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ORIGINAL PAPER

Removal of invasive shrubs reduces rodent consumption of invasive non-native animals and native understory seeds

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Abstract Plant invasions can generate indirect effects on native plants and animals by modifying the behavior and abundance of their consumers. Native consumers can produce positive effects by attacking invasive species and negative effects by attacking native species. However, we lack studies that examine the indirect effects of invasive plants on seasonal patterns of consumer behavior and the consumption of native and invasive organisms. Therefore, we experimentally manipulated the presence of an invasive shrub, *Rhamnus cathartica*, to track seasonal differences in rodent and arthropod consumption of native understory plants (*Caulophyllum thalictroides, Geranium maculatum,* and *Aquilegia canadensis*) and a novel animal invasion, *Amynthas* spp.. We tested the seasonal effects of invasive shrub removal on rodent and arthropod predation of cocoons and seeds using two, 15-day experiments conducted over the summer and autumn seasons. Our results demonstrate that changes in rodent activity caused by invasive shrub presence can generate significant deleterious effects on both invasive animals and native plants during the summer and weakens during the autumn. Invasive shrub removal weakened biotic resistance against *Amynthas* spp. by reducing native rodent activity, but also reduced rodent seed predation on native herbaceous plant seeds. The extended leaf phenology of *R. cathartica* facilitated greater rodent activity during the autumn season; however, greater rodent activity did not translate into differences in consumer pressure and varied in strength by the species consumed. Our results suggest that species traits could predict optimal windows of restoration for native plants and the ability of invasive organisms to successfully invade new environments.

Keywords Invasive plants · Consumer interactions · *Rhamnus cathartica* · *Amynthas* · Biotic resistance · Seasonality

Introduction

Invasive plants can negatively affect the abundance, persistence, and diversity of native plants and animals by generating changes in animal behavior and abundance (Pearson 2009; Ehrenfeld 2010; David et al. 2017). Such changes in the behavior of native animals may be important to understand because they may, in turn, generate important indirect effects (e.g., Orrock et al. 2010b; Guiden and Orrock 2017; Gorchov et al. 2021). For example, the presence of invasive plant species may modify both food availability and habitat structure (Knight et al. 2007; Orrock et al. 2015;

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Ceradini and Chalfoun 2017; David et al. 2017), leading to changes in animal foraging (Mattos and Orrock 2010; Dutra et al. 2011; Mattos et al. 2013; reviewed in Stewart et al. 2021), animal abundance (Malo et al. 2013; Litt et al. 2014), or both (Kelt et al. 2019). Understanding how invasive species may generate consumer-driven indirect effects is important for understanding how to prevent plant invasions (Orrock et al. 2010a, b, 2015; Mattos et al. 2013), for predicting the impacts of plant invasions (Eschtruth and Battles 2009; Vilà et al. 2011; David et al. 2017), as well as for informing the restoration of invaded habitats (Bartowitz and Orrock 2016; Guiden and Orrock 2017).

A major challenge to understanding the effects of invasive plants on animal-mediated interactions is that changes in small mammal attacks on prey can have positive and negative effects depending on the target of consumption (Eschtruth and Battles 2009; Pearson 2009; Dutra et al. 2011; Schlaepfer et al. 2011; Watling et al. 2011; Malo et al. 2013; Connolly et al. 2014; Ceradini and Chalfoun 2017; Guiden and Orrock 2017). Native rodents are highly omnivorous consumers (Landry 1970) that can affect a broad array of species ranging from invasive insects (Elkinton et al. 1996; Ostfeld et al. 1996) to native plants (Bartowitz and Orrock 2016). Therefore, changes in rodent attacks on prey within invaded habitats could have positive effects (e.g., rodent consumption of invasive species) or negative effects (e.g., rodent consumption of native species). For example, invasive plants could generate biotic resistance if invasive plants increase the magnitude at which small mammals consume invasive organisms (Connolly et al. 2014; Averill et al. 2016). In this case, invasive plants may indirectly facilitate increased rodent consumption of invasive organisms and potentially reduce the establishment of other invasive species (i.e., biotic resistance Simberloff and Von Holle 1999). However, invasive shrubs could have negative effects on native species if invasive shrubs lead to increases in rodent attacks on native organisms (Bartowitz and Orrock 2016; Guiden and Orrock 2017). Despite evidence that invasive shrubs affect rodent foraging (Bartowitz and Orrock 2016; Guiden and Orrock 2017) and evidence that small mammals consume diverse types of plant and animal prey (Landry 1970; Elkinton et al. 1996), we lack studies where the effects of a focal native consumer (e.g., rodents) are quantified on both native and invasive organisms living within environments invaded by plants (Fletcher et al. 2019).

Buckthorn (*Rhamnus cathartica*) is an invasive shrub that creates significant changes to the habitat it invades by increasing the density of habitat structure, extending the availability of seasonal habitat cover (i.e., extended leaf phenology), and reducing light penetration to the forest floor (reviewed in Knight et al. 2007; Mattos and Orrock 2010). Increases in habitat structure can reduce the predation risk perceived by rodents by acting as a refuge from predators, which may lead to increases in rodent temporal activity and abundance (Orrock et al. 2010b; reviewed in Prugh and Golden 2014). For example, the extended leaf phenology and habitat structure of invasive shrubs can affect the timing and magnitude of rodent activity (Orrock et al. 2015; Bartowitz and Orrock 2016; Guiden and Orrock 2017, 2019), decrease antipredator behavior (Mattos and Orrock 2010; Dutra et al. 2011), and increase the use of invaded habitat (Malo et al. 2013). Such changes to rodent behavior can generate significant negative effects on native plants via increased predation of native tree and invasive shrub seeds (Bartowitz and Orrock 2016; Guiden and Orrock 2017). However, it is unknown whether changes in rodent consumption within invaded habitats also affect the survival of invasive non-native animals. For example, invasive non-native jumping worms (*Amynthas* spp.) represent a growing novel threat to Midwest forests (Qiu and Turner 2017; Laushman et al. 2018) and produce seed-like propagules (cocoons) with the potential to experience similar predation to that of native seeds (e.g., mistaking cocoons for seeds or attacking cocoons as arthropod prey; Landry 1970). Moreover, despite changes in rodent predation of native tree and invasive shrub seeds, and although understory plants are significant contributors to forest biodiversity and ecosystem function, our understanding of whether invasive shrubs increase rodent predation of understory plant seeds is incomplete (Whigham 2004; reviewed in Gilliam 2007; Orrock et al. 2015).

