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Note

Invasive shrub removal may be more effective at reducing granivory than coating tree seeds with capsaicin

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Abstract

The utility of seed addition to promote tree regeneration can be greatly limited by animals that consume seeds. Moreover, given that restoration often occurs in forests where invasive shrubs are abundant, and evidence that invasive shrubs can increase granivory, it is important to explore whether methods for reducing granivory work equally well in invaded and uninvaded habitats. We used a multi-site field experiment spanning 160 days to explore whether coating seeds of *Prunus serotina* with capsaicin extract leads to reduced granivory in habitats with or without invasive shrubs (*Rhamnus cathartica*). Capsaicin-coated seeds were removed at a similar rate to uncoated seeds, but seeds in invaded plots had a 78.8% higher rate of removal compared to plots without invasive shrubs. Our findings suggest that managers seeking to encourage regeneration of native trees using direct seeding should consider invasive shrub removal as a top priority to limit the loss of seeds once sown.

Key words: seed predation, capsaicin, invasive plants, *Rhamnus cathartica*, *Prunus serotina*

Introduction

The sustainability of temperate forest ecosystems may be compromised by poor recruitment of tree species limiting the regeneration of mature trees (Clark et al. 1999; Royo and Carson 2008). Although the sowing of native tree seeds may be a promising means for promoting regeneration by increasing the number of available germinants (Madsen and Löf 2005; Löf et al. 2019), the effectiveness of sowing tree seeds can be greatly reduced when seeds are consumed by rodent granivores (Madsen and Löf 2005; Birkedal et al. 2010; Bucharova and Krahulec 2020). Rodent seed predation, or granivory, has been shown to limit the recruitment and establishment of plants (Royo and Carson 2008; Dylewski et al. 2020), thereby hindering restoration success via seed addition. As such, understanding the factors that modify rodent granivory on native tree seeds is important in evaluating the effectiveness of regeneration strategies that use seed sowing. A major factor that has been shown to amplify seed predation by rodents within northern temperate forests across the Eastern US is the presence of invasive woody shrubs (McCay and McCay 2009, Mattos et al. 2013; Bartowitz and Orrock 2016; Utz et al. 2020; Connolly et al. 2024). The high amounts of vegetative cover created by invasive woody shrubs has been shown to increase small mammal activity (Guiden and Orrock 2019; Connolly et al. 2024), and this subsequent increase in activity can lead to elevated rates of seed loss within invaded understory (Mattos et al. 2013; Bartowitz and Orrock 2016). While the mechanical removal of invasive shrubs has proven to be an effective means of reducing rodent granivory (Mattos et al. 2013; Bartowitz and Orrock 2016; Keller and Orrock 2023), invasive shrub removal is often expensive, time-consuming, and requires continued site monitoring to suppress any future reestablishment by exotic species (Holl and Howarth 2000; Zavaleta 2000; Anfang et al. 2020). Exploring whether restoration techniques are equally effective in invaded habitats compared to habitats where invasive shrubs have been removed may reveal approaches that allow managers to promote tree regeneration without removing invasive shrubs.

