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Seed harvesting by a generalist consumer is context-dependent: Interactive effects across multiple spatial scales

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Granivore foraging decisions affect consumer success and determine the quantity and spatial pattern of seed survival. These decisions are influenced by environmental variation at spatial scales ranging from landscapes to local foraging patches. In a field experiment, the effects of seed patch variation across three spatial scales on seed removal by western harvester ants *Pogonomyrmex occidentalis* were evaluated. At the largest scale we assessed harvesting in different plant communities, at the intermediate scale we assessed harvesting at different distances from ant mounds, and at the smallest scale we assessed the effects of interactions among seed species in local seed neighborhoods on seed harvesting (i.e. resource–consumer interface). Selected seed species were presented alone (monospecific treatment) and in mixture with *Bromus tectorum* (cheatgrass; mixture treatment) at four distances from *P. occidentalis* mounds in adjacent intact sagebrush and non-native cheatgrass-dominated communities in the Great Basin, Utah, USA. Seed species differed in harvest, with *B. tectorum* being least preferred. Large and intermediate scale variation influenced harvest. More seeds were harvested in sagebrush than in cheatgrass-dominated communities (largest scale), and the quantity of seed harvested varied with distance from mounds (intermediate-scale), although the form of the distance effect differed between plant communities. At the smallest scale, seed neighborhood affected harvest, but the patterns differed among seed species considered. Ants harvested fewer seeds from mixed-seed neighborhoods than from monospecific neighborhoods, suggesting context dependence and potential associational resistance. Further, the effects of plant community and distance from mound on seed harvest in mixtures differed from their effects in monospecific treatments. Beyond the local seed neighborhood, selection of seed resources is better understood by simultaneously evaluating removal at multiple scales. Associational effects provide a useful theoretical basis for better understanding harvester ant foraging decisions. These results demonstrate the importance of ecological context for seed removal, which has implications for seed pools, plant populations and communities.

The importance of spatial scale in ecology is well accepted (Wiens 1989, Levin 1992), and is expected to strongly influence plant–animal interactions, including seed–seed consumer dynamics (Rey et al. 2002, Garćia et al. 2011). Interactive effects of abiotic and biotic drivers of resource selection have been demonstrated to vary across scales (Rey et al. 2002). Additionally, the simultaneous consideration of multiple spatial scales can influence patterns of differential resource harvest (Edwards et al. 1994, Miller et al. 2009). Accordingly, considering variability in resource discovery and selection across a range of spatial scales from smaller (i.e. the resource–consumer interface) through intermediate (i.e. within community level) to larger (i.e. landscape level) scales can offer increased insight into the nuanced role of plant–animal interactions in the regulation of biotic systems (Garćia et al. 2011).

Resources are distributed over the landscape heterogeneously (Reichman 1984, Wilby and Shachak 2000), with both the quantity and quality of the resource varying (Ball et al. 2000). It is reasonable to expect that foraging decisions are made in light of a range of patch characteristics (Wilby and Shachak 2000), including resource quality or quantity (Rey et al. 2002); direct and indirect predation risk (Brown 1999, Sivy et al. 2011); size, composition and arrangement of neighbors (Courant and Fortin 2011); distance to nearby patches (Palmer et al. 2003); and potential rate of harvest (Arthur et al. 2009). The effects of all of these factors depend on the spatial scale considered (Kotliar and Wiens 1990). In this light, there is ample reason to expect that resource harvest is highly context-dependent across a range of spatial scales and that a better understanding of consumer–forager interactions will come from the simultaneous consideration of the interactions across spatial scales.

The local or small scale patch is the most basic and straightforward setting to consider resource–consumer interactions. Foraging granivores are expected to focus on high resource-concentration patches (Root 1972), consistent

with the resource concentration hypothesis, and maximize foraging efficiency by obtaining high quality resources while minimizing risks associated with obtaining those resources (Charnov 1976, Stephens and Krebs 1986), as predicted by optimal foraging theory. However because the quantity and quality of seed resources can be highly variable spatially (Reichman 1984), high foraging efficiency requires consumers to assess and respond to resource variation occurring at a range of spatial scales from local seed neighborhoods through distinct habitats within the foraging range. For example, harvester ants exhibit selectivity among seed types (Kelrick et al. 1986) and, as expected from optimal foraging theory, should become more selective when more desirable food items are in greater supply (Wilby and Shachak 2000).

The probability of a seed being consumed is a function of its own characteristics (e.g. nutritional quality, size, etc.) as well as the characteristics of co-occurring seeds in the immediate neighborhood (Veech 2001); that is, associational effects can be important (Tahvanainen and Root 1972). Associational effects in mixed seed neighborhoods can take the form of associational resistance or associational susceptibility. Associational resistance occurs when a focal species is harvested less when in mixed species patches than when in monospecific patches. This has been widely documented in studies of herbivore foraging in diverse vegetation patches (Stiling et al. 2003, Barbosa et al. 2009, Bee et al. 2009). Alternatively, associational susceptibility occurs when a species suffers greater harvesting when in mixed patches than when in monospecific patches; such associational susceptibility may be more common than ecological reports indicate (White et al. 2006).

At an intermediate spatial scale, granivore foraging patterns can vary strongly within a given community, suggesting a role for within-community structural complexity (Luque and Reyes-López 2007). Habitat structure influences granivore nesting location and foraging patterns, which translate into spatial patterns of seed harvest (Brown et al. 1985, Fewell 1988, Avgar et al. 2008, Azcárate and Peco 2003). The surrounding habitat of central place foraging seed harvesting ants, shaping patterns of seed removal and survival and potentially plant population dynamics (Azcárate and Manzano 2011).

Many factors likely contribute to larger-scale among-community foraging choices. The structure and composition of plant communities influence how foragers negotiate the landscape and use available resources (Crist and Wiens 1994). Different plant communities or even similar communities with different disturbance histories likely vary in seed availability, cover, predation risk, and more, resulting in different foraging patterns (McConkey et al. 2012). For example, variation in seed harvest can be greater among conspecific ant colonies in different plant communities than among heterospecific colonies in the same plant community (Gordon 1993), suggesting large-scale characteristics of the environment have a major impact on seed harvesting.

