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1 **Influence of aboveground vegetation on seed bank composition and distribution in a**
2 **Great Basin Desert sagebrush community**

3

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16 **Abstract**

17
18 The quantity, composition, and spatial dispersion of seed banks can greatly affect
19 community dynamics. While seed banks of hot deserts have been studied extensively, little is
20 known about seed banks in cold deserts, in particular the relationship between the seed bank and
21 the aboveground vegetation. We investigated the relationship between the seed bank and
22 aboveground vegetation and the effect of microhabitat (shrub interspace or beneath shrub) and
23 aboveground community phase (high or low perennial bunchgrass cover) on the seed bank of a
24 Great Basin Desert sagebrush community. The seed bank and aboveground vegetation differed
25 in their most dominant species, resulting in moderately dissimilar species compositions as
26 determined by Sørensen's similarity index and Bray-Curtis distance. In contrast, comparing the
27 seed bank species composition to the aboveground vegetation structure (functional groups) using
28 non-metric multidimensional scaling (NMDS) revealed a correspondence between the two
29 communities. Shrub seed densities were higher beneath shrubs. Neither microhabitat nor
30 community phase explained variation in total seed density or species richness. Therefore, our
31 measures of the aboveground vegetation did not influence seed density across functional groups
32 or species richness, and the similarity between the seed bank and aboveground vegetation varied
33 depending on the aboveground organizational level used in comparisons.

34 Key words: seed bank, aboveground vegetation, shrub, Great Basin Desert, similarity,
35 microhabitat

36
37 **1. Introduction**

38
39 The majority of Great Basin Desert species rely on seeds for propagation; however, seed
40 banks (or seed pools) of this desert are poorly understood (Kemp, 1989). Seed banks may help

41 re-establish species that have become locally extinct aboveground. Evaluations of North
42 American desert seed banks suggest that those of the Great Basin Desert consist of fewer annual
43 and more perennial species than do hot desert seed banks (Kemp, 1989; Guo et al., 1999).
44 Although maximum seed densities are generally similar among the North American deserts,
45 there are some areas of the Great Basin Desert that appear to have very small seed banks (Hassan
46 and West, 1986).

47 Annual species are more likely than perennial species to form persistent seed banks
48 because they tend to produce dormant seeds (Jurado and Flores, 2005). This strategy allows
49 seeds to wait for proper germination cues which may increase the chance of establishment and
50 survival. However, a long-term seed banking strategy may be difficult for annuals to achieve
51 because of seed reductions caused by continuous germination and granivory (Kigel, 1995). Due
52 to the nature of perennial species, seeds are less likely to be dormant, and therefore, seed banks
53 tend to be transient. Species that form transient seed banks are at risk of becoming locally
54 extinct, especially if seed production is limited (O'Connor, 1991). Seed production can be
55 limited by a number of factors, such as invasive species which may cause native perennial
56 species to produce fewer seeds and die prematurely if the density of the invader is high (Vilà and
57 Gimeno, 2007) or by drought years that limit flowering and seed production (St. Clair et al.,
58 2009).

59 The invasion of *Bromus tectorum* (cheatgrass) has altered the structure and composition
60 of Great Basin Desert seed banks. Studies examining seed banks of degraded sagebrush
61 communities have shown shifts to greater annual seed abundance with cheatgrass invasion
62 (Young and Evans, 1975; Humphrey and Schupp, 2001). Even in systems that are not
63 considered to be dominated by cheatgrass, introduced species can still account for 20 percent of

64 the total number of seeds in the seed bank (Guo et al., 1999).

65 The relationship between the seed bank and aboveground vegetation is not well
66 understood in Great Basin Desert sagebrush communities. Plant communities dominated by
67 perennial species usually have relatively low aboveground-belowground similarities, while
68 annual-dominated communities tend to have a greater correspondence between aboveground
69 vegetation and the seed bank (Thompson and Grime, 1979; Ungar and Woodell, 1993; Milberg,
70 1995; Bakker et al., 1996; Osem et al., 2006), at least partly because annual-dominated
71 communities arise yearly from the available seed bank, which reflects vegetation of the previous
72 year (Osem et al., 2006).

