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An omnivorous mesopredator modifies predation of omnivore-dispersed seeds

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Abstract. Post-dispersal seed predation is an important determinant of plant recruitment. Although many plant species are dispersed following consumption by omnivorous vertebrates, the potential for these dispersal agents to indirectly affect seed fate by modifying seed predator behavior is poorly understood. We evaluated the hypothesis that the scat of an omnivorous vertebrate (coyote, *Canis latrans*), which is also a rodent predator, would reduce seed predation by rodent granivores. We also hypothesized that scat would lead to increased removal by arthropod seed predators by providing a resource that attracts ants and other arthropods. We examined the role of omnivore deposition on seed predation of two animal-dispersed species that differed in size: Larger *Prunus serotina* seeds are attacked only by rodents, whereas smaller *Rubus allegheniensis* seeds are attacked by arthropods and rodents. Using an experiment that manipulated the presence of coyote scat and access by different granivore guilds, we found that scat reduced the total number of seeds removed from full-access depots by 12%, but it increased the total number of seeds removed from arthropod-only depots by 43%. Rodent removal of *P. serotina* seeds was 21% lower in the presence of scat. Scat composition was also important in affecting rodent seed predation, with seed predation 50% lower in the presence of meat-rich scat compared with mixed or fruit-rich scat. Arthropod removal of *R. allegheniensis* seeds was 43% higher in the presence of scat. *Prunus serotina* seeds were generally removed at greater rates than *R. allegheniensis* seeds in full-access trays; however, scat reduced this difference in removal rates from 37% more *P. serotina* seeds removed to 18% more *P. serotina* seeds removed. These findings illuminate a new pathway through which omnivores may influence plant populations by modifying post-dispersal seed predation by arthropods and rodents. Moreover, our results indicate that the ultimate effect of vertebrate omnivores on seed survival in a given region may depend upon omnivore diet, dominant seed predator guilds, and differences in granivore seed preference.

Key words: *Canis latrans*; endozoochory; mesopredator; predator cue; *Prunus serotina*; *Rubus allegheniensis*; scat; seed predation.

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Introduction

Seed survival can strongly affect the potential for plant recruitment (Harper 1977, Clark et al. 1998, 2007, Crawley 2000, Turnbull et al. 2000, Auffret et al. 2017); consequently, seed predation can substantially shape patterns of plant establishment and community composition (Howe et al. 2006, Chen and Valone 2017, Dylewski et al. 2020). Understanding patterns of seed predation is therefore important for understanding plant demography (Hobbs 1985, Hulme 1998, Crawley 2000, Orrock et al. 2006), patterns in plant communities (Inouye et al. 1980, Ostfeld et al. 1997, Howe and Brown 2000, Paine and Beck 2007, Larios et al. 2017), plant responses to

climate change (Brown and Vellend 2014), and outcomes of biological invasions (Wolfe et al. 2004, Nuñez et al. 2008, Pearson et al. 2011, Orrock et al. 2015). Understanding the factors that affect granivore foraging provides an important means to understand seed survival because variation in granivore activity and behavior can generate spatiotemporal variation in seed predation (Orrock et al. 2003, Bricker et al. 2010, Lichti et al. 2014, Chandler et al. 2016, Brehm et al. 2019). For example, seeds consumed by granivores may depend critically on the presence of other nearby resources in the environment that serve to attract or distract foraging granivores (Veech 2001, Ostoja et al. 2013, Lichti et al. 2014). Granivore foraging may also be modified by the presence of natural enemies in the environment: Arthropod and rodent granivores are both highly sensitive to risk of attack by predators and modify their activities accordingly (Brown and Kotler 2004, Orrock and Fletcher 2014, Blubaugh et al. 2017). As a result of the importance of the environment in modifying granivore decisions, it is essential to understand whether common, yet unexplored, features of the environment give rise to significant variation in granivore activity and seed survival.

Granivores may often encounter seeds after they have been dispersed by vertebrates: 64% of gymnosperm and 27% of angiosperm plant species are dispersed by vertebrates (Herrera 1989), and thus, their seeds are often found deposited in vertebrate feces (scat). Given that this fate is common for a large number of plant species, the scat of vertebrates may represent a widespread component of the environment in which a seed either dies or survives. Scat might modify granivory by causing changes in the foraging behavior or local abundance of granivores. For example, omnivorous vertebrates (e.g., bears, coyotes, foxes) that are agents of seed dispersal can also be predators of vertebrate granivores. As a cue of predation risk, mesopredator scat can repel rodent granivores (Kats and Dill 1998, Orrock 2010), thereby reducing predation of seeds within scat. In Alaska, where seed-rich bear scat can be a resource subsidy for rodent populations (Shakeri et al. 2018), seeds dispersed in bear scat exhibited decreased removal rates by rodents (Bermejo et al. 1998). Since rodents are known to show greater antipredator behavioral responses to urine of highly carnivorous than omnivorous predators (Nolte et al. 1994, Osburn and Cramer 2013, Scherer and Smee 2016), it is possible that differences in scat composition related to intraspecific diet variation may modify scat's effect on rodent behavior. Conversely, removal of seeds from animal scat by arthropod granivores, particularly ants, is well-documented (Levey and Byrne 1993, Passos and Oliveira 2003, Pizo et al. 2005, Manzano et al. 2010, Fricke et al. 2016), and mammalian scat may increase seed predation when its odor attracts arthropods that utilize additional resources found in scat (Sainz-Borgo 2015). Alternatively, mammalian scat deposition may impede arthropod granivory by reducing seed apparency (Pizo et al. 2005) or by acting as a physical barrier to arthropod handling, much like seed mucilage (LoPresti et al. 2019). To our knowledge, no research has compared the roles of different granivore guilds (e.g., rodents vs. arthropods) in post-dispersal predation of seeds deposited in mesopredator scat. Since rodents and arthropods are known to prefer seeds of different sizes (i.e., arthropods prefer smaller seeds than those preferred by rodents; Orrock et al. 2003, 2006, Orrock and Damschen 2005, Chandler et al. 2016), the effects of mesopredator scat on seed survival may vary with seed size. These potentially important effects of mesopredator scat and its composition for post-dispersal seed fate are largely unexplored because they require intensive experiments that measure seed predation in the presence and absence of mesopredator scat across a gradient of dietary composition.

In this study, we use experimental manipulation of mesopredator scat and granivore guild to test whether the presence of mesopredator scat leads to different patterns of seed predation by arthropod and rodent granivores. Specifically, we determine whether mesopredator scat generates different patterns of seed predation of two animal-dispersed seeds that differ in size (*Prunus serotina* and *Rubus allegheniensis*) from depots that manipulated rodent access in the presence or absence of mesopredator (*Canis latrans*) scat with varying composition (meat-rich, fruit-rich, mix). Further, we compared *P. serotina* removal by rodents in the presence of mesopredator scat and a non-predator omnivore's (*Sus scrofa*) scat to evaluate whether rodent antipredator behavior explained the effect of mesopredator scat and its composition on rodent granivory. Finally, we

compared initial arthropod recruitment to seed piles in the presence and absence of mesopredator scat to test whether scat attracts arthropod granivores. We hypothesized that mesopredator scat would reduce *P. serotina* removal by rodents due to rodent aversion to predator cues (Fig. 1a) and increase *R. allegheniensis* removal by arthropods due to arthropod attraction to scat (Fig. 1b).