Without question the outcomes of plant–animal interactions are influenced by multi-spatial-scale factors and ultimately contribute to community structure and ecosystem function (Levin 2000, Hulme and Kollmann 2005). Although ecologists lack general rules about how biotic interactions operate over multiple scales, the responses across spatial scales may have important implications for natural communities where seed–seed consumer dynamics play an important role in plant population and community dynamics. This may be especially important where invasive species threaten to shift communities from diverse native-dominated communities to those dominated by invasive exotic species (McConkey et al. 2012). Additionally, if seed–seed consumer interactions are affected by invasive species conversions that interrupt consumer–plant feedbacks the implications on plant population, community and associated higher order dynamics may be profound (McConkey et al. 2012).

Here we use the western harvester ant *Pogonomyrmex occidentalis* foraging on five common native grasses, on an annual exotic grass often used in seed selection experiments (*Panicum miliaceum*, millet), and on the annual exotic invasive *Bromus tectorum* (cheatgrass) to address the effects of small, intermediate- and large-scale variation in the environment on seed foraging patterns and test for the occurrence of context dependence and associational effects. The western harvester ant is a generalist seed harvester and one of the most important granivores in semiarid systems of western North America (Mull and MacMahon 1997, MacMahon et al. 2000), removing up to 25% of the viable seed pool per year (Crist and MacMahon 1992). At the larger scale we compared patterns of harvest in intact sagebrush communities versus adjacent highly degraded cheatgrass-dominated communities that have recently undergone a type conversion, a dynamic that may disrupt seed–seed consumer interactions (McConkey et al. 2012). At the intermediate scale we assessed the effects of distance from an ant mound on seed harvesting in both community types. At the smaller scale we investigated the effects of seed neighbor identity on seed removal in patches where seeds were presented in a small seed neighborhood such that the characteristics of the entire patch could be assessed rapidly by foragers. Specifically, we compared the harvesting of seeds of the native species and of millet in monospecific patches versus when in mixture with *B. tectorum* seeds. Lastly, our experimental design allowed us to assess interactions affecting seed harvesting as well; for example, whether small- and intermediate-scale effects differed between sagebrush and cheatgrass-dominated communities (large scale).

We made the following predictions based on previous work and our understanding of the granivore system (Ostoja and Schupp 2009, Ostoja et al. 2009). 1) Native seeds and *P. miliaceum* would be removed in greater quantities than *B. tectorum* seeds under all conditions (Kelrick et al. 1986). 2) Seed removal would be greater in cheatgrass-dominated communities than in sagebrush communities due to greater *Pogonomyrmex occidentalis* population sizes in the former community (Ostoja et al. 2009), and reduced abundance of rodent granivores (Ostoja and Schupp 2009). 3) More seed would be removed from seed patches near than far from nest mounds (Charnov 1976, Crist and MacMahon 1991, 1992). 4) Harvest of *B. tectorum* would be greater when present with highly preferred species (associational susceptibility) but that the reverse would not be true (Veech 2001). Lastly, 5) effects would interact, but a priori

predictions as to whether habitat (large scale), foraging distance (intermediate scale) or seed patch (small scale) would be more important are not clear (Garćia et al. 2011, Rey et al. 2002). In general, by simultaneously accounting for multiple scales of spatial heterogeneity we improve our understanding of ant foraging and to some degree how invasive species type conversions disrupt this type of critical plant–animal interaction (McConkey et al. 2012).

Material and methods

Study site

This study was conducted around the Vernon Hills in Tooele County, west-central Utah, USA (40°07′47″N, 112°22′43″V), approximately 155 km southwest of Salt Lake City, Utah. Six 1.2-ha study plots were established, three in intact sagebrush (sagebrush plots hereafter) and three in nearby annual non-native vegetation dominated by *Bromus tectorum* (>90% standing biomass, Ostoja unpubl.; cheatgrass-dominated plots hereafter). All six plots occur on the Hiko Peak soil series, where the potential plant community is 45% perennial grasses, 15% forbs and 40% shrubs; the dominate shrub is *Artemisia tridentata* ssp. *wyomingensis* (Wyoming big sagebrush; NRCS 2000). Although perhaps not originally identical to the sagebrush plots, all cheatgrass-dominated plots were previously dominated by *A. t.* ssp. *wyomingensis* and were converted to their current state by a fire in 1998 (B. Henderson, USDI BLM Salt Lake Field Office, pers. comm., Schupp unpubl.). Cheatgrass-dominated plots also had other weedy species including *Salsola* spp. and *Lepidium* spp. Vegetation in sagebrush plots was typical of Wyoming big sagebrush communities of the Great Basin. In addition to *A. t.* ssp. *wyomingensis*, other shrubs including *Atriplex canescens*, *Gutierrezia sarothrae*, *Chrysothamnus viscidiflorus* and *Ephedra viridis* were present. The understory was dominated by the grasses *Achnatherum hymenoides*, *Elymus elymoides*, *Poa secunda*, *Hesperostipa comata*, *Leymus cinereus*, *Pseudoroegneria spicata* and some *B. tectorum*.

Ants

The only species found using seed trays was *P. occidentalis*, the most abundant seed-harvesting ant in both plant communities, although it was more abundant in cheatgrass-dominated plots than in sagebrush plots (Ostoja et al. 2009). Mounds of *P. occidentalis* were >40 ha^{-1} in cheatgrass-dominated and ≤20 ha^{-1} in sagebrush plots (Ostoja unpubl.). Nonetheless, it is possible that other species of ants occasionally removed seeds.

Seed species

Seeds of the native perennial grasses *A. hymenoides*, *E. elymoides*, *P. spicata*, *P. secunda* and *L. cinereus* were purchased in Utah. *Panicum miliaceum* was also purchased in Utah. Seeds of *B. tectorum* were collected in the vicinity of the research area by the senior author in 2004 and 2005 and mechanically cleaned and air blown to remove extra coreopsis material from the embryo at Utah State Univ. The native seed species were selected because they are abundant in the region and are commonly used in restoration. *Bromus tectorum* was used because it is locally abundant, it is widespread and still expanding its range, it alters ecosystem processes (e.g. soil morphology, fire regimes, plant–animal diversity), and it might influence target seed choice by granivores (Knapp 1996, Norton et al. 2004, Ostoja and Schupp 2009, Veech 2000, 2001). *Panicum miliaceum* was included because it has been used extensively in seed removal experiments and has been tested with some native species as a potential decoy seed in reseeding projects (Kelrick et al. 1986, Longland and Bateman 1998).

