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Invasive exotic shrub (*Rhamnus cathartica*) alters the timing and magnitude of post-dispersal seed predation of native and exotic species

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Apparent competition; Indirect effects; Invasive exotic species; Multi-species; Seasonality; Seed predation; Small mammals

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Abstract

Aims: Invasive exotic plants may generate deleterious indirect effects on native species, such as increasing consumer pressure on native plants (i.e. apparent competition). Although rarely examined, invasive shrubs may create novel pulses of consumer pressure because their leaves senesce later, providing temporal increases in cover. Apparent competition generated by invasive species may have a strong temporal signal due to extended phenologies of invasive plants. Using an experimental manipulation of the invasive shrub, *Rhamnus cathartica*, we evaluated whether seed predation of multiple species is higher in invaded areas, and if the novel extended phenology of *R. cathartica* leads to temporal changes in seed predation.

Location: University of Wisconsin-Madison Arboretum, Madison, WI, US.

Methods: We removed *R. cathartica* from half of 16 invaded plots. Using three 17-d sessions over two seasons, we quantified seed predation on *R. cathartica* and four native species: *Acer rubrum, A. saccharum, Prunus serotina* and *Quercus rubra*. Studies included autumn sampling to evaluate whether extended phenology of *R. cathartica* led to changes in seed predation. We quantified habitat characteristics and small mammal activity.

Results: *Rhamnus cathartica* removal led to decreased seed removal for *A. rubrum*, *A. saccharum* and *R. cathartica*, but magnitude depended upon season. For *R. cathartica* and *A. rubrum*, autumn seed removal was higher in *R. cathartica* invaded areas, when these areas have substantial leaf cover. Predation of *A. saccharum* seeds was highest in areas with intact *R. cathartica* during the summer. *R. cathartica* removal led to significantly increased light levels at the forest floor, increased leaf litter depth and lower total small mammal captures.

Conclusions: Presence of *R. cathartica* altered seed removal of native and invasive species, and the unique phenology of *R. cathartica* provided cover that generated novel, previously undocumented temporal shifts in consumer pressure. Although our work illustrates how mature *R. cathartica* can increase seed removal, we conclude that apparent competition between seeds of *R. cathartica* and native species is unlikely because higher seed removal caused by *R. cathartica* was seen for *R. cathartica* seeds. Our work highlights how predicting and ameliorating effects of invasive plants may require considering temporal dynamics that are currently poorly understood.

Introduction

Invasion by non-native species can have global ecological and economic consequences: exotic invasive species can reduce biological diversity, alter biological interactions and decrease agricultural productivity (Wilcove et al. 1998; Mack et al. 2000; Pimentel et al. 2005; Vilà et al. 2011). Predicting biological invasions, stopping current invasions and restoring invaded habitats are activities that all hinge upon understanding the primary mechanisms that

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mediate the invasion. For example, invasive plants may have deleterious effects on native plants via two mechanisms that are not mutually exclusive: via direct competition with native plants (i.e. a direct effect; White et al. 2006), by amplifying herbivore or pathogen attack on native plants, an indirect effect termed apparent competition (Holt 1977; Noonburg & Byers 2005; Orrock et al. 2010; Dutra et al. 2011), or both (Menge 1995; Chaneton & Bonsall 2000; Orrock et al. 2015; Smith & Hall 2016). For example, invasive plants may be effective direct competitors because they produce large numbers of seeds (Crawley 1987; Blossey & Notzold 1995; Daehler 2003) or effective indirect competitors because they increase habitat structure or food resources that generate changes in local consumer pressure (Bartuszevige & Gorchov 2006; Pearson & Fletcher 2008; Mattos & Orrock 2010; Dutra et al. 2011; Orrock et al. 2015). From a pragmatic perspective, the distinction between indirect and direct effects is important for restoration because the optimal restoration strategy depends on the primary mechanism whereby the invasive plant might re-invade a habitat. For example, protecting native plants from consumers would be sufficient to promote recovery of native plants if apparent competition is the primary means of invasion, but this approach would be ineffective if exotic plants are successful because of high levels of seed input. Despite the capacity of indirect effects to alter the success of invasive plants, there is little empirical information regarding whether apparent competition is an important process in terrestrial plant invasions (Gordon 1998; White et al. 2006; Meiners 2007; Radtke & Wilson 2015; Sotomayor & Lortie 2015).

