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ARTICLE

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Invasive shrubs amplify seasonal granivory, revealing optimal windows for seed survival following invasive shrub removal

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Abstract

Invasive shrubs dramatically reduce the biodiversity of native plants, making invaded areas important targets of conservation and restoration. Adding seeds of native plant species, in addition to the removal of invasive plants, is a potentially promising means for restoration of native plant communities. However, because seed survival may vary among seasons, it is essential to understand temporal patterns of seed survival. For example, dense habitats created by invasive shrubs exhibit seasonal changes in structure and food resources that could create seasonal variation in seed survival by altering the activity and abundance of native seed-eating rodents. Despite the potential for invasive shrubs to generate seasonal changes in granivory, we lack experimental studies to evaluate changes in granivory caused by invasive plants over a full year. We mechanically removed the widespread invasive species common buckthorn (*Rhamnus cathartica*) from half of 14 sites (20 × 20 m) in a deciduous oak-maple forest to track rodent and arthropod granivory of three native tree species, basswood (*Tilia americana*), black cherry (*Prunus serotina*), and sugar maple (*Acer saccharum*), and the invasive shrub *R. cathartica* over a year. Our results reveal that the effect of invasive shrubs on granivory changed across seasons. Seeds in invaded habitats experienced, on average, 25.9% higher seed removal than seeds in areas with *R. cathartica* removed, with the largest difference in removal occurring in winter. Seed removal was almost entirely due to rodent granivores that removed seeds at similar rates among species. These results indicate that, following removal of invasive shrubs, sowing seeds in winter may optimize seedling establishment by minimizing granivory. Our findings further reinforce the importance of removing invasive shrubs as an important restoration tool because invasions may amplify granivory throughout the year. Understanding the mechanisms that could be affecting seasonal granivory within invaded systems, the important role of rodent granivores, and the similarities in seed consumption between native and nonnative seeds is critical for continual conservation and restoration efforts aimed at promoting forest regeneration.

KEYWORDS
invasive plants, native trees, *Rhamnus cathartica*, seasonality, seed predation, small mammals

INTRODUCTION

Biological invasions can have deleterious effects on ecosystems across the world (Richardson & Rejmánek, 2011; Stewart et al., 2021; Vilà et al., 2011; Zhang et al., 2022), and many of the effects of invasive species on native species may arise because invasive species can modify interactions among native species (Noonburg & Byers, 2005; Pyšek et al., 2012; White et al., 2006). For example, invasive plants can alter the persistence of native species, change the structure and diversity of ecological communities, and modify ecosystem processes (Guiden & Orrock, 2017; McCary et al., 2016; Vilà et al., 2011; Watling et al., 2011). Many of the deleterious effects of invasive species may arise due to the modification in the nature and strength of ecological interactions in the communities they invade (Fletcher et al., 2019; Orrock et al., 2010; White et al., 2006). For example, granivory, or seed predation, is an important ecological interaction linked to variation in plant recruitment, establishment, and diversity, and granivory may be affected by invasive plants (Bartowitz & Orrock, 2016; Clark et al., 2007; Dylewski et al., 2020; Mattos et al., 2013; Pearson et al., 2011; Turnbull et al., 2000). Studying post-dispersal seed predation is essential for informing seed fate because plant recruitment has been linked to seed survival in diverse systems (Brown & Heske, 1990; Connolly et al., 2023; Dylewski et al., 2020; Edwards & Crawley, 1999; Howe & Brown, 2001; Orrock et al., 2006, 2023), including the temperate forests we study (García et al., 2005; Royo & Carson, 2008; Schnurr et al., 2004). Variation in granivory can arise due to changes in habitat structure and resources that affect the activity and abundance of granivorous mammals (Guiden & Orrock, 2017; Mattos & Orrock, 2010; Orrock, Borer, et al., 2015; Orrock, Dutra, et al., 2015). While many studies demonstrate how invasive plants alter spatial patterns of granivory (Dutra et al., 2011; Guiden & Orrock, 2017; Utz et al., 2020), less is known about how invasive plants modify temporal patterns of granivory. This may represent an important knowledge gap because plant species differ in the timing of seed release and subsequent germination (e.g., seeds of many species overwinter prior to germination) and because seed addition can be a promising means of applied ecological restoration (Bucharova & Krahulec, 2020; Clark et al., 2007; Orrock et al., 2023). As a result, understanding seasonal changes in seed survival may be important for understanding the basic ecology of plant communities as well as for informing the optimal timing of restoration and conservation efforts.

