Caching rodents disproportionately disperse seed beneath invasive grass

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Abstract.   Seed dispersal by caching rodents is a context-dependent mutualism in many systems. Plants benefit when seed remaining in shallow caches germinates before being eaten, often gaining protection from beetles and a favorable microsite in the process. Caching in highly unfavorable microsites, conversely, could undermine the dispersal benefit for the plant. Plant invasions could disrupt dispersal benefits of seed caching by attracting rodents to the protection of a dense invasive canopy which inhibits the establishment of native seedlings beneath it. To determine whether rodents disproportionately cache seed under the dense canopy of an invasive grass in southeastern Arizona, we used nontoxic fluorescent powder and ultraviolet light to locate caches of seed offered to rodents in the field. We fitted a general habitat-use model, which showed that disproportionate use of plant cover by caching rodents (principally *Chaetodipus* spp.) increased with moonlight. Across all moon phases, when rodents cached under plants, they cached under the invasive grass disproportionately to its relative cover. A greenhouse experiment showed that proximity to the invasive grass reduced the growth and survival of seedlings of a common native tree (*Parkinsonia microphylla*) whose seeds are dispersed by caching rodents. Biased dispersal of native seed to the base of an invasive grass could magnify the competitive effect of this grass on native plants, further reducing their recruitment and magnifying the effect of the invasion.

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INTRODUCTION

Plant invasions in many parts of the world are reducing the abundance of native plants and altering important species interactions (Vitousek et al. 1997, Shea and Chesson 2002, Levine et al. 2003). Among the important affected species interactions are seed-dispersal mutualisms (Traveset and Richardson 2014). Animal-mediated dispersal associated with foraging occurs primarily through two main mechanisms: frugivory and seed caching (Vander Wall and Beck 2012). Dispersal of native seed can be disrupted by invasive plants bearing attractive fruits, as these can satiate frugivores that then ignore native fruits, which then remain under the parent plant (Heleno et al. 2013, Mokotjomela et al. 2013). In contrast, seed-caching mutualisms, in which animals harvest beyond satiation, should not be disrupted in the same way because satiation does not deter harvest and caching of even less desirable seed. Such mutualisms could be disrupted, however, if seed were transported disproportionately to sites where it has little chance of germinating or surviving. Invasive plants could cause such a disruption by providing a novel, attractive

caching site where native seedlings cannot establish (Traveset and Richardson 2014).

Seed caching is a context-dependent seed-dispersal mutualism (Vander Wall and Beck 2012). It arises when granivorous rodents (Theimer 2005) or birds (Cristol 2005) collect more seed than they can consume and cache the excess in shallow scatter-hoards (Price and Jenkins 1986). Some scatter-hoarded seed remains there if the cacher dies or forgets the cache, or seed may germinate quickly before the cacher returns; in the meantime, such scatter-hoarded seed gains protection from immediate consumption by beetles (McAuliffe 1990), often in a favorable microhabitat for establishment (Vander Wall 1997). Under these conditions, plants may receive a net benefit from harvest by caching animals (Price and Jenkins 1986, Longland et al. 2001). Although animal-mediated seed dispersal may be a facultative mutualism that is not required for establishment in some plant species, others depend on caching to prevent high mortality from beetles and other consumers (McAuliffe 1990). Additionally, although caching interactions may be diffuse, with multiple species caching seed from the same plant populations (Vander Wall and Beck 2012), the mutualism could be disrupted if the disperser community overall shifted to caching seed in sites unfavorable for establishment. The importance of microsites in plant establishment is likely highest in open arid and semiarid landscapes, or in deeply shaded forests (Vander Wall and Beck 2012). The widespread invasion of semiarid regions by dense C_4 grasses (D'Antonio and Vitousek 1992, Williams and Baruch 2000) could therefore undermine the dispersal benefits of caching for plants there, especially where grasses interact with the cover-seeking behavior of caching granivores. These caching animals could magnify the competitive effect of invasive plants on native vegetation by increasing the proximity of native seed to invasive grasses disproportionate to their cover on the landscape.