Temporal dynamics may also be important in the context of understanding indirect effects mediated by invasive plants, especially in situations where invasive plants exhibit novel phenologies that might shift the timing and magnitude of indirect effects (Rodriguez 2006; Strayer et al. 2006; Smith 2013; Smith & Hall 2016). For example, several highly invasive woody plants (e.g. *Rhamnus cathartica*, *Lonicera maackii*) have accelerated and extended leaf phenologies (e.g. they produce leaves earlier and senesce later in the season relative to native plants; Harrington et al. 1989; Knight et al. 2007), adding substantial cover at times when these areas would normally have no leaf cover (Harrington et al. 1989). Invasive woody shrubs also act as large sources of temporally pulsed food resources, producing prodigious quantities of fruit that may cause consumer aggregations (Orrock et al. 2015). Although the timing of resource pulses can dramatically shift dynamics of many systems (Yang et al. 2008) and apparent competition via temporal shifts in cover may give invasive plants a large advantage over native species (Smith & Hall 2016), empirical studies regarding the role of novel invader phenology are rare (Smith 2013). By changing the temporal availability of habitat cover and food resources, invasive plants might generate strong, yet largely unappreciated, changes in consumer pressure, and thus apparent competition on native plants (Smith 2013; Smith & Hall 2016). Removing the structure provided by an invasive plant can be a valuable tool in understanding indirect effects caused by invasive structure presence (Strauss 1991; Dutra et al. 2011). However, evaluating the importance of temporal variation in apparent competition is complicated by the need to track temporal variation in consumer pressure when structure and food provided by the invasive plant has been removed (McCormick & Meiners 2000; Mattos & Orrock 2010; Sotomayor & Lortie 2015).

We coupled the removal of an exotic woody shrub, *R. cathartica* (common buckthorn), with a multi-season study of consumer pressure and consumer activity. *R. cathartica* is optimal for our study because it is a highly invasive woody shrub (Godwin 1943), which extirpates native plant species (Knight et al. 2007; Klionsky et al. 2011) and dominates the mid-storey of deciduous forests it invades, adding a substantial amount of habitat structure (Archibold et al. 1997; Mascaro & Schnitzer 2007). Changes in habitat structure have a unique phenological component because of the extended leaf phenology of *R. cathartica* compared to native plants; habitats invaded by *R. cathartica* have leaf structure at times of the year when uninvaded habitats do not (e.g. in late autumn; Harrington et al. 1989). In addition to altering the timing and availability of habitat structure, *R. cathartica* also provides a food resource: an adult *R. cathartica* plant can produce thousands of fruit every season, many of which fall to the ground (up to 90%; Archibold et al. 1997). Alone or in concert, the changes in habitat structure and food resources caused by *R. cathartica* could alter the abundance and activity of native animals, leading to changes in consumer pressure.

In this study, we coupled the removal of *R. cathartica* shrubs with seed removal experiments, using seeds from invasive *R. cathartica* and multiple native species during summer and autumn 2014 to assess the effect of *R. cathartica* presence and removal on small mammal seed predation of native and invasive seeds. We focus on seed predation by small mammals because granivory by small mammals can have significant impacts on seed survival (Ostfeld et al. 1997; Hulme 1998; Crawley 2000), plant establishment (Orrock et al. 2006) and the structure of plant communities (Brown & Heske 1990; Howe & Brown 2001; Bricker & Maron 2012; Orrock et al. 2015). Invasive plant presence can alter seed predation rates and there can be yearly variation in this trend (Radtke & Wilson 2015). Moreover, the activity, abundance and impact of small mammals may be closely linked to available cover (Manson et al. 1999; Dutra et al. 2011) as well as food resources

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(Orrock et al. 2015), with the potential to alter the establishment of native and exotic species (Connolly et al. 2014; Orrock et al. 2015). We hypothesized that presence of *R. cathartica* would increase activity and abundance of small mammals, especially in late autumn, due to an increase in cover provided by extended leaf phenology, and in turn increase small mammal seed predation.

Methods

This study was conducted at the University of Wisconsin Arboretum, a 485-ha preserve in Madison, WI, that contains a large restored prairie as well as several large tracts of forest. Our work was conducted in a 50-ha portion of a naturally occurring (i.e. not planted) *Quercus rubra*-dominated deciduous forest. Other tree species present include *Carya ovata, Acer saccharum, Acer rubrum* and *Prunus serotina*. The study area contains high densities (50–100% cover) of *R. cathartica* in the understorey (Chidister 2009).