Methods

Study area

We conducted our experiment in a 4-ha early-successional field at the Savannah River Site (SRS), a National Environmental Research Park near Aiken, South Carolina, USA. The field was clear of mature trees and was surrounded on all sides by pine (*Pinus taeda*) plantation. The study area was selected because early-successional habitats are common areas of establishment for the two plant species we examined, *P. serotina* and *R. allegheniensis*. Other plant species commonly found in the study area included *Chaemacrista fasciculata*, *Lespedeza* spp., *Desmodium* spp., *Vitis* spp., *Diospyros virginiana*, *Rubus cuneifolius*, and *Toxicodendron pubescens*. The study area is habitat for vertebrate species (e.g., old-field mouse, *Peromyscus polionotus*) and numerous arthropod species (e.g., *Solenopsis* spp., *Pogonomyrmex badius*, and coleopterans) that are important post-dispersal seed predators (Orrock and Damschen 2005, Orrock et al. 2006, Craig et al. 2011, Chandler et al. 2016). Coyotes are widespread, omnivorous mesopredators that were first documented at SRS in 1989 (Cothran et al. 1991, Gulsby et al. 2017). Coyotes in the southeast are highly omnivorous and exhibit significant variation in their diets (Thornton et al. 2004, Schrecengost et al. 2008, Mastro 2011, Cherry et al. 2016). At SRS, soft mast, chiefly *Prunus* spp. and *Rubus* spp., is the most common food item from spring to late fall, while small mammals are consistently present throughout the year (Schrecengost et al. 2008).

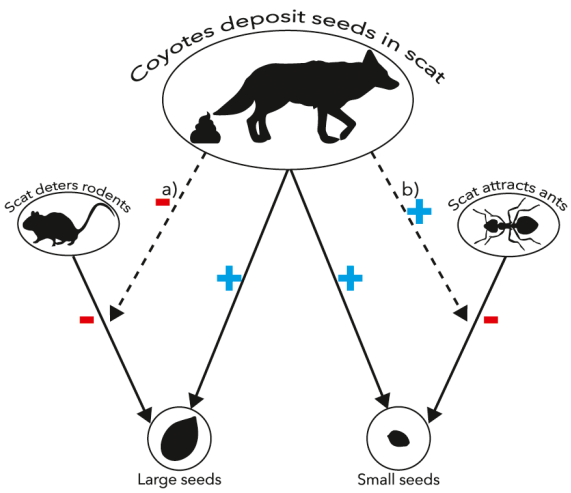

Fig. 1. Coyotes can directly affect seed fate by consuming fleshy fruits and dispersing seeds in scat. We hypothesize that coyotes can indirectly affect seed fate through the effects of scat on granivore foraging behavior. Solid lines represent direct effects of organisms on seeds, and dashed lines represent indirect effects of coyotes on seeds through interaction modifications (Wootton 1994). Positive and negative signs with each line represent whether the organism has a positive or negative effect on seeds (solid lines) or seed–granivore interaction strength (dashed lines). (a) Coyote scat is a cue of predation risk for rodent granivores, so it may decrease rodent foraging activity, reducing the strength of the rodent–seed interaction and increasing survival of seeds favored by rodents (i.e., larger seeds). (b) Coyote scat may attract arthropod granivores, so it may increase the strength of the arthropod–seed interaction, reducing survival of seeds favored by arthropods (i.e., smaller seeds).

Scat composition and granivore identity experiment

Our experiment was conducted from 10 July to 11 August 2018, with three sampling sessions lasting 10 d each (Session 1 10 July 2018–20 July 2018; Session 2 22 July 2018–1 August 2018; and Session 3 1 August 2018–11 August 2018). The timing of this experiment is within the realistic window of when the focal seed species are naturally available at SRS (Schrecengost et al. 2008). The duration of our sampling sessions was longer than typical seed removal studies (Moles and Westoby 2003), and research shows that the majority of seed removal occurs within the first 24 h of deployment (Boman and Casper 1995, Holl and Lulow 1997, Kollmann et al. 1998, Moles and Westoby 2003, Hammond 2020). During each session, we established 10 foraging stations, each containing four seed depots, on a 5 × 2 grid that separated neighboring stations

by 20 m. For each session, a new 5 × 2 grid was established 20 m adjacent to the previous session's grid such that a 5 × 6 grid spanning the three sessions was built (Appendix S1). Each station contained four seed depots to generate a fully factorial cross of scat presence and rodent access. For the two depots that had scat present, we split a single piece of coyote scat in half and put one half in each depot. By splitting the scat in half, we assumed that each half would be equal in its composition (e.g., amounts of animal and plant material), allowing us to control for such factors at the station level. Within a station, depots were randomly placed in a 2 × 2 grid 0.5 m from each other and >1 m from any possible rodent refuge (i.e., woody debris and vegetation cover) or ant nest. Seed depots were 27 × 27 × 11 cm in size with 2.5-cm openings, and they were covered with tight-fitting lids. Lids excluded avian granivores and prevented scat and seed loss from wind and rain. Each depot was filled with 1.5 L of sand, similar to the sandy soils of our study area. One depot was open only to arthropods (hardware cloth at the depot entrance prohibited access by organisms wider than 1.5 cm^2) and did not contain scat; a second depot was open only to arthropods and contained scat; a third depot was open to arthropods and rodents (openings were not barred) and did not contain scat; and a fourth depot was open to arthropods and rodents and contained scat. This general seed depot design has been successfully used to measure seed removal by both arthropod and rodent granivores in numerous ecological settings (Bartowitz and Orrock 2016, Linabury et al. 2019), including our study area (Orrock and Damschen 2005, Craig et al. 2011, Chandler et al. 2016). Because it was not possible to create a treatment where only rodents (and not also arthropods) had access to trays, we assume that the effect of rodents on seed removal is additive to the effect of arthropods. This assumption is also made in other studies with similar experimental designs in our study system (Orrock et al. 2003, Orrock and Damschen 2005). Because *P. serotina* is not removed by arthropods (Orrock and Damschen 2005, Chandler et al. 2016), this assumption is most important for our interpretation of rodent removal of *R. allegheniensis* seeds (since *R. allegheniensis* is removed by both arthropods and rodents). The 0.5 m distance between depots within a station is a standard design utilized in studies evaluating rodent foraging at SRS (Orrock and Danielson 2005, Craig et al. 2011) and studies evaluating the effect of fecal predator cues on rodent foraging in other systems (Orrock 2010). This distance ensures that the paired depots share the same microhabitat, allowing us to assume that other explanations for differences in seed removal rates between paired depots unrelated to our treatments are unlikely.

Within each depot, we scattered 20 seeds of each species (*P. serotina* and *R. allegheniensis*) across the sandy surface. Seeds were procured from a commercial supplier and were free of pulp (Sheffield's Seed Supply, Locke, New York, USA). This amount is representative of natural seed deposition for these species (Smith 1975) and replicates the densities of similar seed removal studies in this system (Orrock and Damschen 2005, Chandler et al. 2016). We chose *P. serotina* because it is the most common *Prunus* species in coyote diets at SRS (Schrecengost et al. 2008). *Rubus allegheniensis* is among the three possible species of *Rubus* found in our study area that are detected in coyote diets (Schrecengost et al. 2008). *Prunus serotina* (6.29–6.71 mm diameter, 0.068–0.084 g; Orrock and Damschen 2005) is significantly larger than *R. allegheniensis* (2.29–2.62 mm, 0.002–0.003 g). We confirmed the presence of common rodent species through camera and live trapping (Appendix S2). We confirmed the presence of common arthropod granivores (e.g., *Solenopsis invicta*) using visual mound surveys and a bait-recruitment assay (Appendix S3). In order to investigate whether scat affected arthropod granivore recruitment to dispersed seeds, we conducted a follow-up experiment comparing arthropod granivore recruitment to *R. allegheniensis* seeds in the presence and absence of coyote scat (see Appendix S3).