73 When comparing the relationship between the seed bank and aboveground vegetation
74 among forest, grassland (including desert), and wetland seed banks, grassland standing
75 vegetation is most similar to the seed banks in terms of species composition (Hopfensperger,
76 2007). In desert grasslands, extreme environmental conditions may select for species that rely on
77 persistent seed banks, resulting in similar above and belowground communities (Henderson et
78 al., 1988). However, higher similarity between the seed bank and aboveground vegetation in
79 desert grasslands is more likely due to limited dispersal and aggregated seed patterns
80 surrounding parent plants (Shaukat and Siddiqui, 2004). In contrast, some studies have found a
81 lack of correspondence between the seed bank and aboveground vegetation in grasslands which
82 has been attributed to different dominant species in the aboveground and seed bank communities
83 (Eriksson and Eriksson, 1997; Kalamees and Zobel, 1997). For example, the most dominant
84 species in the seed bank may be overrepresented due to high production of small seeds (Eriksson
85 and Eriksson, 1997).

86 The aboveground vegetation not only influences the community composition of the seed

87 bank but also the distribution of the seeds. Although the distribution of seeds within desert seed
88 banks is spatially variable, seeds are frequently more abundant under shrub and tree canopies
89 than in interspaces (Nelson and Chew, 1977; Guo et al., 1998; Marone et al., 2004) and exhibit
90 an aggregated seed pattern due to seeds settling close to the mother plant (Shaukat and Siddiqui,
91 2004). A study investigating spatial patterns of species richness found higher species richness at
92 the mid-point and furthest sampling point from shrubs (2 m and 6 m from shrubs ; Li, 2008). In
93 pinyon-juniper woodlands, seed densities and species richness were highest in interspaces and
94 the interface between interspaces and litter under trees (Koniak and Everett, 1983). Shrubs and
95 trees affect the spatial distribution of seeds as they can act as a barrier, altering wind dynamics
96 and subsequent seed deposition patterns. (Guo et al., 1998; Li, 2008; Li et al., 2009). Seeds
97 often accumulate beneath shrubs because they decrease wind velocity and physically trap seeds,
98 leading to deposition close to shrubs (Bullock and Moy, 2004). Seeds can also be redistributed
99 from interspaces to litter beneath shrubs by wind and water (phase II dispersal; Chambers and
100 MacMahon, 1994).

101 This study explores the seed bank and the aboveground vegetation within a Great Basin
102 Desert plant community and how the aboveground vegetation influences the seed bank
103 community composition and seed distributions. Specific goals were to determine the
104 relationship between the compositions of the seed bank and the aboveground vegetation and the
105 effect of shrubs (microhabitat effects) and perennial bunchgrass cover (community phase effects)
106 on the seed bank community composition, seed density, and seed bank species richness.

107 108 **2. Methods**

109 110 111 *2.1. Study site*

112 Soil seed bank samples were collected from the Onaqui Sagebrush/Cheatgrass SageSTEP
113 research site in Tooele County, Utah, USA, about 40 km south of Tooele, UT (40°11'53"N
114 112°27'51"W). The Onaqui site is located on the eastern toeslope of the Onaqui mountains at an
115 elevation of 1750-1850 meters (McIver et al., 2010). Based on Utah Climate Center data from
116 the Vernon climate station (Latitude: 40.1125, Longitude: -112.435; Elevation: 1671 m; Period:
117 1953-2010), about 11.3 km south of the study site and in the same valley, mean monthly
118 temperature ranges from -3.1 C in January to 22.0 C in July, while mean monthly precipitation
119 ranges from 17.5 mm in December to 29.5 mm in May, yielding a mean annual precipitation of
120 264.4 mm. Snow can occur in all months except July and August with a peak in January (Utah
121 Climate Center, 2012). Onaqui has fine-loamy soils (McIver et al., 2010).