Conservation and restoration strategies that involve coating seeds with chemicals to deter rodent granivory have been promising in some studies (Nolte and Barnett 2000; Tewksbury and Nabhan 2001; Willoughby et al. 2011; Lanni et al. 2023), but it is unknown whether this technique is effective in both invaded and recently managed forest understory. Because invasive shrubs are strongly linked to increases in granivorous rodent foraging activity (Mattos et al. 2013; Guiden and Orrock 2019), the use of chemically coated seeds may be less effective in areas invaded by woody shrubs due to high amounts of rodent activity and subsequent granivory. Although invasive shrub removal can reduce rodent seed predation, studies have shown that this effect may be seasonally linked (Mattos et al. 2013; Keller and Orrock 2023, Fuka and Orrock, in review), and therefore requires developing a method to increase seed survival irrespective of invasion status. Capsaicin, from *Capsicum* spp., is the secondary compound found in chili peppers that gives peppers their burning-hot taste, and previous studies have shown that capsaicin can act as a taste deterrent to rodents when applied to plant seeds (Nolte and Barnett 2000; Pearson et al. 2019). Specifically, the use of capsaicin on seeds has been shown to be a cost-effective way to protect the seeds of herbaceous plant species (e.g., *Balsamorhiza sagittate*) (Pearson et al. 2019), fruiting plants (e.g., *Celtis pallida*) (Tewksbury and Nabhan 2001), and small tree seeds (e.g., *Pinus palustris*, *Fraxinus excelsior*, and *Fagus grandifolia*) (Nolte and Barnett 2000; Willoughby et al. 2011; Lanni et al. 2023). Seed coatings with capsaicin may also be more effective at reducing rodent seed consumption than other chemical seed coats (e.g., cinnamamide, quinine sulfate, and ammonium sulfate) (Watkins et al. 1998; Nolte et al. 1994; Willoughby et al. 2011). However, less is known about how capsaicin could affect the consumption of a large-seeded tree species like *Prunus serotina*. Moreover, although *Prunus serotina* is often found in forests invaded by woody exotic shrubs, it is not known whether the effectiveness of capsaicin differs in invaded forests compared to forests where invasive shrubs have been removed due to differences in rodent activity. Additionally, most studies that test for differences in seed consumption using capsaicin-treated seeds are relatively short-term (Nolte and Barnett 2000; Willoughby et al. 2011; Pearson et al. 2019). Because seed removal rates can change over time (Mattos et al. 2013; Keller and Orrock 2023, Fuka and Orrock, in review), we seek to understand the efficacy of capsaicin over multiple seasons relevant to natural timescales of seed dispersal, survival, and recruitment. Examining how invasive shrubs may affect the efficacy of capsaicin-treated seeds across multiple seasons may allow managers to determine the most effective strategies at promoting seed survival using an organic, non-toxic chemical deterrent.

We coupled field-based seed-removal assays with the experimental removal of invasive shrubs to examine the efficacy of *Capsicum chinense* extract, in which capsaicin is a major active ingredient, on seeds of *Prunus serotina.* Seeds were monitored intermittently over a 5-month period in the field to explore whether seed-coat treatment and duration altered rodent granivore deterrence. We hypothesized that (1) *Prunus serotina* seeds coated with capsaicin extract would be consumed less than noncoated seeds, and that (2) the efficacy of capsaicin extract as a deterrent would be less effective in the presence of invasive woody shrubs. By examining the survival of capsaicin-coated seeds, both spatially and temporally, our findings can help to improve our understanding of a practical management strategy for enhancing forest regeneration via seed addition.

Methods

Study area and experimental plot design

This study took place within the Lost City Forest in the University of Wisconsin-Madison Arboretum in Madison, WI. This woodland is heavily invaded by invasive woody shrubs, primarily *Rhamnus cathartica*, throughout the understory and the canopy consists of *Acer saccharum*, *Prunus serotina*, and *Quercus rubra*. In 2014, we established ten, 400 m^2 plots where all invasive shrubs were removed from half of the plots using mechanical removal followed by herbicide application to each cut stem (Bartowitz and Orrock 2016). This treatment method has been maintained by removing any new *R. cathartica* that appear in *R. cathartica* removal plots each year.

Capsaicin extraction

To extract pure capsaicin from *C. chinense*, we used commercially available Bhut Jolokia powder. Each extraction process, which yielded approximately 160 mL of capsaicin extract, used 45 g of *C. chinense* powder and 300 mL of 200-proof ethanol (Lanni et al. 2023). Following extraction, *Prunus serotina* seeds were soaked in capsaicin extract for 30 s to ensure a full coating before they were set out to dry in the lab for 3 days prior to field deployment. This application method and extraction protocol allowed us to measure the amount of capsaicin present in the capsaicin extract following seed coating. We used colorimetric assays (González-Zamora et al. 2015, Lanni et al. 2023) to compare between known concentrations of capsaicin and the amount present on randomly selected seeds that were collected from the field following deployment as well as seeds immediately following drying and before deployment in the field. This was done by creating concentrations of capsaicin extract (displaying peaks at 280 nm) with varying ethanol dilution levels to develop a standard curve of average absorbance (Lanni et al. 2023). Standard concentrations ranged from a maximum of 75% capsaicin extract to a minimum of 0.01% capsaicin extract. Capsaicin was stripped from seed coats using a 48 h ethanol soak followed by a 1 min vortex.