In this study, we experimentally removed common buckthorn (*R. cathartica*) to determine if the presence of a common invasive shrub affects biotic resistance to invasive non-native earthworms (*Amynthas* spp.) by modifying rodent consumer interactions. Furthermore, we evaluated if the removal of invasive buckthorn mediates rodent predation of native herbaceous

plant seeds. The presence of *R. cathartica* alters the spatiotemporal dynamics of risk within ecosystems by extending the seasonal availability and density of habitat structure for rodents (Knight et al. 2007; Guiden and Orrock 2017, 2019). Therefore, we tested three main hypotheses centered on whether the presence of *R. cathartica* may modify rodent consumer interactions with invasive non-native cocoons and native seeds. (1) Removing the dense habitat structure provided by *R. cathartica* will reduce the activity of rodents leading to decreases in the predation of *Amynthas* cocoons. (2) The reduced activity of rodents will reduce the magnitude of predation on understory herbaceous seeds in habitats with *R. cathartica* removed relative to *R. cathartica* intact. (3) Changes in rodent predation of cocoons and seeds in invaded habitats will be greatest during times of the year when native vegetation undergoes leaf senescence prior to *R. cathartica* (late-autumn) and weakest during the growing season (mid-summer) relative to habitats with *R. cathartica* removed. We predict that the extended leaf phenology of *R. cathartica* will facilitate high levels of rodent activity and predation on cocoons and herbaceous seeds within the autumn season (Bartowitz and Orrock 2016; Guiden and Orrock 2017, 2019).

Methods

Our study was conducted within a 50-ha deciduous oak-hickory forest at the University of Wisconsin–Madison Arboretum in Madison, Wisconsin, United States (43°02′30.3"N 89°25′04.8"W). The forest has experienced a widespread invasion of *R. cathartica* throughout the understory; *Rhamnus cathartica* first invaded in 1955 and now represents 50–100% of all forest cover (Guiden and Orrock 2017). During the summer of 2014, we delineated fourteen 20×20 m experimental plots to examine the effects of *R. cathartica* removal (Bartowitz and Orrock 2016). Each plot was dominated by *R. cathartica* cover, with stems of the non-native invasive shrub *Lonicera maackii* rarely present (Bartowitz and Orrock 2016). Therefore, seven plots were randomly selected to have all invasive shrubs removed to mimic a common management technique employed in habitat restoration, and seven plots left the dense understory invasive shrubs left intact as a control (Bartowitz and Orrock 2016). Invasive shrubs were cut at ground-level using loppers, handsaws, and brush cutters before being treated with herbicide (Garlon 4—triclopyer; Bartowitz and Orrock 2016). Since the summer of 2014, we have maintained each removal plot to prevent the regrowth of *R. cathartica* within a plot and encroachment from the surrounding invaded-forest matrix. No other invasive shrub species have been noted within our plot since the initial removal in 2014. The vegetation present at the plots represent seven years of natural reestablishment of native herbaceous and woody plants. The plots where *R. cathartica* was left intact were characterized by dense understory cover throughout the summer and autumn seasons. In contrast, during the autumn there was little to no understory vegetation at plots where *R. cathartica* was removed (Appendix S1: Table S1). We conducted habitat measurements (e.g., proportion of herbaceous and woody cover, stem density, and woody debris) once during the summer (July 11, 2020) and autumn (November 6, 2020) to demonstrate the stark differences in habitat characteristics due to the effect of invasive shrub removal and seasonality; methods, results, and data on the density of *R. cathartica* can be found in Appendix S1: Table S1. We measured photosynthetically active radiation (PAR) using a light meter (LQM 70–10; Apogee Instruments, Logan, UT, USA) to capture potential differences in light intensity driven by the availability of seasonal habitat structure and the removal of *R. cathartica*. We collected ground-level measurements of PAR at the center of each plot, where each foraging depot was located, within one hour of solar noon on a cloudless day during the middle of the experiment (July 10, 2020 and November 5, 2020).

Cocoon collection

We collected the cocoons of *Amynthas tokioensis* and *Amynthas agrestis* from four locations within the deciduous forests of the University of Wisconsin-Madison Arboretum where high densities of worms have previously been surveyed. Four, 1 m x 1 m x 7 cm soil quadrats were excavated in November 2019 and stored at 0 °C until cocoons could be extracted (Johnston and Herrick 2019). Cocoons were sieved from the soil, refrigerated at 3 °C, then suspended in deionized water and heated in a drying oven at 50 °C for 15 days to render cocoons nonviable (Johnston

and Herrick 2019). After heat treatment, cocoons were stored at 3 °C until deployed during the experiment described below.

