RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

PRACTICE AND TECHNICAL ARTICLE

THEMATIC SERIES Arid Lands

Granivorous ants prefer small and unprotected seeds—implications for restoration in arid ecosystems

Trace E. Martyn[1,2,3], Christina L. Kwapich[4], Albert Kline[1], Elise S. Gornish[1]

Successful seed-based restoration in dryland systems is difficult due to the many limitations associated with germination and establishment. Seed predators, including granivorous ants, can consume or move applied seeds offsite reducing restoration success. Granivorous ants in the U.S. southwest move and store tens of thousands of seeds and show preferences for seeds based on weight, size, nutrient content, and novelty. In this study, we examine which seed traits most influence seed predation rates in a grassland in southwestern Arizona, U.S.A. We presented 24 seed types from native species with restoration value in three cafeteria-style selection areas installed adjacent to *Pogonomyrmex* nests. We also installed pitfall traps to assess the diversity of ant species that may have visited the cafeterias. Our results showed that among offered seeds, 3–99% were collected by granivorous ants, with small seeds and those with no structure the most preferred. Across all cafeterias, we had 11 ant species in our pitfall traps, with over half of those being known seed predators. From our study, we found that seed traits do influence ant seed preference and our results can help inform practices that could aid in keeping seed on the ground and increasing the chance of germination and establishment.

Key words: ant-seed predation, granivory, *Pogonomyrmex*, seed traits

Implications for Practice

- Consider using larger-seeded species in restoration mixes and including seeds with a variety of structures on or surrounding the seed.
- Reducing the amount of processing of the seed to maintain seed coatings and other seed structures (awns, pappus) reduced ant predation, though impacts of reduced processing on germination probability need to be considered for restoration application.
- Seeds used in restoration should be in low density and away from obvious ant nests to reduce seed predation.

Introduction

Successful seed-based restoration in dryland systems is difficult due to the many limitations associated with germination and establishment (Kildisheva et al. 2016). Generally, managers tend to identify drought and heat stress (Balazs et al. 2020), herbivory (Pearson et al. 2019), and competition with other plants (Rinella et al. 2015) as some of the more critical challenges for effective revegetation. However, these biotic and abiotic conditions only become a significant obstacle to restoration if germination occurs, which is only possible if seed remains on the ground. Several studies, however, suggest that for many restoration projects, seeds are not maintained in the location where they are broadcast, and instead are consumed or moved offsite (DeFalco et al. 2010; Suazo et al. 2013; Elliott et al. 2021).

In dryland systems, there is a high potential for restoration to fail due to significant seed loss by granivory (Elliott et al. 2021). For example, one study found that, collectively, granivorous ants and rodents removed on average circa 40% of seed from nine different species over 1 year on a restoration site (Suazo et al. 2013). Another study described percent seed taken ranging from 28% of the seed in early summer and 54% of seed in late summer (primarily driven by an increase in insect predation; Linabury et al. 2019). It appears that seed-based restoration projects can be dissimilarly affected by such seed predation and for projects implemented in the summer in particular, insect-based seed predation could be an issue. This is clearly a critical challenge that needs to be addressed as a majority of seed-based projects in the U.S. southwest are implemented in the summer before the monsoon (as this is the critical time when most of the annual rain occurs in this area; e.g. Abella 2009).

Granivorous insects are known to be key ecosystem engineers of arid plant communities (Clive et al. 1994; Folgarait 1998) and

Author contributions: TEM, CLK, ESG developed the project; TEM, AK implemented the research; TEM wrote the manuscript with contributions from all authors.

[1]School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ 85721, U.S.A.
[2]Address correspondence to T. Martyn, email martyn.ecology@gmail.com
[3]Present address: Yale School of the Environmental, Yale University, New Haven, CT 06511, U.S.A.
[4]Department of Biological Sciences, The University of Massachusetts Lowell, Lowell, MA 01854, U.S.A.

doi: 10.1111/rec.13759
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.13759/suppinfo

ants, especially, create complex relationships with seeds, interacting with them in many ways, including as dispersers, predators, and parasites (reviewed in Penn & Crist 2018). In arid and semiarid regions in the United States, the most common granivorous ants are harvester ants in the genera *Pogonomyrmex*, *Pheidole*, *Solenopsis*, and *Veromessor* (Brown et al. 1979; Johnson 2000). These ants can move and store tens of thousands of seeds each season and have been shown to collect a wide variety of seeds across U.S. dryland and forest landscapes. In the Sonoran Desert, *Veromessor pergandei* colonies harvest enough seeds to produce 3.4 kg of dry, insect biomass per hectare, each year (Kwapich et al. 2017). Likewise, *Pogonomyrmex rugosus* colonies store up to 70 mg of seeds per worker (Mackay 1981; MacKay 1984), while mature *Pogonomyrmex badius* colonies can amass a cache of 300,000 seeds, representing up to 58 species from 20 plant families (Tschinkel & Domınguez 2017). Even very large seeds are not safe from some *Pogonomyrmex* species, which rely on germination, rather than mechanical processing to access seeds. By waiting for large seeds to germinate in underground chambers, the ants increase the upper range of seed sizes available to them (Tschinkel & Kwapich 2016).