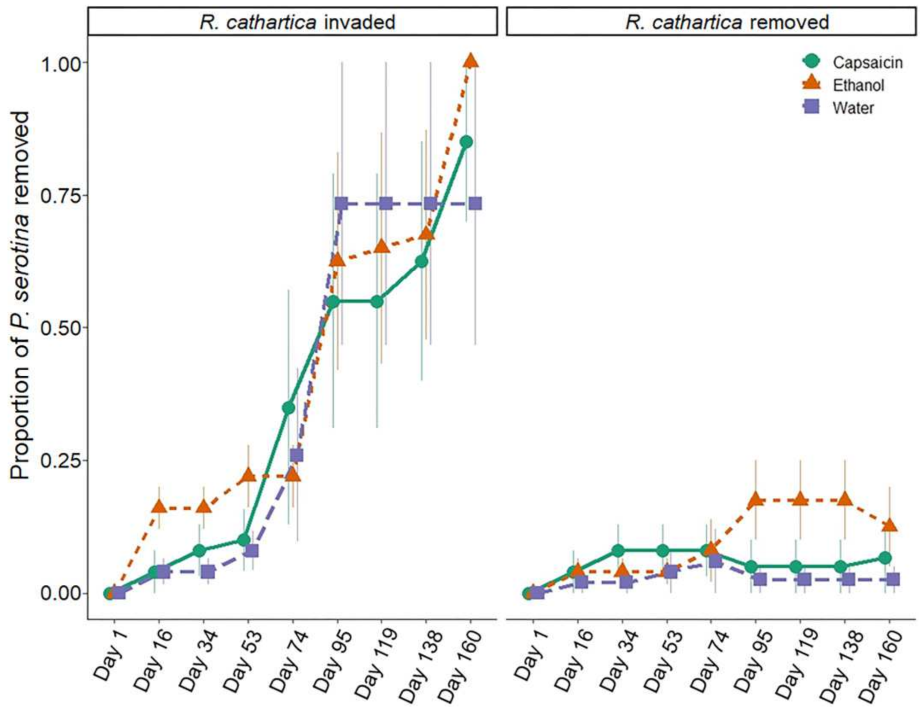
Seed predation and capsaicin treatment

To quantify seed predation, three, 3.78 L seed-removal depots were placed in a triangular pattern 0.3 m apart within each of the ten plots, totaling 30 removal depots. Seed-removal depots have been used successfully to quantify rodent seed removal in invaded versus uninvaded habitats in previous studies (Bartowitz and Orrock 2016; Keller and Orrock 2023; Fuka and Orrock, in review). Within each depot, 10 *Prunus serotina* seeds, locally obtained from the Wisconsin Department of Natural Resources, were randomly distributed on top of a sand substrate. Each depot consisted of a different, randomized seed coating treatment and therefore each plot contained one replicate depot per seed-coating treatment. Prior to deployment, each set of 10 seeds was treated with either water, capsaicin extract, or an ethanol-only control. The use of an ethanol treatment was due to the use of ethanol in extracting pure capsaicin, allowing us to determine if different rates of seed predation were caused by traces of ethanol used during extraction, or the capsaicin extract itself. Seed depots were deployed during the early winter (2 December 2022) and remaining seeds were monitored eight times approximately every 20 days during the deployment prior to depot collection in spring (10 May 2023), totaling a 160-day deployment.