Invasive plants may be particularly important for generating temporal variation in granivory because many invasive plants exhibit temporal changes in vegetative structure (e.g., distinct timing of leaf out and leaf drop) in comparison with native plants (Fridley, 2012; Gallinat et al., 2015; Knight et al., 2007; Wolkovich & Cleland, 2011), produce large seasonal resource pulses (e.g., production of fruits consumed by animals) (Orrock, Borer, et al., 2015; Orrock, Dutra, et al., 2015), or both. Leaf senescence and the associated loss of vegetative cover of invasive shrubs has been linked to changes in the magnitude of granivory within invaded systems (Bartowitz & Orrock, 2016; Keller & Orrock, 2023). Previous studies have shown increases in the magnitude of granivory when invasive shrubs were present (Bartowitz & Orrock, 2016; Keller & Orrock, 2023), but these studies have been limited to a few sampling periods that do not include the winter and spring periods that can be essential for seed survival. However, winter foraging by seed predators can limit plant diversity and survival during the growing season (Guiden & Orrock, 2019, 2021; Korslund & Steen, 2006), and resource scarcity in winter may alter granivore seed preferences (Berl et al., 2017; Guiden & Orrock, 2021; Schnurr et al., 2002, 2004).

Seasonal trends in the effect of invasive shrubs on granivory may also depend on which seed predators are most responsible for seed loss within a system (Bartel & Orrock, 2021; Berl et al., 2017; Chandler et al., 2020). Two of the most common granivore guilds, rodents and arthropods, often exhibit preferences among seed species, and both are capable of substantially altering plant distribution and abundance through their consumption of seeds (Hulme, 1998; Maron & Simms, 1997; Turnbull et al., 2000; Willson & Whelan, 1990). Rodents, in particular, are geographically widespread and abundant seed predators capable of reducing recruitment for specific species (Peters et al., 2004; Siepielski & Benkman, 2008) and affecting the composition of plant communities (Maron et al., 2012; Ostfeld et al., 1997; Pearson et al., 2011; Turnbull et al., 2000). Determining whether rodents or arthropods are responsible for the greatest amount of tree seed loss seasonally, as well as whether one granivore guild exhibits preferences for particular seed species, is important for understanding the ecology of granivory. Moreover, this information can help inform applied strategies, like seed additions, to reduce granivory and maximize restoration and conservation of native plant species.

We experimentally removed invasive shrubs to quantify seasonal patterns of rodent and arthropod granivory by conducting multi-season field experiments using seeds of several woody plant species. Common buckthorn, *Rhamnus cathartica*, is an invasive woody shrub commonly found in deciduous forest understory (Knight et al., 2007; Mascaro & Schnitzer, 2007). *R. cathartica* is highly shade tolerant, capable of rapid growth, and produces high levels of rodent-dispersed seeds (Knight et al., 2007). The unique leaf phenology of *R. cathartica* allows its leaves to senesce later into the autumn and leaf-out earlier in the spring, which can create vegetative cover for rodent granivores during times of the year when no native canopy cover exists (Fridley, 2012; Gallinat et al., 2015; Guiden & Orrock, 2019; Knight et al., 2007; Schuster et al., 2021; Wolkovich & Cleland, 2011), potentially leading to changes in perceived predation risk (Guiden & Orrock, 2019; Orrock et al., 2010). We quantified seasonal patterns of granivory across four seasons and among four species: basswood (*Tilia americana*), black cherry (*Prunus serotina*), sugar maple (*Acer saccharum*), and the invasive shrub *R. cathartica* to illuminate differences in seed removal. Using plots where *R. cathartica* was either removed or left intact, we quantified granivory across all four seasons, evaluating rodent and arthropod granivory on three native tree species, basswood (*T. americana*), black cherry (*P. serotina*), sugar maple (*A. saccharum*), and the invasive shrub *R. cathartica* to illuminate differences across early and late summer, autumn, winter, and spring. We hypothesized that seed predators would use the vegetative cover provided by the late autumn leaf senescence and early spring leaf-out of *R. cathartica* to avoid risk of predation and therefore remove a higher proportion of seeds within invaded habitats. Additionally, due to large differences in vegetative cover between summer and winter, we hypothesized that seed removal would be highest in the summer and lowest in the winter irrespective of invasion status. By examining when seeds are most vulnerable and which species may be at greatest risk, our results will provide land managers with insights to inform the timing and composition of seed additions.

METHODS

Study area and invasive shrub manipulation

This study was conducted at the University of Wisconsin-Madison Arboretum in Madison, WI, within a 50-ha deciduous oak-hickory dominated woodland heavily invaded by *R. cathartica* in the understory. Native tree species in the overstory include broadleaf, deciduous species (e.g., *T. americana*, *A. saccharum*, and *P. serotina*). The majority of the small mammal granivore community is comprised of white-footed mice (*Peromyscus leucopus*) (Bartowitz & Orrock, 2016; Guiden & Orrock, 2017, 2019). Sites consisted of fourteen 20×20 m plots established in the summer of 2014 with half containing intact *R. cathartica* and half with all *R. cathartica* removed (Bartowitz & Orrock, 2016). Since initial plot establishment, each *R. cathartica* removal site has been monitored for *R. cathartica* encroachment and maintained to keep the invasion from spreading within plots by routine mechanical removal of *R. cathartica* (Bartowitz & Orrock, 2016).