Despite collecting numerous seeds, harvester ant foragers are selective and discriminate among the breadth of available seed species in their environment, including novel seeds. Attributes influencing seed preference include ant body size (Holldobler 1976; Hansen 1978; Chew & Chew 1980), relative seed availability (Davison 1982), seed novelty (Fewell & Harrison 1991), seed caloric value (Pirk & de Casenave 2010), and seed lipid content (Gordon 1980). Since seed traits appear to be critical for ant choice and handling, these traits might provide utility for addressing seed predation in a restoration setting.

When developing seed mixes for human-mediated restoration work, seed traits are rarely considered (Chambers & Macmahon 1994). To keep seed on the landscape where it is initially deployed, it is important to understand the relationship between seed traits and seed predation to help inform restoration seed mixes. Here, we test two main questions: (1) What is the ant predation rate on 20 commonly used native grass and forb species? and (2) What seed traits influence this predation rate?

Methods

Cafeteria Study

We installed a cafeteria study in September 2020 on a private ranch in the Altar Valley, southwest of Tucson, Arizona. Our study area was within a horse pasture dominated by invasive Lehmann's lovegrass (*Eragrostis lehmanniana* Nees), mesquite (*Prosopis* sp.), and various native grasses and forbs. It has a loamy soil, an average annual precipitation of 620 mm, an annual maximum temperature of 27.2°C, and an annual minimum temperature of 8.4°C.

We selected three ant mounds of the same granivorous ant species (*Pogonomyrmex rugosus*) to establish our study. In this area, *P. rugosus* mounds are large in diameter with noticeable foraging trunks and have 1–2 m of vegetation cleared around each mound. Cafeterias were installed approximately 5 m away from the mound, adjacent to an established ant trail on the right-hand side of the trail when facing the ant mound. We dug a shallow pit and installed 24 petri dishes in five rows (Fig. 1) at each cafeteria, covered with 0.6 cm mesh to prevent rodent- and bird-seed predation. We used petri dishes with masking tape added to the edges for ease of ant entrance and exit from the trays (Jacob et al. 2006). We used seed from 20 different species of common restoration species from a local native seed distributor, Borderlands Restoration (Table S1; Borderlands Restoration Network 2021). Species were chosen based on their use among local restoration projects (Gornish unpublished data) as well as requests by the landowner. In addition to the 20 species of non-modified seeds, we also included 4 replicates of seeds without the seed coat, for a total of 24 seed types. We modified seeds for four species by removing the seed coat (for grass, this consisted of lemma, palea) with tweezers by hand: three grasses

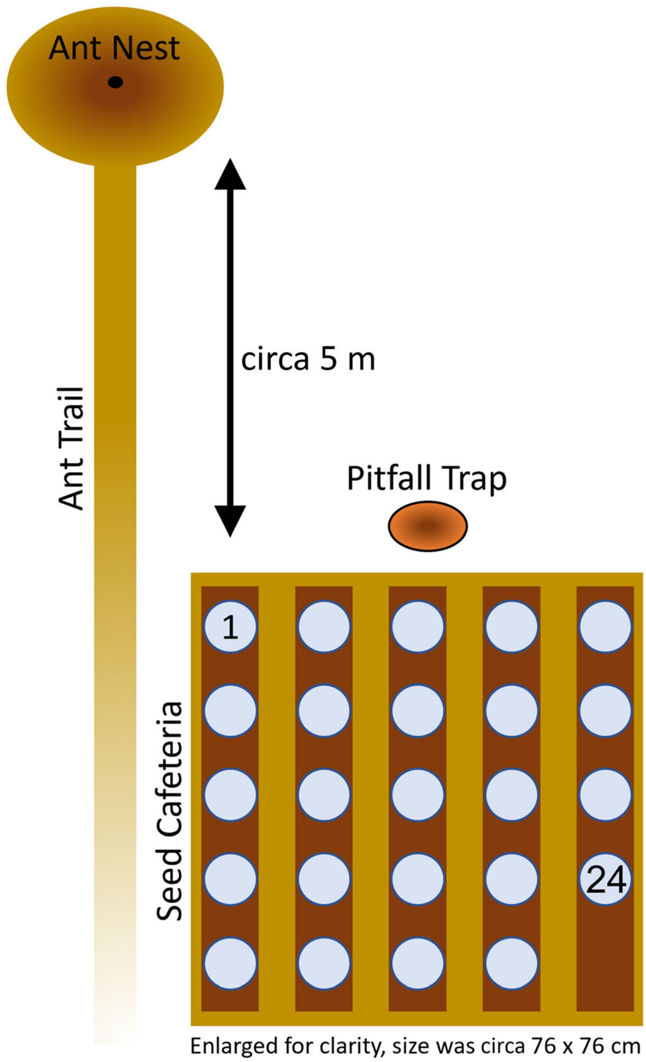

Figure 1. Diagram of experiment location and layout. Notably, 24 petri dishes were laid in 5 rows within the cafeteria approximately 5 m away from the ant mound (see first and last dish labeled). The pitfall trap was established at the top of the middle row of the cafeteria.