Seed trays

To quantify seed harvesting by ants and to determine whether the presence of cheatgrass seeds in a mixture affected harvesting of other seeds, we designed a cafeteria-style seed removal experiment using ant-specific seed trays fashioned out of seven-day plastic pill boxes with a 10-mm diameter hole placed on each side of each individual day compartment 5 mm above the bottom to allow access of ants to seeds while excluding rodents and birds (Supplementary material Appendix A1). In one set of trials, seeds of all seven species were offered individually (monospecific treatment). A seed patch was 2 g of one seed species placed randomly in a 'day compartment' of the seven-day box. Thus, all species were presented simultaneously and within centimeters of one another, but individual seed patches were of only a single species. In another set of trials, seeds of the five native grasses and of *P. miliaceum* were presented in mixture with *B. tectorum* seeds (mixture treatments). A seed patch consisted of 1 g of one of these six seed species combined with 1 g of cheatgrass seed. Each of these distinct mixed seed patches was then placed randomly in one of the 'day compartments' of the seven-day box, leaving one compartment empty. This resulted overall in 13 unique types of seed patches.

Due to the nature of the experimental design and the research questions we used seed weights rather than seed density, which resulted in different numbers of seeds for the different seed species. Ultimately, however, because we were primarily interested in understanding whether the ecological context in which seeds are encountered changes seed removal, our use of seed weight rather than density is not a problem; the absolute removal is not as important as changes in relative removal with changes in context.

In each of the six 1.5-ha plots a monospecific or a mixture tray was placed at one of four distances from a different individual active *P. occidentalis* nest mound in a random direction from the mound center. Distances were: 1) at the edge of the mound clearing (mound), 2) 1 m from the mound clearing (1 m), 3) 3 m from the mound clearing (3 m), and 4) 5 m from the mound clearing (5 m). Each seed treatment × distance combination was replicated ten times per plot during the months of August and September 2005 and mounds were not used in a trial more

than once. After 48 h, seed trays were collected and seeds were separated and reweighed by species to determine the amount of seed removed by species.

Statistical analyses

Seed harvest was analyzed with split-plot MANOVA. The split-plot factor was plant community. We performed three separate sets of analyses to assess: 1) the amount of seed harvested in monospecific treatments, 2) the amount of non-*B. tectorum* seed harvested in mixture treatments, and 3) the amount of *B. tectorum* seed harvested in mixture treatments (small spatial scale responses). Predictor variables were: seed species, distance from a mound (intermediate spatial scale), plant community (large spatial scale), and the interaction between distance from mound and plant community. The response variable was the proportion of seeds removed. The error term for the plant community effect (main plot) was trial within plant community. In all cases the proportions of seeds removed were arcsine transformed in order to conform to the assumptions of parametric tests. When results of the MANOVA were significant ($p \leq 0.05$) we conducted individual ANOVA's for each species and report the ANOVA decomposition of the MANOVA accordingly.

MANOVA was also used to evaluate the effects of mixed species seed neighborhoods by considering the harvest of each non-*B. tectorum* species in mixed seed patches relative to the harvest of *B. tectorum* in the mixture. The response variable was the $\log_e$ ratio of the proportion of non-*B. tectorum* seeds removed to the proportion of *B. tectorum* seeds removed. The predictor variables and error terms were the same as for the MANOVAs described above. Interpretively the *y*-axis ranges from 3 to −3, and if the ratio is positive this indicates more of the focal seed than *B. tectorum* seed was removed. Alternatively if the ratio is negative then more *B. tectroum* seed was removed than target seed. Finally, we evaluated the mean proportional shift in removal for each non-*B. tectorum* seed species between monospecific and mixture treatments to assess the potential occurrence of associational interactions among the seed species tested. All analyses were conducted with SYSTAT 11. Significance for all analyses was declared at $\alpha \leq 0.05$.

Results

Seed harvest in monospecific treatments

The multivariate results indicates that there was a significant interaction between plant community and distance from mound in the monospecific seed harvest trials (Wilk's $\lambda = 0.276$, $F_{21,138} = 3.729$, $p \leq 0.0001$). The only species where this effect was not significant was *Bromus tectorum* (Supplementary material Appendix A2). In general, more seed was removed in sagebrush than in cheatgrass-dominated plots, but the effect of distance differed between plant communities (Fig. 1, Supplementray material Appendix A2). In addition, the effect of distance appeared to differ among seed species (Fig. 1). The most preferred seeds were *Achnatherum hymenoides* and *Panicum miliaceum*, whereas the least preferred species was *B. tectorum* (Fig. 1). The general trend in cheatgrass-dominated plots was for less seed to be harvested at increasingly greater distances from mounds, although the greatest amount of *B. tectorum* seed was removed at the greatest distance from the mounds (Fig. 1). In contrast, seed harvest in sagebrush plots tended to be greatest at the mound and at 5 m from the mound, with generally less removal at intermediate distances (Fig. 1).

Non-*B. tectorum* seed harvest in mixture treatments

The multivariate results indicates that there was a significant interaction between plant community and distance from mound in the mixed seed harvest trials (Wilk's $\lambda = 0.672$, $F_{6,106} = 3.729$, $p = 0.002$). The only species where this effect was not significant was *P. secunda* (Supplementary material Appendix A3). Similar to monospecific results, non-*B. tectorum* seed harvest from mixtures was generally greater in sagebrush than in cheatgrass-dominated plots although the pattern was not as strong (Fig. 2). Again, seed species differed in the proportion harvested in both cheatgrass-dominated and sagebrush plots (Fig. 2, Supplementary material Appendix A3). In contrast with monospecific results, seed harvesting tended to be greatest at 1 m, especially in cheatgrass-dominated plots (Fig. 2). The influence of distance on removal rates in sagebrush plots was largely due to less seed harvested at 3 m than at other distances (Fig. 2).

B. tectorum seed harvest in mixture treatments

According to the multivariate analysis, *B. tectorum* seed harvest was significantly affected by an interaction between plant community and distance in all species mixtures except *P. secunda* (Fig. 3, Supplementary material Appendix A4). More *B. tectorum* was harvested from mixtures at 1 m than at other distances in cheatgrass-dominated plots, except when *B. tectorum* was present with *P. secunda* (Fig. 3). In contrast, in sagebrush plots *B. tectorum* seed harvest was greatest either at the mound or at 5 m (Fig. 3, Supplementary material Appendix A4).