Heteromyid rodents (pocket mice and kangaroo rats), common seed-caching granivores across southwestern North America, can function as net mutualists for some plants. Tracking seed fates for *Oryzopsis hymenoides* with and without the presence of rodents demonstrated a net increase in seed survival and germination from rodent activity (Longland et al. 2001). Observations of desert plants such as *Simmondsia chinensis* (Sherbrooke 1976, 1977) and *Parkinsonia microphylla* (McAuliffe 1986, 1990) successfully establishing primarily from rodent caches have led to hypotheses that scatter-hoarding by heteromyids can be an important dispersal mutualism for these species. The survival of *P. microphylla* seed increased when scatter-hoarded by rodents, as shallow burial prevented more destructive bruchid beetle predation (McAuliffe 1990).

The foraging and caching behavior of the larger, bipedal heteromyid genus *Dipodomys* (kangaroo rats) has often been studies in comparison with that of the smaller, quadrupedal genera *Chaetodipus* and *Perognathus* (pocket mice). The quadrupedal genera in particular have a well-documented tendency to forage for and scatter-hoard seed under cover (e.g., in Swartz et al. 2010). Manipulations of owl presence and illumination have demonstrated that cover-seeking in heteromyids is related to the risk of predation by owls (Brown et al. 1988). In that sense, owl predation risk may drive biased dispersal of seeds cached by quadrupedal heteromyids such as *Chaetodipus* to favorable microsites under native shrubs (McAuliffe 1986), providing a further benefit to scatter-hoarded seed (Vander Wall 1997, Vander Wall and Longland 2004). If an invasive plant provided superior cover from owls, however, the cover-seeking behavior of a site dominated by *Chaetodipus* rodents could result in seed being disproportionately dispersed to the base of that invasive plant.

Rocky slopes in the Sonoran Desert are being invaded by the dense C_4 bunchgrass *Pennisetum ciliare*, which is associated with lower abundances of native plants such as *P. microphylla* (Olsson et al. 2012*a*, *b*). The heteromyid community on rocky slopes tends to be dominated by the smaller quadrupedal species (Reichman and Vandegra 1973), which could drive biased dispersal toward the grass. Any negative effect of the invasive grass on the successful establishment of native seedlings could be increased if rodents disproportionately scatter-hoarded seed under the invasive grass.

In this study, we quantified the degree to which rodents cached seed under the invasive grass disproportionate to its local relative availability, and the effect that might have on

establishment of native seedlings. First, we conducted a greenhouse study to determine the effect of the mature grass on the establishment of seedlings of the native tree *P. microphylla*. We focused on this tree because it is common on invaded hillsides and is one of the species suggested to benefit from heteromyid caching and potentially facilitation by native shrubs (McAuliffe 1990). We studied caching behavior in the field at a grass-invaded site by offering seed trays dusted in fluorescent powder, then using handheld ultraviolet light to follow rodent trails and locate caches. Using a model of resource selection and availability, we estimated how the propensity to cache seed under the invasive grass interacted with its local cover. We expected that caching under the grass would be consistently more attractive to rodents, particularly quadrupedal heteromyids, due to its dense canopy.

METHODS

Greenhouse experiment

To determine how proximity to the invasive grass affects germination or survival of a native seedling in the absence of consumers, we planted 24 scarified seeds of the native tree *Parkinsonia microphylla* in each of 18 tubs outside the greenhouse at the University of Arizona in August 2013. Six of the tubs received mature tussocks of invasive grass transplanted from the Tucson Mountains. Six other tubs received mature individuals of a native shrub, *Ambrosia deltoidea*, which is a common ground cover of similar height and diameter to the invasive grass, and which has been suggested to facilitate seedling survival (McAuliffe 1986). The final six tubs had no adult plant. All tubs contained soil from the Tucson Mountains. Tubs were arranged randomly within spatial blocks of equal numbers of adult plant treatments. Supplemental water (4 s daily, 5 d/week) was provided throughout the five-week experiment to provide conditions suitable for seedling establishment. Temperatures during the experiment ranged from 19° to 42°C, with 10–94% relative humidity. We harvested the seedlings and then dried them for 3 d at 60°C before weighing them. We compared the percentage of seedlings germinating in each tub, percentage surviving in each tub at harvest, and mean biomass per surviving seedling between adult plant treatment levels. For the analysis, we used linear mixed models in package lme4 (Bates et al. 2014) in R v. 3.2.2 (R Core Team 2015), with spatial block as a random effect.