122 Characteristic vegetation of this site includes Wyoming big sagebrush (*Artemisia*
123 *tridentata* ssp. *wyomingensis*), shadscale saltbush (*Atriplex confertifolia*), yellow rabbitbrush
124 (*Chrysothamnus viscidiflorus*), Sandberg bluegrass (*Poa secunda*), squirreltail (*Elymus*
125 *elymoides*), Indian ricegrass (*Achnatherum hymenoides*), bluebunch wheatgrass
126 (*Pseudoroegneria spicata*), basin wildrye (*Leymus cinereus*), and cheatgrass (*Bromus tectorum*).

127 Seed bank germination assays were conducted at the Utah State University Research
128 Greenhouse Facility in Logan, UT.

129 130 2.2. Experimental design

131 This study presents the results of baseline sampling of the seed bank of the Onaqui
132 sagebrush-cheatgrass site of the SageSTEP network (McIver et al., 2010). The sagebrush-
133 cheatgrass portion of SageSTEP is a large experimental study addressing the effects of
134 restoration treatments (control, prescribed burn, mow, tebuthiuron herbicide, and imazapic
135 [Plateau[®]] pre-emergent herbicide) on sagebrush ecosystems. Burn, mow, and tebuthiuron

136 treatments were designed to reduce shrub cover, while imazapic is used to reduce the emergence
137 and establishment of exotic annuals. All results presented in this paper are pretreatment and thus
138 do not address the effects of treatments; nonetheless, we describe the experimental design and
139 refer to sampled plots and subplots by their treatment names because treatment effects will be
140 addressed in a subsequent paper. In the present study, the treatment plots should be viewed
141 simply as replicate plots of untreated sagebrush ecosystems.

142 Control, prescribed burn, mow, and tebuthiuron treatments were applied at the whole plot
143 level (75 acres; 30.4 ha), while imazapic was applied at the subplot level (0.1 ha) as a split-plot
144 factor in all whole plots. In the seed bank studies at Onaqui the mow treatment was excluded,
145 leaving three plot-level treatments and one subplot-level treatment.

146 In each sampled plot, subplots with two levels of perennial bunchgrass cover were
147 sampled. Community phases were chosen by dividing the cover of perennial bunchgrasses into 3
148 ranges. Subplots with greater than 19 percent perennial bunchgrass cover were considered phase
149 1 communities, those with 10-19 percent bunchgrass cover were considered phase 2, and those
150 with less than 10 percent perennial bunchgrass cover were considered phase 3 communities. In
151 the present study only phase 1 and 3 communities were sampled in order to examine the effects
152 of high and low native bunchgrass covers on seed banks. Four phase 1 subplots and four phase 3
153 subplots that did not receive Plateau[®] were sampled in the control (CO), prescribed burn (FI),
154 and tebuthiuron (TE) plots, and four phase 1 subplots and four phase 3 subplots that did receive
155 Plateau[®] also were sampled in the control plot for a total of 32 subplots. Although the set of the
156 control subplots that received Plateau are not from a true plot, we refer to these subplots as the
157 control-Plateau[®] plot (CP) for convenience.

158
159 *2.3. Seed bank sampling*

160
161 Soil seed bank samples were collected 14-17 and 22-24 August 2006. Within each 0.1-ha
162 (30 x 33 m) subplot, four 28-m transects were laid out so as to not interfere with vegetation
163 surveys. Transects ran north-south and were located at 3, 10, 20, and 27 meters from the
164 northwest corner of the subplot. A composite sample consisting of 5 subsamples from within a
165 25 x 25-cm frame was collected every 3 meters along each of the 4 transects for a total of 10
166 composite samples per transect and 40 per subplot. Collecting many small samples has been
167 shown to increase the precision of estimates of seed numbers in the soil (Bigwood and Inouye,
168 1988). If necessary, sampling locations were shifted slightly in order to assure that all 5
169 subsamples were from the same microhabitat (see below). Subsamples measured 6.1 cm in
170 diameter and were taken to a depth of 4 cm with PVC couplings. Litter and soil layers were
171 collected together. Microhabitat (shrub interspace or beneath shrub) was recorded for each
172 composite sample collected.