Quantifying seed removal

We examined the seasonal effects that the presence of *R. cathartica* can have on small mammal seed removal over a 7-month period. Sessions consisted of 17-day deployment periods of seed removal depots. Seed depots were 3.78-L, translucent plastic containers fitted with lids to eliminate potential predation by birds and large mammals in addition to keeping seeds protected from wind and rain (Chandler et al., 2020; Mattos et al., 2013). We used two types of depots to quantify seed removal by arthropods (arthropod-access depots) and seed removal by both arthropods and rodents (all-access depots) (Bartowitz & Orrock, 2016; Chandler et al., 2020). Two, 5-cm^2 square openings cut into each side allowed for rodent and arthropod access (Chandler et al., 2020; Mattos et al., 2013). An arthropod-access depot was placed adjacent (<0.1 m) to each all-access depot consisting of two, 5-cm^2 openings covered by hardware cloth to exclude rodents. By quantifying both rodent and arthropod seed removal, we were able to estimate the magnitude of rodent seed removal. Within each depot, 10 seeds of each species (*A. saccharum*, *T. americana*, *P. serotina*, and *R. cathartica*) were uniformly dispersed across a sand substrate (Bartowitz & Orrock, 2016; Chandler et al., 2020; Mascaro & Schnitzer, 2007; Mattos et al., 2013). *R. cathartica* seeds were obtained from the University of Wisconsin-Madison Arboretum, and all other seeds were purchased from the Wisconsin Department of Natural Resources.

We selected deployment periods to capture variation in vegetative cover of *R. cathartica* based on its leaf phenology and the availability of native overstory cover. Deployment periods occurred during late summer (September 17, 2021 to October 4, 2021), autumn (November 5, 2021 to November 22, 2021), winter (December 3, 2021 to December 20, 2021), spring (May 10, 2022 to May 27, 2022), and early summer (June 21, 2022 to July 8, 2022). Following each session, we counted remaining seeds and seed fragments within each depot as well as any seeds found directly outside of each depot entrance. The depots in our design have been used in previous studies to assess differences in rodent foraging based on vegetative cover (Bartowitz & Orrock, 2016; Chandler et al., 2020; Keller & Orrock, 2023; Mattos et al., 2013); we have confirmed that patterns of rodent activity (e.g., rodent photo captures around seed depots) are significantly correlated with patterns of seed removal (M. E. Fuka & J. L. Orrock, unpublished data). Seeds were classified as removed if they were not present within a depot or if they were present but clearly destroyed. We assume that seed removal is analogous with seed death as our study species have no structures to promote secondary dispersal (e.g., elaiosomes), and evidence suggests nearly all moved seeds are typically destroyed (e.g., 95% of recovered seeds in a previous study in these sites were destroyed; Guiden & Orrock, 2017).

Measuring habitat characteristics

Because local habitat characteristics can affect the abundance and activity of granivores (Guiden & Orrock, 2017; Manson & Stiles, 1998; Orrock et al., 2003; Orrock & Damschen, 2005), we measured plot-level features that can affect seed removal. Stem density of all woody species was measured once using 1-m^2 quadrats at four central plot locations 5 m from the plot edge during October 2021. Plot-level downed woody debris was counted and separated into medium (11–20 cm) and large (>20 cm) diameter size classes following Bowman et al. (2000). To assess canopy coverage of both the native tree canopy and *R. cathartica* vegetation, light penetration was measured as photosynthetically active radiation (PAR) using a light bar (Apogee Instruments, LQM 70–10). PAR was quantified at the plot center with three measurements spaced 0.5 m apart at ground level (10 cm), chest height (1 m), and overhead height (2 m), totaling nine measurements taken within an hour of solar noon on clear, sunny days (Bartowitz & Orrock, 2016; Chandler et al., 2020; Guiden & Orrock, 2019). Following the first two sessions, light penetration was measured at an additional four locations, 5 m from the plot center in each cardinal direction to capture a larger plot-level measurement of light penetration.

Data analysis

We tested the effects that treatment (*R. cathartica* invaded and *R. cathartica* removed), season (late summer, autumn, winter, spring, and early summer), and granivore access (all-access and arthropod-only access) had on the proportion of seeds removed. We used linear mixed-effects models (LMMs) (package: "lme4"; Bates et al., 2015) with invasion treatment, season, and access as fixed effects, along with all possible interaction terms. In all analyses, plot was modeled as a random effect, totaling 14 plots for each season. Models used the proportion of seeds removed from each depot as the response variable and linear contrasts (package: "emmeans"; Lenth et al., 2020) were used to examine differences in seeds removed between treatment groups. All proportions were logit transformed (Keller & Orrock, 2023; Warton & Hui, 2011), and plots of model residuals were used to verify model assumptions of normality, homoscedasticity, and linearity. Because arthropod seed removal was negligible (see *Results*), we evaluated rodent seed removal using seeds removed from all-access depots using LMMs with invasion treatment, season, PAR, and their interaction as fixed effects. We evaluated PAR differences across treatments and season using LMMs that accounted for the repeated-measures nature of PAR sensor data with invasion treatment, season, and their interaction as fixed effects. Lastly, we examined species-specific patterns of removal using separate LMMs with each species as a response variable and invasion treatment and season as fixed effects. In all analyses, depots destroyed by animal activity were omitted. This reduced the depot total to 130, with each access category losing five total depots. All analyses were conducted using R (R Core Team, 2023).