(*Bouteloua gracilis*, *Bouteloua curtipendula*, and *Bothriochloa barbinodis*) and one forb (*Sphaeralcea ambigua*). We chose these three grass species because of ease of seed coat removal and representation of seed coatings (coat and hair coat) and we chose the forb because it was the only forb with a papery seed coat (Table S1). For each trial, 100 seeds of each seed type were placed in an individual petri dish; however, because of lack of availability of *Helianthus annus* seed, we only used 80 seeds for each trial. We randomly assigned each seed type to a different petri dish for each cafeteria. We added seed to the petri dishes in the late afternoon, at the peak of ant activity, and collected the dishes at the same time the following day. We then left the cafeterias empty for 24 hours before repeating the trial. We repeated the trial three times over the course of 7 days. Weather was similar across all trials. For each trial, we randomly assigned the location of each seed type. After dishes were collected from the field, they were brought into the lab and remaining seeds were counted. If a seed was stuck to the masking tape, that seed was counted as "unavailable" and not included in the calculation for proportion taken. We calculated proportion seed taken as:

$$\text{Proportion taken} = 1 - \frac{\text{Number of seeds remaining}}{\text{Number of seeds available}}$$

We chose locations specifically to capture seed predation rates for *P. rugosus*, however, we also wanted to determine the entire species composition of ants that visited the cafeterias. To do this, we installed one pitfall trap beside each cafeteria. Pitfall traps were made out of a plastic cup and funnel installed so the lip of the funnel was level with the ground. Pitfalls were installed on the edge of the cafeteria closest to the *Pogonomyrmex rugosus* nest and in line with the center row of the cafeteria's dishes (Fig. 1). We installed the pitfalls 24 hours after we first placed seed on the cafeterias. The pitfall traps were emptied and reinstalled every 24 hours and we kept the pitfall traps open for four consecutive days (despite 2 of the days not having seed installed) so that we could acquire a complete picture of the ant species composition surrounding the site. Ants were transported to the lab and frozen at −30°C. Ants were then identified to species when possible and quantified for each cafeteria for each day. In some instances, ants were damaged or we did not have sufficient data to identify to species, in such cases samples were identified to genus. We then identified which ant species were potential or known seed predators, and which were not seed predators (Table S4; see supplemental material for keys used).

Seed Traits

We quantified mass and volume of the seed and the additional structures of all seed types used in the cafeterias. We weighed a set number of seeds and then divided that bulk mass by the number of seeds to determine individual seed mass (Table S1). We then used digital calipers to measure the length, width, and thickness of the seeds. For seeds that were cylindrical or spherical, we only measured width (diameter) and length. Using these measurements, we calculated the volume of the seed using basic geometric calculations for a cylinder, sphere, and triangular prism based on the shape of the seed (Table S1). For seeds that had other structures, such as hairy or papery coats or awns, we also measured the length, width, and thickness of these as well. The collective seed and structure volume was the sum of the structure and the seed within any coating. We also calculated seed density as seed mass divided by seed volume. In addition, we calculated a "seed to seed plus structure" volume ratio to quantify the amount of volume taken up by the actual seed (the actual part used by the ant) compared to the entire seed and structure volume (the total volume the ant would have to transport or interact with) (Table S1).

We categorized the seeds into five different seed structure categories to examine if any one structure appeared more favorable than others. There categories included: coat (papery coating completely surrounding the seed), hair (awn or pappus on top of the seed, but seed is still exposed), hair coat (seed is completely coated in a papery coat that has numerous hairs), flake (a distinct structure for one species, *Zinna acerosa*, that is a paper wing on top of the seed, but the seed is still exposed), and none (no distinct papery seed coat or appendage; example images in Fig. S1).

Statistical Analyses

We ran a mixed effects model to test the impact of different seed traits on the proportion of seed taken. Using *glmer()* (*lme4* package, Bates et al. 2015) and a binomial family error distribution with a logit link function, we modeled cafeteria nested within day as a random effect as well as dish location as a random effect and six different traits as fixed effects: seed plus seed structure length, seed plus seed structure thickness or diameter (mm), individual seed mass (g), seed plus structure volume (mm^3), seed plus structure density (g/mm^3), and seed to seed plus structure ratio based on volume. We compared model fit across all models based on Akaike information criteria (AIC), Bayesian information criteria (BIC), log-likelihood values, and model deviance (from *lmerTest* package, Kuznetsova et al. 2017). For each analysis, we considered the best model to be the model, which had the lowest AIC/BIC value by at least two points (Burnham & Anderson 2002), the lowest log-likelihood values, and the lowest deviance values. We also used marginal and condition r^2 values (*rsquared()* from *piecewiseSEM* package, Lefcheck 2016) to identify model fit. Marginal r^2 values show the variance explained by only the fixed effects whereas the condition r^2 values consider both the random and fixed effects.