173
174 *2.4. Vegetation surveys*

175 Aboveground vegetation surveys were conducted on transects located at 2, 7, 15, 23, and
176 28 meters from the northwest corner of each subplot. The line-point intercept method was used
177 to measure the cover of each species present along each transect (Herrick et al., 2005). Species
178 intercepted by the pin were recorded every half meter totaling 60 points per transect and 300
179 points per subplot. Subplots were then surveyed to account for any additional species that were
180 not encountered on transects and were assigned a dominance class. Class 1 represents rare
181 species (1-2 plants per subplot); class 2 represents sparse species (<5% cover); class 3 represents
182 common species (5-25% cover); class 4 represents co-dominant species (25-50% cover), and
183 class 5 represents dominant species (>50% cover). Of the additional species found in the subplot

184 survey, none had a higher dominance than 3. Dominance classes were then converted to relative
185 abundance for analysis. Class 1 was converted to 0.0033 (equivalent to a species being hit once
186 during line-point intercept). Class 2 was converted to 0.04 (4% cover), and class 3 was
187 converted to 0.15 (15% cover). Vegetation surveys were conducted in summer 2006.

188 Nomenclature for all plant species followed the USDA NRCS PLANTS Database (2009).

189 190 *2.5. Evaluating the seed bank*

191
192 The germinable seed bank was evaluated by direct germination in a greenhouse following
193 cold-moist stratification, which has been shown to be an efficient and reliable method for
194 determining species presence in the germinable seed bank (Gross, 1990). Each composite
195 sample was moistened to field capacity and kept in an unlighted refrigerator at 2°C. After 60
196 days of stratification, samples were removed from the refrigerator and spread over a 2-cm layer
197 of sand in planting trays with drainage holes. Planting trays were divided into three 25.4 X 16.9-
198 cm compartments, each containing one soil sample. Spread out soil samples had a depth of ≈ 1.3
199 cm and a volume of $\approx 585 \text{ cm}^3$. Samples were kept moist, and seedlings were identified, counted,
200 and removed as they emerged. Individuals that were not identified in the seedling stage were
201 transplanted and grown until mature.

202 Due to the high volume of samples collected, not all seed bank samples were evaluated at
203 the same time. Therefore, depending on the availability of greenhouse space, varying numbers
204 of samples were randomly selected from each treatment combination for each germination assay.
205 Eleven of the 40 samples from each treatment combination were germinated and evaluated for
206 each of the first and second germination assay. Six samples from each treatment combination
207 were germinated and evaluated for the third germination assay, and nine samples were
208 germinated and evaluated for the fourth germination assay. Thus, a total of 37 of the 40 samples

209 per subplot were germinated. Each germination assay lasted 150 days. Emergence was initially
210 censused for 115 days, at which point emergence was noticeably reduced. Samples were then
211 dried out for 14 days and mixed, after which watering was resumed and emergence was censused
212 for an additional 21 days.

213 The first germination assay ran from mid-January to mid-June 2007. The second
214 germination assay ran from mid-June to mid-November 2007. The third germination assay ran
215 from mid-January to mid-June 2008, and the fourth germination assay ran from mid-June to mid-
216 November 2008. First and third germination assays and second and fourth assays ran during the
217 same time of year so as to control for potential seasonal germination effects that could bias
218 results.

219 2.6. Statistical Analysis

220 *Sørensen's similarity index (C_s) and Bray-Curtis distance (BC) were calculated in R*
221
222 version 2.6.2 (R Development Core Team, 2008) to compare the seed community to the
223 aboveground community. These two similarity/distance metrics compare two communities in
224 different ways. Sørensen's similarity is based strictly on presence/absence: $C_s = 2w / (2w + A + B)$
225 where w is the total number of species found in both communities, A is the number of species
226 exclusive to aboveground, and B is the number of species exclusive to belowground. A C_s of 0
227 represents completely dissimilar communities and C_s of 1 represents identical communities at the
228 level of presence/absence. In contrast to Sørensen's similarity index, Bray-Curtis distance
229 incorporates information on relative abundance (or cover). This metric normalizes relative
230 abundance for communities being compared by dividing the absolute differences by the
231 summation: $BC = \sum_i^n |x_{ij} - x_{ik}| / \sum_i^n x_{ij} + x_{ik}$ where x_{ij} is the relative abundance of species i in
232