RESULTS

All season access seed removal

In all-access depots, 38.2 ± 4.2% (mean ± SE) of seeds were removed, and seed fragments were found in 29.2%

of these depots. In arthropod-access depots, 2.38 ± 0.58% of seeds were removed. Intact seeds were found displaced outside of 13.8% of depots. Total seed removal was significantly higher ($F_{1,12} = 73.1$, $p < 0.01$) (Table 1) in all-access depots than in arthropod-only access depots across all seasons (Figure 1a). Seed removal was significantly higher in plots invaded by *R. cathartica* across seasons ($F_{1,12} = 4.56$, $p = 0.05$) (Table 1), and there was a significant effect of season on total seed removal ($F_{4,86} = 2.57$, $p = 0.04$) (Table 1).

All season species-specific seed removal

In all-access depots, 38.0 ± 4.63% of *T. americana*, 38.9 ± 5.01% of *P. serotina*, 44.3 ± 5.31% of *A. saccharum*, and 31.6 ± 4.43% of *R. cathartica* seeds were removed. In arthropod-access depots, 0.46 ± 0.26% of *T. americana*, 0.46 ± 0.26% of *P. serotina*, 0.46 ± 0.34% of *A. saccharum*, and 3.38 ± 1.06% of *R. cathartica* seeds were removed. Seed removal was significantly higher in invaded plots than in removed plots for *P. serotina* ($F_{1,12} = 12.7$, $p < 0.01$), *A. saccharum* ($F_{1,12} = 7.57$, $p = 0.01$), and *R. cathartica* seeds ($F_{1,12} = 6.29$, $p = 0.02$) (Table 2).

Season-specific seed removal

Compared to invaded plots, total seed removal was significantly lower in plots without *R. cathartica* during the winter ($t = 2.14$, df = 12, $p = 0.05$) and marginally significantly lower in spring ($t = 2.03$, df = 12, $p = 0.06$) (Figure 1b). Total seed removal in invaded plots was not significantly different across all seasons ($F_{4,21} = 0.23$, $p = 0.91$), but was significantly different within removal plots across all seasons ($F_{4,21} = 3.29$, $p = 0.02$). Removal of *P. serotina* seeds was significantly higher in invaded plots in winter ($t = 3.31$, df = 12, $p < 0.01$) and early summer ($t = 2.18$, df = 12, $p = 0.04$), but not significantly different in any other season (Figure 2). Removal of *A. saccharum* seeds was significantly higher in invaded plots in winter ($t = 2.62$, df = 12, $p = 0.02$) and spring ($t = 2.11$, df = 12, $p = 0.05$), but not significantly different in any other season (Figure 2). Removal of *R. cathartica* seeds was significantly higher in invaded plots in spring ($t = 2.31$, df = 12, $p = 0.03$) and marginally in early summer ($t = 2.05$, df = 12, $p = 0.06$), but not significantly different in any other season (Figure 2).

TABLE 1 *F* ratios and *p* values for evaluating effects of treatment (*Rhamnus cathartica* invaded and *R. cathartica* removed), season (early and late summer, autumn, winter, and spring), and granivore access (all-access and arthropod-only access) on the proportion of seeds removed (linear mixed-effects model).

Effect	*F*	df	*p*
Invasion	4.56	1, 12	0.053†
Season	2.57	4, 86	0.043*
Access	73.1	1, 12	<0.001***
Treatment × Season	0.90	4, 86	0.466
Treatment × Access	4.39	1, 12	0.057†
Season × Access	1.88	4, 86	0.120
Treatment × Season × Access	0.37	4, 86	0.826

†$p < 0.1$;
*$p < 0.05$; ***$p < 0.001$.

Microhabitat characteristics

Across all seasons, total stem density was positively associated with increasing total seed removal ($F_{1,10} = 4.63$, $p = 0.05$) and total stem density was significantly higher in invaded plots ($F_{1,12} = 8.37$, $p = 0.01$). On average, there were 10 times more stems per *R. cathartica*-invaded plot than in *R. cathartica*-removed plots. Plot-level downed-woody debris was not significantly different between treatments ($F_{1,11} = 0.008$, $p = 0.93$) and was not significant in increasing total seed removal across all seasons ($F_{1,6} = 1.08$, $p = 0.33$). Ground-level PAR was significantly different across all seasons ($F_{4,43} = 6.03$, $p < 0.01$), but was not significantly different between removal treatments ($F_{1,12} = 2.66$, $p = 0.12$). No significant effect of ground-level PAR on total seed removal across seasons and treatments was found ($F_{1,33} = 0.66$, $p = 0.42$). No significant differences were detected between PAR readings based on height across seasons ($F_{2,179} = 0.459$, $p = 0.63$).