Cocoon and seed predation

We conducted experiments to quantify the predation of *Amynthas* spp. cocoons and the seeds of understory plants using plastic foraging depots (Bartowitz and Orrock 2016; Bartel and Orrock 2020; Chandler et al. 2020). Two foraging depots were placed in the center of each plot and deployed for 15 days during the summer and autumn seasons (July 3 – 18 and October 28 – November 12, 2020, respectively). Each depot consisted of a covered, translucent container (1.89 L); two rectangular holes (8 × 10 cm holes) were created on opposite sides of each container to allow access by rodents and arthropods (Mattos and Orrock 2010; Mattos et al. 2013; Chandler et al. 2020). One depot was used to measure seed and cocoon removal by rodents and arthropods together, while the openings of the second depot were covered with 1 cm^2 mesh hardware cloth to exclude rodents but allow access by all granivorous arthropods within our study area. The paired depot design allowed us to differentiate between rodent and arthropod predation of cocoons and seeds. Within each depot, we randomly scattered ten *Amynthas* spp. cocoons together with ten seeds of *Aquilegia canadensis*, *Geranium maculatum,* and *Caulophyllum thalictroides* on top of 0.5 L of sifted, fine-grained sand. Each herbaceous plant species was present within our study area and are of restoration interest within Midwestern deciduous forests following management. No *Amynthas* species were present at our experimental plots; thereby, cocoons of these species may be perceived as a novel food source similar to earthworm cocoons of other species present within the study area (Chang et al. 2021). To more closely mimic the natural situation where seeds and cocoons co-occur in the soil and could be simultaneously encountered by a foraging small mammal, we presented all seed species and cocoons together in each depot. All seeds were obtained from a commercial supplier and were checked for viability prior to delivery (Prairie Moon Nursery, Winona, MN, USA). Cocoons and seeds were handled using nitrile gloves to prevent any cues that could deter rodents or arthropod foraging.

Rodent activity

We monitored rodent activity and the activity of non-target consumers (e.g., birds, mesocarnivores, and larger mammals) at each plot using motion-activated wildlife camera traps. Wildlife camera traps were paired with each depot during the seed and cocoon removal experiments. We recorded the date, time, and species captured within each photograph. We estimated plot-level activity for each species using the total number of photographs captured at each plot. Each camera was positioned to capture individuals entering and exiting each depot. We allowed for a five-minute rest period between consecutive visits to mark an independent, single occurrence for each individual of a given species (Hicks et al. 1998). Lastly, it is important to note that the home range of our focal small mammal species, *Peromyscus leucopus*, is much smaller (~0.1 ha [17.8 m], Myton 1974; Lackey et al. 1985) than the distance between our experimental plots (each plot is located a minimum of 90 m apart; Bartowitz and Orrock 2016), and we have never observed individuals moving between plots in our previous small-mammal live-trapping studies (unpublished data). These observations suggest that foraging by the same individual at multiple sites is unlikely.

Data analyses

We evaluated the effects of buckthorn removal (*R. cathartica* presence and removal) and seasonality (summer and autumn) on light intensity using a linear mixed-effects model (LMM); light intensity was log-transformed. Buckthorn removal, season, and their interaction were included as fixed effects with plot as a random effect. We evaluated the effects of buckthorn removal and seasonality on white-footed mouse, *Peromyscus leucopus*, activity with a zero-inflated generalized linear model with a Poisson distribution using the *glmmTMB* package (Brooks et al. 2017); buckthorn removal, season, and their interaction were included as fixed effects with plot as a random effect. We confirmed model assumptions used diagnostic plots to examine the distribution of the data and residual plots to check for linearity between covariates and overdispersion. We calculated the proportion of *Amynthas* cocoons and herbaceous seeds consumed from each depot. To evaluate the effects

of buckthorn removal, season, and exclosure (rodent and arthropod access versus rodent exclusion) on cocoon and seed consumption, we used LMMs to test for significant differences in the proportion of *Amynthas* cocoons consumed and the proportion of each seed species consumed (all proportions were logit transformed; Warton and Hui 2011). For each model examining the cocoons and seeds, buckthorn removal, season, exclosure, and their interactions were included as fixed effects, while exclosure was nested with plot and included as a random effect. Each model was constructed in R ver. 3.6.3 using the *nlme* package (version 3.1–152; Pinheiro et al. 2021) to account for the split-plot nature of the design. We confirmed assumptions of normality, linearity, and homoscedasticity by evaluating plots of model residuals. We performed Tukey pair-wise comparisons to examine differences between the treatment groups and estimated the marginal means using the *emmeans* package (Lenth et al. 2020).

Results

Light intensity

There was strong evidence demonstrating that light intensity was greater when *R. cathartica* was removed ($F_{1,12}=62.06$, $P<0.001$): plots with *R. cathartica* removed had a greater mean light intensity (304.0 ± 89.9 µmol m^{-2} s^{-1}) than plots with *R. cathartica* intact (20.4 ± 4.4 µmol m^{-2} s^{-1}). There was very strong evidence demonstrating that light intensity differed seasonally at plots where *R. cathartica* was removed ($F_{1,12}=45.70$, $P<0.001$; Appendix S1: Figure S1), such that the mean autumn light intensity at plots where *R. cathartica* was removed (595.0 ± 58.0 µmol m^{-2} s^{-1}) was greater than the mean light intensity at plots with *R. cathartica* intact during the summer (7.3 ± 1.03 µmol m^{-2} s^{-1}) and autumn (33.4 ± 3.6 SE µmol m^{-2} s^{-1}), as well as compared to plots with *R. cathartica* removed in the summer (12.6 ± 1.9 SE µmol m^{-2} s^{-1}).

Rodent foraging activity

Wildlife camera traps yielded 11,459 photos of animals over the course of 960 camera-trapping nights. Camera traps captured 3928 photographs of *Peromyscus leucopus*, as well as 1059 photographs of *Tamias striatus* across all plots. There was very strong evidence that *Peromyscus leucopus* was the dominant forager relative to *T. striatus* ($F_{1,\ 12}=15.45$, $P=0.002$), such that the mean number *P. leucopus* independent occurrences per plot (187.0 ± 44.4 SE) was higher than the number of mean independent occurrences by *T. striatus* (81.5 ± 29.1 SE). There was very strong evidence demonstrating that the activity of *P. leucopus* was greater when *R. cathartica* was intact ($\chi^2=58.20$, $P<0.001$), such the mean number of occurrences of *P. leucopus* (254.0 ± 44.1 SE) was much higher at plots where *R. cathartica* was intact compared to plots with *R. cathartica* removed (52.3 ± 9.87 SE). There was no evidence that *P. leucopus* activity changed by season ($\chi^2=2.69$, $P=0.10$). However, there was very strong evidence demonstrating that season and *R. cathartica* removal interacted to affect *P. leucopus* activity ($\chi^2=32.24$, $P<0.001$), such that there were substantially lower mean autumn occurrences at plots where *R. cathartica* had been removed (261 ± 52.0 SE) compared to plots where R. cathartica was intact (7.0 ± 0.0 SE; Fig. 1. Appendix S1: Table S2).