Field study site and species

The caching experiment was conducted on a rocky slope invaded by *Pennisetum ciliare* near Tucson, Arizona (32°10′50″ N, 111°02′00″ W, elevation 830 m), typical of invaded sites (Abella et al. 2012). The soil is shallow, well-drained, and rocky, with rocky outcroppings. Dominant native perennials include *P. microphylla* and *Simmondsia chinensis*, both of which potentially benefit from caching by heteromyids (Sherbrooke 1976, 1977, McAuliffe 1990). Where *P. ciliare* is absent, the habitat is open, with substantial bare ground between dispersed shrubs, trees, and succulents. Average annual rainfall is approximately 300 mm, with about half arriving as summer thunderstorms (WRCC 2015).

Although our question and methods focus on the overall effects of a community of caching granivores, because the hypothesis in large part derives from literature on heteromyid behavior it is worth noting that likely granivorous rodents at the site based on habitat characteristics include the genera *Chaetodipus*, *Neotoma*, and *Peromyscus*. The species of *Chaetodipus* most likely present based on habitat, in-person observations, and video recordings was *C. intermedius*, although *C. baileyi* could also potentially inhabit the site (Reichman and Vandegra 1973). The only species of *Neotoma* (*N. albigula*) and most likely species of *Peromyscus* (*P. eremicus*) present at this site have not been recorded to make shallow scatter-hoarding caches, although other members of both *Neotoma* have been seen to larder-hoard (Post and Reichman 1991) and some other species of *Peromyscus* do scatter-hoard (Vander Wall et al. 2001, Hollander and Vander Wall 2004).

Sampling design

To locate recent rodent caches, we provided trays of seed dusted in fluorescent powder on eight nights between July and September 2015 (Appendix S1), a period when rodent activity tends to be high (Reichman and Vandegra 1973). Each paper tray, 15 cm in diameter, was covered in approximately 0.75 g of loose nontoxic fluorescent powder (Glow, Severn, Maryland, USA)

and 14 g of millet that had been coated previously in fluorescent powder. Millet is often used for field studies of desert rodents because it is within the size range of available native seed (Price 1983) and is an attractive resource that elicits a large response. It is an order of magnitude smaller than the seeds of *P. microphylla* used in the greenhouse study, although it is on par with the size of some native seeds, which thus provides more opportunity for rodents to subdivide their harvest into caches. Approximately 50 trays were arranged in a grid at sunset, with each tray approximately 5 m from the next, although they were often much farther in practice, especially as we excluded potential grid points that did not have at least one *P. ciliare* individual within 3 m. This spacing provided a compromise between spacing trays far enough apart that foraging animals would not detect a continuous array, while providing sufficient coverage of the landscape that the trays would attract sometimes sparsely spaced rodents. For each survey, we returned 24 h later with handheld ultraviolet lights to search for caches. On subsequent surveys, we located a new grid adjacent to, but not overlapping with, previous grids, to avoid resampling locations and animals.

Locating caches

To find caches, we employed a technique similar to that of Longland and Clements (1995) by following fluorescing rodent trails leading from the trays, scanning for visible fluorescing seed or signs of disturbed soil. We considered a cache to be a group of three or more seeds in contact with one another that were separated clearly from the tray, such that they were unlikely to have spilled together. For each cache, we recorded the plant species canopy directly over the seed, if any, the estimated number of individual grains (as it was not always possible to recover whole caches from the rocky substrate), and the distance to the tray from which the cache was made. Trails were almost always sufficiently distinct to determine which tray had been visited. From the second survey onward, we measured the mass of seed remaining at each tray. From the third survey onward, we recorded all animal types that might have visited the tray based on fluorescing footprints correlated with video data. We verified our ability to identify rodent trails to genus by