DISCUSSION

Seasonal variation in seed survival is important to understand because periods of elevated seed consumption may place strong constraints on plant recruitment (Bricker et al., 2010; Chambers & MacMahon, 1994; Dylewski et al., 2020; Turnbull et al., 2000) as well as delimit optimal seasons for conservation, restoration, and management action. Using an invasive shrub removal and experimentally measuring seed removal across all seasons, our results reveal how an invasive plant creates temporally heterogenous patterns of rodent granivory. In finding that invasive shrubs generate strong temporal intra-annual consistency in rodent seed predation for both native trees and invasive shrubs, our results suggest several implications. First, because seed removal was

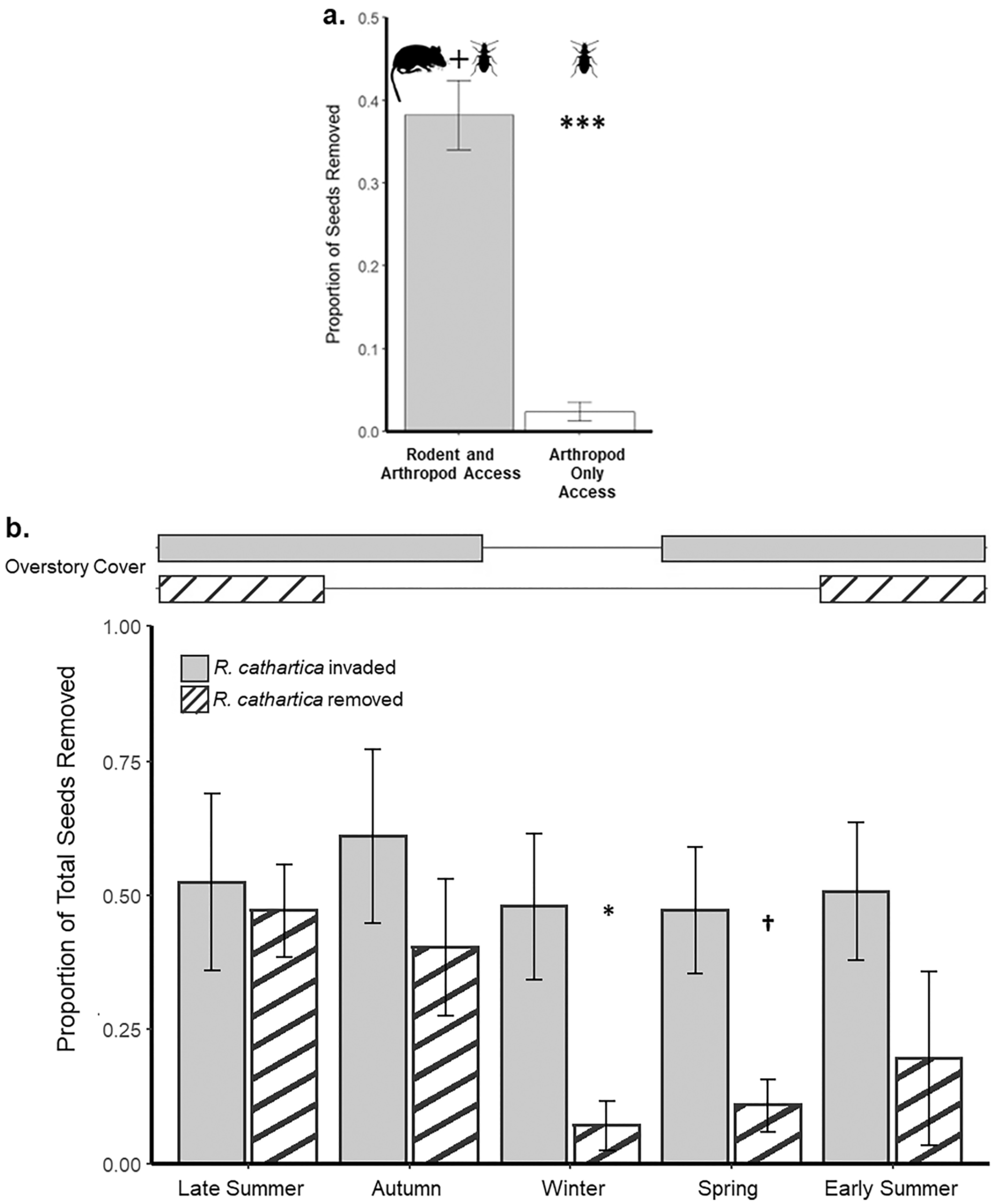

FIGURE 1 (a) Bar plot showing the proportion of seeds removed from arthropod-only access depots and all-access depots (mean ± SE). (b) Bar plot of the proportion of seeds removed from all-access seed depots across seasons and invasive-shrub removal treatments. Potential overstory cover refers to the hypothetical vegetative cover present in plots based on treatment and season differences. Error bars depict one SE. Asterisks indicate significant pairwise differences. $^{\dagger}p < 0.1$; $^{*}p = 0.05$; $^{***}p < 0.001$.

lowest in the winter and spring in the absence of invasive shrubs, this indicates an optimal window for potentially successful seed additions of native tree species as well as a potential factor leading to tree recruitment failure. Second, restoration and conservation strategies that deter rodent granivory may be an effective technique for reducing native tree seed loss in both invaded and uninvaded forests. Finally, given consistent consumption of both native and exotic species, rodent granivores may be important in limiting invasive shrub introduction into uninvaded woodlands or hinder establishment in managed habitat.