Predation of Amynthas cocoons

There was moderate evidence that the proportion of cocoons consumed was reduced by the removal of *R. cathartica* ($F_{1,12}=5.13$, $P=0.04$), with the mean proportion of cocoons consumed in *R. cathartica* removed plots being lower (0.06 ± 0.03 SE) than in plots with *R. cathartica* left intact (0.15 ± 0.05 SE). There was very strong evidence the proportion of cocoons consumed was affected by season ($F_{1,\ 24}=25.6$, $P<0.001$), with the mean proportion of cocoons consumed in the summer (0.18 ± 0.05 SE) being substantially greater than the proportion consumed in the autumn (0.02 ± 0.01 SE). Furthermore, there was moderate evidence demonstrating that the proportion of cocoons consumed was affected by the exclusion of rodents ($F_{1,\ 12}=6.83$, $P=0.022$; Fig. 2), such that when rodents were excluded the mean proportion of cocoons consumed was lower (0.05 ± 0.02 SE) compared to when rodents had access (0.15 ± 0.06 SE).

There was weak evidence that cocoon consumption was affected by the interaction between *R. cathartica* removal and season ($F_{1,\ 24}=3.68$, $P=0.067$), as

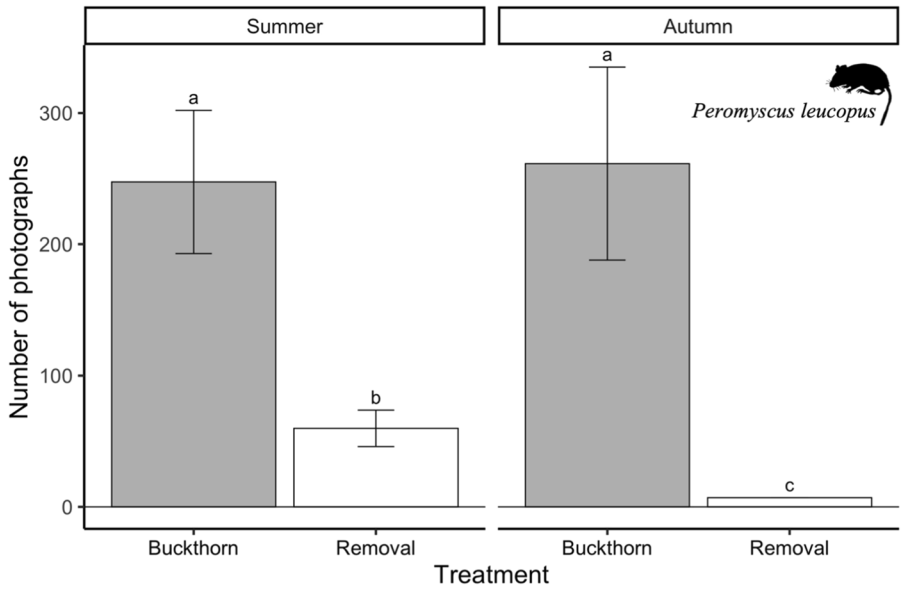

Fig. 1 The seasonal effects of *Rhamnus cathartica* on the average activity of white-footed mice, *Peromyscus. leucopus*, (number of photographs) at plots where *R. cathartica* was removed relative to plots with *R. cathartica* intact. Error bars represent one standard error. Letters indicate significant differences in Tukey pair-wise comparisons across the treatments and across seasons ($P \leq 0.05$)

well as *R. cathartica* removal and rodent exclusion ($F_{1,\ 12} = 4.03$, $P = 0.068$). During the summer, the mean proportion of *Amynthas* cocoons consumed was higher within plots with *R. cathartica* intact (0.26 ± 0.07 SE) compared to when *R. cathartica* was removed (0.10 ± 0.03 SE); the mean proportion of cocoons consumed was lower in the autumn at plots with *R. cathartica* intact (0.03 ± 0.02 SE) and at plots with *R. cathartica* removed (0.02 ± 0.01 SE). When *R. cathartica* was intact, the mean proportion of summer cocoon predation was higher when rodents had access to depots (0.44 ± 0.06 SE) compared to when rodents were excluded and when *R. cathartica* was removed ($F_{1,\ 24} = 1.72$, $P = 0.202$; Fig. 2); this pattern emerged because of the strong evidence demonstrating that the exclusion of rodents reduced the mean proportion of cocoons consumed ($F_{1,\ 24} = 14.21$, $P < 0.001$), such that during the summer the mean proportion consumed when rodents had access (0.30 ± 0.06 SE) was lower than when rodents were excluded in the summer (0.07 ± 0.02 SE); the mean proportion of cocoons removed was negligible during the autumn regardless of rodent access (Fig. 2).

Predation of understory plant seeds

The effect of *R. cathartica* removal on seed predation varied by plant species. There was moderate evidence demonstrating that the mean proportion of *C. thalictroides* seeds consumed (0.08 ± 0.03 SE; $F_{1,\ 12} = 5.32$, $P = 0.04$), but not *G. maculatum* or *A. canadensis* (Table 1), was lower with the removal of *R. cathartica* compared to when *R. cathartica* was left intact (0.18 ± 0.03 SE). We found very strong evidence that *G. maculatum* ($F_{1,\ 24} = 11.17$, $P = 0.003$) and strong evidence *A. canadensis* ($F_{1,\ 24} = 6.18$, $P = 0.02$) experienced a higher mean proportion of seed consumed during the summer (0.24 ± 0.04 and 0.20 ± 0.02 (SE) respectively) relative to the autumn season (0.06 ± 0.03 and 0.08 ± 0.01 (SE) respectively; Fig. 3). There was weak evidence demonstrating that when *R. cathartica* was removed the mean proportion of *C. thalictroides* consumed was higher during the summer relative to autumn (Table 1). In contrast, there was no evidence to demonstrating that the removal of R. cathartica interacted with season to affect the mean proportion of *G. maculatum* and *A. canadensis* consumed (Table 1).