examining fluorescent trails made from trays whose visitors were captured by wildlife cameras. On 25 May and 6 June 2015, we set up eight motion-triggered infrared wildlife video cameras (Bushnell Trophy Cams) approximately 0.5 m away from seed trays with fluorescent powder to survey granivores present at the site and ensure we could distinguish their tracks. Rodent genera created tracks that were distinct from one another. *Neotoma* and *Chaetodipus* could appear superficially similar, but were usually distinguishable by size and by destination to a midden or a burrow. Tracks by *Peromyscus* were more distinct in movement and were typically correlated with small amounts of seed removed from the trays. Larger animals, such as squirrels, foxes, or birds, created larger areas of disturbance and clearer footprints. Thin, sinuous and continuous ant trails were easily visible and distinguishable. From the fourth survey onward, we recorded trails linking multiple trays that indicated that the same animal was foraging at both. In assigning caches to individual animals in earlier surveys before this was recorded, we took a conservative approach of assuming caches made from adjacent trays may have been made by the same individual. Caches of fluorescing seed are less visible under dense grass than under diffuse native shrubs or in the open. Although we did not measure detection probabilities, we were naturally more likely to underestimate the number of caches under *P. ciliare*. Our estimate of the rodents' disproportionate use of dense grass for caching is thus a conservative one. This research was conducted under IACUC protocol 15-586.

Quantifying vegetation cover

To quantify the vegetation locally available to animals under which they might scatter-hoard seed, we identified and measured plants within 3 m of trays, creating circular plots of 28 m². This scale was the largest feasible with trays typically just over 5 m apart and characterized the cover immediately available for caching rodents to use. We measured the average diameter of each plant to the nearest 10 cm. Plant diameters ranged from 0.3 to 4.0 m. We included only the portion of the plant within the plot for those on the border and accounted for overlapping plants by subtracting the area under two plants from the total. We measured vegetation cover for all trays

with caches and for an additional subsample of nine trays per survey grid to determine whether vegetation availability affected the probability of tray visitation or caching rates.

Model definition

We defined a general model for estimating disproportionate use of invasive grass from the probability p_i that cache i under some plant is under the invasive grass rather than under native vegetation. If rodents cache seed under plant types proportional to their relative cover, the null expectation of caching under the invasive grass would be its relative cover r_i near the tray from which cache i was made. Spatially random caching therefore results in $p_i = r_i$.

If rodents seek out the dense cover of the invasive grass for caching seed, their propensity for caching there may interact with the availability of the grass to determine the actual probability of caching under the invasive grass. We therefore introduced a parameter α for use disproportionate to availability that could be estimated with existing statistical methods and that maintained the scale at which the proportion of caches was measured (Chesson 1983). We defined the probability p_i of seed being cached under the invasive grass as a function of the grass's relative cover r_i and the parameter of disproportionate use α:

$$p_i = \frac{\alpha r_i}{(1 - \alpha)(1 - r_i) + \alpha r_i}. \tag{1}$$

When rodents exhibit no disproportionate likelihood of caching beneath the invasive grass, $\alpha = 0.5$ (odds of 1:1) and Eq. 1 simplifies to the null expectation of $p_i = r_i$. Estimation of α was made with binary logistic regression with Eq. 2 converted from a probability to an odds ratio that a cache is under the invasive grass (Chesson 1983):

$$\frac{p_i}{1 - p_i} = \left(\frac{\alpha}{1 - \alpha}\right)\left(\frac{r_i}{1 - r_i}\right). \tag{2}$$

The natural log both sides of Eq. 2 converts this formula into a logit model,

$$\ln\left(\frac{p_i}{1 - p_i}\right) = \ln\left(\frac{\alpha}{1 - \alpha}\right) + \ln\left(\frac{r_i}{1 - r_i}\right) \tag{3}$$

which can be fit to empirical data with common logit regression techniques (Appendix S2).

This general form for estimating disproportionate use of caching cover can be modified to account for additional factors known to affect rodent behavior, such as frequency-dependent use of cover types. The likelihood of caching under the invasive grass could change with its relative cover, as animals habituate to it or fill all space under it with caches. Such frequency-dependent disproportionate use of the grass would be reflected in the logit formulation by a slope not equal to 1.0 of the log-odds of the relative grass cover. To include moonlight in the model, which may affect cover-seeking behavior, we estimated a slope for how cache cover type changed with moon phase during survey j. Finally, disproportionate use could vary with differences between individual animals k (nested within surveys) or between survey grids due to variables not measured. We captured animal effects as random intercepts in the model of cache cover types.