233 community j , x_{ik} is the relative abundance of species i in community k , and n is the total number
234 of species. A BC of 0 represents most similar communities, and a BC of 1 represents most
235 different communities. C_s and BC were calculated for the entire site and for each plot using
236 relative cover of the aboveground community and relative abundance of the germinable seed
237 bank community to avoid differences in sampling scales.

238 To further compare the community composition of the germinable seed bank to that of
239 the aboveground vegetation, seed bank composition data were ordinated by non-metric
240 multidimensional scaling (NMDS) with a Bray-Curtis distance measure using the metaMDS
241 function in the Vegan package in R version 2.11.1 (Oksanen et al., 2008; R Development Core
242 Team, 2008). Specifically, seed bank composition was compared to the aboveground vegetation
243 structure by assigning one of seven functional groups to all species present aboveground: annual
244 forbs, annual grasses, perennial forbs, perennial grasses, *Poa secunda*, shrubs, and trees. As with
245 the similarity and distance metrics, relative cover of the aboveground community and relative
246 abundance of the germinable seed bank community were used to avoid differences in sampling
247 scales. Functional groups were based on different morphologies and root systems. *Poa secunda*
248 was considered a different functional group than perennial grasses because *P. secunda* is a
249 shorter grass that has a shallower root system compared to the other perennial grasses. The
250 relative covers of aboveground functional groups were fitted and plotted onto the seed bank
251 species composition ordination solution using the envfit function in the Vegan package in R
252 version 2.11.1 with $P < 0.05$ to determine significance (Oksanen et al., 2008; R Development
253 Core Team, 2008). NMDS on densities of germinable seed bank species was also used to
254 compare beneath shrub (S) and shrub interspace (I) community compositions and to compare
255 phase 1 and phase 3 community compositions.

256 To determine the number of dimensions for each NMDS, stress values were assessed.
257 Stress is a measure of how much the distances in the reduced ordination space depart from the
258 distances in the original p-dimensional space. High stress values indicate a possibility that sites
259 are randomly being placed without any relation to the original distances. Therefore, ordinations
260 with the lowest possible stress are desirable; values up to 20 are acceptable and can be
261 interpreted ecologically (Clarke, 1993). Regardless of the number of dimensions chosen, all
262 figures are shown in two dimensions because the third dimension did not seem to alter results
263 upon inspection.

264 A mixed-model factorial ANOVA (analysis of variance) was performed to detect
265 differences in total seed density and species richness (total number of species present) between
266 aboveground microhabitat and community phase using the MIXED procedure in SAS version
267 9.1.3 (SAS Institute, 2003) and $P < 0.05$ to determine significance. Microhabitat and community
268 phase were treated as fixed effects, and plot and subplot were random effects. Because seed
269 bank species composition data were sparse and did not meet the assumptions of normality and
270 heteroscedasticity, seed bank species were grouped into functional groups and analyzed to
271 understand how aboveground microhabitat and community phase affect the structure of the seed
272 bank community. The same ANOVA model described above was used to detect seed density
273 differences within each of six functional groups: annual forb, annual grass, perennial forb,
274 perennial grass, *Poa secunda*, and shrub. One tree species (*Tamarix ramosissima*) was found in
275 the germinable seed bank but was not analyzed as a functional group due to very low seed
276 densities and only one species present. Species richness was not analyzed within functional
277 group because sample sizes were too low and assumptions of normality and heteroscedasticity
278 were unable to be met.

279 Total seed density and species richness across functional groups were log transformed to
280 meet the assumptions of normality and homogeneity of variance. Seed densities within the
281 perennial grass, perennial forb, annual forb, *Poa secunda*, and shrub functional groups were
282 square root transformed. Seed density within the annual grass functional group was log
283 transformed. For significant main effects, least squared means were compared using Tukey's
284 test. Least squared means and standard errors were back-transformed for figures.