We used nonmetric multidimensional scaling (NMDS) to explore the variation in seed-type preferences and ant composition across cafeterias and days. Using proportion taken per species as the response, we ran a NMDS (using Bray-Curtis differences, *metaMDS()* in the *vegan* package, Oksanen et al. 2018) using the data for each day and cafe combination as an individual record. We then added vectors of the top three seed traits based on the model selection above. We then ran a cluster analysis on the data using Bray-Durtis dissimilarity (using *vegdist()* and *hclust()* as well as for plotting from package, Oksanen

Table 1. Proportion seed taken by cafeteria and day. Values reported are proportion seed taken by ants at three different cafeteria locations across 4 days. Values are averaged across all seed species.

	Cafeteria		
Day	*1*	*2*	*3*
1	0.44	0.52	0.17
2	0.65	0.53	0.37
3	0.60	0.63	0.22
4	0.76	0.72	0.53

et al. 2018). We looked for distinct clustering of that could be indicative of differences between different cafeterias and different days. We performed a similar method for ant composition across cafeterias and days to determine if the diversity of ant species changed over time and space.

Results

Proportion of seed species taken by ants ranged from 0.03 to 0.99 with the average being 0.51 across all cafeterias and days

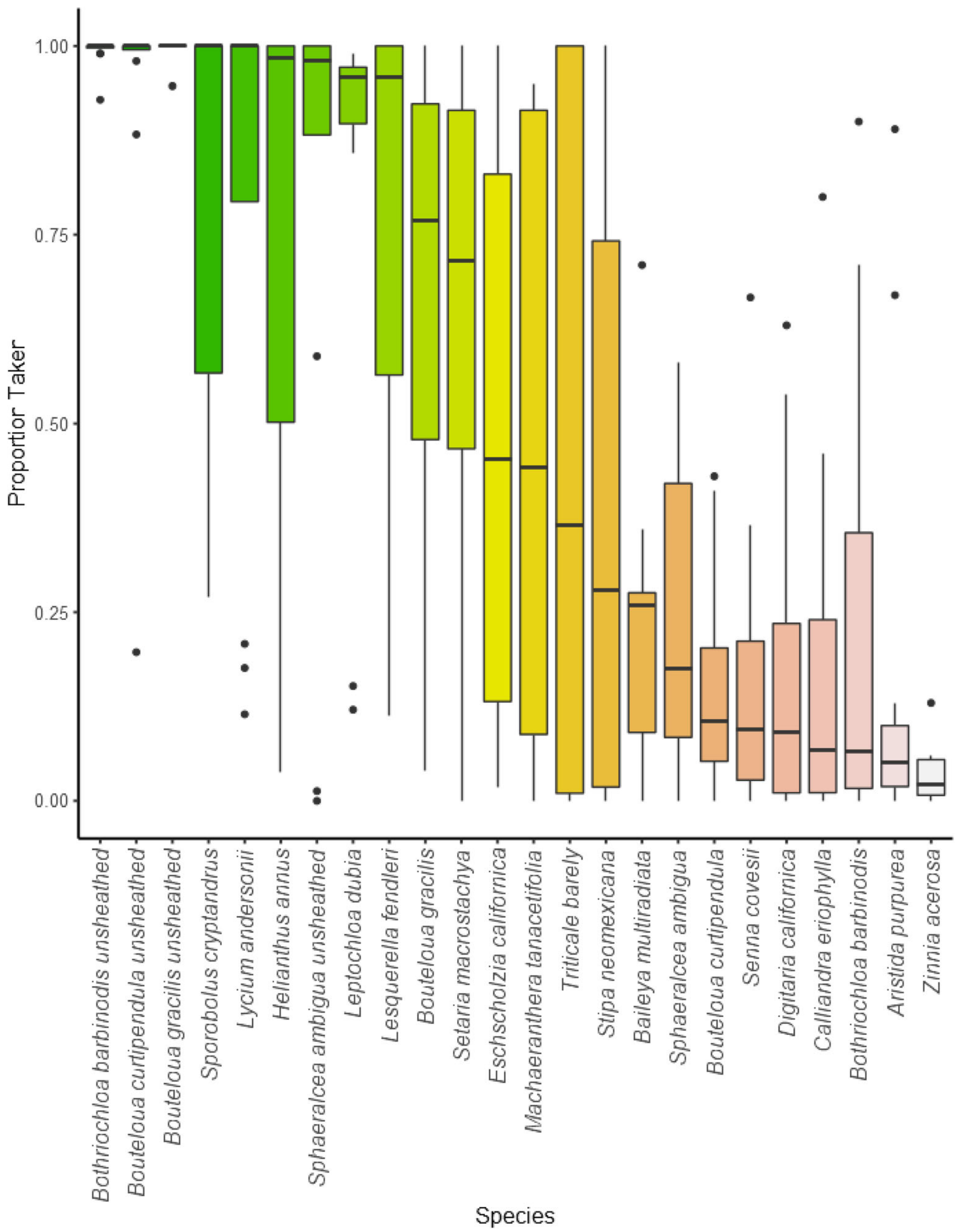

Figure 2. Proportion of seeds taken by ants for each restoration plant species. Shown is proportion of seed taken for each species (values are averaged across all days and cafeterias). Species are ordered from left to right with decreasing median proportion taken values.