Sixteen 20 × 20 m plots were selected randomly throughout the study area (see Appendix S1). Eight plots were then randomly selected to have *R. cathartica* removed (removed plots) and eight plots were left with *R. cathartica* intact (intact plots). *R. cathartica* removal took place during late spring (18–31 May 2014) using loppers, handsaws and brush cutters. Each cut *R. cathartica* stem was cut at ground level and spot-treated with the herbicide Garlon 4 (triclopyr) to prevent regrowth (Archibold et al. 1997; Pergams & Norton 2006). Spot treatment with Garlon 4 was conducted carefully to ensure non-target plants were not treated with the herbicide. During removal, we visited intact plots to control for the disturbance created during the *R. cathartica* removal in the removed plots. During these visits, *R. cathartica* shrubs and trees were shaken and branches were dragged through plots to simulate activities that occurred during removal in the removal plots.

Quantifying changes in habitat characteristics related to *R. cathartica* invasion

Before and after *R. cathartica* removal (17 May 2014 and 3 Jun 2014), light measurements were taken at nine points in each plot, at midday on clear days using a light sensor (LQM 70-10; Apogee Instruments, Logan, UT, USA) held at ground level. Prior to *R. cathartica* removal (17 May 2014), we performed *R. cathartica* stem counts in 1 × 1 m quadrats at the nine points. Leaf litter depth was measured on 9 Nov 2014 at two of the established quadrats. In early summer (19 Jun 2014) and late summer (25 Aug 2014), ground cover measurements were taken at the same two quadrats as leaf litter depth: bare ground, herbaceous, leaf litter and downed woody debris percentage cover were visually estimated within those quadrats.

Quantifying seed removal

To test whether *R. cathartica* presence altered seed predation by small mammals, we conducted seed removal experiments at three time periods using seeds of four native species (*P. serotina, Q. rubra, A. saccharum* and *A. rubrum*) and seeds of exotic *R. cathartica*. Species were selected based on common tree species present in the study area (K. Bartowitz, pers obs), and are typically found in Wisconsin forests invaded by *R. cathartica* (Mascaro & Schnitzer 2007). These species are of ecological and commercial importance in deciduous forests throughout the US (Brockman & Merrilees 2001). Seed removal experiments were conducted using covered 1-gallon white translucent plastic buckets as seed removal depots. Two rectangular 8 × 10 cm holes were cut into opposite sides of each bucket, 2.5 cm from the bottom of the bucket to allow small mammal access. One depot was placed in the centre of each plot. Ten seeds of *P. serotina, A. saccharum, A. rubrum* and of *R. cathartica* and two acorns of *Q. rubra* were allotted to each depot on top of 0.3 L of sifted sand. Three sessions of seed removal experiments were conducted during the summer from 17 Jun–5 Jul 2014, early autumn from 14 Sept–2 Oct 2014, and late autumn from 9 to 25 Nov 2014. We did not quantify invertebrate post-dispersal seed predation (e.g. by ants or beetles) because post-dispersal seed predation by ants is rare in the temperate zone for tree species (Ostfeld et al. 1997; Hulme 1998). Small mammal abundance has strongly predicted seed removal rates in a similar study, suggesting that small mammals are key agents of seed mortality in Midwestern deciduous forests (Mattos et al. 2013). We assume that seed removal is analogous to seed death (Moles et al. 2003; Hillyer & Silman 2010; Mattos et al. 2013). This assumption is supported by observations of destroyed seeds in our study (seed fragments were found in 93% of our depots), as well as by additional studies at our field sites (P. Guiden, unpubl data) and other forest systems (Hillyer & Silman 2010) showing that secondary dispersal is extremely rare.

Assessing small mammal activity and abundance

We sampled small mammals using live trapping in midsummer (7–11 Jul 2014) and late summer (1–5 Aug 2014). Trapping occurred in all plots using Sherman live mammal traps (7.6 × 8.9 × 22.9 cm) to compare mammal activity and abundance between plots with *R. cathartica* intact removed plots. We placed ten traps at each plot in a cross pattern. Traps were baited with whole oats coated in peanut butter. Pre-baiting took place on the first day of trapping; traps were baited and propped open. Traps were checked twice daily, once in the morning and then in the afternoon, and re-baited with oats as needed. Upon capture, we marked animals with a unique tag, and determined gender, age and reproductive status. Due to logistical constraints, mass and morphology measurements were only taken for the smaller of the two species captured (i.e. white-footed mouse, *Peromyscus leucopus*).

