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# Rodent Granivores Generate Context-specific Seed Removal in Invaded and Uninvaded Habitats

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ABSTRACT.—Invasive plants threaten biodiversity and impact natural ecosystems through both well-studied direct effects and lesser known indirect effects. We examined one indirect effect: whether the presence of an invasive exotic shrub, *Lonicera maackii,* changes seed predation of native shrub species by providing dense cover that might harbor shared seed predators (*i.e.*, apparent competition). Our study quantified removal of seeds of exotic *L. maackii* and native plant species by granivores in invaded and uninvaded plots during winter and spring trials. We found that the presence of *L. maackii* did not change removal of native seeds in either season and that rodent granivores contributed significantly to seed removal compared to arthropods. Removal of *L. maackii* seeds by rodent seed predators was significantly greater than the native species studied in the spring (*Cornus drummondii*), suggesting that rodents may have negative effects on *L. maackii* in some ecological contexts by consuming seeds. Our findings highlight the need for future research to understand the context-specific mechanisms that determine the nature and strength of indirect effects in biological invasions.

## INTRODUCTION

Biological invasions can have transformative effects on the communities they invade (Vitousek, 1990; Wilcove *et al.*, 1998; Pimentel *et al.*, 2005; Theoharides and Dukes, 2007). While direct effects, such as competition and herbivory, are commonly studied in the field of invasion ecology (reviewed in Levine *et al.*, 2004), a growing literature suggests that indirect effects mediated through other species may play an under-appreciated role in biological invasions (Borgman and Rodewald, 2004; Noonburg and Byers, 2005; White *et al.*, 2006; Orrock *et al.*, 2010; Dutra *et al.*, 2011). One such indirect effect is apparent competition, where the presence of one species leads to reduced density and population size of another species by increasing the impact of a shared enemy (Holt, 1977; White *et al.*, 2006). Although apparent competition may have important effects in both terrestrial and aquatic plant communities (Connell, 1990; Menge, 1995; Chaneton and Bonsall, 2000), few studies have examined the role of apparent competition in mediating plant invasions.

In this paper, we evaluated indirect interactions between invasive and native plants mediated through shared seed predators to determine if apparent competition could be

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affecting plant invasion in different ecological contexts (*e.g.,* as a function of plant invasion, predator identity, and season). We examined whether seed removal rates differed among sites invaded by mature *Lonicera maackii* and uninvaded sites, and further analyzed the role of different seed predators by quantifying seed removal by rodents separately from removal by arthropods in two seasonal studies. *Lonicera maackii* has been shown to change rodent foraging behavior and increase foraging activity because it provides increased cover that rodents can use as a refuge while foraging (Mattos and Orrock, 2010; Dutra *et al.*, 2011). The presence of *L. maackii* shrub cover has also been shown to increase rates of seed removal of native species (Meiners, 2007), consistent with apparent competition. Though these studies suggest that components of apparent competition are present (*e.g.,* higher native seed removal in shrub cover, Meiners, 2007; preference for foraging under shrub cover, Mattos and Orrock, 2010; increased activity under shrub cover, Dutra *et al.*, 2011), they do not address one important prediction of apparent competition: the differential removal of native and exotic seeds in invaded habitats. Our study quantified removal of exotic *L. maackii* as well as the removal of seeds of native *Symphoricarpos orbiculatus* and *Cornus drummondii*. We expected apparent competition to facilitate further plant invasion in this system if consumers preferred native seed species to *L. maackii* in areas where invasive shrub cover was present. Alternatively, if *L. maackii* seeds were consumed more than native seeds, we expected that spread of the invasive shrub may be inhibited by seed predators, *i.e.,* that native consumers provide biotic resistance (Levine *et al.*, 2004) to further spread of *L. maackii*. We hypothesized that seed predators will facilitate apparent competition by preferentially removing native seeds in invaded habitats.