The model is general for exploring disproportionate use of a resource type in any choice. Although described in detail for the probability of caching under the canopy of the invasive grass rather than under native vegetation, we also applied the same approach to whether caches were made under vegetation of any kind as opposed to in the open, based on the total vegetation cover v_{ijk}, and the log-odds of total vegetation cover.

Analysis

We modeled the probability p_{ijk} of caches under a plant being specifically under the invasive grass with a generalized linear mixed model (GLMM) with a logistic link and a binomial error structure, using package lme4 (Bates et al. 2014) in R version 3.2.3 (R Core Team 2015). We classified moon phase based on date, ranging from 0 at the new moon to 14 at the full moon. We included a random intercept structure for individual animal. We used a likelihood ratio test on the fitted model results for nested models including grass cover, moon, or their interaction to ask which factors affect caches being under the invasive grass (Bates 2010). We back-calculated the average animal's preference α and its bootstrapped 95% confidence interval from estimates of intercept β_0 and moonlight (if included as significant in the model). We considered whether

the slope of the log-odds of relative grass cover was different from one to determine whether use changed disproportionately with availability, using the bootstrapped 95% confidence interval.

Similarly, we fitted a GLMM with a binomial link function using lme4 (Bates et al. 2014) in R (R Core Team 2015) to ask whether the probability of caches being under vegetation of any kind, rather than in the open, varied with total vegetation cover and moonlight. We included animal nested within survey as a random intercept, compared the results of nested models with likelihood ratio tests (Bates 2010) for the fixed effects of vegetation cover, moon, and their interaction. We again back-calculated the average animal's preference α and its bootstrapped 95% confidence interval from estimates of intercept β_0 and other covariates when included in the best model. We considered whether the slope of the log-odds of vegetation cover was different than one, using the bootstrapped 95% confidence interval, to determine whether use changed disproportionately with availability.

We also assessed whether vegetation cover or grass cover differed between trays that were or were not visited by *Chaetodipus*, and whether they differed between visited trays with and without caches found, using linear mixed models with survey as a random effect in lme4 (Bates et al. 2014) in R v. 3.2.2 (R Core Team 2015).

RESULTS

Across all eight surveys, we located 99 caches, 74 of which were under vegetation and 45 of which were under *Pennisetum ciliare* (Appendix S1). Cache sizes varied from 12 grains to approximately 2,000 grains. Their structures varied from fully buried under loose soil to visible in an excavated depression and were sometimes under a pile of pebbles or deep in rock crevices. Distance from the tray to the cache ranged from 0.39 to 11.08 m, with a mean distance of 3.07 m and a median of 2.84 m.

All caches found were associated with tray visits and trails by either *Chaetodipus* or *Neotoma*. The majority of caches (93%) were associated with *Chaetodipus* trails, but we found four shallow caches (4% of total caches) clearly made by *Neotoma* and three other caches (3% of total) for which neither *Neotoma* nor *Chaetodipus* could be

ruled out as the cacher. We found no evidence of any other animals creating scatter-hoard caches.

We found that rodents cached seed under the invasive grass disproportionate to its availability. The following results are the model estimate followed by the 95% confidence interval. Disproportionate use α of the grass relative to native plants was 0.71 (0.56, 0.87), back-calculated from the intercept β_0 of 0.90 ($z = 2.10$, $P = 0.036$; red line, Fig. 1). Use of invasive grass for caching cover did not change significantly differently from proportional to its relative cover, as evidenced by its slope estimate interval containing 1.0 (0.24, 1.19).

Whether rodents cached seed disproportionately under plant cover overall depended on the level of illumination by moonlight. Near the new moon, rodents cached seed under vegetation roughly proportional to plant cover in the area, with α of 0.48 (0.20, 0.99). At the full moon, rodents cached seed under plant cover disproportionately relative to available area, with α of 0.90 (0.79, 1.00; blue line, Fig. 1). Despite the overlap of these confidence intervals, the slope β_2 of the moon phase of 0.18 (−0.030, 0.31) is significantly different from zero ($z = 2.46$, $P = 0.014$), meaning that α changes significantly with moon phase. Use of vegetation overall did
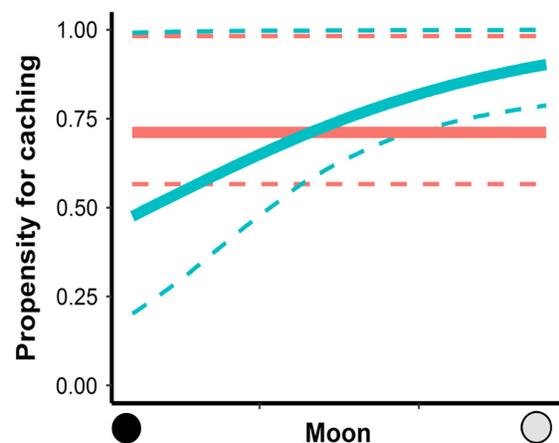