285 286 **3. Results**

287 288 289 *3.1. Relationship between the germinable seed bank and aboveground vegetation*

290 A total of 47 species germinated from the seed bank, and 43 species were recorded
291 aboveground (Appendix A; Appendix B). The germinable seed bank and aboveground
292 vegetation were moderately different in terms of species presence at the overall site scale
293 according to Sørensen's similarity index ($C_s = 0.447$). Results were similar for all individual
294 plots (CO $C_s = 0.421$; FI $C_s = 0.436$; TE $C_s = 0.511$; CP $C_s = 0.433$). When relative abundance
295 was incorporated, Bray-Curtis distance showed a similar trend, where the germinable seed bank
296 and aboveground vegetation were moderately dissimilar at the overall site level and the
297 individual plot levels (Site $BC = 0.609$; CO $BC = 0.580$; FI $BC = 0.587$; TE $BC = 0.627$; CP $BC =$
298 0.638). Sørensen's similarity index concluded that the CO plot had the most dissimilar
299 aboveground-belowground communities while Bray-Curtis distance found that CP had the
300 highest dissimilarity. According to Sørensen's similarity index the aboveground-belowground
301 communities were most similar in the TE plot. However, Bray-Curtis distance identified the CO
302 plot as having the most similar aboveground-belowground communities.
303

304 The NMDS with two dimensions was an acceptable representation of the original

305 germinable seed bank data (stress = 7.18). Four of the seven aboveground structure variables
306 (functional groups) were significantly correlated with the germinable seed bank community, with
307 correlations being highly significant for annual grasses and annual forbs, as expected (Table 1).
308 The two most dominant annual grass species present in the germinable seed bank, *Bromus*
309 *tectorum* (brte) and *Vulpia octoflora* (vuoc), were positively correlated with the cover of the
310 aboveground annual grass functional group (Fig. 1).

311
312 *3.2. Effects of microhabitat and aboveground community phase on germinable seed bank*
313 *community, seed densities, and species richness*

314
315
316 *3.2.1. Germinable seed bank community*

317
318 The NMDS plot constructed to compare microhabitats with three dimensions was an
319 acceptable solution (stress=19.88). Interspace and beneath shrub communities did not display
320 distinct community compositions as indicated by the lack of separation in the ordination plot
321 between the two microhabitats (Fig. 2).

322 The NMDS comparing aboveground community phase required three dimensions to
323 achieve an acceptable stress level of 17.38. There was no obvious separation of phase
324 1 and phase 3 community compositions (Fig. 3).

325
326 *3.2.2. Seed density*

327
328 ANOVA showed that seed density was not significantly affected by microhabitat, phase,
329 or the microhabitat x phase interaction (Table 2). Shrub seed density was the only functional
330 group significantly affected by any of the factors (Table 2). Microhabitat had a significant effect
331 on shrub seed density, with more seeds found beneath shrubs (6.74 ± 3.12) than in interspaces
332 (3.17 ± 4.46).

333
334 3.2.3. *Species richness*

335 ANOVA showed that species richness of the germinable seed bank was not significantly
336 affected by microhabitat, phase, or the microhabitat x phase interaction (Table 2).

337
338 **4. Discussion**

339
340
341 4.1. *Relationship between the germinable seed bank and aboveground vegetation*

342
343 Despite findings that desert grassland germinable seed bank communities may
344 correspond to the aboveground vegetation as a result of limited seed dispersal and clustered
345 seeds surrounding parent plants (Shaukat and Siddiqui, 2004), our results from the similarity and
346 distance metrics did not strongly support this expectation. Both Sørensen's similarity index and
347 Bray-Curtis distance indicate that the germinable seed bank and aboveground community
348 compositions were moderately different at the overall site and individual plot levels. At the plot
349 level, Sørensen's similarity index and Bray-Curtis distance give conflicting results as to which
350 plot had the most and least similar aboveground-belowground communities. This is likely due to
351 Sørensen's similarity index giving greater importance to rare species. The germinable seed bank
352 and aboveground vegetation only shared 19 of the total of 71 species encountered in this study.
353 However, for most species present in both the germinable seed bank and aboveground
354 vegetation, relative abundances were similar except that *Alyssum desertorum* and *Ceratocephala*
355 *testiculata* were vastly over-represented in the germinable seed bank relative to the aboveground
356 vegetation while *Artemisia tridentata* was over-represented in the aboveground vegetation
357 relative to the seed bank (Appendix A; Appendix B).