We assume that removed seeds were consumed and not secondarily dispersed for several reasons. Explicit tracking of 28,000 *Quercus nigra* seeds in nearby old-field habitats like the one used in this study during the same season as this study found no evidence of directed dispersal by rodents in this ecosystem (Bartel and Orrock 2020). Excavation of *P. polionotus* burrows found large quantities of seed fragments but no intact seeds (Gentry and Smith 1968). *Solenopsis invicta*

was the primary arthropod granivore in our experiment (Appendix S3) and is known to be a highly effective seed predator (Ready and Vinson 1995, Zettler et al. 2001, Seaman and Marino 2003, Ness and Bronstein 2004). Past work conducted in our study area shows that the number of seed-coat fragments in full-access foraging trays correlates with seed removal (Craig et al. 2011), and other studies in our system have also found destroyed seeds (Chandler et al. 2016), supporting past evidence that seed removal by arthropods and rodents is indicative of seed death (Orrock and Damschen 2005, Orrock et al. 2006; Bartel and Orrock 2020).

Coyote scat was collected by surveying roads across an ~80,000-ha area at SRS. We collected only fresh coyote scat for each sampling session 0–3 d prior to deployment. Field-collected scat was inspected prior to the experiment, and the composition of the scat was categorized by a single observer (SLB). Scat was classified as meat-rich scat (>75% animal material), fruit-rich scat (>75% fleshy fruit material), or a fruit-meat mix (>50% plant material with visible animal material). A total of 30 pieces of coyote scat were used for this experiment: nine meat-rich scat, eight fruit-rich scat, and 13 mixed-composition scat. Scat compositions were stratified across the three sessions.

Rodent responses to predator and non-predator scat experiment

In order to examine whether the effect of coyote scat on rodent seed removal was driven by rodents avoiding the scat of a predator rather than simply an aversion to scat itself, we conducted an experiment comparing rodent foraging responses to coyote scat (omnivorous predator) and feral hog scat (*S. scrofa*; omnivorous non-predator). This experiment was conducted in 15 July–20 July 2019 at the same field as the past experiment. We established 20 foraging stations, each containing three seed depots, on a 10 × 2 grid that separated neighboring stations by 20 m. Each of the three seed depots allowed rodent access and contained 20 *P. serotina* seeds. One depot contained coyote scat, one depot contained hog scat, and one control depot did not contain scat. To replicate the methods of the first experiment, all scat was locally collected within 0–3 d prior to deployment, and depots within a station were randomly placed in a triangular grid 0.5 m from each other and >1 m from any habitat structure that might affect rodent foraging by serving as a predation refuge (Orrock et al. 2004). At the end of the deployment period, we counted the number of seeds remaining in the depots.

Statistical analyses

We used generalized linear mixed-effects models (GLMMs) with a binomial response distribution to examine the proportion of seeds removed. All analyses were conducted in R ver. 3.5.1, and GLMMs were constructed using the lme4 package (Bates et al. 2015). To evaluate how forager identity and scat affected *R. allegheniensis* seed removal, we examined depot access, scat presence, and scat composition as fixed effects with intercepts varying among stations and rodent access treatments within a station. To evaluate how scat composition affected *R. allegheniensis* arthropod responses to scat in arthropod-only depots, we examined scat presence and scat composition as fixed effects with station as a random intercept. To evaluate how scat and scat composition affected *P. serotina* seed removal by rodents in full-access depots, we examined scat presence and scat composition as fixed effects and station as a random intercept. To evaluate whether scat changed the difference in removal rates between the two species, we used the difference in seeds remaining as the dependent variable, scat and scat composition as fixed effects, and station as a random intercept. To evaluate whether rodent seed predation was more strongly affected by the scat of an omnivorous predator than that of an omnivorous non-predator, we examined the scat treatment (coyote, hog, or control) as a fixed effect with station as a random intercept.

Results

Scat composition and forager identity

Arthropods did not remove *P. serotina* seeds, and allowing rodents access always increased the number of *P. serotina* seeds removed (Fig. 2a). In full-access depots, the removal of *P. serotina* seeds was significantly affected by scat ($\chi^2 = 16.95$, $P < 0.001$; Table 1). Scat decreased *P. serotina* removal by 21% in full-access depots (Fig. 2a). Seed removal of *P. serotina* in full-access

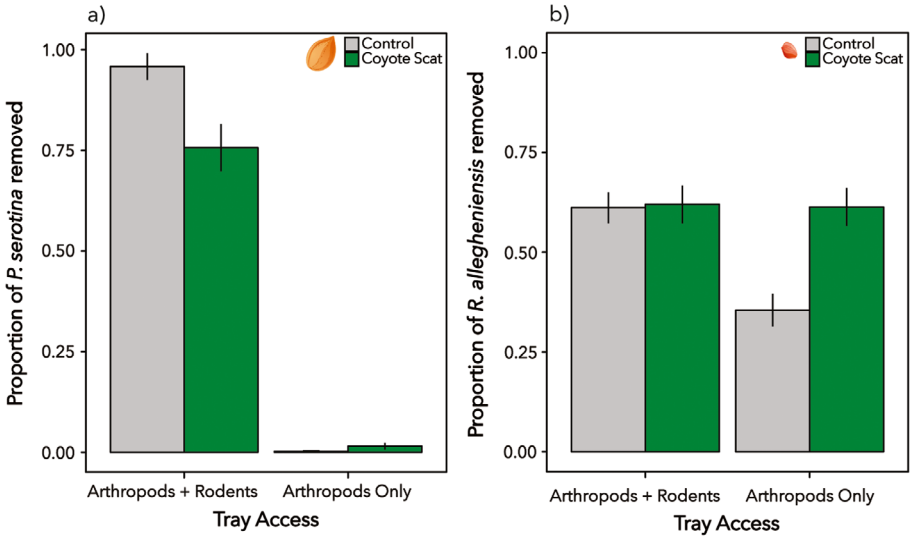

Fig. 2. Bar graphs depict the average seed removal rates of each seed species based on granivore access and scat treatment combination. Error bars represent one standard error. (a) *Prunus serotina* seeds were only removed from full-access depots. In full-access depots, scat significantly decreased the proportion of *P. serotina* seeds removed. (b) *Rubus allegheniensis* seed removal was significantly affected by the interaction of rodent access and scat presence. In full-access depots, there was no effect of scat on *R. allegheniensis* seed removal. In arthropod-only depots, *R. allegheniensis* seed removal was significantly greater in the presence of scat. Significant increases in *R. allegheniensis* seed removal when rodents had access to scat-free control trays suggest that rodents visiting control trays did contribute to *R. allegheniensis* seed removal, just as *P. serotina* removal was greater in control trays. In the absence of rodents, scat led to an increase in *R. allegheniensis* seed removal.