Fig. 1. Disproportionate use (α) of the invasive grass relative to native plants (red line). Disproportionate use (α) of vegetation cover (blue line) rather than open cache sites occurred only with fuller moon phases. Dashed lines indicate bootstrapped 95% confidence intervals.

not change significantly differently from proportionally in relation to percent cover, as evidenced by its slope estimate interval containing 1.0 (−3.11, 2.24).

Relative grass cover was similar ($t = −0.125$, $P = 0.90$) between trays visited by *Chaetodipus* (40.4% ± 7.84) and those not visited (41.3% ± 11.56). Overall vegetation cover was also similar ($t = −1.81$, $P = 0.07$) between trays with (55.0% ± 5.29) and without (62.9% ± 8.04) *Chaetodipus* visits. Vegetation cover ($t = 0.04$, $P = 0.97$) and grass cover ($t = 1.31$, $P = 0.19$) were similar between trays from which caches were (vegetation: 58.5% ± 4.70, relative cover of grass: 39.0% ± 6.67) and were not located (vegetation: 58.0% ± 4.90, relative cover of grass: 41.2% ± 7.06). When ants were the sole visitor type to a tray (11 trays), they removed only an average of 10.0% (±3.49) of available seed, and *Peromyscus* visits alone (6 trays) removed an average of 26.7% (±13.54) of seed. These low removal rates contrast with trays that had been visited only by *Chaetodipus* (161 trays) or *Neotoma* (12 trays), or disturbance from a larger animal such as a fox (6 trays), which all had more than 90% of the seed removed (*Chaetodipus*: 93.1 ± 2.72, *Neotoma*: 90.2 ± 10.33, other: 95.3 ± 9.23). Although cache sizes were larger on average under native vegetation (149.1 seeds ± 122.4) than under the invasive grass (62.6 seeds ± 43.3) or with no cover (82.4 seeds ± 38.8), their sizes varied substantially and their bootstrapped confidence intervals overlap substantially.

Presence of the invasive grass reduced the early survival of native seedlings in the greenhouse experiment (Fig. 2), though not their germination rates. *Parkinsonia microphylla* seeds germinated at similar rates when grown with the invasive grass (97.2% ± 1.56), with the native shrub (97.2% ± 2.43; $t = 0$, $P = 1.0$), and without any adult plant (94.4% ± 3.09; $t = −1.65$, $P = 0.13$). After five weeks, however, only two-thirds on average of seedlings grown with grass were still alive (66.4% ± 17.7), which was less than those grown with a native shrub (98.6% ± 2.36; $t = 4.11$, $P = 0.002$) or those grown without grass (98.5% ± 1.66; $t = 4.10$, $P = 0.002$; Fig. 2). The seedlings that did survive with grass had accumulated less than a quarter of the biomass (11.4 mg ± 4.06) of seedlings
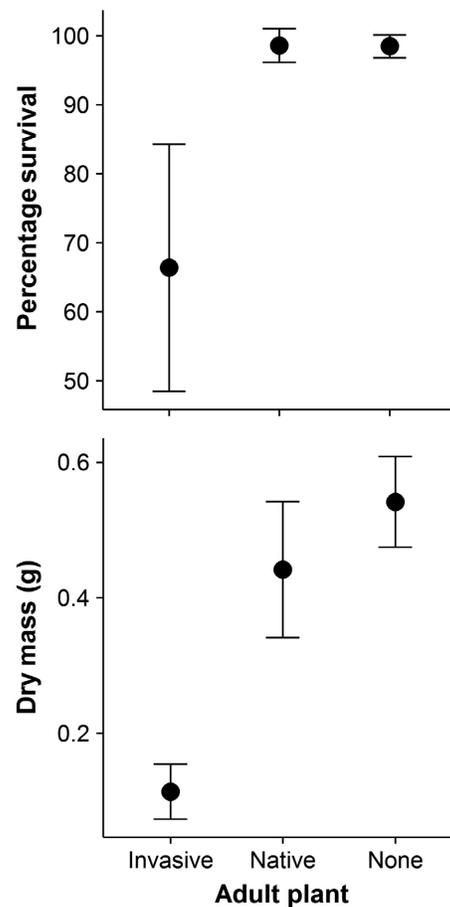