Mixed neighborhood and associational effects

A major interest in the current research was how seed removal by ants might be influenced by the seed neighborhood in which seeds are encountered. In particular, we were interested in whether the small scale effect of seed neighborhood differed according to distance from a focal mound (intermediate scale) as well as how patterns might differ among the plant communities (large scale). However, in the current experimental framework, statistical comparison of the quantity of seed removed from monospecific treatments with 2 g of seed and from mixture treatments with only 1 g of seed is not straightforward. To address the effects of seed mixture on harvest we first analyzed least square means of the ratio of non-*B. tectorum* seed removal to *B. tectorum* seed removal in the mixture treatments.

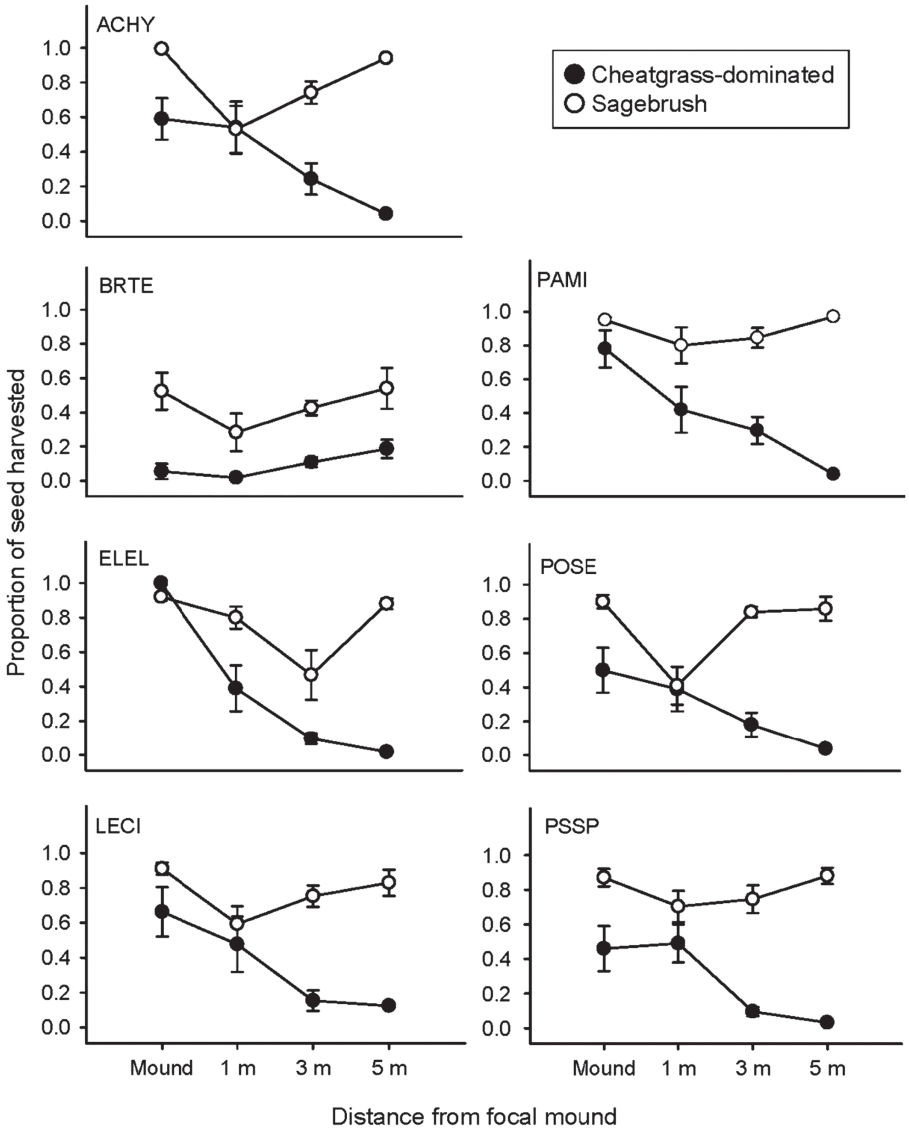

Figure 1. Mean (± 1 SE) of the weight of seeds harvested in monospecific treatments at each of the sampled distances from focal mounds in cheatgrass-dominated and in sagebrush plots. See Supplementary material Appendix A1 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSE, *Poa secunda*; and PSSP, *Pseudoroegneria spicata*.

The ratio between native seed harvest and *B. tectorum* seed harvest varied by distance, between the plant communities and among the six native species (Wilk's $\lambda = 0.099$, $F_{18,37} = 2.624$, $p = 0.006$). In general, *A. hymenoides*, *E. elymoides*, *P. miliaceum* and *P. spicata* were harvested proportionally more than *B. tectorum* in cheatgrass-dominated plots, but less than *B. tectorum* in sagebrush plots (Fig. 4, Supplementary material Appendix A5). The amounts of *L. cinereus* and *B. tectorum* harvested were similar in both plant communities, although in sagebrush proportionally fewer *B. tectorum* seeds were harvested at the mound. A significantly lower proportion of *P. miliaceum* than of *B. tectorum* was harvested in sagebrush across all distances (Fig. 4). In sum, for most species the ecological context not only affected the total harvest of individual species, but also affected the relative harvest of the species encountered in mixtures.

To consider the occurrence of associational effects we compared the proportion of non-*B. tectorum* seed removed from the monospecific treatments to the proportion of the same seed removed from the mixture treatments, despite the potential importance of density dependence of seed harvesting (Price and Heinz 1984). Because of the shortcomings of this approach, we only consider three possible qualitative alternative outcomes of ecological interest: 1) no difference in proportional removal between the two treatment types (neutral effect), 2) proportionally more non-*B. tectorum* seed removed from mixtures than from monospecific treatments (associational susceptibility), or 3) proportionally less non-*B. tectorum* seed removed from mixtures than from monospecific patches (associational resistance). Seed harvest for all species suggests associational resistance, especially in the sagebrush plots (Fig. 5). Interestingly, this means ants harvested a