## METHODS

### STUDY SYSTEM

*Lonicera maackii* (Amur honeysuckle) is native to northeastern Asia and has invaded forests in the eastern half of the United States (Collier *et al.*, 2002). *Lonicera maackii* invasion has been correlated with decreased growth and diversity of forest plant species (*e.g.,* Collier *et al.*, 2002; Miller and Gorchov, 2004). *Lonicera maackii* fruits are berries containing an average of 3.8 seeds per fruit (Williams *et al.*, 1992), with seeds measuring approximately 3 mm along the longest axis. *Cornus drummondii* (rough-leafed dogwood, Cornaceae) and *Symphoricarpos orbiculatus* (coralberry, Caprifoliaceae) are both native forest shrubs that occur naturally in our study area and have similar fruiting phenology and seed size to *L. maackii*. Both *C. drummondii* and *S. orbiculatus* produce drupes containing one seed, measuring approximately 5 mm and 2 mm along the longest axis, respectively. Seed, and not fruit, removal was examined in this study because seeds of our focal species are typically dispersed by birds and mammals, such that seeds are free of pulp during the time when they are exposed to seed predators (*i.e.,* after dispersal). We chose to provide the same number of seeds for each species, rather than providing the same total mass of each species (which would have led to different seed numbers per species). We held seed number constant because this has the advantage of allowing us to focus on the role of seed identity in affecting seed removal, whereas differences in removal observed when constant seed masses are presented could arise due to differences in seed traits, differences in relative numbers of seeds among species, or both. The use of standardized numbers of seeds is common in seed-removal studies (*e.g.,* Orrock and Damschen, 2005; Craig *et al.*, 2011).

*Peromyscus leucopus* was the only rodent active at our sites during our sampling (*see* Results). *Peromyscus leucopus* is an abundant small mammal in North American deciduous forests and seeds comprise an important part of its diet (Lackey *et al.*, 1985). Invasive shrubs

may increase mouse population densities and consumer pressure on native plants by subsidizing food resources (Pearson and Callaway, 2008) and providing preferred foraging habitat (Meiners, 2007; Orrock *et al.*, 2008; Mattos and Orrock, 2010; Dutra *et al.*, 2011). While predation of *Lonicera maackii* seeds by *P. leucopus* has never been examined, *Peromyscus maniculatus* has been shown to consume *L. maackii* seeds (Williams *et al.*, 1992).

This study was conducted at the August A. Busch Memorial Conservation Area in St. Charles County, Missouri, USA (38°42′18″N, 90°44′50″W). We chose 12 sites of mixed hickory-oak deciduous forest; visual surveys indicated that six sites had very low or no *Lonicera maackii* presence (''uninvaded'' sites, mean number of *L. maackii* stems per 1 m radius circular plot = 0.03 ± 0.03 SE) and six sites were characterized by high densities of *L. maackii* (''invaded'' sites, mean number of *L. maackii* stems per 1 m radius circular plot = 2.64 ± 0.39 SE, P-value < 0.001). All sites were separated by a distance of at least 400 m, a distance much larger than the average home range of the most common seed predator, *Peromyscus leucopus*, (1000 $m^2$, Lackey *et al.*, 1985, *i.e.*, an area of approximately 30 × 30 m).

### DATA COLLECTION

Seeds were collected from naturally occurring plants throughout the study area in Oct. and Nov. 2008. Seeds were removed from fruits, washed clean of pulp, air-dried, and stored at room temperature until placed in the field. We performed two seed removal studies from 17 Nov. 2008 to 17 Dec. 2008 and from 3 Apr. 2009 through 30 Apr. 2009. On the first day of each period, seed removal depots (translucent white 18 × 18 × 12 cm plastic buckets with two 5 × 5 cm holes on the sides and white plastic lids) were placed in pairs at each of the twelve study sites. Seed depots are often used in predation studies to provide a standardized habitat in which to measure removal rates and food preferences (*e.g.,* Orrock and Damschen, 2005; Craig *et al.*, 2011). Previous work in this study system has also shown that granivorous animals will readily use these depots for foraging (Mattos and Orrock, 2010), and depots eliminated the effects of heavy precipitation and raccoon disturbance. One depot in each pair had its access holes covered in hardware cloth (1-cm openings) to allow access to arthropods only; the other depot was open to both rodent and arthropod seed predators. Depots were filled with 400 g of dried, sifted fine sand to provide a substrate for seed presentation, a common practice in seed-removal studies (Orrock and Damschen, 2005; Craig *et al.*, 2011). In the winter period three pairs of seed removal depots were used per site (six depots per site for twelve sites, n = 72) with 10 *Lonicera maackii* seeds, 10 *Cornus drummondii* seeds, and 10 *Symphoricarpos orbiculatus* seeds scattered randomly on the surface of the sand with 5–50 mm between individual seeds. In the spring period, limited seed availability forced us to use two pairs of depots per site (four depots per site for 12 sites, n = 48) with 10 *L. maackii* seeds and 10 *C. drummondii* seeds only.