Fig. 2. Mean survival (top) and dry mass (bottom) of seedlings of the native tree *Parkinsonia microphylla* when grown in tubs with invasive grass, a native shrub, or the absence of a mature competitor. Survival is mean per tub ($n = 24$ seeds/tub), and dry mass is a mean per tub of per-seedling mass for those still surviving after five weeks.

grown with native plants (44.1 mg ± 9.94; $t = 5.87$, $P < 0.001$) or with no adult plant (54.2 mg ± 6.71; $t = 7.66$, $P < 0.001$).

DISCUSSION

We found that rodents disproportionately cached seed under the invasive grass *Pennisetum ciliare* rather than under native plants at our study site, given equal availability (red line, Fig. 1). The preference for caching under cover is consistent with studies of other heteromyids (e.g., *Perognathus longimembris*) that more often

cache seed under plant cover than in the open (Swartz et al. 2010). Foraging under cover has been associated with predation risk from owls (Brown 1988), which could explain why the denser canopies of the invasive grass are more heavily used. We also found that the cover-seeking caching more generally increased with brighter moon phases at our site, which agrees with past work showing that quadrupedal heteromyids increasingly seek cover in response to greater illumination (Brown et al. 1988).

We were primarily interested in quantifying the overall effect of seed caching by the community of rodent granivores from a plant's perspective rather than quantifying the dynamics of any given rodent species. Nevertheless, our hypothesis was driven by the past work on behavior of quadrupedal heteromyids, which we expected to be prevalent on rocky hillsides. The majority of tray visits and seed removals were indeed by *Chaetodipus*, judging from trail patterns, the burrows trails led to, and personal observations of *Chaetodipus* individuals covered in fluorescent powder during surveys. Although *Neotoma* also appeared to cache seed, their caches were also near the invasive grass, and the overall outcome matters more to the plant populations than the specific actor. Nonrodent granivores did not remove enough seed to interfere with these results in this case. Ants are the other major class of granivores typically considered in seed-removal studies in the Sonoran Desert (e.g., Reichman 1979), but accounted for very low seed removal overall in our study. Very few trays (2.9%) in this experiment were visited only by ants, and those had an average of 10% of the seed removed, compared with trays visited only by *Chaetodipus* (41.8%), which removed on average more than 90% of the seed.

Heteromyid rodents actively move seed between scatter-hoards and also to their burrows (Reichman 1979, Longland et al. 2001, Swartz et al. 2010), as do other caching rodents (Hirsch et al. 2012, Yi et al. 2014), and they also pilfer one another's caches (Pyare and Longland 2000, Leaver and Daly 2001, Longland et al. 2001, Murray et al. 2006). Our results likely best reflect initial scatter-hoarding sites, as surveys were completed only 24 h after seed was offered, although secondary management of rapidly made caches or even pilfering could already have

occurred. Other studies have found that pilfered seed can be recached within a single night, again under or near shrub cover (Swartz et al. 2010). Seedlings germinating under the canopy of the invasive grass, whether seed was placed there during initial or secondary caching, will experience the competitive effects of the grass.

