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

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ABSTRACT

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.

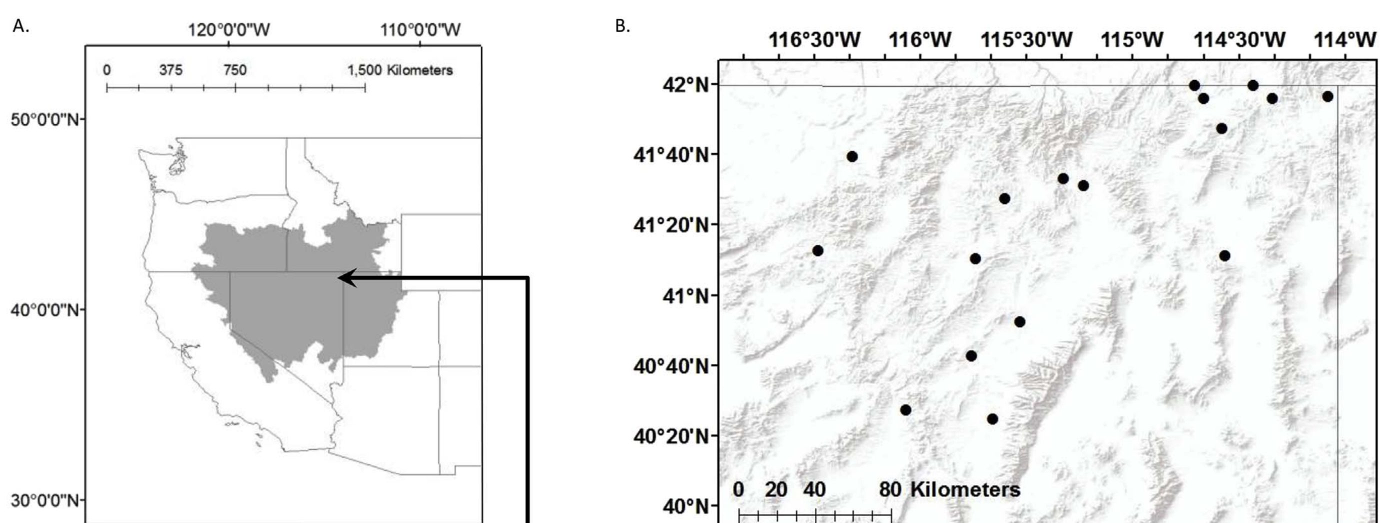

Fig. 1. Map of field sites showing (A) the western United States with the floristic Great Basin highlighted in gray and (B) north-eastern Nevada site locations within two sagebrush steppe dominated ecoregions, as designated by the U.S. Environmental Protection Agency (13M - Central Basin and Range, 80A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