Statistical analyses

We used a generalized linear mixed model (package: “glmmTMB”; Brooks et al. 2017) to test for the effects that invasion (*R. cathartica* invaded vs. *R. cathartica* removed), seed

Fig. 1. Time-series plot of the proportion of *Prunus serotina* seeds removed based on seed treatment for the duration of the deployment window split by habitat.



treatment (water, capsaicin, or ethanol), and time (day of year), had on *Prunus serotina* removal. We modelled invasion, seed treatment, and time as fixed effects, and included a first-order autoregressive term as a random effect to account for covariance among sites sampled during repeated sessions. Linear contrasts (package: “emmeans”; Lenth et al. 2020) were used to examine significant main effects and interaction terms associated with our a priori hypotheses that capsaicin would decrease seed removal and that this effect would be greatest in plots with invasive shrubs removed due to lower granivorous rodent activity associated with cleared plots (Mattos and Orrock 2010; Guiden and Orrock 2019; Keller and Orrock 2023). During the study, six depots (haphazardly distributed across sites and treatments) were disturbed and excluded from analyses. Analyses were conducted with R (R Core Team 2024).

Table 1. χ^2-values and *p*-values for evaluating effects on proportion of total *Prunus serotina* seeds removed between habitat (*R. cathartica* invaded vs. *R. cathartica* removed), seed treatment (water, capsaicin, or ethanol), and time (day of year). Asterisks indicate significant differences in the proportion of seeds removed. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

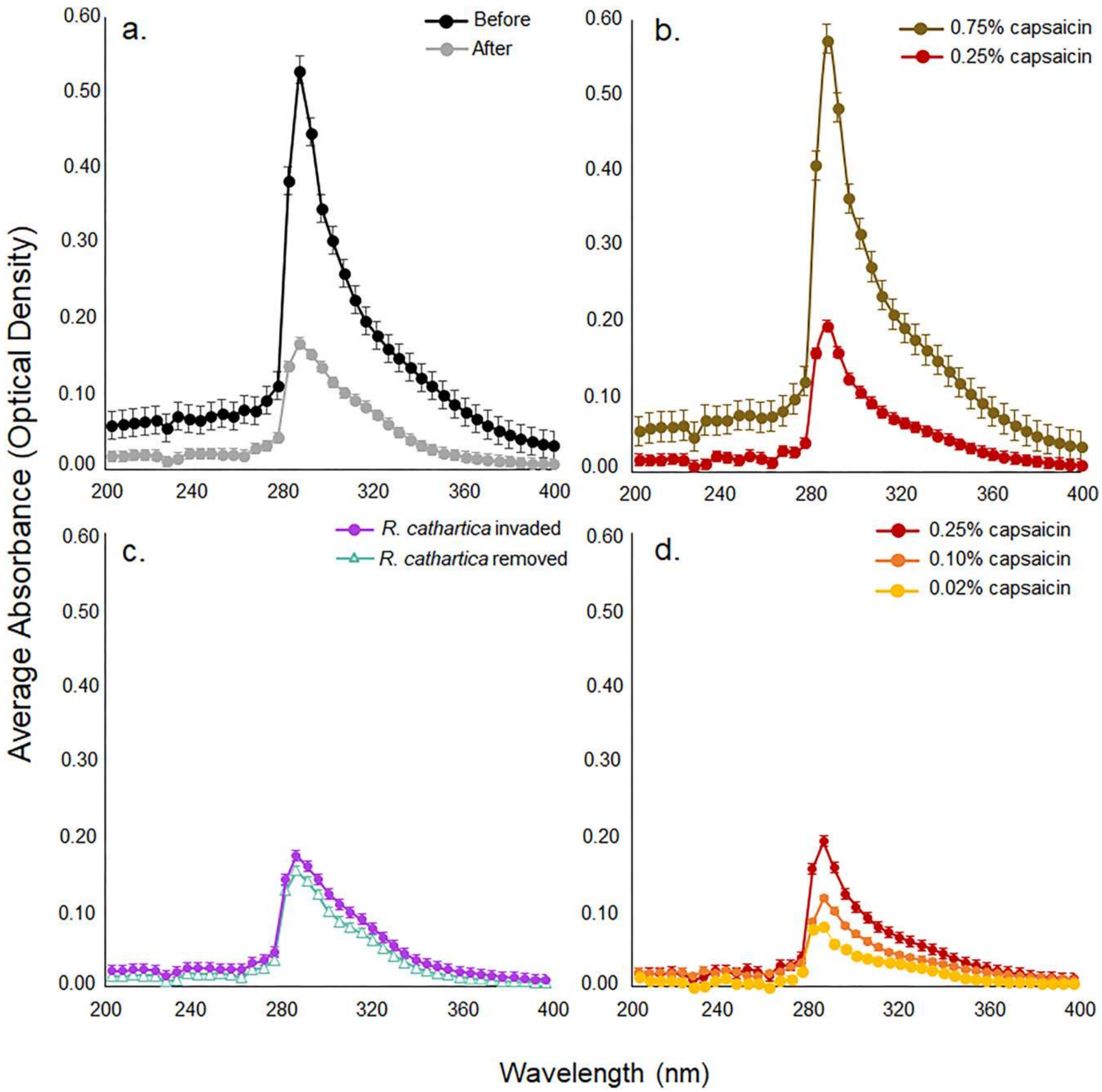
Effect	χ^2-value	df	*p*-value
Treatment	3.06	2	0.215
Habitat	0.15	1	0.718
Time	30.24	1	<0.001***
Treatment x habitat	1.55	2	0.458
Treatment x time	1.94	2	0.379
Habitat x time	14.16	1	<0.001***
Treatment x habitat x time	4.18	2	0.123