Table 1. Coefficients, test statistics, and *P*-values for our binomial GLMMs evaluating the effects of scat and scat composition on seed removal.

	Prunus serotina (full-access)			*Rubus allegheniensis* (arthropod-only)		
Effect	β	χ^2	*P*	β	χ^2	*P*
Scat	−2.91	16.95	<0.001***	−1.30	17.27	<0.001***
Composition	3.36	3.77	0.152	−0.46	0.91	0.339
Scat × composition	−3.69	8.65	0.013*	0.26	2.49	0.288

Notes: GLMMs, generalized linear mixed-effects models. Since arthropods do not remove *P. serotina*, only data from full-access depots were analyzed to understand how scat and scat composition modify rodent behavior. In order to understand how scat and scat composition specifically modify arthropod behavior, only *R. allegheniensis* removal data from arthropod-only depots were analyzed.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

depots was significantly affected by the interaction of scat and composition (Table 1, Fig. 3c). The effect of meat-rich scat on *P. serotina* removal was over 50% greater than that of fruit-rich and mixed scat (Fig. 3d). *Rubus allegheniensis* seed removal was significantly affected by rodent access ($\chi^2 = 16.85$, $P < 0.001$) and the interaction of rodent access and scat ($\chi^2 = 8.420$, $P = 0.004$; Fig. 2b). Scat did not change the removal of *R. allegheniensis* in full-access depots, but it increased removal by 43% in arthropod-only depots (Fig. 2b). Seed removal of *R. allegheniensis* in arthropod-only depots was not significantly affected by the interaction of scat and composition (Table 1, Fig. 3a, b). The difference between *R. allegheniensis* and *P. serotina* seeds remaining in the depots was not significantly affected by the interaction of rodent access and scat

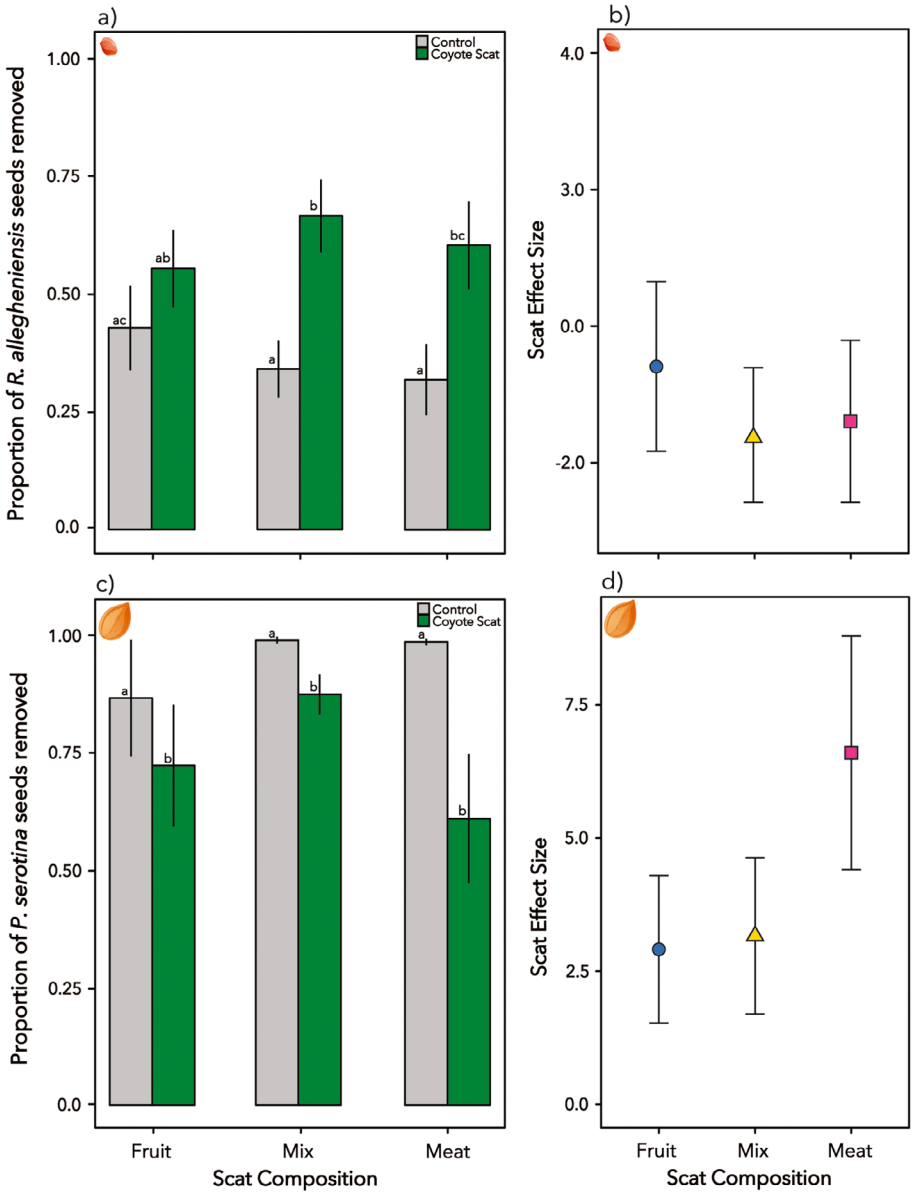

Fig. 3. Bar graphs on the left depict the average seed removal rates of each seed species for each scat treatment and scat composition. Graphs on the right plot the effect size of the scat treatment on seed removal for each scat composition category. Error bars represent one standard error; bars that share a letter represent means that are not significantly different (i.e., $P>0.05$). (a) In arthropod-only depots, scat significantly increased *Rubus allegheniensis* seed removal in mix and meat-rich scat, but there was no significant interaction of scat and scat composition on seed removal by arthropods. (b) There was no difference in the strength of scat's effect on *R. allegheniensis* seed removal by arthropods between the different types of scat composition. (c) In full-access depots, scat and the interaction of scat and scat composition significantly affected *Prunus serotina* seed removal by rodents. (d) Meat-rich scat had a greater negative effect on *P. serotina* removal by rodents than mix or fruit-rich scat.

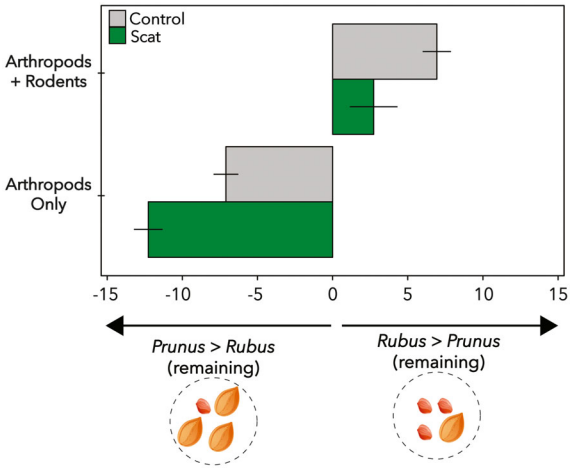

Fig. 4. For each seed depot, we subtracted the number of *Prunus serotina* seeds remaining from the number of *Rubus allegheniensis* seeds after the deployment period to estimate how scat and granivore access modified the difference in removal rates between the two species. Bar graphs depict the average for each granivore access and scat treatment combination. Error bars represent one standard error. In full-access depots, *P. serotina* always had greater removal rates than *R. allegheniensis*, but scat significantly reduced this difference. In arthropod-only depots, *R. allegheniensis* always had greater removal rates than *P. serotina*, and this difference was greatest in the presence of scat.