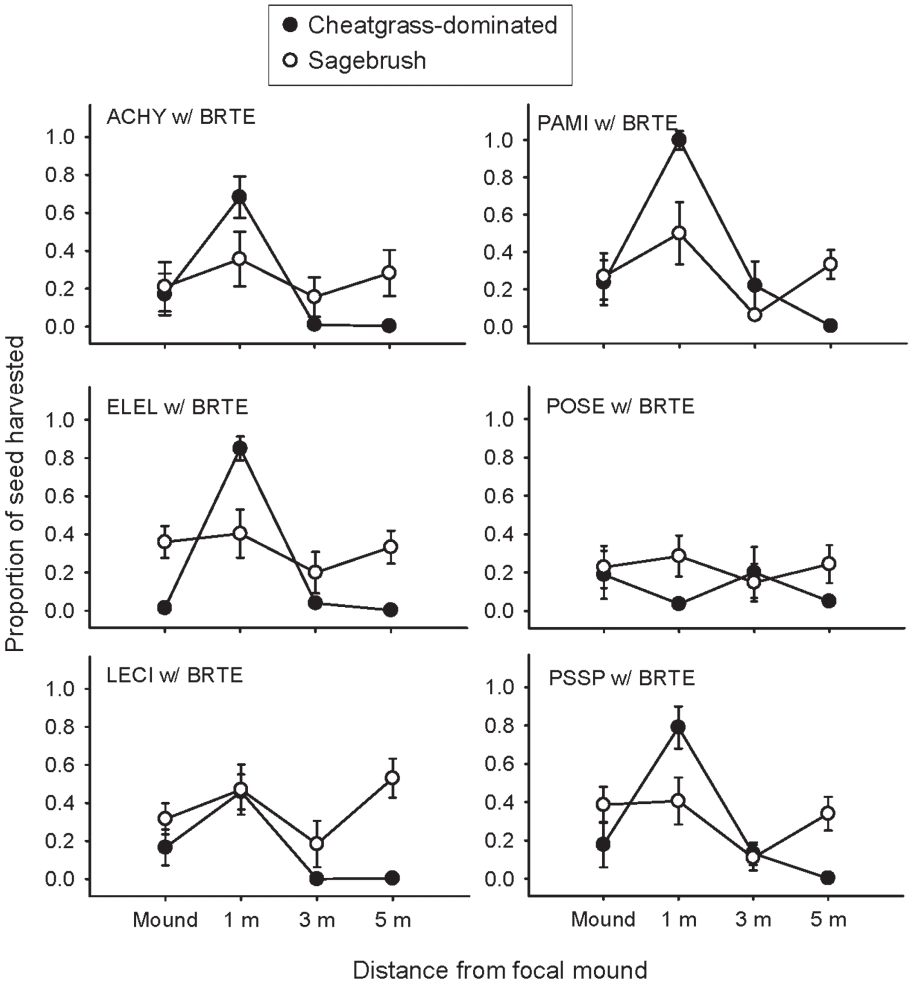

Figure 2. Mean (± 1 SE) of the weight of non-*B. tectorum* seed harvested in mixture treatments in cheatgrass-dominated and sagebrush plots at each of the distances from focal mounds. See Supplementary material Appendix A2 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSE, *Poa secunda*; and PSSP, *Pseudoroegneria spicata*.

smaller proportion of the seed when there was less of it initially available (that is, from the mixture treatments), suggesting that the results are not due to satiation. While these results are strongly compatible with associational resistance, they are not conclusive.

Discussion

Generally, it is thought that seed removal by seed-harvesting ants like *Pogonomyrmex occidentalis* follows two general patterns consistent with foraging theory (Charnov 1976). First, because they are trunk-trail central place foragers more seeds are thought to be collected nearer the mound than farther from the mound (Crist and MacMahon 1991, 1992, Anderson and MacMahon 2001). Second, ant foraging is expected to be concentrated in high-density seed patches (Mull and MacMahon 1997, MacMahon et al. 2000). Although we did not test the density-dependent expectation, we did show that seed harvesting by ants varied as a function of distance from the mound, the intermediate scale effect. In addition, we showed that harvesting varied as a function of background plant community, the large scale effect, and as a function of seed neighborhood, the small scale effect. Indeed, the fates of seeds were very dependent on the ecological context in multiple ways. Such interactive effects of varying spatial scales have been demonstrated for larger foraging vertebrates (Baraza et al. 2006, Bee et al. 2009, Miller et al. 2009) but not for seed harvesting ants in North American deserts, nor have the interactive effects across spatial scales been considered in the context of invasive species type conversion, an alarming occurrence throughout western North American arid landscapes.

Seed preferences

There was a clear preference for native seeds, especially *Achnatherum hymenoides*, and for *Panicum miliaceum*, over the non-native *B. tectorum* seeds, a result consistent with our prediction and other findings (Kelrick and MacMahon 1985, Kelrick et al. 1986, Crist and MacMahon 1991). These preference rankings were not related to individual seed weight, in contrast to other