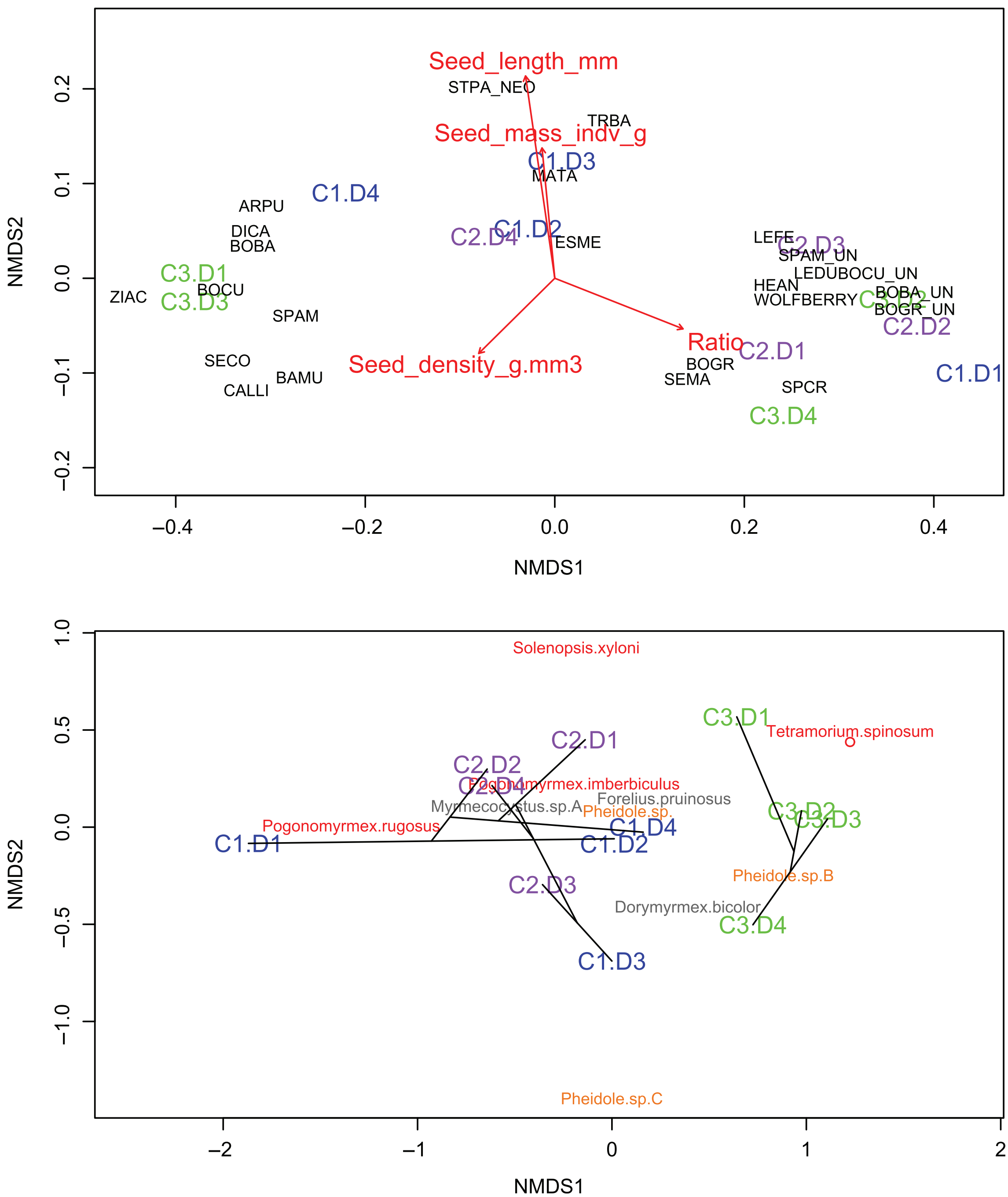

Figure 3. Results from nonmetric multidimensional scaling (NMDS) for seed preference (top panel) and ant composition (bottom panel) across day and cafeteria. In the top panel, seed species (small black text) are plotted on two NMDS axes. Vectors are the best fitting seed traits. Cafeteria numbers and days are added to the figure as well; for example cafeteria 3 on day 1 is "C3.D1." Cafeteria 1 is shown in blue, cafeteria 2 is shown in purple, and cafeteria 3 is shown in green. In the bottom panel, ant species (small text) are plotted on two NMDS axes. Ant species that are in red are known seed predators; ant species names in orange are suspected seed predators but we were unable to confirm because we could not identify to species; ant species with names in black are not seed predators. Cafeteria and day labelings are the same as above. Clustering branches show high degree of similarity between cafeterias and days. See Table S1 for species codes used in the top panel.

(Table 1; Fig. 2). Cafeterias 1 and 2 had similar proportions in seeds taken (ranging from 44 to 76%), whereas cafeteria 3 had circa 30% less predation of seeds on average and had values ranging from 40 to 185% less than the other two cafeterias (Table 1). Eleven seed types had over 70% of seeds taken (median values) across all cafeterias and days; three species had between 70 and 30%; and 10 species had less than 28% proportion taken (Table S2; Fig. 2). Seeds types with no structure or coating were most preferred (average 62% of seeds taken), compared to seeds with a coating (47%), awn (32%), hairy coating

(20%), or flake (3%) (Table S1). There is no trend in preference of a particular restoration species or functional groups (grass, forb, shrub)—except for the three grass seeds species where the paper coat is removed (*Bouteloua gracilis*, *B. curtipendula*, and *Bothriochloa barbinodis*); these seed types were highly preferred (0.92 proportion taken on average). *Zinnia acerosa* was the least preferred species on average with 3% taken on average.