Results

Over the 160-day span of our experiment, we quantified removal of 116 seeds from a total of 240 total seeds (Fig. 1). Significantly more water-coated *Prunus serotina* seeds ($n = 60$) were removed in *R. cathartica* invaded plots compared to *R. cathartica* removed plots ($z = 2.74$, $p = 0.04$), marginally more ethanol-coated seeds ($n = 30$) were removed in *R. cathartica* invaded plots compared to removed plots ($z = 2.51$, $p = 0.08$), and extract-coated seeds had no significant differences in removal based on habitat type ($z = 2.27$, $p = 0.15$). Within habitat type, no seed coating treatment was removed significantly more than another ($\chi^2 = 1.55$, df = 2, $p = 0.458$).

Averaged across all sessions, 51.4 ± 17.9% (SE) of extract-coated *Prunus serotina* seeds were removed, followed by 50.0 ± 18.1% (SE) of ethanol-coated seeds and 32.9 ± 17.5% (SE) of water-coated seeds. In the presence of invasive shrubs, 86.0 ± 9.5% (SE) of all *Prunus serotina* seeds were removed. In the absence of invasive shrubs, 7.2 ± 3.3% (SE) of all *Prunus serotina* seeds were removed. The proportion of *Prunus serotina* removed over time between habitat types was significantly different ($\chi^2 = 14.1$, df = 1, $p < 0.01$) (Table 1). The predicted slopes of seed removal differed by habitat ($z = 3.43$, $p < 0.01$), and the slope was different than zero in

Fig. 2. Average absorbance spectra from 200 to 400 nm (5 nm increments) for varying capsaicin concentrations: (*a*) absorbance following ethanol soak of *Prunus serotina* seeds before and after field deployment, (*b*) standard capsaicin concentrations of 0.75% and 0.25%, (*c*) absorbance following ethanol soak of *Prunus serotina* seeds after field collection split by habitat treatment, (*d*) standard capsaicin concentrations ranging from 0.25% to 0.02%.



R. cathartica invaded plots ($z = 6.12$, $p < 0.01$) but not in *R. cathartica* removed plots ($z = 1.21$, $p = 0.40$), indicating that the rate of seed removal was significantly greater in *R. cathartica* invaded plots compared to plots without invasive shrubs present.