Our greenhouse results demonstrated that although the invasive grass does not inhibit germination of a native tree, *Parkinsonia microphylla*, under favorable water conditions, it reduces survival and growth within the first month of life (Fig. 2). The growth and survival of native tree seedlings under a native shrub of similar stature to the grass, on the other hand, were indistinguishable from that of seedlings grown with no adult plant. Like many C_4 grasses, *P. ciliare* is a strong competitor due to its high water-use efficiency (Cox et al. 1988, Williams and Black 1994, Stevens and Fehmi 2009, Ens et al. 2015), nitrogen-use efficiency (Sage and Zhu 2011, Ens et al. 2015), and a dense, fibrous network of roots able to effectively take up resources as they become available (Carino and Daehler 2002, Bond 2008, Cech et al. 2010). Above ground, its dense canopy, while attractive to caching rodents, could also limit light availability for seedlings (Hoffmann and Haridasan 2008, Haling et al. 2013). Introduced pasture grasses can block several times as much radiation as the native legumes they compete with (Kalmbacher and Martin 1983, Cruz and Sinoquet 1994). By increasing the spatial overlap of native plants with the invasive grass, caching rodents would increase the total resource niche overlap of native plants and the invasive grass, increasing the likelihood that the inferior competitor would be excluded (Chesson and Kuang 2008).

Biased dispersal of seed to the base of *P. ciliare* individuals intensifies resource competition with the grass regardless of whether the rodents function as a net mutualist or consumer of native plants. In locations or years when rodents otherwise would serve as net mutualists (e.g., Longland et al. 2001), biased dispersal to such an unfavorable site could reduce the benefit or even lead to a net cost to the plant. In times or places where the caching rodents otherwise function as net consumers, the cost to the plants of having seed harvested and cached would further increase, as the few seeds that otherwise

might escape consumption and germinate would then be inhibited by the invasive grass. Future work should extend these results to quantifying the impact on population growth of native plants.

Mutualism disruption has received more attention where vertebrate pollinators and dispersers have gone extinct, raising concerns about the future of the widow species (Aslan et al. 2013). Our results suggest the potential for threats to positive interactions extend beyond vertebrate partner extinctions to include other disruptions of plant reproductive mutualisms. Granivory is an important dispersal syndrome in semiarid regions where seedlings sometimes require favorable microhabitats to successfully establish (Vander Wall and Beck 2012) and which are increasingly invaded by exotic grasses (Williams and Baruch 2000). Other communities in which seed-caching animals are important dispersers could therefore also experience disrupted seed dispersal due to grass invasions. Context-dependent mutualisms may be the most easily disrupted, as many context-dependent mutualists are sensitive to shifts in the relative abundance of the partners and the addition of third parties (Bronstein 1994). Disruption of mutualisms that are facultative and diffuse is considered less likely to have a large effect on the plant populations (Bond 1994), although changes in the outcome of interactions may be more common than is currently realized (Chamberlain et al. 2014).

Although we demonstrate behaviorally mediated changes to a potential seed-caching mutualism, future work should also consider how changes in rodent densities due to the grass might affect the context of such a context-dependent mutualism. Such disruptions can be used to better understand the outcome of species interactions on community composition (Shea and Chesson 2002, Ignace and Chesson 2014). The density of rodents affects whether seed caching on balance benefits plants because the quantity of seed remaining in caches during the germination window depends on each consumer collecting more than they will eat (Price and Jenkins 1986, Theimer 2005). Thus, seed caching is more likely to be a net mutualism in years or locations where rodents are at low density relative to the seed produced (Vander Wall 2010). This may occur as a result of masting or of weather patterns driving large fluctuations in seed production, with rodent populations lagging (Zhang et al. 2008, Vander Wall 2010). The addition of a new plant species to the community, especially a water-efficient prolific seed producer, could buffer the variability in seed availability, maintaining a higher minimum rodent density than was previously present, and reducing the benefit of high seed-production years for native plants.

Conclusions

We found evidence consistent with the disruption of a context-dependent dispersal mutualism through seed caching. To our knowledge, this is the first evidence that seed-caching dispersal mutualisms could be disrupted by grass invasions. Behavioral interactions of caching consumers at this site increase the spatial proximity of native plants to an invasive grass, potentially undermining the benefits of dispersal by caching for native plants, and increasing the competitive overlap of the invasive grass with native plants. As grass invasions increasingly change ecological contexts of the invaded communities, they may reveal more interactions to be context-dependent than previously realized. The outcomes of interactions between mutualism, predation, and competition may be heavily influenced by behavioral responses that generate spatial and ultimately population-level consequences.

Acknowledgments

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