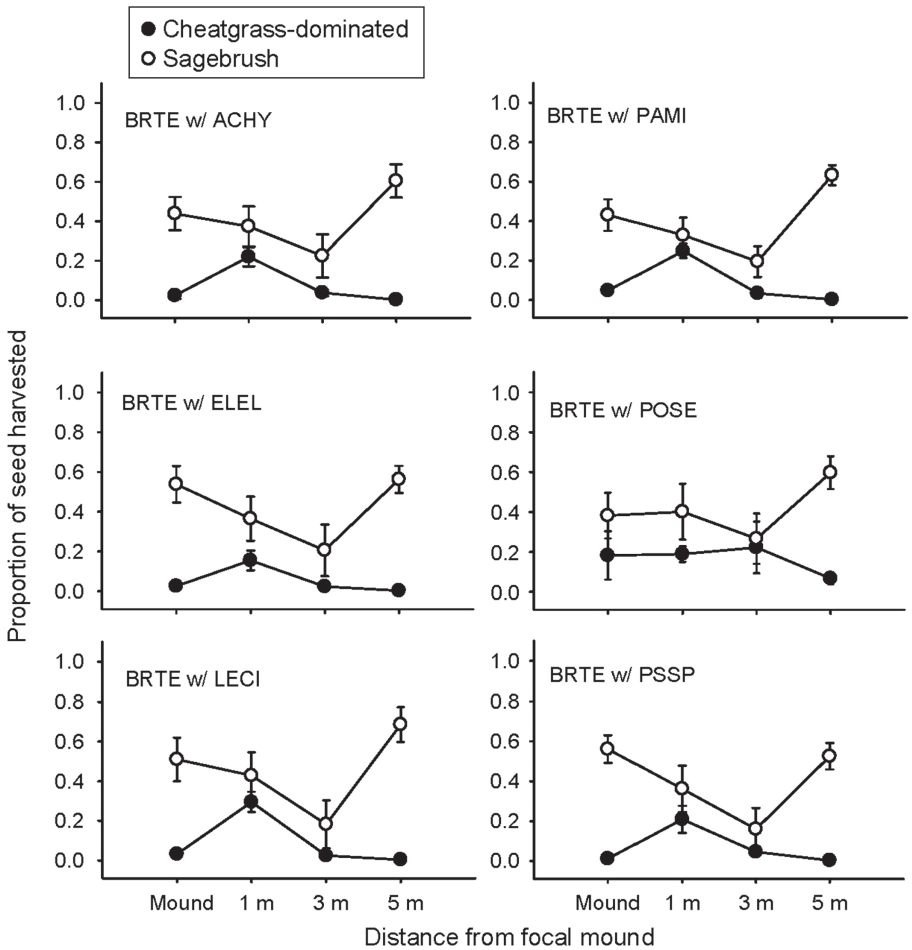

Figure 3. Mean (± 1 SE) of the weight of *B. tectorum* seed harvested in mixture treatments in cheatgrass-dominated and sagebrush at each of the distances from focal mounds. See Supplementary material Appendix A3 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSE, *Poa secunda*; and PSSP, *Pseudoroegneria spicata.*

studies where seed size and shape were selected more for another seed harvesting ant species (Azcárate and Peco 2006). The low harvest rate of cheatgrass was likely due to low nutritional value and to persistent awns which make handling difficult. Interestingly, *B. tectorum* went virtually un-harvested from seed trays in cheatgrass-dominated plots. While there was greater harvest of *B. tectorum* in sagebrush plots, our results reinforce the conclusion that cheatgrass is a relatively undesirable seed for ants. Although *B. tectorum* accounted for the majority of seed harvested by *P. occidentalis* in a Wyoming sagebrush steppe (Mull and MacMahon 1996), this was probably due to the high abundance of cheatgrass seeds at the site (60% of total), not preference per se. In our study, the low preference for *B. tectorum* seeds combined with its overwhelming abundance in the background seed pool, especially in cheatgrass-dominated sites where seeds can be in excess of 12 000 per m^2 (Crist and MacMahon 1991, 1992, Humphrey and Schupp 2001), may explain the low removal from trays.

Of the *B. tectorum* seeds harvested by *P. occidentalis*, large numbers are later discarded in refuse piles, and many of these are partially eaten and effectively removed from the seed pool (Mull 2003). For surviving discarded *B. tectorum* seeds the effectiveness of dispersal by harvester ants depends on how many seeds subsequently move from refuse piles to favorable establishment sites (Schupp 1993, Schupp et al. 2010). In this light, despite the low preference for cheatgrass seeds it has been argued that harvester ants could indirectly facilitate increased densities of *B. tectorum* near their mounds (Mull and MacMahon 1996, 1997) due to the open conditions that are suitable for germination and growth and the high densities of discarded *B. tectorum* seeds (Nowak et al. 1990).

Large scale effects: plant community

Overall, seed harvesting by *P. occidentalis* was strongly influenced by the context of plant community. Seed removal patterns by *Messor* spp. harvester ants in Spain were also affected by the spatial structure of the ecosystem (Azcárate and Peco 2003), suggesting this larger-scale context dependence of seed harvesting is widespread.

In monospecific treatments, more seed was harvested in sagebrush than in cheatgrass-dominated plots for nearly all seed species and distances, which is contrary to our

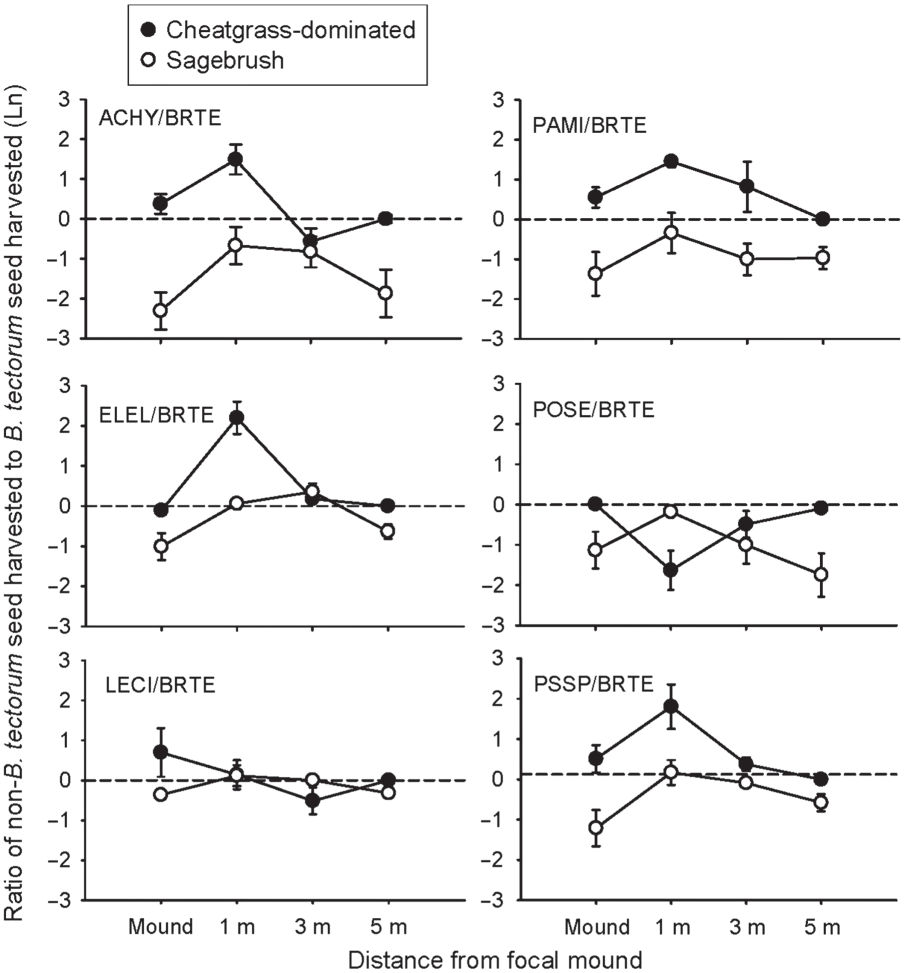

Figure 4. Mean ratio of the amount of non-*B. tectorum* seed harvested to *B. tectorum* seed harvested (± 1 SE) for cheatgrass-dominated and sagebrush plots at each of the four distances from a given focal mound. Values greater than zero indicate more non-*B. tectorum* seed relative to *B. tectorum* seed was harvested. Conversely, values below zero indicate that the amount of non-*B. tectorum* seed harvested was less than the amount of *B. tectorum* seed harvested. Note the y-axis is shown on the natural log (ln) scale. See Supplementary material Appendix A4 for statistical results. Species codes are ACHY, *Achnatherum hymenoides*; BRTE, *Bromus tectorum*; ELEL, *Elymus elymoides*; LECI, *Leymus cinereus*; PAMI, *Panicum miliaceum*; POSE, *Poa secunda*; and PSSP, *Pseudoroegneria spicata.*