Seasonal variation in seed removal may provide a window for management action

Removal of invasive woody shrubs is a primary restoration approach that is often followed by seed addition to reintroduce native species (Bucharova & Krahulec, 2020;

TABLE 2 *F* ratio and *p* values for evaluating effects of treatment (*Rhamnus cathartica* invaded and *R. cathartica* removed) and season (early and late summer, autumn, winter, and spring) on the proportion of seed species removed by rodents and arthropods combined (linear mixed-effects models).

Effect	F	df	p
Tilia americana			
Treatment	0.24	1, 12	0.631
Season	4.05	4, 43	0.007**
Treatment × Season	0.57	4, 43	0.679
Prunus serotina			
Treatment	12.7	1, 12	0.003**
Season	1.32	4, 43	0.277
Treatment × Season	0.78	4, 43	0.538
Acer saccharum			
Treatment	7.57	1, 12	0.017*
Season	3.23	4, 43	0.020*
Treatment × Season	0.83	4, 43	0.508
R. cathartica			
Treatment	6.29	1, 12	0.027*
Season	0.93	4, 43	0.454
Treatment × Season	0.66	4, 43	0.621

*$p < 0.05$; **$p < 0.01$.

Gorchov & Trisel, 2003; Hartman & McCarthy, 2004), and studies have shown that abundance and richness of native species often increase following the removal of invasive shrubs (Connolly et al., 2023; Orrock, Borer, et al., 2015; Orrock, Dutra, et al., 2015). Direct seeding native tree species as a means of reforestation can be an efficient and cost-effective alternative to seedling additions (Grossnickle & Ivetić, 2017; Löf et al., 2019; Madsen & Löf, 2005; Villalobos et al., 2020). Our results highlight the value of removing invasive shrubs for reducing granivory and suggest that implementing seed additions during the winter and spring may enhance seed survival (Boone & Mortelliti, 2019; Pearson et al., 2014; Schnurr et al., 2004; Tourville & Dovciak, 2023). Because seed survival is a critical stage in the life cycle of plants and studies demonstrate that seed survival is directly linked to plant establishment (Dylewski et al., 2020; Larios et al., 2017; Ostfeld et al., 1997; Turnbull et al., 2000), our results further imply that winter and spring may be the times of year when added seeds are most likely to escape granivory. Moreover, rodent granivory has been linked to altering plant recruitment for species used in our study (Royo & Carson, 2008; Schnurr et al., 2004) as well as within similar systems (e.g., temperate forests) (García et al., 2005; Royo & Carson, 2008; Schnurr et al., 2004), and rodent

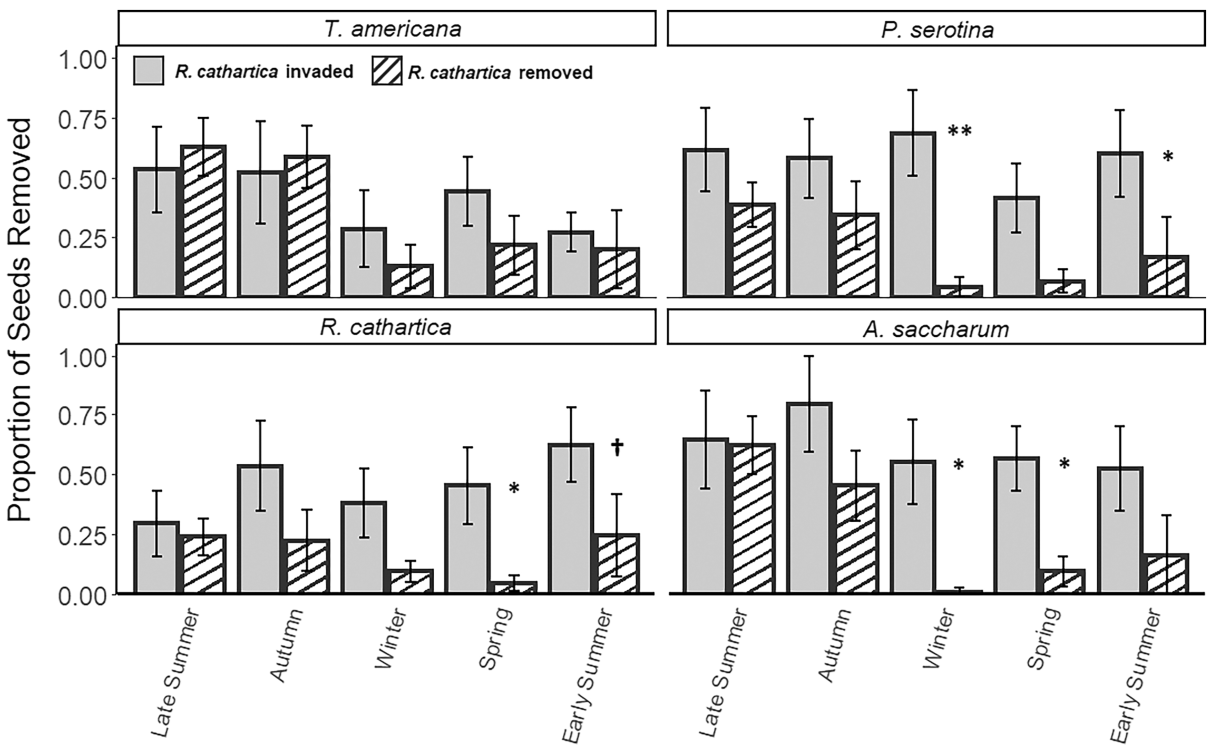

FIGURE 2 Bar plot grid of *Tilia americana*, *Prunus serotina*, *Acer saccharum*, and *Rhamnus cathartica* seed removal across seasons and invasive-shrub removal treatments (mean ± SE).