There was very strong evidence that the removal of each seed species was lower with the exclusion of rodents (Table 1). During the summer, the mean proportion of seeds removed when rodents had access was higher for all seed species relative to when rodents were excluded (Fig. 3). In autumn, the mean proportion of seeds removed was lower regardless of rodent access, such that both rodents and arthropods consumed a relatively small fraction of seeds. There is weak evidence that the effect of rodent access on the mean proportion of seeds consumed varied with the removal of *R. cathartica,* such that the exclusion

Table 1 Degrees of freedom, *F*-test statistic, and *P*-values for each model evaluating the effects of treatment (*Rhamnus cathartica* removal), season (summer and autumn), and exclosure (rodent and arthropod access compared to arthropod only) on the proportion of *Caulophyllum thalictroides, Geranium maculatum,* and *Aquilegia canadensis* seeds consumed (linear mixed-effects models)

Effect	*C. thalictroides*			*G. maculatum*			*A. canadensis*		
	ndf, ddf	*F*	*P*	ndf, ddf	*F*	*P*	ndf, ddf	*F*	*P*
Treatment	1, 12	5.32	0.040*	1, 12	1.88	0.196	1, 12	2.37	0.150
Season	1, 24	3.43	0.076	1, 24	11.17	0.003**	1, 24	6.18	0.020*
Exclosure	1, 12	43.20	< 0.001**	1, 12	13.03	0.004**	1, 12	13.53	0.003**
Treatment:Season	1, 24	3.61	0.069	1, 24	0.08	0.784	1, 24	1.50	0.232
Treatment:Exclosure	1, 12	3.49	0.087	1, 12	4.36	0.059	1, 12	0.00	0.973
Season:Exclosure	1, 24	3.43	0.076	1, 24	4.61	0.042*	1, 24	7.83	0.010*
Treatment:Season: Exclosure	1, 24	3.61	0.069	1, 24	1.81	0.191	1, 24	1.40	0.249

of rodents led to a lower mean proportion of *C. thalictroides* and *G. maculatum* seeds consumed (Table 1; Fig. 3). Lastly, there is no evidence to suggest that the removal of R. cathartica, season, and exclusion of rodents interact to affect the mean proportion of seeds removed for any species (Fig. 3).

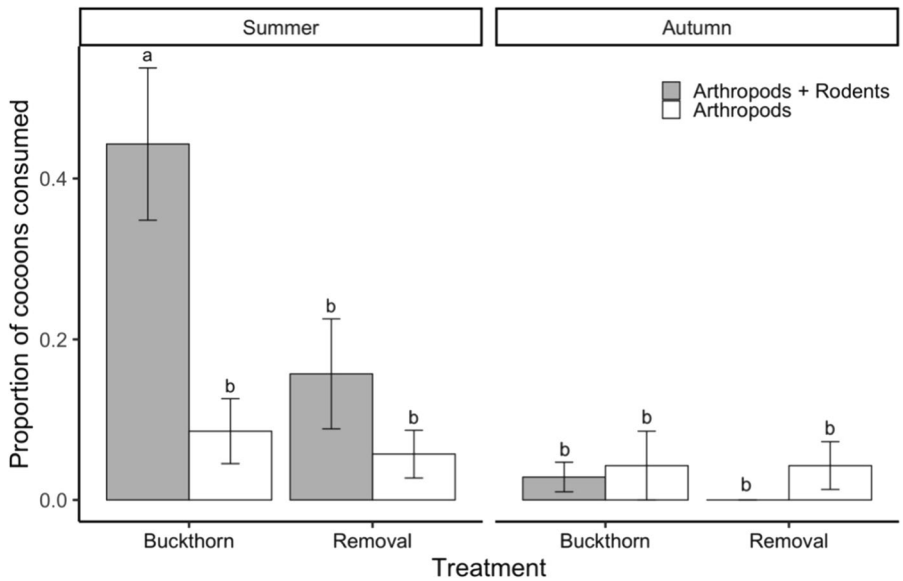

Fig. 2 The seasonal effects of *Rhamnus cathartica* and rodent access on the mean proportion of *Amynthas* spp. cocoons consumed at plots where *R. cathartica* was removed relative to plots with *R. cathartica* intact. Error bars represent one standard error. Letters indicate significant differences in Tukey pair-wise comparisons across the treatments and across seasons ($P \leq 0.05$)

Discussion

Our study demonstrates that the removal of invasive shrubs may generate indirect effects via native rodent consumers that strongly influence the survival of propagules of both invasive non-native animals (Fig. 2) and the seeds of native understory plants (Fig. 3). These indirect effects arise due to the greater activity of rodents in habitats dominated by the invasive shrub *R. cathartica* compared to habitats where *R. cathartica* had been removed. Our findings have three main implications. First, our results indicate that the removal of invasive shrubs (a common restoration method) may unintentionally facilitate the colonization or increase the abundance of invasive non-native worms by weakening the biotic resistance produced by native consumers. Second, changes in rodent activity generated by the removal of invasive shrubs may