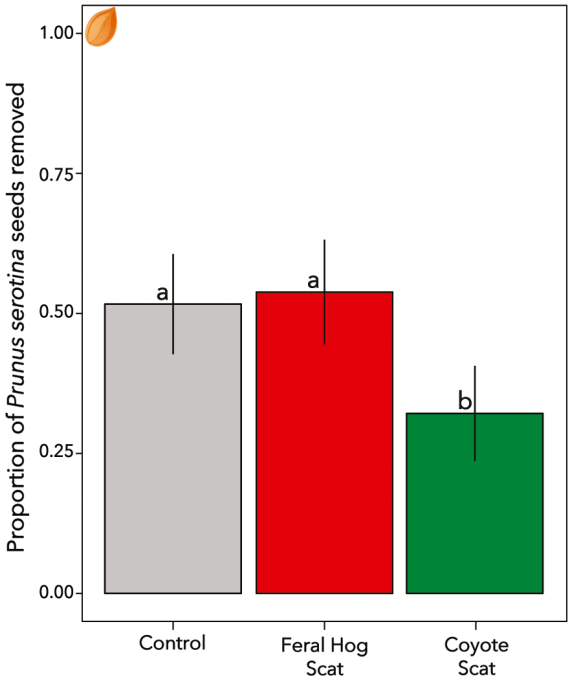

Fig. 5. Bar graphs depict the average seed removal rates of *Prunus serotina* for each scat treatment. Error bars represent one standard error; bars that share a letter represent means that are not significantly different (i.e., $P>0.05$). Seed removal of *P. serotina* was significantly lower in depots containing coyote scat than in depots containing feral hog scat or no scat. There was no difference in the proportion of *P. serotina* seeds removed in depots containing feral hog scat and depots containing no scat.

($F = 0.24$, $P = 0.625$), but there was a significant effect of scat ($F = 9.10$, $P = 0.004$) and access ($F = 80.81$, $P < 0.001$). In full-access depots, *P. serotina* was always removed at a greater rate than *R. allegheniensis* (Fig. 4), but scat significantly reduced this difference in removal ($t = 3.02$, $P = 0.004$). In arthropod-only depots, *R. allegheniensis* always experienced greater removal than *P. serotina*, especially in the presence of scat ($t = 3.71$, $P = 0.001$).

Rodent responses to predator and non-predator scat

In the additional experiment testing rodent foraging on *P. serotina* in the presence of coyote or hog scat, there was a significant effect of the scat treatment ($\chi^2 = 14.65$, $P < 0.001$) on *P. serotina* seed removal. Rodents removed significantly less *P. serotina* seeds in the presence of coyote scat than in the presence of hog scat or no scat (Fig. 5). There was not a significant difference in *P. serotina* seed removal between depots with hog scat and depots without scat (Fig. 5).

Discussion

Seed predation can play an important role in plant population establishment and persistence. Our study illustrates that coyotes can play multiple roles in plant recruitment: In addition to their roles in dispersing seeds and limiting rodent granivore populations (Howe and Smallwood 1982, Willson 1993, Herrera and Pellmyr 2002, Mastro 2011), we show that coyotes may also affect seed predation by modifying the behavior of multiple granivore guilds. In finding that a reduction or enhancement in post-dispersal seed predation is an unappreciated consequence of endozoochory by coyotes, our work adds an

important facet to our increasing appreciation of the myriad roles that omnivorous vertebrates play in food webs (Fagan 1997, McCann et al. 1998, Williams and Martinez 2000, Levey et al. 2002, Emmerson and Yearsley 2004, Duffy et al. 2007, Rudolf 2007, Thompson et al. 2007). Our findings have several implications. First, our study shows that post-dispersal seed survival of coyote-dispersed seeds is contingent upon seed traits (Fig. 4). Additionally, coyote diets are known to be highly variable (Andelt et al. 1987, Mastro 2011), and our results show that variation in coyote scat composition modifies seed predation, which may contribute to large-scale variation in post-dispersal seed fate (Fig. 3). Finally, our findings suggest that changes in coyote abundance and diet could have unappreciated effects on seed fate.

The effect of coyote omnivory on post-dispersal seed predation is contingent upon seed traits

If rates of seed predation can be linked to seed traits (e.g., size), this may provide a powerful way to make general predictions about rates of predation among different plant species (Moles and Westoby 2003, Orrock and Damschen 2005, Larios et al. 2017). Seed size may be particularly important for predicting predation by specific granivore guilds, as evidenced by a recent meta-analysis finding that seed size predicted global patterns of seed predation by small mammals (Dylewski et al. 2020). We found that coyote scat reduced post-dispersal removal of the larger *P. serotina* seeds by rodents in full-access depots. In contrast, scat increased seed removal of the smaller *R. allegheniensis* seeds by arthropods in arthropod-only depots and had no effect on overall *R. allegheniensis* removal in full-access depots (Fig. 2). One explanation for the absence of an effect of coyote scat on overall *R. allegheniensis* removal is that arthropod attraction to scat compensated for rodent aversion to coyote scat. Significant increases in *R. allegheniensis* seed removal when rodents had access to control depots suggests that rodents visiting control depots did contribute to *R. allegheniensis* seed removal, just as *P. serotina* removal was greater in control depots (Fig. 2). Results from our ant-recruitment assay found that ants were more likely to recruit to scat-associated *R. allegheniensis* seeds first (Appendix S3), indicating that ant attraction to scat may explain increased *R. allegheniensis* removal in arthropod-only depots. Those findings, coupled with further results showing that rodent removal of *P. serotina* seeds was reduced in the presence of coyote scat but not feral hog scat (Fig. 5), provide additional evidence that coyote scat promotes *P. serotina* seed survival through rodent repulsion but has no effect on *R. allegheniensis* survival due to the contrasting responses to scat by its two predator guilds. Interpretation of these results hinges on the assumption that rodent and arthropod granivory is additive (see *Methods*). Although past work has found evidence of antagonistic interactions between rodents and arthropods in which rodent access led to a decrease in overall *R. cuneifolius* seed removal by arthropods, this interaction was strongly dependent on the distance to the mound of an invasive ant species, *S. invicta* (Chandler et al. 2016), a factor that was not evaluated in our study. Moreover, Chandler et al. (2016) reported substantially lower rates of *P. serotina* seed removal rates (22% on average) in full-access depots than what our study detected (86% on average). This difference in *P. serotina* removal suggests that rodents were less abundant or less active in the previous study site than in our study site. Our finding of an increase in seed removal with rodent access suggests a lack of antagonistic interactions possibly due to these differences in study design and rodent activity.