Statistical analyses

Differences in light penetration before and after *R. cathartica* removal were compared using a general linear mixed model that accounted for the repeated-measures nature of the data (i.e. light measured twice at the same sites) using a compound symmetry covariance structure (Littell et al. 2006). We used a *t*-test to compare *R. cathartica* stem counts before the *R. cathartica* removal treatment. For comparison of habitat characteristics after *R. cathartica* removal, i.e. differences in light penetration, leaf-litter depth, bare ground, downed woody debris, herbaceous cover and canopy cover, we used *t*-tests to compare data from *R. cathartica*-intact and *R. cathartica*-removed plots.

We evaluated seed removal using a repeated-measures generalized linear mixed model with a compound symmetry covariance structure (Littell et al. 2006) and a binomial response distribution. This model used *R. cathartica* removal, species, session of seed removal experiment and all interactions as fixed effects. Site was modelled as a random effect and session was modelled as a repeated measure to account for the split-plot, repeated measures design. We removed *Q. rubra* from the seed removal analysis because seeds were nearly entirely removed in each of the three seed removal sessions (i.e. Jul, Sept, Nov; 98% of seeds; ancillary analyses found no difference in *Q. rubra* removal between intact and removed plots).

Mammal trapping data were evaluated using a repeated-measures generalized linear mixed model with a structure identical to the seed removal model, using *R. cathartica* removal, species and session of small mammal trapping as fixed effects, with site as a random effect and session as a repeated measure (Littell et al. 2006). Models utilized a Poisson distribution for count data. We focus our analysis of the mammal data primarily on the total number of captures, instead of the number of unique individuals captured, because the total number of captures represents both animal abundance and activity, and both may be affected by *R. cathartica* cover. We provide the results of analyses for the total number of individuals in Appendices S5 and S6.

All generalized linear mixed models were evaluated for over-dispersion, and all model residuals were evaluated using QQ plots to ensure they were normally distributed. All analyses were conducted in SAS v 9.4 (SAS institute, Cary, NC, US).

Results

Habitat characteristics

Before experimental removal of *R. cathartica,* there was no difference in *R. cathartica* stem count (t = 0.23, df = 14, P = 0.81) or understorey light (F = 0.93, df = 27.81, P = 0.34; Appendix S2) in plots assigned to have *R. cathartica* removed vs plots where it was to be left intact. After removal of *R. cathartica* shrubs, light penetration increased significantly in the removed plots (Table 1). Overstorey canopy cover was not significantly different between plots with *R. cathartica* intact and plots with *R. cathartica* removed (Table 1). Six months after *R. cathartica* removal, leaf litter depth in removed plots was significantly higher than leaf litter depth in intact plots (Table 1).

Seed removal

Total seed removal across three sessions was significantly different between *R. cathartica* removed and intact sites (Appendix S3). Total seed removal between removed and intact plots was significantly different by species (Appendix S3). There was no significant difference for the main effect of session (Appendix S3). There was a significant interaction between species and session (Appendix S3), and a significant interaction between species, session and *R. cathartica* removal (Appendix S3). There was no significant difference in seed removal rates across sessions for *P. serotina* between removed and intact plots (Fig. 1). During July, there was no difference in *R. cathartica* and *A. rubrum* seed removal between removed and intact plots (Fig. 1). In Sept and Nov, there were significantly more *R. cathartica* seeds removed (Fig. 1, Appendix S3) and marginally more *A. rubrum* seeds removed (Fig. 1, Appendix S3) between plots with *R. cathartica* removed and plots with *R. cathartica* intact. There was marginally higher *A. saccharum* seed removal between removed and intact plots in Jul, Sept and Nov (Fig. 1, Appendix S3).

On average, total seed removal was lower in sites with high levels of light penetration (F = 19.31, df = 1, 14, P < 0.0; Appendix S3). Total seed removal was lower in sites with higher cover of leaf litter (F = 6.16, df = 1, 14, P = 0.03).

Small mammal activity and mass

We captured two species of small mammal over the course of the two small mammal trapping sessions: *P. leucopus* and

Table 1. Habitat characteristics in plots invaded by *R. cathartica* and invaded plots where *R. cathartica* was removed. Values are mean ± SE.