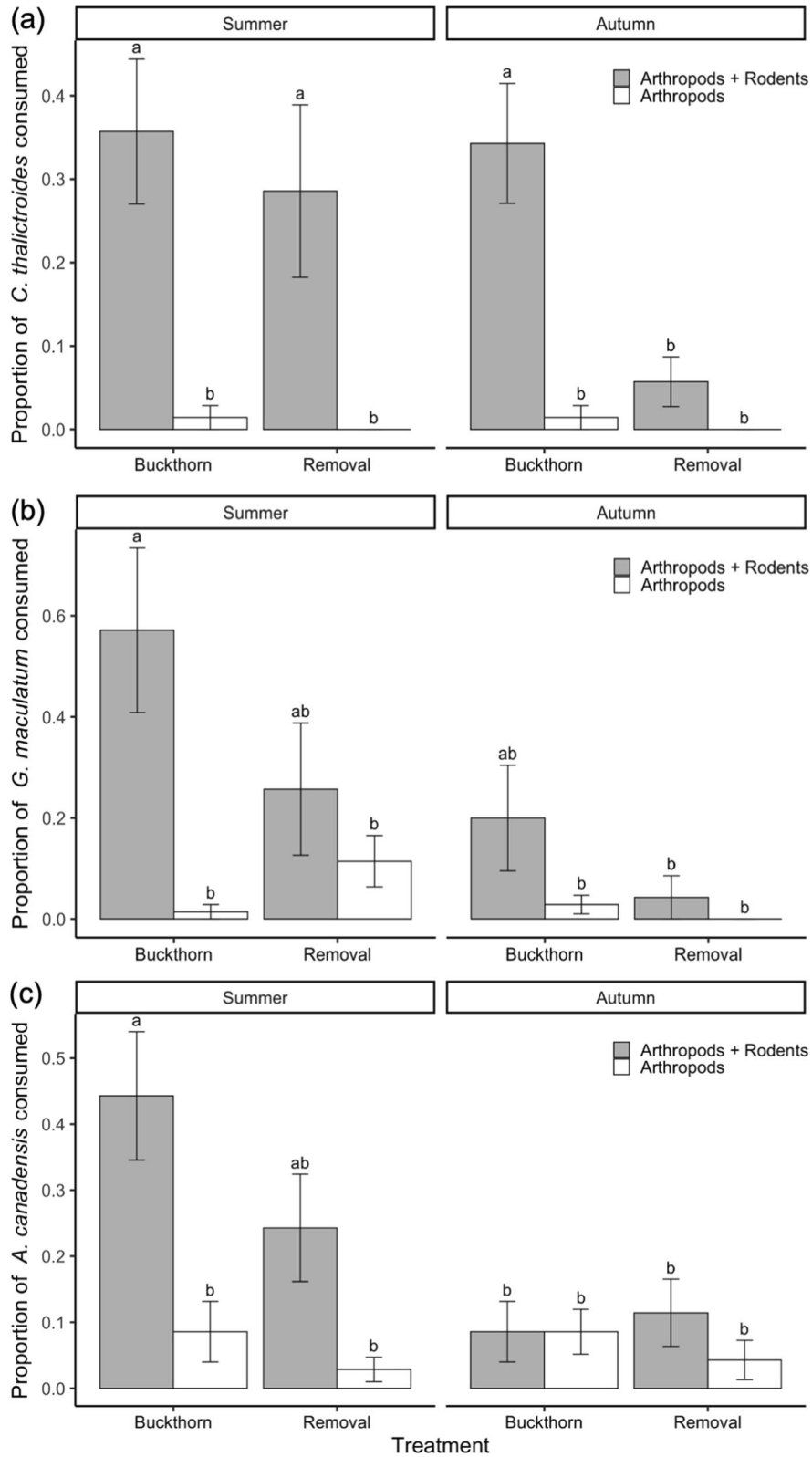

Fig. 3 The seasonal effects of *Rhamnus cathartica* and rodent access on the mean proportion of **a** *Caulophyllum thalictroides*, **b** *Geranium maculatum*, and **c** *Aquilegia canadensis* consumed at plots where *R. cathartica* was removed relative to plots with *R. cathartica* intact. Error bars represent one standard error. Letters indicate significant differences in Tukey pair-wise comparisons across the treatments and across seasons ($P \leq 0.05$)

have unappreciated consequences for the restoration and conservation of native understory plant populations by reducing granivory and potentially increasing seedling establishment. Lastly, our results suggest that the success of restoration that relies on the removal of invasive shrubs could depend on the timing of restoration, given that changes in rodent predation of the propagules of invasive non-native animals and the seeds of native understory plants can vary significantly among seasons. Furthermore, studies conducted within a single season may misrepresent the full consequences of shrub-invasions, as our result indicate that the presence of invasive shrubs may produce significant variation in rodent attacks on native seeds and invasive non-native animal propagules during one season but not during another (e.g., the presence of *R. cathartica* increased *Amynthas* cocoon predation in summer but not autumn; Figs. 2–3).

Removal of invasive shrubs may weaken biotic resistance against invasive non-native worms

Understanding how native consumers respond to restoration techniques (i.e., invasive shrub removal) that are in widespread use is vital to ensuring successful habitat restoration (Hartman and McCarthy 2004; Orrock et al. 2010a, b; Guiden and Orrock 2017; Maynard-Bean and Kaye 2019). Our results demonstrate that one negative effect of the removal of a widespread invasive shrub species may be to weaken biotic resistance against an invasive non-native earthworm: the removal of *R. cathartica* reduced the activity of native rodents, leading to a significant decline in the consumption of invasive non-native earthworm cocoons by rodents but not arthropods. Arthropods can significantly reduce the survival of adult *Amynthas* earthworms (Gorsuch and Owen 2014), however, we found that arthropod predation of cocoons was negligible and that arthropod consumers did not generate biotic resistance to early life history stages of an invasive non-native earthworm. Quantifying how invasive plants might affect multiple native consumer species can help to determine which species may be driving patterns of resistance to animal invasions (Fletcher et al. 2019) and could provide essential information for management decisions. In particular, management that reduces the abundance of invasive shrubs and the activity of rodent consumers (e.g., timber harvest, forest restoration; Pardini et al. 2005; Zwolak 2009) may also have the potential to reduce biotic resistance to invasive non-native earthworm colonization. Importantly, our findings suggest that the efficacy of techniques used to control *Amynthas* worms (Ikeda et al. 2015; reviewed in Chang et al. 2021), may depend on the direct effect of management on adult *Amynthas* and the indirect effects on *Amynthas* cocoon survival that arise when management also affects rodents.