prediction. Differences in harvester ant population sizes cannot explain our results; the most abundant seed-harvesting ant species in our sites was *P. occidentalis*, which was three-times more abundant in cheatgrass-dominated than in sagebrush plots (Ostoja et al. 2009). In addition, harvester ant mound density was approximately twice as high in cheatgrass-dominated as in sagebrush plots (Ostoja et al. 2009). It is likely that background seed resources are at least partly responsible for the greater harvesting of seeds from sagebrush. Substantially more seeds are available in cheatgrass-dominated compared to sagebrush communities (Mull and MacMahon 1996, Anderson and MacMahon 2001, Humphrey and Schupp 2001), although the quality of the resource is relatively poor (i.e. dominated by *B. tectorum*). Perhaps ants were to some extent satiated in cheatgrass-dominated plots.

Differences in granivore competitive interactions between the two plant communities may also partially explain our results. In contrast to *P. occidentalis*, granivorous rodent communities were greatly reduced in cheatgrass-dominated communities relative to intact sagebrush (Ostoja and Schupp 2009). Potentially, then, competitive interactions for seed resources shift from intense ant-rodent competition in sagebrush to more ant–ant competition in cheatgrass-dominated communities. Evidence for such an interaction is suggested by Brown and Davidson (1977) who noted the important role rodent granivores have in limiting the abundance of seed-harvesting ants through resource competition. In the face of strong competition from rodents in sagebrush communities, seed-harvesting ants might forage more efficiently on a per colony basis than those living in cheatgrass-dominated communities.

Intermediate scale effects: foraging distance

To some degree our results indicate seed removal decreased with increasing distances from the mound, as predicted, although this result was most evident in cheatgrass-dominated plots. Similar patterns of removal were demonstrated in sagebrush habitats in Wyoming (Mull and

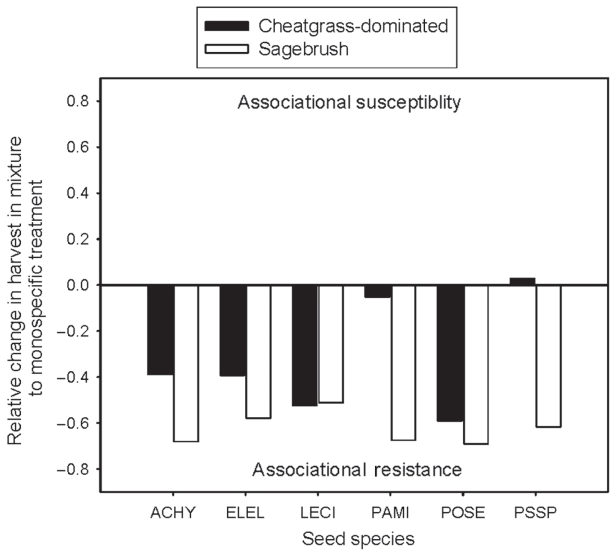

Figure 5. Relative change in seed harvest in mixture compared to seed harvest in monoculture in cheatgrass and sagebrush plots combining all distances. Relative change was measured as the ratio of mean proportion of a non-*B. tectorum* seed species harvested from a mixture treatment to the proportion of that seed harvested in the monospecific treatment. Positive values indicate an overall increase in harvest in mixture compared to monospecific treatments (associational susceptibility). Conversely, negative values indicate an overall reduction in harvest when in mixture compared to monospecific harvest (associational resistance).

MacMahon 1997, Anderson and MacMahon 2001). However, in our sagebrush plots the greatest amount of seed removed was at the mound clearing and again at 5 m from the mound. Various context-dependent factors have been noted to influence within habitat foraging patterns of ants, including resource availability, topographic features and associated obstacles including vegetation, intra-specific colony distance (i.e. competition) and predation risk (Azcárate and Peco 2003, Crist and MacMahon 1991). Similar factors have been suggested with foraging patterns of more mobile organisms (Garćia et al. 2011).

Such context dependence could arise in a number of ways. The increased density of *P. occidentalis* in cheatgrass-dominated communities could result in increased inter-colony competition, shifting foraging closer to the mound in contrast to more diffuse foraging in sagebrush communities. Vegetation structure might also contribute to the differing distance patterns. Because *P. occidentalis* foragers have greater running speeds and net energetic gain when using trunk trails, they tend to use cleared paths over vegetated areas (Fewell 1988). Because cheatgrass can thickly reinvade cleared trails annually, it likely impedes the use of foraging trails in areas with high cheatgrass densities, concentrating foraging nearer to nests. In contrast, trails likely remain clear for longer periods in sagebrush communities where cheatgrass is much less dense, facilitating foraging at greater distances from the nest. Foraging trails radiating from mounds in cheatgrass-dominated sites are very difficult to locate at distances of greater than 2 or 3 m, while they are easily located at distances of more than 5 m in sagebrush plots. Further, the complete loss of shrubs in cheatgrass-dominated plots could also help explain the reduced seed removal at more distant locations from mounds in these plots since shrub structure is thought to provide visual references for foraging *P. occidentalis* (Crist and MacMahon 1991).

Lastly, it is possible that the overall patterns of distance-dependent seed harvesting were not strong in sagebrush due to using a maximum distance of 5 m. Others have found that harvest and/or selectivity shifted at distances >9 m (Kelrick et al. 1986), at 7 m (Crist and MacMahon 1991), and >10 m (Davidson 1978) from the mound. Unfortunately, we were constrained to a 5 m limit in this study due to the very high mound densities in cheatgrass-dominated plots.