Habitat Characteristic	*R. cathartica* Removed Plots	*R. cathartica* Intact Plots	*df*	*t*	*P*
Light Penetration	359.40 ± 49.90	44.3 ± 10.3	14	6.55	<0.01
Autumn Leaf Litter Depth (cm)	5.98 ± 0.38	1.89 ± 0.36	14	7.82	<0.01
Bare ground (% Cover)	23.30 ± 3.12	37.2 ± 5.31	14	3.24	0.05
Downed Woody Debris (% Cover)	12.50 ± 1.10	14.38 ± 2.65	14	0.65	0.53
Herbaceous (% Cover)	21.40 ± 3.80	25.16 ± 4.46	14	0.64	0.53
Overstorey Canopy (% Cover)	81.90 ± 4.27	75.71 ± 3.63	14	1.10	0.29

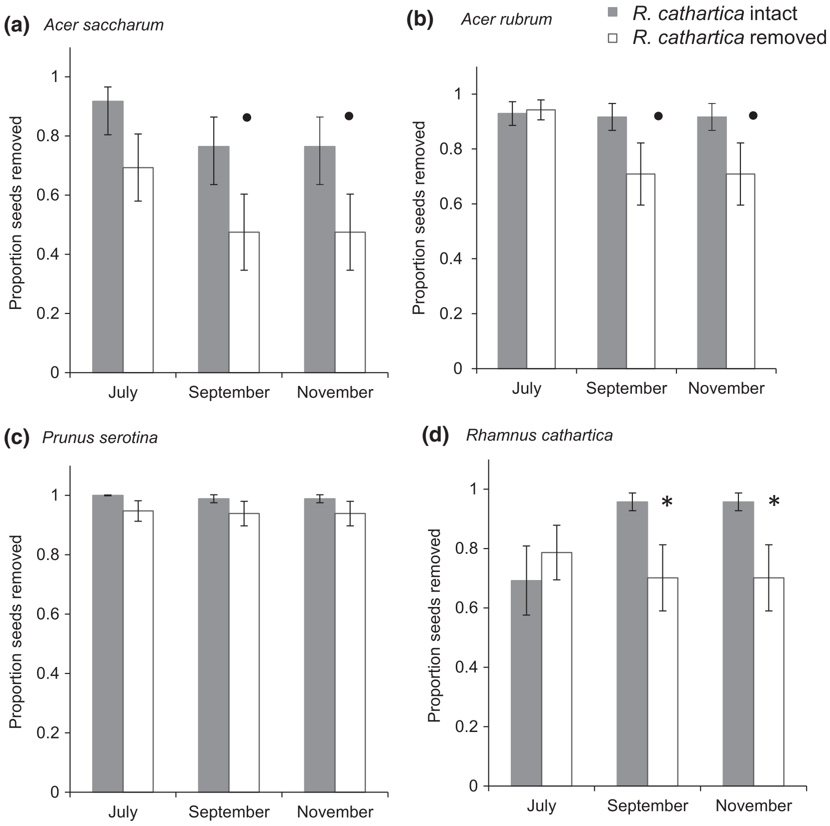

Fig. 1. Proportion of seeds removed for (**a**) *A. saccharum*, (**b**) *A. rubrum*, (**c**) *P. serotina* and (**d**) *R. cathartica* in Jul, Sept and Nov in plots in which *R. cathartica* was removed vs plots in which *R. cathartica* was left intact. Asterisks indicate significant pair-wise differences ($P \leq 0.05$) between plots with *R. cathartica* intact vs *R. cathartica* removed, while dots indicate marginally significant differences ($0.05 < P < 0.10$). Bars illustrate means ± 1 SE.

Tamias striatus (eastern chipmunk). Total small mammal captures were significantly higher in *R. cathartica* intact plots (5.40 ± 0.79) than *R. cathartica* removed plots (2.80 ± 0.65; Table 2). There were significantly more *P. leucopus* captures (10.50 ± 0.97) than *T. striatus* captures (1.44 ± 0.36; Table 2). There was no significant main effect of session (i.e. Jul or Aug; Table 2). There was no interaction between the *R. cathartica* removal treatment and species for *P. leucopus,* and there were more *T. striatus* total captures in *R. cathartica* intact plots (Fig. 2), although this trend was only marginally significant. Qualitatively similar, but less pronounced, trends were also observed for the *R. cathartica* removal treatment if the number of unique individuals captured was evaluated as the response variable (instead of the total number of captures; see Appendices S5 and S6). Traps were disturbed during our sampling, but the number of disturbed traps did not differ between intact and removed plots in either trapping session ($t = 0.80$, $df = 14$, $P = 0.44$; $t = 0.05$, $df = 14$, $P = 0.96$).