The removal of invasive shrubs has the potential to affect the stage-specific mortality of invasive earthworms (i.e., *Lumbricus* spp; Madritch and Lindroth 2009). We find that the removal of invasive shrubs may increase propagule survival for *Amynthas* by reducing rodent consumption of cocoons (Fig. 2). As such, native rodent consumption of invasive non-native earthworm cocoons could potentially play a role in the decreased survival of early demographic stages when invasive shrubs are present, but not when shrubs are removed. This suggests that invasive shrubs may have the potential to limit the initial colonization of invasive non-native worms via rodent consumption of cocoons (Fig. 2) but may promote the survival of adult worms once established within invaded habitats (Bethke and Midgley 2020). Furthermore, rodent population size can exhibit significant variation in time and space (Korslund and Steen 2006; Nater et al. 2018; Kelt et al. 2019); therefore, years when rodent populations are low could increase the susceptibility to invasive non-native worm colonization within habitats invaded by shrubs. Although we currently lack studies of *Amynthas* demography, future research that examines how seasonal variation in the effect of native consumers influences *Amynthas* population dynamics may provide insight into the factors influencing successful invasions.

The seasonal effects of invasive shrub presence on the consumption of invasive animals have rarely been examined yet represents an important knowledge gap for understanding the co-invasion of multiple species (Fletcher et al. 2019). Rodent consumption of worm cocoons closely mirrored the removal of seeds of similar size (*G. maculatum*: $r = 0.77$; *A. canadensis*: $r = 0.70$; Figs. 2–3b), suggesting that rodents may either mistake cocoons for seeds or select cocoons contingent on seasonal energy constraints. We observed high levels of summer cocoon predation when invasive shrubs we present but not when removed, followed by a substantial decline in

autumn cocoon consumption (Fig. 2). This suggests that the strength of biotic resistance against *Amynthas* may be seasonally dependent, but that the removal of invasive shrubs may consistently reduce biotic resistance by decreasing rodent consumption of cocoons. The decline in rodent consumption of cocoons during the autumn could be particularly important within the context of biotic resistance against invasive jumping worms because *Amynthas* differs in the seasonal production and availability of cocoons (Görres et al. 2016; Moore et al. 2018; Nouri-Aiin and Görres 2019). The production of *Amynthas* cocoons begins mid-summer, but the majority of cocoons are believed to be produced during the autumn season once adults have matured and prior to complete adult winter mortality (Chang et al. 2021). Therefore, *Amynthas* may be able to escape long-term consequences of biotic resistance because the timing of propagule production coincides with the period when rodent consumer pressure is lowest. Yet, the demographic consequences of rodent cocoon predation remain unclear, as demographic studies have not been conducted on *Amynthas* spp. nor has it been determined if *Amynthas* populations are limited by the number of cocoons produced (Chang et al. 2021). Much of what is known about *Amynthas* cocoon production and abundance comes from laboratory experiments and seasonal field surveys of cocoon abundance; neither of which account for the effects of native consumers on the abundance of adult worms and cocoons nor the ability of cocoons to survive within the soil bank for multiple years (reviewed in Chang et al. 2021).

Past studies have examined the potential importance of invasive shrubs in facilitating the success of earthworms (Heneghan et al. 2007; Dávalos et al. 2015; Qiu and Turner 2017; Ziter and Turner 2019; Gorchov et al. 2021), however, we lack studies that account for how invasive shrubs may influence the strength of native consumer pressure on invasive worm abundance. Our study is the first to demonstrate the effects of rodent consumption of *Amynthas* cocoons (Chang et al. 2021) and highlights that seasonal patterns of rodent cocoon consumption may be important to consider in light of the timing of field studies of *Amynthas* cocoon abundance. For example, field studies conducted during the summer may represent a time when rodent consumption of cocoons may strongly affect the abundance of cocoons in the soil; in contrast, studies conducted in the autumn, when the highest cocoon abundance is often observed (reviewed in Chang et al. 2021), could represent the abundance of cocoons when no longer influenced by rodent propagule consumption. Therefore, the current abundance of *Amynthas* cocoons found during a given sampling period may depend on four factors: (1) the cocoons present within the soil bank from previous years, (2) the ongoing seasonal production of cocoons, (3) the magnitude of seasonal rodent consumption of cocoons, and (4) the presence of invasive shrubs.

Like all ecological studies, the inference possible from our results must be interpreted within the temporal and spatial scales of our study. The strength of our study lies in our ability to measure the outcomes of rodent consumer interactions at biologically, temporally, and spatially relevant scales (Orrock et al. 2010a), but we did not track the long-term outcome of rodent consumer interactions on *Amynthas* population dynamics. We cannot know the full extent to which small mammal predation of cocoons affects *Amynthas* population dynamics without explicit knowledge of how cocoon survival affects demography. As such, future empirical studies that evaluate which density-dependent and independent factors may limit seasonal cocoon abundance and influence *Amynthas* population dynamics would be highly informative. Our study focuses on a single deciduous forest landscape, and as a result, it is necessary for future studies to assess the extent to which these findings can be applied to other forests and landscapes. For example, invasive plants have been demonstrated to affect the behavior of many native animal species across different ecosystems (reviewed in Stewart et al. 2021). Therefore, our findings could lead to exciting future work exploring the generality (or lack thereof) of biotic resistance to jumping worms via other native consumer species.