Small scale effects: mixed species seed neighborhoods and associational effects

The occurrence of altered susceptibility to attack due to local or small scale resource neighborhoods has received much attention with plants and herbivores but much less with seed consumers. The susceptibility of a seed species to attack by granivores depends on conditions of the local environment, on the seed species' abundance and associated traits, and on the availability of other seed species (Veech 2000, Azcárate and Peco 2003). Our study on seed harvesting ants corroborates these results as well as other resource–consumer systems (Bee et al. 2009). Generally, patterns of removal of non-*B. tectorum* seeds in mixture with *B. tectorum* differed from patterns of removal for the same species in monospecific treatments, suggesting seed neighborhoods matter. Moreover, in most cases significantly lower proportions of seeds were removed when in combination with *B. tectorum* than when in monospecific patches. To our knowledge, this is the first study looking at within-patch effects on seed removal by seed harvesting ants. Thus, although our results are contrary to our prediction, our null prediction was a default based on a lack of previous research with ants, although this issue has been addressed with rodent granivores (Veech 2000, 2001, Caccia et al. 2006). For example, Veech (2001) found a negative indirect effect of highly preferred *Oryzopsis hymenoides* (*A. hymenoides*) seeds on less preferred *Astragalus cicer* seeds, due to rodents foraging less in patches with only *A. cicer* seeds than in patches with seed mixtures. In contrast, *A. cicer* did not affect harvest of *O. hymenoides*.

While the nature of our design had limitations for rigorously testing associational interactions among seeds, even still our results strongly suggest that *B. tectorum* seeds provided associational resistance to seeds of the other species. Thus, in contrast to Veech (2001), it appeared that the less preferred species affected the fate of the more desirable species. This is compatible with theory (Atsatt and O'Dowd 1976). Predation on desirable seeds could be reduced when in an undesirable seed neighborhood that repels seed predators (McNaughton 1978, Atsatt and O'Dowd 1976, Hay 1986), resulting in protection from predation. Similarly selectivity should increase where increased abundances of desirable resources occur (Wilby and Shachak 2000). Such associational resistance (Tahvanainen and Root 1972) has been documented in herbivory studies

(Holmes and Jepson-Innes 1989, Callaway et al. 2005, Bee et al. 2009), and strongly suggested now for seed-harvesting ants.

Causes of context dependence and associational effects in this study are unknown. Given the chemical sensitivity of ants, it is possible that target seeds simply were less detectable when in mixture with cheatgrass seeds. Alternatively, the persistent awns on cheatgrass might increase the handling time of more desirable seeds in mixture, diminishing their desirability, as predicted by foraging theory (Charnov 1976). In this scenario, the seed patch as a whole would be less preferred if handling time increased due to the presence of cheatgrass in the patch.

Interestingly, associational resistance appeared to be greater in sagebrush than in cheatgrass-dominated plots. In addition, when ants encountered seed mixtures they tended to disproportionately harvest non-*B. tectorum* seed in cheatgrass-dominated plots but disproportionately harvest *B. tectorum* seed in sagebrush plots, despite the overall low preference for *B. tectorum*. These results highlight the strong interaction between spatial scales, and are likely related to the overall background seed communities. Cheatgrass-dominated plots clearly had much greater quantities of cheatgrass in the background seed pool than did sagebrush plots. Thus, in cheatgrass-dominated communities all available desirable seeds are likely mixed with many cheatgrass seeds so that ants abandoning such mixed seed patches are unlikely to gain by encountering a more pure desirable seed patch. In contrast, mixed patches with many cheatgrass seeds are probably less common in sagebrush communities and abandoning these mixed patches likely leads to encountering higher quality patches with a greater relative abundance of more desirable seeds.

Combined effects: context dependence is extensive

Foragers are able to simultaneously negotiate and evaluate several scales prior to selecting resources. The net effects of consumer foraging decisions are a result of the sum of interactions among choices made at a range of spatial scales (Miller et al. 2009). However, most studies have evaluated consumers that are able to move across large tracks of land and make foraging decisions based on factors associated with landscape scales and then smaller scale characteristics. For example, red deer select vegetation patches within a landscape based on the relative quality of the overall patch and then select which individual plants to eat based on the relative qualities of individuals in the patch (Bee et al. 2009). In contrast, the seed harvesting ants evaluated in this study do not individually or even at a colony level move across the community types considered, yet we demonstrated a strong interaction among plant community, distance, and seed neighborhood. As shown here the interactive effects of multi scale processes suggest that seed harvesting is a complex outcome of processes occurring across a variety of spatial scales, even for foragers that are more fixed in location compared to larger vertebrate consumers. Our results demonstrate that we cannot completely understand the effect of distance from a nest without also understanding the effects of plant community and seed neighborhood.

Invasive species and interactive effects among scales

In North American arid systems granivory is arguably the most critical plant–animal interaction in terms of shaping patterns of plant population dynamics and community structure (Heske et al. 1993, Longland et al. 2001). The two most abundant and potentially important granivore groups in the Great Basin Desert, rodents and ants, differed significantly in total abundance between intact sagebrush sites and nearby sites that had undergone type conversion to invasive annual cheatgrass communities (Ostoja and Schupp 2009, Ostoja et al. 2009). With such marked shifts in consumer communities it is reasonable to expect some translation to higher order effects such as seed–seed consumer interactions. Patterns of consumer foraging effort across community types (our large scale) have been shown to differ in other systems (Garćia et al. 2011), which may in part explain the variation among the cheatgrass and sagebrush sites but it is important to recognize that human alterations have altered ant foraging patterns in other systems as well (Díaz 1992). The occurrence of differential harvest among vegetation types demonstrated in the current study is not unexpected, but is noteworthy in the context of one of the systems having been recently converted from a native shrubland to an annual grassland. It is possible that the manner in which granivores interact with native seeds (i.e. increased survival) when in the context of the more abundant cheatgrass seed present in the background seed neighborhood may shape plant community patterns in time. How these resultant dynamics of seed survival translate to potential patterns within the plant populations individually is not known, but effects are likely (Avgar et al. 2008).

Ants appear to induce associational resistance to all but one native seed species when present with cheatgrass, however the effect is weakened in the cheatgrass sites compared to the sagebrush sites. Because native seeds are already rare, if present, in cheatgrass-dominated communities, it is encouraging that they are not increasingly more susceptible to harvest by ants when present with cheatgrass in the background seed neighborhood. Because ants are primarily considered seed predators in this ecosystem, seed harvest will likely reduce the chances of subsequent dispersal and future germination and establishment which could be dire for increasing or even retaining native plants within the invaded landscape.

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Supplementary material (available as Appendix O19969 at <www.oikosoffice.lu.se/appendix>). Appendix A1–A5.