exclusion studies have provided evidence that rodents are a key limiting factor in reducing plant recruitment from seeds (Brown & Heske, 1990; Connolly et al., 2023; Howe & Brown, 2001; Pearson et al., 2011). Madsen and Löf (2005) found that the direct seeding of oak acorns had higher establishment success when sown in the spring than in the autumn, with approximately 20%–40% higher establishment. In our study, in the absence of invasive shrubs, seed removal was 29.6% lower in the spring than in the autumn. Taken together, the findings of Madsen and Löf (2005) highlight that seed additions of native trees can be a useful approach, but the timing of seed additions is crucial. Our results suggest that there may be predictable periods when survival is highest, translating into more effective management when assuming that recruitment is limited only by seed survival.

Despite a lack of vegetative cover in the winter that we hypothesized would reduce winter granivory, we found that total seed predation rates in the presence of *R. cathartica* were similar across all seasons (Figure 1b). A possible explanation for these findings is that *P. leucopus* often forage in areas that are defined by a high level of structural complexity (Guiden & Orrock, 2017; Manson & Stiles, 1998). Additionally, dense canopies of invasive plant cover have been linked to limited tree and native plant recruitment (Aronson & Handel, 2011; Fagan & Peart, 2004; Greene & Blossey, 2012; Orrock, Dutra, et al., 2015), and our results provide a possible mechanism for these findings. Because habitats invaded by *R. cathartica* typically have high densities of vertical woody stems (e.g., we recorded a total of 265 more stems in invaded plots than in removal plots within our system), these stems may provide year-long structural complexity that maintain high rates of rodent granivory and have been shown to be important in affecting rodent activity and abundance (Guiden & Orrock, 2019; Kotler & Brown, 1988; Ostfeld et al., 1997; Utz et al., 2020). Our findings suggest that differences in stem density could be having strong effects on rodent granivory because of the vertical structure provided by these stems. Dueser and Shugart (1978) found that rodents more often occurred at sites with higher densities of woody stems, and our results suggest that stems are an important habitat feature that can provide seasonal benefits to rodents, allowing them to consume large quantities of seeds throughout the year. Our results complement and extend their findings by demonstrating that stem density may be an unappreciated contributor to changes in rodent activity and granivory by potentially providing rodents with a source of refuge when vegetative cover is no longer available. While the effect of habitat structural complexity on granivory may be a more general mechanism that could be generated by native shrubs, we currently lack any studies to suggest that cover from native plants may alter granivory. As such, habitat structural complexity may provide a means to predict when the strength of seasonal changes may be greatest.

Measures aimed at reducing rodent granivory may be most effective at reducing tree seed loss

Both rodents and arthropods can profoundly affect plant populations and communities through seed predation (Bricker et al., 2010; Christian, 2001; Crist & Macmahon, 1992; Maron et al., 2012; Maron & Simms, 1997), although rodents and arthropods often differ in the seeds they consume (Chandler et al., 2020; Keller & Orrock, 2023). Our results corroborate the findings of other studies that found that seed predation by arthropods is often comparatively less than that by rodents (Chandler et al., 2020; Hulme, 1998; Hulme & Borelli, 1999; Keller & Orrock, 2023; Ostfeld et al., 1997). Rodent seed predators, like *P. leucopus*, are significant consumers of tree seeds in temperate deciduous forests (Bartowitz & Orrock, 2016; Guiden & Orrock, 2017; Webb & Willson, 1985). The lack of seed predation by arthropods in our study may be because the seeds we used were relatively large (all over 15 mg), and many arthropods consume much smaller seeds (Chambers & MacMahon, 1994; Crist & Macmahon, 1992; Ness et al., 2004). For example, Crist and Macmahon (1992) found that the size range of seeds removed by ants was between 0.26 and 0.50 mg, approximately 30 times lighter than the lightest seed used in our study. Given the significant consumption of tree seeds by rodents (Figure 1a) and other studies implicating rodents as the largest impediment to successful tree establishment following seed additions (Birkedal et al., 2010; Löf et al., 2019; Madsen & Löf, 2005; Villalobos et al., 2020), restoration and conservation strategies that seek to deter rodent granivory, such as chemically treating seeds, could be useful. For example, capsaicin is a common taste deterrent for rodents used to reduce granivory (Curtis et al., 2000; Jensen et al., 2003; Pearson et al., 2019), although few studies have tested the efficacy of capsaicin on large-seeded tree seeds similar to those used in our study (see Lanni et al., 2023). Therefore, our results suggest that if seeds cannot be added during the winter due to logistical constraints, the use of granivory deterrents (e.g., chemical seed coatings, hardware cloth exclosures, seed burials, protective tubing) (Lanni et al., 2023; Madsen & Löf, 2005; Maron & Simms, 2001; Nilson et al., 2013) will be important to protect seeds during times when seeds may be more vulnerable.