Table 2. Results of generalized linear mixed model analysis of the effect of *R. cathartica* removal, small mammal species (*P. leucopus* and *T. striatus*) and session on total captures of small mammals.

Effect	Num *df*	Den *df*	*F*	*P*
R. cathartica Removal	1	14	5.77	0.031
Species	1	42	56.3	<0.01
R. cathartica Removal × Species	1	42	3.47	0.07
Session	1	42	0.07	0.789
R. cathartica Removal × Session	1	42	0.38	0.499
Species × Session	1	42	0.53	0.539
R. cathartica Removal × Species × Session	1	42	0.43	0.436

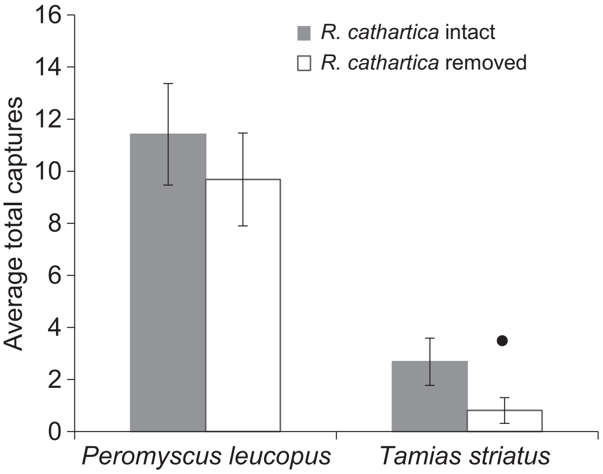

Fig. 2. Average total captures of *P. leucopus*, and *T. striatus* in plots in which *R. cathartica* was removed vs plots in which *R. cathartica* was left intact. Dots indicate marginally significant pairwise differences (0.05<*P*<0.10) between plots with *R. cathartica* intact vs. *R. cathartica* removed, while . Bars illustrate means ± one SE.

Average individual *P. leucopus* mass was higher in *R. cathartica* intact plots in the Jul session (t = 3.78, df = 14, P = 0.002), and there was no difference in *P. leucopus* mass the Aug session (t = 1.79, df = 14, P = 0.10). There was no difference in reproductive status or gender of *P. leucopus* in *R. cathartica* removed and intact sites (see Appendix S7).

Discussion

Increasing evidence suggests that invasive plants can change the magnitude of consumer pressure (Pearson & Fletcher 2008; Dutra et al. 2011; Orrock et al. 2015). However, less appreciated is that invasive plants that exhibit novel phenologies may alter timing of consumer pressure. Using an experimental removal of mature *R. cathartica*, our study reveals that the presence of *R. cathartica* changes the magnitude and timing of seed removal for several species, including *R. cathartica*. Our results have several important implications. First, by changing the magnitude of seed predation at particular times of year, *R. cathartica* may have unappreciated effects on the survival and recruitment of several woody species. Second, our results indicate that apparent competition among seeds may not be a primary mechanism promoting the persistence of *R. cathartica* in invaded habitats. Third, our study adds to the growing evidence that small mammal consumers are directly affected by the presence of invasive woody shrubs, suggesting that changes in consumer pressure may be a widespread mechanism altering dynamics of temperate forest communities.

Temporal shifts in seed predation caused by novel phenology

Our results illustrate the capacity for novel phenologies of exotic plants to alter the temporal dynamics of seed predation for multiple species. Higher levels of seed predation of *R. cathartica* and *A. rubrum* coincided with novel extended leaf phenology of *R. cathartica*. *R. cathartica* seeds disperse Sept–Dec (Gill & Marks 1991), while *A. rubrum* seeds are dispersed in Jul–Aug, and germinate in late summer–autumn (Walters & Yawney 1990). The largest difference in *R. cathartica* seed removal occurred when seeds of *R. cathartica* were naturally available in the environment, suggesting that the temporal increase in seed removal may affect this species at a crucial time for the seed survival. The largest difference in *A. rubrum* seed removal occurred when the seeds of this species are beginning to germinate after dispersal, so a portion of these seeds are still available in the environment at this time. Conversely, for *A. saccharum* significant differences in seed removal in Jul did not coincide with natural dispersal times from Oct–Dec (Olson & Gabriel 1974). Shifts in other temporal dynamics due to global climatic changes may also lead to reduced seed survival (Connolly & Orrock 2015), which could act in conjunction with increased seed predation due to the novel phenology of an exotic shrub, leading to the potential for increasingly larger decreases in recruitment and subsequent spatial variation in plant communities (Maron et al. 2012).