Since our study measured seed removal of two species of different sizes, we are limited in our understanding of the role of seed size in generating these patterns of differential removal. Future experiments measuring removal across a greater breadth of seed species and sizes will be necessary to fully elucidate the importance seed traits in this system. The patterns of differential seed removal by rodents and arthropods in our study match the results of past experiments using *P. serotina* and *Rubus* spp. seeds in our study area (Orrock and Damschen 2005, Chandler et al. 2016), indicating that environmental factors with contrasting effects on rodent and arthropod behavior may have consequences for plant communities. Although their study did not evaluate guild-specific seed removal, reduced *P. serotina* seed removal in full-access depots containing scat is consistent with the results found in a study by Bermejo et al. (1998) examining seed

removal of bear-dispersed seeds in Alaska. Our findings that arthropod seed removal increased in the presence of scat contrast with the findings of Pizo et al. (2005) that arthropod seed removal in Brazilian tropical forests was reduced by mammalian scat. Viewed in light of the strong effects of scat we observed, these studies provide additional evidence that scat-mediated changes in seed fate may be important in different ecosystems. Importantly, the study-specific variation in the effect of scat on seeds suggests that scat effects may be context-specific and that future studies are needed to evaluate how the strength of scat effects may be modified by local variation in abiotic and biotic conditions. For example, *S. invicta* was the only ant species that we visually detected foraging in our study (Appendix S3); however, research in habitats containing more diverse ant communities found that competitive displacement of other ant species by *S. invicta* generates spatial variation in *Rubus* seed removal, contingent on distance to *S. invicta* mounds (Chandler et al. 2016). Spatial patterns in scat deposition relative to *S. invicta* mounds may be important in the nature of seed removal from scat when multiple ant species are present. Further, our follow-up experiment found *S. invicta* recruitment to scat-associated seeds occurred within 0–20 min whereas seeds that were not associated with scat experienced no recruitment within the 60-min observation window (Appendix S3), indicating that scat may improve the ability of *S. invicta* to detect seeds. Our results indicate that the effect of scat on post-dispersal seed removal is contingent upon granivore guild, and the fate of scat-dispersed seeds may diverge among systems containing different granivore communities.

Changes in seed predation rates among plant species can elicit changes in plant communities (Inouye et al. 1980, Howe and Brown 2000, Howe et al. 2006, Paine and Beck 2007). In finding that scat has contrasting effects on seed predation of *P. serotina* and *R. allegheniensis*, our results suggest that scat presence and composition may promote differential survival of one plant species over another. Past experiments conducted on another animal-dispersed plant species, *Phytolacca americana*, in our study system found that seed predation by rodents and arthropods is a limiting factor on plant recruitment (Orrock et al. 2003, 2006). We therefore expect that scat-mediated changes in granivore behavior documented in our study have the potential to generate consequences for plant recruitment in our system. However, since plant dynamics are also the result of many processes, including seed dispersal, seed predation, and herbivory (Vander Wall 1994, Auffret et al. 2017), future studies that explicitly incorporate scat and the role of mesopredators as seed dispersers into multistage experiments will be needed to understand the effect of scat-mediated changes in predation on local plant communities. Importantly, we were not able to track potential secondary seed dispersal events in our experiment, though significant evidence suggests that these events are extremely rare in our system (see *Methods*). Future studies that track secondary seed dispersal may be important for understanding how coyote scat determines seed fate in ecosystems where it is more common.

Coyote diet variability affects rodent granivory

Coyote scat reduced *P. serotina* seed removal by rodents, and meat-rich scat had a significantly stronger effect on rodent granivory than fruit-rich or mix scat. It is possible that rodents reduced *P. serotina* seed removal in the presence of coyote scat because rodents detected it as a cue of predation risk (Kats and Dill 1998) or a cue of disease risk (Buck et al. 2018). Since rodent removal of *P. serotina* seeds was not affected by feral hog scat, an omnivore that is not a predator (Fig. 5), we expect that the negative effect of coyote scat on rodent foraging was driven by rodent antipredator responses. Past research in our study system found that rodents did not respond differently to the urine of a suite of native and non-native predators (fox, bobcat, coyote, and ocelot) than to native deer urine or water (Orrock et al. 2004). Our findings that rodent seed removal was reduced by predator scat and not by non-predator scat indicate that the ability of prey to discriminate between the cues of predators and non-predators may be contingent upon the type of cue that is deposited (e.g., urine, scat, or mucus; Kats and Dill 1998). The significantly stronger effect of meat-rich coyote scat than that of fruit-rich or mix coyote scat on *P. serotina* seed removal by rodents also suggests that rodents may equate an individual's degree of carnivory to an indicator of predation risk (Nolte et al. 1994).

Coyote ranges and abundances have increased rapidly across the globe due to a combination of anthropogenic disturbances (Parker 1995, Crooks and Soulé 1999, Prugh et al. 2009). These changes in coyote populations have been shown to modify prey populations and behavior, generating cascading effects on primary producers and disease transmission (Prugh et al. 2009, Brashares et al. 2010, Levi et al. 2012). Our results illuminate an unappreciated consequence of such changes for seed predation through coyote endozoochory (Fig. 1), indicating that fluctuations in coyote densities may cause fluctuations in seed predation of animal-dispersed seeds. Further, coyote diets are highly variable, and our results show that factors driving changes in diets could affect seed fate. For example, the proportions of fruit and animal matter in coyote diets can vary not only seasonally (Andelt et al. 1987, Quinn 1997, Schrecengost et al. 2008) but also spatially in relation to human disturbance (Morey et al. 2007, Grigione et al. 2011, Wallace and Gipson 2014). As the ways in which human activities modify predator–prey interactions become more appreciated (Guiden et al. 2019), it is important to consider how human-induced changes in coyote diets may modify rodent responses to predator cues and generate cascading effects on seed fate.

Conclusions and Future Directions

Coyotes have the potential to indirectly affect post-dispersal seed predation through the direct effects of coyote scat on granivore behavior. Since granivore guilds that vary in their seed preferences also show differing responses to coyote scat (i.e., attraction vs. aversion), coyote scat may cause differential seed predation, making the benefits of this mode of dispersal contingent upon seed traits related to granivore preferences. In this study, we show that the nature and magnitude of the effects of coyote scat on seed predation were contingent upon granivore identity, seed species, and scat composition. In order to understand whether these patterns in seed fate modify plant recruitment, long-term studies comparing recruitment of animal-dispersed species in the presence and absence of coyotes are necessary. Since variation in scat composition can yield variation in nutrient availability and consequently determine seedling establishment (Traveset et al. 2001), future studies that explicitly track the effects of individual-level diet choice on both seed predation and subsequent recruitment are needed to understand the ultimate consequences of coyote omnivory for plant populations.

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Literature Cited

Andelt, W. F., J. G. Kie, F. F. Knowlton, and K. Cardwell. 1987. Variation in coyote diets associated with season and successional changes in vegetation. Journal of Wildlife Management 51:273–277.

Auffret, A. G., Y. Rico, J. M. Bullock, D. A. P. Hooftman, R. J. Pakeman, M. B. Soons, A. Suárez-Esteban, A. Traveset, H. H. Wagner, and S. A. O. Cousins. 2017. Plant functional connectivity – integrating landscape structure and effective dispersal. Journal of Ecology 105:1648–1656.

Bartel, S. L., and J. L. Orrock. 2020. Past and present disturbances generate spatial variation in seed predation. Ecosphere 11:e03116.

Bartowitz, K. J., and J. L. Orrock. 2016. Invasive exotic shrub (*Rhamnus cathartica*) alters the timing and magnitude of post-dispersal seed predation of native and exotic species. Journal of Vegetation Science 27:789–799.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Bermejo, T., A. Traveset, and M. Willson. 1998. Post-dispersal seed predation in the temperate rainforest of Southeast Alaska. Canadian Field-Naturalist 112:510–512.