The first and second axes for the NMDS accounted for 55 and 8% of the variation, respectively. The first axis that accounted for most variation among seed types appeared to lie along a spectrum of covered versus uncovered seeds (driven by the seed to seed plus structure ratio). Species with lower values on this axis were those with a seed structure or coat whereas species with higher values were those without any structure or coating. The second axis appeared to differentiate seed size, with larger seeds separating on the high end of the axis. The traits that best explained proportion seed taken included those that considered seed structure length (based on model fit r^2) and seed to seed and structure volume ratio (using AIC, BIC, loglik, and deviance; Table S3).

For the ant composition, we had up to 11 ant species across the three cafeterias and the 4 days of the trial (Table S4). *Pogonomyrex rugosus* was the dominant species at both cafeterias 1 and 2 but not cafeteria 3. At cafeteria 3, there was no one dominant ant species present across all days. Four ant species made up about 80% of the ant composition in the cafeteria 3 pitfalls: *Dorymyrmex biocolor*, *Forelius pruinosus*, *Pheidole* species B, and *Solenopsis molesta* (Table S4). From the NMDS, the first and second axes accounted for 46 and 15%, respectively. Clustering within the NMDS supported that cafeterias 1 and 2 were most similar in their composition of ants. The NMDS also shows a distinct cluster of ant composition for cafeteria 3 (Fig. 3).

Discussion

Seed movement by granivores is likely an underestimated challenge for restoration success. Granivores can remove (predate) native seed spread on the landscape (Linabury et al. 2019), assist native seed movement (Brewer & Rejmanek 1999), and even increase exotic seed movement (Ortiz et al. 2021; Wandrag et al. 2021). For grasslands, understanding and reducing ant-seed predation could be important components of restoration success. Our study showed that seed traits do influence ant seed preference and using these results can help inform practices that could aid in keeping seed on the ground and increasing the chance of germination and establishment.

Structure Impacts Seed Preference

We determined that seed length (including the structure) and seed to seed plus structure ratios were the best predictors of proportion of seed taken by ants explaining 31 and 27% of the variation in the proportion of seeds collected, respectively. Using these results, we found that for our site, grass species *Bothriochloa barbinodis* and *Bouteloua curtipendula* (with hairy/papery coating), forb species *Sphaeralcea ambigua*, and shrub species *Zinnia acerosa* would be most likely to success because of the increased seed to seed plus structure ratio and the presence of a flake (*Zinnia* sp.).

Our results compliment those of previous studies that showed a seed structure or coating can reduce seed predation by ants. For example, Wandrag et al. (2021) conducted a comparative study with three exotic seed species naturally with no awns, three native seed species with awns intact, and the same three native species with the awns removed in an Australian grassland. They found that seed removal rate by ants was highest for the exotic species but that removing the awns increased these rates almost fivefold. Further, Pan et al. (2021) found that seeds characterized by a mucilage-coating were less likely to be removed by harvester ants *Pogonomyrmex subdentatus*. They concluded that this was most likely because these seeds would become attached to the soil surface and were difficult for the ants to remove.

Our results also contrast some studies that note that awns or similar seed structures can make seeds easier to notice, manipulate, and move. A study by Azcarte et al. (2005) showed that larger or heavier seeds (which often have awns or other structures) were preferred by harvester ant *Messer barbarus*. The authors of that study postulated that the preference could be due to increased potential of detection and retention on the soil surface when compared to small, smooth seeds. Another study by Pullman and Brand (1975) found that mandible structure for *Pogonomyrmex* ants makes movement of small, smooth seeds difficult. The authors noted, however, that the presence of an awn, papery coating, or other structure could facilitate easy manipulation and movement of seed.

The results from our study highlight that when a variety of restoration plant species are being considered for a project, the presence of seed appendages should be a consideration. Further, our work suggests that the costly and laborious process of seed cleaning to remove seed coats might enhance ant granivory of seeded species. In cases where seed appendages do not restrict germination (see Pedrini et al. 2018 for study on seed processing and germination), they should remain intact to enhance restoration outcomes. Seed enhancement technologies could also reduce seed predation via seed coatings or amalgamation; however, they require further study to understand how effective they could be in reducing ant-seed predation.

Differences Among Cafeterias

Seed predation rates in our results were distinctly different between cafeteria 3 and the other two cafeterias. We concede that this stands out as a distinct difference likely because of a small sample size (three cafeteria replicates). We, however, postulate below potential reasons for the differences in seed preference. We think this is because of a difference in ant abundance and composition of the ants present. Compared to the *Pogonomyrmex* sp., which dominated cafeterias 1 and 2, cafeteria 3 was dominated by *Pheidole* species. *Pheidole* workers captured in our pitfall traps were smaller than *Pogonomyrmex rugosus*, which may have influenced the difference in seed choice (Hansen 1978; Chew & Chew 1980) as we found that the seeds preferred at cafeteria 3 were also smaller on average. These results suggest that knowledge of local seed eating ants can help guide plants species selection for restoration, based on seed size.