Specific to seed predation, our work suggests that seed removal studies may yield very different conclusions depending on when they are conducted, highlighting the importance of multi-season studies (e.g. Wilson & Whelan 1990; Mattos et al. 2013). Not only is within-year variation an important factor in seed removal studies, year-to-year variation may also be in a driving factor in seed predation of invaded habitats (Radtke & Wilson 2015). Future multi-year studies would help elucidate if there are yearly fluctuations in seed removal in woody invaded habitats. Our work is one of the first experimental studies to demonstrate how indirect effects of invasive woody shrubs require experiments explicitly designed to detect temporal variation in biological interactions. Studies that explicitly incorporate the potential for temporal variation and novel phenology are likely to lead to the greatest insights.

Apparent competition via seed predation does not facilitate woody invasive seed recruitment in invaded habitats

While our study illustrates that *R. cathartica* presence is indirectly affecting several native plant species by increasing small mammal seed predation, *R. cathartica* seeds were consumed as heavily as native seeds. This suggests that apparent competition via seed predation may not be an important mechanism for promoting recruitment of *R. cathartica* in invaded habitats. While we did not observe apparent competition via seed predation between *R. cathartica* and native seeds in our study, increased seed predation of native seeds in the presence of *R. cathartica* could be working in conjunction with other direct effects of *R. cathartica* to benefit *R. cathartica* over native plants. Although the lack of apparent competition in our study was contrary to a part of the predicted outcome of a model of apparent competition mediated through extended leaf phenology, our results still agree with the conclusion that novel leaf phenology often favours the invader through direct or indirect competition, or both (Smith & Hall 2016). Predation of *R. cathartica* seeds has been hypothesized to limit *R. cathartica* invasion into mature, un-invaded deciduous forests (McCay & McCay 2009), and our work suggests that it may be a limiting factor in invaded forests. Future studies will be needed to understand if the density-dependent attack on *R. cathartica* seeds (i.e. a form of a Janzen-Connell effect; Janzen 1970) is important for recruitment of *R. cathartica* in later stages of invasion.

Although our work suggests that *R. cathartica* does not benefit from apparent competition, the ultimate effect of consumers on recruitment may depend upon the total number of seeds that survive predation, not just the fraction of seeds consumed (Crawley 2014). For example, although small mammals consumed similar proportions of native and exotic seeds, these native plants typically produce fewer and more variable numbers of viable seeds (50–600 seeds·m^{-2}; Houle 1994) than *R. cathartica* (620 seeds·m^{-2}, Archibold et al. 1997). As such, seed predation may reduce the total number of native seeds so that all suitable microsites are not located, whereas *R. cathartica* may still have sufficient absolute numbers of surviving seeds. Therefore, even at the high levels of predation we documented, it is unclear whether seed predation by small mammals will limit seed availability for *R. cathartica* in areas where seed inputs are high.

Invasive woody shrub increases habitat structure and consumer abundance

Our experimental removal of *R. cathartica* demonstrates how a woody invasive shrub alters habitats: it increases mid-storey cover, and decreases light penetration and leaf litter depth (Table 1). While these direct habitat changes have been well documented (Archibold et al. 1997; Anderson et al. 2003; Knight et al. 2007), our results highlight shifts in subsequent biological interactions, such as small mammal abundance and seed predation of multiple species. The significant relationship detected between habitat characteristics and seed predation suggests that shifts in habitat characteristics driven by *R. cathartica* are a primary means through which *R. cathartica* alters small mammal abundance and activity (as measured by total captures) and subsequently seed predation. While studies have shown that *R. cathartica* increases cover and decreases leaf litter (Heneghan et al. 2004), and that leaf litter presence can decrease seed predation (Myster & Pickett 1993), our study provides the first empirical linkage of these *R. cathartica*-mediated changes in habitat characteristics to subsequent changes in seed predation. Our results illustrate how a single species can alter consumer activity via alteration of the above-ground environment (i.e. light penetration) as well as alteration of the ground-level environment.