Blubaugh, C. K., I. V. Widick, and I. Kaplan. 2017. Does fear beget fear? Risk-mediated habitat selection triggers predator avoidance at lower trophic levels. Oecologia 185:1–11.

Boman, J. S., and B. B. Casper. 1995. Differential post-dispersal seed predation in disturbed and intact temperate forest. American Midland Naturalist 134:107–116.

Brashares, J. S., L. R. Prugh, C. J. Stoner, and C. W. Epps. 2010. Ecological and conservation implications of mesopredator release. *In* J. W. Terborgh and J. A. Estes, editors. Trophic cascades. Island Press, Washington, D.C., USA.

Brehm, A. M., A. Mortelliti, G. A. Maynard, and J. Zydlewski. 2019. Land-use change and the ecological consequences of personality in small mammals. Ecology Letters 22:1387–1395.

Bricker, M., D. Pearson, and J. Maron. 2010. Small-mammal seed predation limits the recruitment and abundance of two perennial grassland forbs. Ecology 91:85–92.

Brown, J. S., and B. P. Kotler. 2004. Hazardous duty pay and the foraging cost of predation. Ecology Letters 7:999–1014.

Brown, C. D., and M. Vellend. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change. Proceedings of the Royal Society of London B: Biological Sciences 281: 20141779.

Buck, J. C., S. B. Weinstein, and H. S. Young. 2018. Ecological and evolutionary consequences of parasite avoidance. Trends in Ecology and Evolution 33:619–632.

Chandler, J. L., J. L. Orrock, and J. Resasco. 2016. Invasive ants generate heterogeneity in patterns of seed survival. American Midland Naturalist 176:289–297.

Chen, T. C., and T. J. Valone. 2017. Rodent granivory strengthens relationships between seed size and plant abundance in a desert annual community. Journal of Vegetation Science 28:808–814.

Cherry, M. J., K. L. Turner, M. Brent Howze, B. S. Cohen, L. Mike Conner, and R. J. Warren. 2016. Coyote diets in a longleaf pine ecosystem. Wildlife Biology 22:64–70.

Clark, J. S., E. Macklin, and L. Wood. 1998. Stages and spatial scales of recruitment limitation in Southern Appalachian forests. Ecological Monographs 68: 213–235.

Clark, C. J., J. R. Poulsen, D. J. Levey, and C. W. Osenberg. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. American Naturalist 170:128–142.

Cothran, E. G., M. H. Smith, J. O. Wolff, and J. B. Gentry. 1991. Mammals of the Savannah River Site. SRO-NERP-21. Savannah River Site, Aiken, South Carolina, USA.

Craig, M. T., J. L. Orrock, and L. A. Brudvig. 2011. Edge-mediated patterns of seed removal in experimentally connected and fragmented landscapes. Landscape Ecology 26:1373–1381.

Crawley, M. J. 2000. Seed predators and plant population dynamics. Pages 167–182 *in* M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. Second edition. CABI, Wallingford, UK.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Duffy, J. E., B. J. Cardinale, K. E. France, P. B. Mcintyre, E. T. Bault, and M. Loreau. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology Letters 10:522–538.

Dylewski, Ł., Y. K. Ortega, M. Bogdziewicz, and D. E. Pearson. 2020. Seed size predicts global effects of small mammal seed predation on plant recruitment. Ecology Letters 23:1024–1033.

Emmerson, M., and J. M. Yearsley. 2004. Weak interactions, omnivory and emergent food-web properties. Proceedings of the Royal Society of London B: Biological Sciences 271:397–405.

Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. American Naturalist 150: 554–567.

Fricke, E. C., D. C. Haak, D. J. Levey, and J. J. Tewksbury. 2016. Gut passage and secondary metabolites alter the source of post-dispersal predation for bird-dispersed chili seeds. Oecologia 1:905–910.

Gentry, J. B., and M. H. Smith. 1968. Food habits and burrow associates of *Peromyscus polionotus*. Journal of Mammalogy 49:562–565.

Grigione, M. M., P. Burman, S. Clavio, S. J. Harper, D. Manning, and R. J. Sarno. 2011. Diet of Florida coyotes in a protected wildland and suburban habitat. Urban Ecosystems 14:655–663.

Guiden, P. W., S. L. Bartel, N. W. Byer, A. A. Shipley, and J. L. Orrock. 2019. Predator-prey interactions in the Anthropocene: reconciling multiple aspects of novelty. Trends in Ecology and Evolution 34:616–627.

Gulsby, W. D., J. C. Kilgo, M. Vukovich, and J. A. Martin. 2017. Landscape heterogeneity reduces coyote predation on white-tailed deer fawns. Journal of Wildlife Management 81:601–609.

Hammond, D. S. 2020. Post-dispersal seed and seedling mortality of tropical dry forest trees after shifting agriculture, Chiapas, Mexico. Journal of Tropical Ecology 11:295–313.

Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.

Herrera, C. M. 1989. Frugivory and seed dispersal by carnivorous mammals, and associated fruit characteristics, in undisturbed Mediterranean habitats. Oikos 55:250–252.

Herrera, C. M., and O. Pellmyr. 2002. Plant-animal interactions: an evolutionary approach. Wiley-Blackwell, Hoboken, New Jersey, USA.

Hobbs, R. J. 1985. Harvester ant foraging and plant species distribution in annual grassland. Oecologia 67:519–523.

Holl, K. D., and M. E. Lulow. 1997. Effects of species, habitat, and distance from edge on post-dispersal seed predation in a tropical rainforest. Biotropica 29:459–468.

Howe, H. F., and J. S. Brown. 2000. Early effects of rodent granivory on experimental forb communities. Ecological Applications 10:917–924.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

Howe, H. F., B. Zorn-Arnold, A. Sullivan, and J. S. Brown. 2006. Massive and distinctive effects of meadow voles on grassland vegetation. Ecology 87:3007–3013.

Hulme, P. E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. Perspectives in Plant Ecology, Evolution and Systematics 1:32–46.

Inouye, R. S., G. S. Byers, and J. H. Brown. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. Ecology 61:1344–1351.

Kats, L. B., and L. M. Dill. 1998. The scent of death: chemosensory assessment of predation risk by prey animals. Écoscience 5:361–394.

Kollmann, J., D. A. Coomest, and S. M. Whitet. 1998. Consistencies in post-dispersal seed predation of temperate fleshy-fruited species among seasons, years and sites. Functional Ecology 12:683–690.

Larios, L., D. E. Pearson, and J. L. Maron. 2017. Incorporating the effects of generalist seed predators into plant community theory. Functional Ecology 31:1856–1867.

Levey, D. J., and M. M. Byrne. 1993. Complex ant-plant interactions: rain-forest ants as secondary dispersers and post-dispersal seed predators. Ecology 74:1802–1812.

Levey, D. J., W. R. Silva, and M. Galetti. 2002. Seed dispersal and frugivory: ecology, evolution, and conservation. CABI, New York, New York, USA.

Levi, T., A. M. Kilpatrick, M. Mangel, and C. C. Wilmers. 2012. Deer, predators, and the emergence of Lyme disease. Proceedings of the National Academy of Sciences USA 109:10942–10947.

Lichti, N. I., M. A. Steele, H. Zhang, and R. K. Swihart. 2014. Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758.