Potential seasonal differences in rodent granivory between native trees and invasive shrubs

Among differences in consumption of specific seed species, our results reveal comparable consumption of native tree seeds and *R. cathartica* seeds by rodent granivores (Figure 2). Rodent granivores often choose seeds based on size and ease of handling (Kerley & Erasmus, 1991; Muñoz & Bonal, 2008), and the large seed species used in our study have been positively correlated with high energy content, a trait that is more preferable to rodent granivores than seed abundance or availability (Boone & Mortelliti, 2019; Celis-Diez et al., 2004; Chambers & MacMahon, 1994; Moore et al., 2021; Schnurr et al., 2004). Because we used large-seeded species that reflected the tree communities in our study area, size differences between the seeds available may not have been great enough to drive rodent preference for any one species over another. A lack of difference in consumption of native tree seeds versus *R. cathartica* seeds could either (1) foster future plant invasions or (2) support biotic resistance by not allowing invasive shrubs to establish linked to a high consumption of *R. cathartica* seeds. At the same sites used in our study, Bartowitz and Orrock (2016) also found no differences in seed removal between native tree seeds and the invasive shrub *R. cathartica*. Because *R. cathartica* produces a large amount of viable seeds relative to the native tree species used in our study, it may be difficult to measure the impacts that rodent granivores may have on invasion success (Clark et al., 1999, 2007; Henry et al., 2021; Houle, 1994). While studies have found different rates of seed consumption between native and invasive species (Mattos et al., 2013; Pearson et al., 2011) as well as between multiple invasive species (Bierker et al., 2023), these studies were seasonally constrained and did not allow for the examination of seed consumption when differences in ambient seed inputs were present. Our study design allowed us to examine differences in consumption rates based on the seasonal variation associated with seed production and fruit inputs, specifically in the presence of *R. cathartica* where fruit fall is often prolific (Archibold, 1997; Knight et al., 2007). Our results suggest that these seasonal pulses in seed fall and fruit drop did not lead to changes in seed preference for rodent granivores. In the future, the ability to link seed removal of invasive species to future invasive plant establishment can allow us to better understand whether there is strong evidence to support granivore-mediated biotic resistance or lead to greater establishment success for invasive shrub–based high levels of seed outputs by invasive shrubs in comparison with native trees (Archibold, 1997; Houle, 1994; Mattos et al., 2013; Pearson et al., 2014).

Conclusions and future directions

Temporal variation in seed survival is important to understand because extended dormancy periods for many species may render seeds vulnerable to post-dispersal seed predation, because invasive plants may influence the magnitude of seed mortality, and because successful conservation and restoration ultimately require seed survival. Our study helps to better inform management decisions for seed addition timing and emphasizes the need for understanding intra-annual variation in granivory (Bartowitz & Orrock, 2016; Mattos et al., 2013; Willson & Whelan, 1990). By revealing that vertical stem density is a primary mechanism associated with seasonal variation in rodent granivory in invaded and uninvaded habitats, our work highlights a key habitat feature affecting seed loss throughout the year. Our results also help identify future studies that will be important to fully characterize the role of invasive shrubs in modifying granivory and tree recruitment. For example, future studies might explore how the effect of invasive shrubs may depend upon landscape context: Our study was done in an urban forest, which may differ from rural forests in terms of the foods available for small mammals, the presence of small mammal predators, or other factors that could modify granivory (Borden & Flory, 2021; Faeth et al., 2005; Lyons et al., 2017; Mazza & Guenther, 2021; Shochat et al., 2010). Additionally, while our results provide evidence for differences in seasonal seed removal using a 7-month duration, the majority of seed removal studies are often limited to single removal periods and short exposure times (Hargreaves et al., 2019; Moles et al., 2003; Orrock, Borer, et al., 2015). Therefore, future studies examining seasonal variation in granivory under a seasonal lens would benefit from considering multi-year analyses due to the inherent temporal variation that exists between years (e.g., weather patterns, background seed availability, rodent populations) (Schnurr et al., 2002). Understanding both seasonal and temporal variations in granivory may be critical to linking changes in granivory to more large-scale patterns of plant recruitment. By implementing direct seeding strategies, future studies may link seasonal patterns of granivory to potential shifts in plant communities.

AUTHOR CONTRIBUTIONS

Mark E. Fuka and John L. Orrock conceptualized the study and project design. Mark E. Fuka conducted fieldwork, data collection, data analysis, and wrote the initial draft of the manuscript. Mark E. Fuka and John L. Orrock both contributed to manuscript revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Fuka, 2024) are available from Figshare: https://doi.org/10.6084/m9.figshare.23802342.

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