Following initial seed coating, spectrophotometric absorbance detected 0.75% capsaicin present on seed coats, while seeds collected from the field following deployment detected an average of 0.25% capsaicin present, indicating a 66% reduction in capsaicin concentration (Fig. 2). The amount of capsaicin present on seed coats did not significantly differ between habitat type following recovery ($t = -1.07$, df $= 80$, $p = 0.14$). Significantly more capsaicin was detected on seeds following initial coating compared to those collected from the field ($t = 4.45$, df $= 80$, $p < 0.01$) (Fig. 2).

Discussion

The practice of direct seeding native tree species can provide a reliable and cost-effective means to promote reforestation (Madsen and Löf 2005; Grossnickle and Ivetić 2017). In finding that extract-coated *Prunus serotina* seeds were removed at a similar rate to ethanol and water treated seeds, as well as seeds in invaded habitats having higher rates of removal over time, our results reveal several implications. First, the strength of capsaicin as a taste deterrent to rodent granivores in our study may not have been strong enough to deter rodents from consuming highly desirable, large-seeded species, regardless of whether those seeds fell in areas with *R. cathartica* present or absent. Second, based on our findings from our colorimetric assays, the loss of capsaicin on *Prunus serotina* seeds over the duration of the deployment may reveal an important characteristic of capsaicin when applied to seeds. Third, because invasive shrubs were the primary factor in facilitating seed loss by rodents for the duration of the deployment, these results support seed loss findings for other woody and herbaceous plant species (Bartowitz and Orrock 2016; Keller and Orrock 2023; Fuka and Orrock, in review) and further reinforce how invasive shrub removal may be a powerful restoration and conservation tool when preparing a site for reforestation by direct seeding.

The duration of capsaicin on seeds may be limited and lose efficacy over time

The use of capsaicin has emerged as an effective means to reduce rodent granivory on a variety of small-seeded species, including *Helianthus annuus*, *Balsamorhiza sagittata*, and *Pseudoroegneria spicata* (Pearson et al. 2019; Taylor et al. 2020). Lanni et al. (2023) found that for *Acer rubrum*, *Pinus banksiana*, and *Pinus resinosa* extract-coated seeds were removed 50% less than untreated seeds during a 4-day removal period in uninvaded forested plots. During a longer duration of 137 days using *Fagus grandifolia* seeds, Lanni et al. (2023) found that 17% more seeds were removed if untreated with capsaicin extract, although this longer session was conducted in an old field rather than a forest understory. These findings, coupled with our own, suggest that the length of time since coating seeds may affect the efficacy and strength of capsaicin as a deterrent. Pearson et al. (2019) concluded that capsaicin coating technology may not be persistent enough to fully protect seeds for over-wintering, and following our seed collection, we detected 66% less capsaicin on seeds, lending support for a loss of capsaicin strength over time. A factor that may have a strong influence on the efficacy of capsaicin as a long-term taste deterrent could be related to application method, and studies that have tested coating seeds with capsaicin often use different techniques. Application methods have included applying *C. chinense* powder directly onto seeds (Pearson et al. 2019), using a clay slurry mixed with *C. chinense* applied to seeds (Nolte and Barnett 2000), or using an adhesive seed moisturizer mixed with extracted capsaicin applied to seed coats (Lanni et al. 2023). While our method of applying capsaicin had the advantage of allowing us to reliably determine whether capsaicin coverage decreased during the 160-day field-deployment period, our findings potentially indicate a lack of any deterrence effect prior to the first depot monitoring. Despite this, field-based capsaicin studies using tree seeds have shown less than a 20% reduction in granivory (Willoughby et al. 2011; Leverkus et al. 2013; Lanni et al. 2023), while the presence of invasive shrubs in our study increased granivory by 1094%. Therefore, our findings further reinforce the importance of invasive shrub removal as a primary strategy to protect seeds from rodent granivores. To detect small differences in seed removal based on capsaicin seed coatings, we suggest that future studies monitor seed loss earlier following deployment and more frequently to better capture the efficacy of using capsaicin. Importantly, while the seeds we deployed retained some capsaicin after 160 days, there was a significant decrease in capsaicin coverage over the deployment period. As a result, our findings suggest that seed coatings with capsaicin are likely to be less effective for tree species with a long soil residence time pre-germination (e.g., *Prunus serotina*) and may be more effective for species known to germinate quickly after sowing (e.g., *Pinus resinosa*). In our study, we found that the timing of when seeds were monitored was significant in affecting the removal of *Prunus serotina*, and therefore suggests the need for more frequent monitoring to capture when the concentration of capsaicin is too low to have an effective deterrent effect.