Linabury, M. C., N. E. Turley, and L. A. Brudvig. 2019. Insects remove more seeds than mammals in first-year prairie restorations. Restoration Ecology 27:1300–1306.

LoPresti, E. F., V. Pan, J. Goidell, M. G. Weber, and R. Karban. 2019. Mucilage-bound sand reduces seed predation by ants but not by reducing apparency: a field test of 53 plant species. Ecology 100: e02809.

Manzano, P., F. M. Azcárate, B. Peco, and J. E. Malo. 2010. Are ecologists blind to small things? The missed stories on non-tropical seed predation on feces. Oikos 119:1537–1545.

Mastro, L. L. 2011. Life history and ecology of coyotes in the Mid-Atlantic states: a summary of the scientific literature. Southeastern Naturalist 10:721–730.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

Moles, A. T., and M. Westoby. 2003. Latitude, seed predation and seed mass. Journal of Biogeography 30:105–128.

Morey, P. S., E. M. Gese, and S. Gehrt. 2007. Spatial and temporal variation in the diet of coyotes in the Chicago Metropolitan area. American Midland Naturalist 158:147–161.

Ness, J. H., and J. L. Bronstein. 2004. The effects of invasive ants on prospective ant mutualists. Biological Invasions 6:445–461.

Nolte, D. L., J. R. Mason, G. Epple, E. Aronov, and D. L. Campbell. 1994. Why are predator urines aversive to prey? Journal of Chemical Ecology 20:1505–1516.

Nuñez, M. A., D. Simberloff, and M. A. Relva. 2008. Seed predation as a barrier to alien conifer invasions. Biological Invasions 10:1389–1398.

Orrock, J. L. 2010. When the ghost of predation has passed: Do rodents from islands with and without fox predators exhibit aversion to fox cues? Ethology 116:338–345.

Orrock, J. L., and E. I. Damschen. 2005. Corridors cause differential seed predation. Ecological Applications 15:793–798.

Orrock, J. L., and B. J. Danielson. 2005. Patch shape, connectivity, and foraging by oldfield mice (*Peromyscus polionotus*). Journal of Mammalogy 86:569–575.

Orrock, J. L., B. J. Danielson, and R. J. Brinkerhoff. 2004. Rodent foraging is affected by indirect, but not by direct, cues of predation risk. Behavioral Ecology 15:433–437.

Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of predator-prey interactions: Corridors and patch shape influence seed predation. Ecology 84:2589–2599.

Orrock, J. L., H. P. Dutra, R. J. Marquis, and N. Barber. 2015. Apparent competition and native consumers exacerbate the strong competitive effect of an exotic plant species. Ecology 96:1052–1061.

Orrock, J. L., and R. J. Fletcher. 2014. An island-wide predator manipulation reveals immediate and long-lasting matching of risk by prey. Proceedings of the Royal Society of London B: Biological Sciences 281:20140391.

Orrock, J. L., D. J. Levey, B. J. Danielson, and E. I. Damschen. 2006. Seed predation, not seed dispersal, explains the landscape-level abundance of an early successional plant. Journal of Ecology 94:838–845.

Osburn, D. J., and M. J. Cramer. 2013. Foraging response of *Erethizon dorsatum* and *Lepus americanus* to specialized and generalized predator scents. American Midland Naturalist 169:66–73.

Ostfeld, R. S., R. H. Manson, and C. D. Canham. 1997. Effects of rodents on survival of tree seeds and seedlings invading old fields. Ecology 78:1531–1542.

Ostoja, S. M., E. W. Schupp, S. Durham, and R. Klinger. 2013. Seed harvesting is influenced by associational effects in mixed seed neighbourhoods, not just by seed density. Functional Ecology 27:775–785.

Paine, C. E. T., and H. Beck. 2007. Seed predation by neotropical rain forest mammals increase diversity in seedling recruitment. Ecology 88:3076–3087.

Parker, G. 1995. Eastern coyote: the story of its success. First edition. Nimbus Publishing, Halifax, Nova Scotia, Canada.

Passos, L., and P. S. Oliveira. 2003. Interactions between ants, fruits and seeds in a restinga forest in south-eastern Brazil. Journal of Tropical Ecology 19:261–270.

Pearson, D. E., R. M. Callaway, and J. L. Maron. 2011. Biotic resistance via granivory: Establishment by invasive, naturalized, and native asters reflects generalist preference. Ecology 92:1748–1757.

Pizo, M. A., P. R. Guimarães, and P. S. Oliveira. 2005. Seed removal by ants from faeces produced by different vertebrate species. Écoscience 12:136–140.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

Quinn, T. 1997. Coyote (*Canis latrans*) food habits in three urban habitat types of western Washington. Northwest Science 71:1–5.

Ready, C. C., and S. B. Vinson. 1995. Seed selection by the red imported fire ant (Hymenoptera: Formicidae) in the laboratory. Environmental Entomology 24:1422–1431.

Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. Ecology 88:2697–2705.

Sainz-Borgo, C. 2015. Bird feces consumption by fire ant *Solenopsis geminata* (Hymenoptera: *Formicidae*). Entomological News 124:295–299.

Scherer, A. E., and D. L. Smee. 2016. A review of predator diet effects on prey defensive responses. Chemoecology 26:83–100.

Schrecengost, J. D., J. C. Kilgo, D. Mallard, H. S. Ray, and K. V. Miller. 2008. Seasonal food habits of the coyote in the South Carolina Coastal Plain. Southeastern Naturalist 7:135–144.

Seaman, R. E., and P. C. Marino. 2003. Influence of mound building and selective seed predation by the red imported fire ant (*Solenopsis invicta*) on an old-field plant assemblage. Journal of the Torrey Botanical Society 130:193–201.

Shakeri, Y. N., K. S. White, and T. Levi. 2018. Salmon-supported bears, seed dispersal, and extensive resource subsidies to granivores. Ecosphere 9: e02297.

Smith, A. J. 1975. Invasion and ecesis of bird-disseminated woody plants in a temperate forest sere. Ecology 56:19–34.

Thompson, R. M., M. Hemberg, B. M. Starzomski, and J. B. Shurin. 2007. Trophic levels and trophic tangles: the prevalence of omnivory in real food webs. Ecology 88:612–617.

Thornton, D. H., M. E. Sunquist, and M. B. Main. 2004. Ecological separation within newly sympatric populations of coyotes and bobcats in south-central Florida. Journal of Mammalogy 85:973–982.

Traveset, A., T. Bermejo, and M. Willson. 2001. Effect of manure composition on seedling emergence and growth of two common shrub species of Southeast Alaska. Ecology 155:29–34.

Turnbull, L. A., M. J. Crawley, and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238.

Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. Ecology 75:1911–1926.

Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. Behavioral Ecology 12:467–474.

Wallace, M. C., and P. S. Gipson. 2014. Comparison of coyote (*Canis latrans*) diets in continuous and fragmented short-grass prairie in the Texas Panhandle. Texas Journal of Science 66:25–41.

Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. Nature 404:180–183.

Willson, M. F. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67:159–176.

Wolfe, L. M., J. A. Elzinga, and A. Biere. 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. Ecology Letters 7:813–820.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–466.

Zettler, J. A., T. P. Spira, and C. R. Allen. 2001. Ant-seed mutualisms: Can red imported fire ants sour the relationship? Biological Conservation 101:249–253.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3369/full