606–615. http://dx.doi.org/10.1111/jvs.12382.

Peco, B., Ortega, M., Levassor, C., 1998. Similarity between seed bank and vegetation in mediterranean grassland: a predictive model. J. Veg. Sci. 9, 815–828.

Pekas, K.M., Schupp, E.W., 2013. Influence of aboveground vegetation on seed bank composition and distribution in a Great Basin Desert sagebrush community. J. Arid Environ. 88, 113–120. http://dx.doi.org/10.1016/j.jaridenv.2012.08.013.

Prevéy, J.S., Germino, M.J., Huntly, N.J., Inouye, R.S., 2010. Exotic plants increase and native plants decrease with loss of foundation species in sagebrush steppe. Plant Ecol. 207, 39–51. http://dx.doi.org/10.1007/s11258-009-9652-x.

Pringle, H.J.R., Landsberg, J., 2004. Predicting the distribution of livestock grazing pressure in rangelands. Austral Ecol. 29, 31–39.

Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. J. Appl. Ecol. 39, 294–309. http://dx.doi.org/10.1046/j.1365-2664.2002.00718.x.

R Development Core Team, 2016. R: a Language and Environment for Statistical Computing.

Scheinost, P., Scianna, J., Ogle, D., 2010. Plant Guide for Rubber Rabbitbrush (Ericameria Nauseosa). (Pullman, WA).

Simpson, R., Leck, M., Parker, V., 1989. Seed banks: general concepts and methodological issues. In: Leck, M., Parker, V., Simpson, R. (Eds.), Ecology of Soil Seed Banks. Academic Press, San Diego, CA, pp. 3–8.

Smith, R.S., Shiel, R.S., Millward, D., Corkhill, P., Sanderson, R.A., 2002. Soil seed banks and the effects of meadow management on vegetation change in a 10-year meadow field trial. J. Appl. Ecol. 39, 279–293. http://dx.doi.org/10.1046/j.1365-2664.2002.00715.x.

Thompson, K., Grime, J.P., 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. J. Ecol. 67, 893–921.

Tilley, D., St John, L., 2012. Plant Guide for Yellow Rabbitbrush (Chrysothamnus Viscidiflorus). (Aberdeen, ID).

USDA NRCS, 2017. The PLANTS Database - National Plant Data Team. U.S. Department of Agriculture, Natural Resources Conservation Service, Greensboro, NC , Accessed date: 13 February 2017.

Venable, D.L., 2007. Bet hedging in a guild of desert annuals. Ecology 88, 1086–1090. http://dx.doi.org/10.1890/06-1495.

West, N.E., 1999. Synecology and disturbance regimes of sagebrush steppe ecosystems. In: Entwistle, P.G., Debolt, A.M., Kaltenecker, J.H., Steenhof, K. (Eds.), Sagebrush Steppe Ecosystems Symposium. Bureau of Land Management, Idaho State Office, Boise, ID, USA, Boise, ID, pp. 15–26.

Xiong, S., Nilsson, C., 1999. The effects of plant litter on vegetation: a meta-analysis. J. Ecol. 87, 984–994. http://dx.doi.org/10.1046/j.1365-2745.1999.00414.x.

Young, J.A., Evans, R.A., 1975. Germinability of seed reserves in a Big Sagebrush community. Weed Sci. Soc. Am. 23, 358–364.

Young, J.A., Evans, R.A., 1974. Population dynamics of green rabbitbrush in disturbed Big Sagebrush communities. J. Range Manag. 27, 127–132.

Young, J.A., Evans, R.A., Major, J., 1972. Alien plants in the Great Basin. J. Range Manag. 25, 194–201.