Our experiment provides the first demonstration that *R. cathartica* presence directly increases the abundance and activity of small mammals, and supports other studies that have found changes in consumer pressure in invaded habitats. For example, invasion by *R. cathartica* can increase non-native earthworm presence (Heneghan et al. 2007; Madritch & Lindroth 2009) and the presence of large mammals such as coyotes (*Canis latrans*) and opossums (*Didelphis virginiana*; Vernon et al. 2014). Also, previous research suggests *P. leucopus* prefer dense cover of a similar exotic woody shrub, *Lonicera maackii* (Mattos & Orrock 2010), leading to increased activity of mammals in invaded habitats (Dutra et al. 2011). Removal of *L. maackii,* has shown both decreased *P. leucopus* abundance (Dutra 2011) and increased *P. leucopus* abundance, although it is unclear whether these changes are maintained over longer periods (Shields et al. 2014). Consumer response to invasive plant presence can vary depending on the system (Ostoja & Schupp 2009; Litt et al. 2014), showing that responses of native species differ by focal exotic plant present (e.g. woody shrubs, grasses). Our results suggest that changes in habitat characteristics and subsequent small mammal abundance may be a general mechanism driving increases in seed predation in habitats invaded by *R. cathartica*.

Our results imply that the condition of small mammals may also be affected by *R. cathartica*: mass of *P. leucopus* was generally lower in sites where *R. cathartica* was removed. We did not find differences in gender, age or reproductive status of small mammals between removed and intact plots, suggesting that differences in mass may be due to increased foraging activity in invaded plots, rather than changes in demographic structure. The change in mass we noted may also be caused by increased food resources provided by *R. cathartica*: 90% of *R. cathartica* fruits fall to ground before being dispersed (Archibold et al. 1997), and *P. leucopus* is known to consume fruits of other invasive woody shrubs, such as *L. maackii* (Rose et al. 2014). Increased food availability from *R. cathartica* fruit presence could be a driving force behind increased small mammal activity and seed predation, however it is difficult to tease apart the impact of increased leaf cover and increased food availability on small mammal activity. Future studies investigating the fate of *R. cathartica* fruits and small mammal preference of leaf cover vs increased food availability would be a profitable next step for determining whether fruits from *R. cathartica* drive changing consumer pressure, as has been found for *L. maackii* (Orrock et al. 2015).

Conclusions and future directions

The success of invasive species and their impact on native communities can depend upon indirect effects of consumers (White et al. 2006; Orrock et al. 2015). Our study provides evidence that the presence of *R. cathartica* in a deciduous forest increases small mammal abundances and indirectly alters the temporal dynamics of seed predation. Removal of *R. cathartica* could directly facilitate restoration or recovery of native flora in invaded sites by increasing light levels, and indirectly by decreasing seed predation on native species. Our results also highlight that seasonal indirect effects can play an important role in invaded plant communities, and illustrate how the magnitude of indirect effects depend upon the novel extended leaf phenology of an invasive plant. While several studies have examined *R. cathartica*-mediated changes in interactions such as herbivory and germination (Fagan & Peart 2004; Klionsky et al. 2011; Grady et al. 2012), and the potential for multiple, synergistic effects of exotic shrubs certainly exists (Orrock et al. 2015), exactly how *R. cathartica*-driven changes in different consumer-mediated interactions work in concert to affect native communities is not known. Future multi-season studies that track success of plants in invaded habitats through multiple life stages (e.g. germination success, seedling survival) are needed to link seed predation patterns we saw with differential recruitment patterns. Our work suggests that seed removal studies may yield different conclusions depending on when they are conducted, highlighting the importance of studies that utilize multi-season approaches to understand indirect effects of invasive plants.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Map of study site.

Appendix S2. Results of generalized linear mixed model analysis of the effect of *Rhamnus cathartica* removal and time period of *R. cathartica* removal on light penetration.

Appendix S3. Results of generalized linear mixed model analysis of the effect of *Rhamnus cathartica* removal, seed species and session on post-dispersal seed removal for five seed species.

Appendix S4. Plot of proportion of seeds removed plotted against light penetration.

Appendix S5. Summary table of GLMM of total individual small mammal captures.

Appendix S6. Species-specific graphs of total individual small mammal captures.

Appendix S7. Table of mammal gender, age and reproductive status.