The pairs of depots were evenly spaced approximately 6 m from the center of the each site, with less than 1 m between each depot in a pair. Depots were left out for 30 d in the winter and 28 d in the spring to allow consumer access to seeds. The sites were checked twice during this period to record raccoon disturbance. If depots were disturbed, they were set upright and any sand and seeds that could be located were replaced. Upon completion of each study period, seeds were recovered and quantified. Depots were classified as having experienced foraging activity if one or more seeds of one or more species were missing. Because *Peromyscus leucopus* is not primarily a hoarding species and because depredated fragments of seeds were found in the trays, we assumed that seed removal was equivalent to seed predation.

*Peromyscus leucopus* abundance was measured using live trapping. Three Sherman live traps were placed within 1 m of the each of the winter paired depot positions (nine traps per site).

After a one-day acclimation period when baited traps were propped open and left at the sites, traps were checked, emptied, re-baited and reset at dawn each day from 31 Mar. 2009 until 3 Apr. 2009. Captured rodents were identified to species, marked with a metal ear tag, and released near the site of capture.

### DATA ANALYSIS

Our seed removal experiment represents a split-plot design with three levels of experimental unit. Within each seed removal depot, seeds were of a particular species (*Lonicera maackii, Cornus drummondii, Symphoricarpos orbiculatus*). Within a site, half of the depots excluded rodents and half of the depots allowed rodent access (exclosure treatment). Finally, each site's habitat was classified as either invaded or uninvaded. Because we had replicate seed-removal depots within each site (*i.e.*, three pairs per site for winter trials, two pairs per site for spring trials), we pooled seed removal data within a session and site to avoid pseudo-replication. We performed two analyses for each season of the study. The first analysis examined whether overall seed removal differed between habitat type (invaded or uninvaded) and seed species by quantifying overall seed removal in trays with exposure to rodents and arthropods, examining habitat (invaded or uninvaded) and seed species as fixed effects and site as a random effect. The second, species-specific analysis examined habitat type (invaded or uninvaded) and exclosure treatment as fixed effects and site as a random effect to evaluate the role of rodents in seed removal for each species. All analyses examined the proportion of seeds removed in each depot using generalized linear mixed models with a binomial response distribution (Littell *et al.*, 1996), except the analysis that examined rodent contributions to seed removal for *C. drummondii* in winter which required an arcsine square-root transformation of the proportion of seeds removed because the linear model would not converge. Data from one invaded and one uninvaded site in the winter and one invaded site in the spring were discarded because of severe raccoon disturbance at the sites. All mixed models used the Kenward-Roger approximation to calculate appropriate error terms for testing the hypotheses of our split-plot design (Littell *et al.*, 1996). Rodent abundance data were analyzed using *t*-tests to compare the total numbers of unique captures at invaded versus uninvaded sites. All analyses were conducted using SAS 9.1 (Littell *et al.*, 1996); all means are presented ±1 Standard Error (SE).

## RESULTS

### WINTER SEED REMOVAL

Of the 60 depots that were used in the winter period (excluding two raccoon-disturbed sites), 30 experienced foraging activity, sixteen in invaded plots and fourteen in uninvaded plots. Direct evidence of seed mortality (*i.e.*, gnawed seeds and fragments of chewed seed coats) was found in 23% of foraged trays with rodent access. Overall, seed removal across species and treatments was low, with average proportions of seeds removed ranging from 0 to 0.27 across treatments (Fig. 1A).