The timing of direct seeding may be more effective than seed coating for seed survival

In finding a significant interaction effect of *R. cathatica* removal and day of year on *Prunus serotina* removal, our results point to the value of implementing seed additions during the winter and spring in the absence of invasive shrubs. The generality of this seasonal pattern is also supported by other recent studies that use multiple tree species in the same study system (Fuka and Orrock, in revision). The small mammal community present within our study system primarily consists of *Peromyscus leucopus*, *Tamias striatus*, and *Sciurus carolinensis* (Guiden and Orrock 2017, 2019; Fuka and Orrock, in revision). While rodents often forage in areas dominated by shrub cover due to a lower perceived risk of predation associated with vegetative refugia (Mattos et al. 2013; Guiden and Orrock 2019), seed loss can also be altered seasonally (e.g., seed loss is often high regardless of shrub cover in the summer) (Bartowitz and Orrock 2016; Keller and Orrock 2023; Fuka and Orrock, in revision). Recent work done in our study system revealed that seed loss under invasive shrub cover remained high across all four seasons (Fuka and Orrock, in revision). These results, coupled with the results presented here, indicate that winter seed predation is primarily driven by the presence of invasive woody shrubs largely due to the high level of structural complexity created by *R. cathartica* that is utilized by foraging rodents (Dueser and Shugart 1978, Manson and Stiles 1998, Guiden and Orrock 2017). Irrespective of the use of capsaicin, our study highlights the importance of not only where seeds may most likely survive, but when. Therefore, the timing of conservation and restoration efforts, like direct seeding, may be more important, and potentially more effective, than coating seeds with chemicals to deter rodent granivory.

Conclusions and future directions

To promote success seed additions of native trees without relying on costly and time-consuming nursey seedling production (Bullard et al. 1992, Atondo-Bueno et al. 2018, García-Hernández and López-Barrera 2024), examining the efficacy of seed coat technology is important to understand for both forest management and practical restoration. By revealing that the strength of capsaicin may deteriorate over time, our work underscores the need to test capsaicin on seed coats using long-term field experiments. Future studies seeking to test the efficacy of capsaicin may consider direct comparisons of capsaicin coating techniques as well as developing novel methods for stripping capsaicin from seed coats to further understand the longevity of capsaicin when applied in different ways (e.g., clay slurries, powders, and adhesives) (Nolte and Barnett 2000; Pearson et al. 2019; Lanni et al. 2023). Additionally, while our findings illuminate the efficacy of capsaicin on a single native tree species, *Prunus serotina*, future studies would benefit from testing a variety of large native tree species to more fully capture whether capsaicin seed coating techniques may be a viable option to promote seed survival during seed addition. Because seed selection is often associated with seed size, nutritional value, and ease-of-handling (Kerley and Erasmus 1991; Moore et al. 2021), future studies could potentially illuminate preferences for certain seeds that could therefore modify the efficacy of capsaicin in deterring granivorous rodents. In finding that invasive shrub cover contributed to variation observed in seed loss, our work helps to reinforce the positive impacts that invasive shrub removal can have on promoting forest regeneration and provides a clearer understanding of the efficacy of using capsaicin on tree seeds using a field experiment.

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Data availability

Data analyzed in this paper can be found on FigShare: https://figshare.com/s/d5174f308dd3b60b5bc8.

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Competing interests

The authors declare there are no competing interests.

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