358 Eriksson and Eriksson (1997) have attributed a lack of correspondence between the
359 germinable seed bank and aboveground vegetation to the fact that the dominant species often

360 differ between the two communities. *A. tridentata* was the most dominant species aboveground
361 at the Onaqui site. Young and Evans (1989) found that no *A. tridentata* seeds germinated from
362 the seed bank when collected before fall when *A. tridentata* seeds mature. In contrast, in the
363 present study germinable *A. tridentata* seeds were found in seed bank samples collected in
364 August, before seed dispersal, but at low densities. Therefore, *A. tridentata* was over-
365 represented aboveground, which decreased the similarity between the germinable seed bank and
366 aboveground vegetation. Conversely, *A. desertorum* and *C. testiculata* were abundant in the
367 germinable seed bank but had lower cover aboveground. Annual species such as *A. desertorum*
368 and *C. testiculata* that produce small abundant seeds generally may be over-represented in the
369 germinable seed bank (Eriksson and Eriksson, 1997). Although many factors potentially
370 contribute to seed traits, in general annuals are expected to invest more resources in seed
371 production and, all else equal, produce smaller seeds relative to perennials (Silvertown and
372 Charlesworth, 2001). Also, being annuals, *A. desertorum* and *C. testiculata* can produce large
373 germinable seed banks and use seed banking as a bet hedging germination strategy (Philippi and
374 Seger, 1989; Gutterman, 2002; Mistro et al., 2005). *A. desertorum* and *C. testiculata* may be
375 maintaining dormant seeds to spread the risk of germination over time, allowing seeds to wait for
376 more favorable germination conditions which may increase the chance of establishment and
377 survival. Another possibility for the over-representation of *A. desertorum* and *C. testiculata*
378 belowground is the simple fact that these plants were not frequently encountered aboveground
379 during data collection using the line-point intercept method due to their relatively small size (the
380 probability of a pin hitting a smaller plant is lower than the probability of hitting a larger plant)
381 and due to primarily actively growing much earlier in the season than when the aboveground
382 sampling occurred.

383 In contrast to the similarity and distance metrics, the NMDS suggested that the
384 germinable seed bank and aboveground vegetation were in fact moderately similar. One reason
385 for this disagreement is the organizational level of the aboveground vegetation used in
386 comparisons. For the similarity and distance metrics, relative abundances were compared at the
387 species-level. However, the NMDS compared the relative abundance of each species in the
388 germinable seed bank to the relative abundance of aboveground vegetation functional groups, i.e.
389 aboveground vegetation structure. Therefore, at the species-level the germinable seed bank and
390 aboveground vegetation communities were only moderately similar, but similarities were
391 considerably greater when comparing germinable seed bank species abundances to the
392 aboveground functional groups. There were a number of species that were only present above or
393 belowground (Tables A.1 and A.2) which decreased similarity between the germinable seed bank
394 and aboveground vegetation. However, the differences between each species present in either
395 community were no longer detected when using functional group as the aboveground
396 organizational level of comparison.