Holldobler (1976) found that distance from the nest and seed density both influence forager recruitment and seed predation in *P. rugosus*, which may forage up to 40 m from their nests (Hölldobler 1974). Because colonies deploy a limited number of foragers, seed predation rates decline when seeds are farther from ant nest entrances, and when seed density is low. *Pognomyrmex rugosus* are central place foragers, and their nests are reported to occur at an average distance of 19.4 m apart (Holldobler 1976). Placing arrays of seeds of high restoration value away from the large, bare discs that surround *P.* nests, or at intermediate distances between nests, may increase seed survival. Likewise, increasing space between seeds during restoration may decrease mass recruitment to seed patches in defended territories. It has been suggested that the foraging trunk routes of *Pogonomyrmex rugosus* allow colonies to recruit to and exploit patchy seed resources, while the independent foraging behavior of some other *Pogonomyrmex* species represents an adaptation to scattered seeds (Holldobler 1976).

Ants clearly can play a large role in restoration seeding projects especially in arid systems. Further understanding and matching the ecology and size of the ants of the area to the seeds in seed mixes could be helpful in increasing seed germination rates (e.g. smaller ants you could use large-seeded species). Though we concede that this is small study and further research is needed to draw general conclusions, it is promising that we have found some general trends across diverse seed species.

Acknowledgment

The authors acknowledge S. Zuniga for help in the field.

LITERATURE CITED

Abella SR (2009) Post-fire plant recovery in the Mojave and Sonoran deserts of western North America. Journal of Arid Environments 73:699–707. https://doi.org/10.1016/j.jaridenv.2009.03.003

Azcarte FM, Arqueros L, Sanchez AM, Peco B (2005) Seed and fruit selection by harvester ants, *Messor barbarus*, in Mediterranean grassland and scrubland. Functional Ecology 19:273–283. https://doi.org/10.1111/j.0269-8463.2005.00956.x

Balazs KR, Kramer AT, Munson SM, Talkington N, Still S, Butterfield BJ (2020) The right trait in the right place at the right time: matching traits to environment improves restoration outcomes. Ecological Applications 30:1–7. https://doi.org/10.1002/eap.2110

Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models usinglme4. Journal of Statistical Software 67:48. https://doi.org/10.18637/jss.v067.i01

Borderlands Restoration Network (2021) Borderlands Nursery and Seed

Brewer SW, Rejmanek M (1999) Small rodents as significant dispersers of tree seeds in a Neotropical forest. Journal of Vegetation Science 10:165–174. https://doi.org/10.2307/3237138

Brown JH, Davidson DW, Reichman OJ (1979) An experimental study of competition between seed-eating desert rodents and ants. Integrative and Comparative Biology 19:1129–1143. https://doi.org/10.1093/ICB/19.4.1129

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. second ed. Springer, New York

Chambers JC, Macmahon JA (1994) A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. Ecology 25:263–292. https://doi.org/10.1146/annurev.es.25.110194.001403

Chew AE, Chew RM (1980) Body size as a determinant of small-scale distributions of ants in evergreen woodland southeastern Arizona. Insectes Sociaux 27:189–202. https://doi.org/10.1007/BF02223663

Clive JG, Lawton JH, Shachakl M (1994) Organisms as ecosystem engineers. Pages 130–147. In: Ecosystem Management

Davison EA (1982) Seed utilization by harvester ants. Pages 1–6. In: Buckley RC (ed) Ant-plant interactions in Australia. Springer, Netherlands, Dordrecht

DeFalco LA, Esque TC, Nicklas MB, Kane JM (2010) Supplementing seed banks to rehabilitate disturbed Mojave desert shrublands: Where do all the seeds go? Restoration Ecology 20:85–94. https://doi.org/10.1111/j.1526-100x.2010.00739.x

Elliott CP, Commander LE, Williams MR, Golos PJ (2021) Seed movement in small-scale vegetation restoration. Ecological Management and Restoration 22:274–279. https://doi.org/10.1111/emr.12516

Fewell JH, Harrison JF (1991) Flexible seed selection by individual harvester ants, *Pogonomyrmex occidentalis*. Behavioral Ecology and Sociobiology 28:377–384. https://doi.org/10.1007/BF00164118

Folgarait PJ (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221–1244. https://doi.org/10.1023/A:1008891901953

Gordon SA (1980) Analysis of twelve Sonoran Desert seed species preferred by the desert harvester ant. Madrono 27:68–78. http://www.jstor.org/stable/41424254

Hansen SR (1978) Resource utilization and coexistence of three species of *Pogonomyrmex* ants in an Upper Sonoran Grassland Community. Oecologia 35:109–117. https://doi.org/10.1007/BF00345544

Hölldobler B (1974) Home range orientation and territoriality in harvesting ants. Proceedings of the National Academy of Sciences 71:3274–3277. https://doi.org/10.1073/pnas.71.8.3274