Removal of invasive shrubs may decrease understory seed predation by rodents

The removal of invasive shrubs can significantly decrease rodent consumption of tree seeds (Bartowitz and Orrock 2016; Guiden and Orrock 2017); however, we know little about how invasive shrub removal affects the survival of native understory seed species, which are often important components of biodiversity and targets of restoration (Whigham

2004). In finding that rodents were the primary guild consuming understory plant seeds, our work contributes to a larger body of research finding that arthropods have smaller effects on post-dispersal predation of overstory and understory plant seeds (Hulme and Borelli 1999; Hulme and Hunt 1999; Schnurr et al. 2004; Chandler et al. 2020). Greater seed predation by native rodents within deciduous forests may significantly affect the ability of native understory plants to persist (Turnbull et al. 2000; Lichti et al. 2017) and could contribute to reduced species richness and abundance of understory plants within invaded habitats (Orrock et al. 2015). Therefore, the reduction in rodent activity driven by invasive shrub removal could represent an effective tool that may increase the natural regeneration of native understory plants and help to conserve the critical resources they provide to deciduous forests (Whigham 2004; Gilliam 2007). Lastly, it is important to note that although rodent population abundance often varies annually which could affect spatiotemporal patterns of seed consumption (Nater et al. 2018; Kelt et al. 2019); our study found similar patterns of rodent seed predation as previously conducted research at our plots during years where rodent abundance was likely different (e.g., 2014—Bartowitz and Orrock 2016; and 2015—Guiden and Orrock 2017). This similarity suggests that although rodent abundance likely differs annually, patterns of rodent consumption when invasive shrubs are present and removed remain qualitatively consistent.

Our findings also demonstrate that, just as invasive shrubs generate seasonal patterns in the consumption of tree seeds (Bartowitz and Orrock 2016; Guiden and Orrock 2017), invasive shrubs may also generate seasonal changes in rodent consumption of understory plant seeds, and the strength of this effect may depend upon the plant species being evaluated (Fig. 3, Table 1). Previous research conducted at our experimental plots demonstrated that the removal of *R. cathartica* leads to substantial reductions in rodent activity and predation of large-seeded tree species during the autumn relative to when *R. cathartica* is present (Bartowitz and Orrock 2016; Guiden and Orrock 2017). Although we found similar patterns for larger-seeded plant species in our study (e.g., Bartowitz and Orrock 2016; Guiden and Orrock 2017; Fig. 3), consumption of the smallest species we examined (*G. maculatum* and *A. canadensis*) was not only lower in autumn, but also was not significantly different when invasive shrubs were present or removed (Fig. 3). Rodent may select larger seed species based on seasonal energetic constraints (e.g., thermoregulation) that increase the costs of foraging during cooler months (Kotler et al. 1993; Shaner et al. 2007). Therefore, smaller-seeded species (e.g., herbaceous plants) that undergo autumn seed set (e.g., A. canadensis; LaRoche 1978) may experience fewer attacks by rodents and have the potential to persist in greater abundance within invaded and removal habitats (Janzen 1971; Hulme 1998; Dylewski et al. 2020). Understanding seasonal variation in rodent seed predation under invasive shrub presence and removal may help identify optimal windows in the restoration of native understory plants (Anderegg et al. 2021). We suggest that the restoration of larger-seed species, which experience substantial summer seed death by rodents in invaded habitats (Bartowitz and Orrock 2016; Guiden and Orrock 2017), may require the removal of invasive shrubs and late-autumn seed additions when the risk of predation is lowest. In finding that when invasive shrubs are removed, smaller-seeded species experience substantially lower summer and autumn predation relative to larger seeds (Fig. 3; Bartowitz and Orrock 2016), smaller understory plant seeds may be less at risk of being consumed by rodents and have a wider window in which successful restoration could occur (e.g., late summer and autumn seed sowing). Importantly, rodent granivory can greatly influence plant recruitment and is often used to predict changes in plant establishment (Dylewski et al. 2020); yet, future empirical studies are needed to fully appreciate how seasonal patterns of granivory affect plant population dynamics and represent exciting new research directions (Hulme 1998; Hulme and Kollmann 2005).

Conclusions and future directions

Ultimately, management and restoration efforts aimed at reducing rodent granivory may offer the greatest likelihood of overstory and understory seed survival (i.e., invasive plant removal, seasonal and species-specific seed additions). The use of restoration strategies that take into account life-history traits to predict which plant species may escape consumption (Dylewski et al. 2020), coupled with a rodent deterrent (e.g., capsaicin and rodent exclosures; Pearson

et al. 2019), could reduce the predation of more vulnerable plant species. In finding that invasive shrubs can indirectly generate both biotic resistance to invasive non-native animals and increased consumption of native plants, our results also highlight areas where additional studies may help further improve our ability to predict and mitigate the effects of invasive shrubs. For example, because the removal of worm cocoons closely mirrored the removal of seeds of similar size (Figs. 2–3b), we suggest that future research studies should evaluate the utility of a trait-based classification of species for predicting the magnitude of rodent consumption both native plant seeds (Dylewski et al. 2020) and invasive non-native animals. The ability to predict the magnitude of rodent consumer pressure based on shared traits of species represents a potentially powerful tool in predicting the ability of both invasive plants and animals to invade new habitats and the success of future restoration strategies. Given that associational effects could be common during biological invasions (Orrock et al. 2010b), studies that evaluate the positive or negative associational effects between native seed and invasive non-native cocoon consumption may provide greater insight into what makes *Amynthas* a successful invader. For example, rodent predation of cocoons may be influenced by the quantity or identity of the seeds present within our study via associational effects (Underwood et al. 2014). As such, manipulative studies that explore how seed species, size, or density affects the predation of cocoons could be of useful in predicting biotic resistance within an ecosystem. Lastly, future studies that examine the temporal dynamics of cocoon abundance and predation could represent a valuable research direction in understanding potential the limitations invasive non-native worms may face when colonizing new habitats.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests CBK and JLO declare they have no financial interests.

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