397 The germinable seed bank and aboveground vegetation tend to be more similar in annual
398 communities than in perennial communities (Thompson and Grime, 1979; Ungar and Woodell,
399 1993; Milberg, 1995; Bakker et al., 1996; Osem et al., 2006). NMDS results from the present
400 study did show a significant correlation between the annual germinable seed bank and
401 aboveground structure, but also a significant correlation between the perennial germinable seed
402 bank and aboveground structure. The unexpected correspondence between the perennial
403 germinable seed bank species and aboveground vegetation structure could simply be a function
404 of the comparison between species and functional groups. As displayed by the similarity and
405 distance metrics, the similarity between germinable seed bank and aboveground species

406 compositions was relatively low. However, comparing germinable seed bank species
407 composition to aboveground structure yielded the opposite result. Although the germinable seed
408 bank and aboveground vegetation were not similar at the species level, the germinable seed bank
409 species composition was similar to the aboveground vegetation functional group categories. For
410 example, both *Achnatherum hymenoides* and *Elymus elymoides* were positively correlated with
411 the aboveground perennial grass functional group.

412
413 *4.2. Aboveground community phase and microhabitat effects*
414

415
416 Shrub was the only functional group whose seed density was significantly affected by
417 microhabitat. The beneath shrub microhabitat contained more shrub seeds than interspaces,
418 which has been observed in other studies (Nelson and Chew, 1977; Guo et al., 1998; Marone et
419 al., 2004). Shrub seed densities tend to be higher under shrub canopies due to seeds falling
420 beneath and adjacent to the parent plant (phase I dispersal; Shaukat and Siddiqui, 2004). Shrubs
421 might have decreased wind velocity, physically trapping seeds beneath shrubs (Bullock and
422 Moy, 2004). Another explanation for higher beneath shrub densities is seeds could have been
423 transported by wind or water from interspaces and trapped in the litter beneath shrubs (phase II
424 dispersal; Chambers and MacMahon, 1994). However, if this was the primary reason we would
425 expect to have higher densities of other seed types beneath shrubs as well.

426 There are few studies investigating the spatial pattern of species richness of seeds in
427 desert shrub communities, but Li (2008) reported species richness was highest 2 m and 6 m from
428 shrubs. Results from the present research can neither corroborate nor contradict this finding.
429 Species richness was not significantly affected by any of the factors of interest.

430 The invasive grass *Bromus tectorum* was the most dominant annual grass on site.

431 However, annual grass seed density was not affected by aboveground community phase,
432 microhabitat, or the community phase x microhabitat interaction. Although we did not directly
433 examine the effects of *Bromus tectorum* on the seed bank, the invasion of *Bromus tectorum* can
434 create shifts to greater annual seed abundance (Young and Evans, 1975; Humphrey and Schupp,
435 2001) which can in turn affect the aboveground vegetation. Regardless of the differences in
436 perennial bunchgrass cover aboveground (community phase), annual grass seed density was not
437 affected—*Bromus tectorum* seed densities were relatively high as was aboveground cover
438 (Appendix A; Appendix B). Even if an invader can be eradicated aboveground, it may be
439 impossible to restore the vegetation community to the composition of an uninvaded community
440 (Vilà and Gimeno, 2007) due to invasive species persisting in the seed bank. Total seed density
441 and species richness, and seed density and species richness for all other functional groups
442 individually, were not significantly affected by aboveground community phase or microhabitat.
443 Seed banks of semiarid deserts can vary extensively spatially (Marone et al., 2004; Coffin and
444 Lauenroth, 1989) which may make it difficult to detect strong effects of these factors on seed
445 density and species richness.

446 In addition to seed density and species richness, the germinable seed bank species
447 composition was not strongly affected by community phase or microhabitat, or at least NMDS
448 did not detect such effects. Due to variability in seed dispersal patterns among species, distinct
449 germinable seed bank communities as a function of microhabitat and aboveground community
450 phase may not exist.

451 Prior to our research, the relationship between the seed bank and aboveground vegetation
452 had not yet been examined in cold desert plant communities. Our study found that seed
453 densities, species richness, and the germinable seed bank community composition were not

454 affected by aboveground community phase or, with the exception of shrub functional group seed
455 densities, microhabitat. Species compositions were moderately dissimilar when the germinable
456 seed bank and aboveground vegetation were compared at the species level but were moderately
457 similar when the germinable seed bank was compared to the aboveground vegetation functional
458 groups. These findings provide new insight into seed banks of cold deserts and their potential to
459 influence the aboveground vegetation.

460

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465

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475

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