Holldobler B (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. Behavioral Ecology and Sociobiology 1:3–44. https://doi.org/10.1007/BF00299951

Jacob HS, Minkey DM, Gallagher RS, Borger CP (2006) Variation in post dispersal weed seed predation in a crop field. Weed Science 54:148–155. https://doi.org/10.1614/WS-05-075R.1

Johnson RA (2000) Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. Sociobiology 36:89–122. http://periodicos.uefs.br/index.php/sociobiology/issue/archive

Kildisheva OA, Erickson TE, Merritt DJ, Dixon KW (2016) Setting the scene for dryland recovery: an overview and key findings from a workshop targeting seed-based restoration. Restoration Ecology 24:S36–S42. https://doi.org/10.1111/rec.12392

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82:1–26. https://doi.org/10.18637/jss.v082.i13

Kwapich CL, Gadau J, Holldobler B (2017) The ecological and genetic basis of annual worker production in the desert seed harvesting ant, *Veromessor pergandei*. Behavioral Ecology and Sociobiology 71:1–14. https://doi.org/10.1007/s00265-017-2333-1

Lefcheck JS (2016) piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579. https://doi.org/10.1111/2041-210X.12512

Linabury MC, Turley NE, Brudvig LA (2019) Insects remove more seeds than mammals in first-year prairie restorations. Restoration Ecology 27:1300–1306. https://doi.org/10.1111/rec.13004

MacKay W (1984) Why do harvester ants store seeds in their nests? Sociobiology 9:31–47. http://periodicos.uefs.br/index.php/sociobiology/issue/archive

Mackay, WP (1981) A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). Ph.D. thesis. University of California, Riverside

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn DJ, et al. (2018) vegan: Community ecology package

Ortiz DP, Elizalde L, Pirk GI (2021) Role of ants as dispersers of native and exotic seeds in an understudied dryland. Ecological Entomology 46:626–636. https://doi.org/10.1111/een.13010

Pan VS, McMunn M, Karban R, Goidell J, Weber MG, LoPresti EF (2021) Mucilage binding to ground protects seeds of many plants from harvester ants: a functional investigation. Functional Ecology 35:2448–2460. https://doi.org/10.1111/1365-2435.13881

Pearson DE, Valliant M, Carlson C, Thelen GC, Ortega YK, Orrock JL, Madsen MD (2019) Spicing up restoration: can chili peppers improve restoration seeding by reducing seed predation? Restoration Ecology 27:254–260. https://doi.org/10.1111/rec.12862

Pedrini S, Lewandrowski W, Stevens JC, Dixon KW (2018) Optimising seed processing techniques to improve germination and sowability of native grasses for ecological restoration. Plant Biology 21:21415–21424. https://doi.org/10.1111/plb.12885

Penn HJ, Crist TO (2018) From dispersal to predation: a global synthesis of ant–seed interactions. Ecology and Evolution 8:9122–9138. https://doi.org/10.1002/ece3.4377

Pirk GI, de Casenave JL (2010) Influence of seed size on feeding preferences and diet composition of three sympatric harvester ants in the Central Monte Desert, Argentina. Ecological Research 25:439–445. https://doi.org/10.1007/s11284-009-0673-7

Pullman HR, Brand MR (1975) The production and utilization of seeds in plains grassland of southeastern Arizona. Ecology 56:1158–1166. https://doi.org/10.2307/1936155

Rinella MJ, Hammond DH, Bryant AEM, Kozar BJ (2015) High precipitation and seeded species competition reduce seeded shrub establishment during dryland restoration. Ecological Applications 25:1044–1053. https://doi.org/10.1890/14-1110.1

Suazo AA, Craig DJ, Vanier CH, Abella SR (2013) Seed removal patterns in burned and unburned desert habitats: implications for ecological restoration. Journal of Arid Environments 88:165–174. https://doi.org/10.1016/j.jaridenv.2012.08.016

Tschinkel WR, Domınguez DJ (2017) An illustrated guide to seeds found in nests of the Florida harvester ant, *Pogonomyrmex badius*. PLoS One 12:1–14. https://doi.org/10.1371/journal.pone.0171419

Tschinkel WR, Kwapich CL (2016) The Florida harvester ant, *Pogonomyrmex badius*, relies on germination to consume large seeds. PLoS One 11:1–34. https://doi.org/10.1371/journal.pone.0166907

Wandrag EM, Copeland HR, Duncan RP (2021) Ant preference for seeds without awns increases removal of exotic relative to native grass seeds. Ecological Entomology 46:500–503. https://doi.org/10.1111/een.12980

Supporting Information

The following information may be found in the online version of this article:

Table S1. A table of all species used in study.
Table S2. Proportion seed taken for each species at each cafeteria.
Table S3. Model fit for Proportion Taken given different seed traits.
Table S4. Ant composition across the three cafeterias and 4 days.
Figure S1. Photos of some example seeds used in the study.

Coordinating Editor: David Eldridge

Received: 11 February, 2022; First decision: 21 March, 2022; Revised: 4 June, 2022; Accepted: 3 July, 2022