There were marginally significant differences in overall seed removal in trays open to both arthropods and rodents between the different species offered ($F_{2,\ 24} = 2.81$, $P = 0.08$), with higher removal of *Lonicera maackii* (mean proportion of seeds removed = 0.11 ± 0.08) and *Symphoricarpos orbiculatus* (0.11 ± 0.08) than of *Cornus drummondii* (0.07 ± 0.05, Fig. 1). There were no differences between different habitats when overall seed removal was analyzed ($F_{1,\ 7.70} = 0.44$, $P = 0.53$); however, there was a suggestive, marginally significant interaction between habitat and seed species ($F_{2,\ 24} = 3.19$, $P = 0.06$, Fig. 1A). This interaction was due to significant differences in removal among species in uninvaded sites

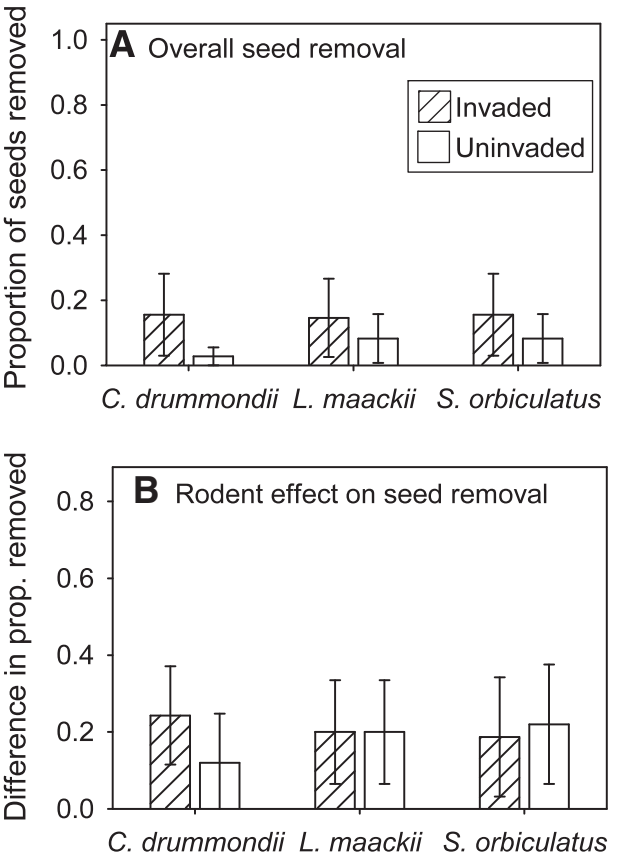


FIG. 1.—Proportion of seeds removed after exposure to rodents and arthropods in winter (30 d) in invaded and uninvaded areas **(A)** and the difference in proportion removed between trays with both rodent and arthropod access and trays with only arthropod access (representing removal by rodents; **(B)** Bars illustrate means +/− one standard error

(linear contrast, $F_{2,\ 24} = 5.82$, $P = 0.01$). There was no difference in removal among seed species in invaded sites (linear contrast, $F_{2,\ 24} = 0.02$, $P = 0.98$).

When analyzing each species individually for the contribution of rodents to seed removal, all three species showed strong trends towards higher removal in depots with rodent and arthropod access than in depots with only arthropod access (Fig. 1B). For *Symphoricarpos orbiculatus* and *Lonicera maackii* the effect of the exclosure was marginally significant (*S. orbiculatus*: $F_{1,\ 8.44} = 4.24$, $P = 0.07$; *L. maackii*: $F_{1,\ 8.44} = 4.46$, $P = 0.07$) with higher predation when all seed predators had access (mean proportion of seeds removed *S. orbiculatus*: $0.12 \pm 0.08$; *L. maackii*: $0.14 \pm 0.07$) than when only arthropods had access (*S. orbiculatus*: $0.02 \pm 0.02$; *L. maackii*: $0.03 \pm 0.02$). For *Cornus drummondii* the effect of the exclosure was significant ($F_{1,\ 16} = 4.88$, $P = 0.04$) with higher predation when both arthropod and rodent seed predators had access ($0.19 \pm 0.06$) than when only arthropods had access ($0.01 \pm 0.06$). The effect of habitat was not significant for any of the three species (*S. orbiculatus*: $F_{1,\ 6.48} = 0.32$, $P = 0.59$; *L. maackii*: $F_{1,\ 7.14} = 0.12$, $P = 0.74$; *C. drummondii:* $F_{1,\ 16} = 1.97$, $P = 0.18$) nor was the interaction

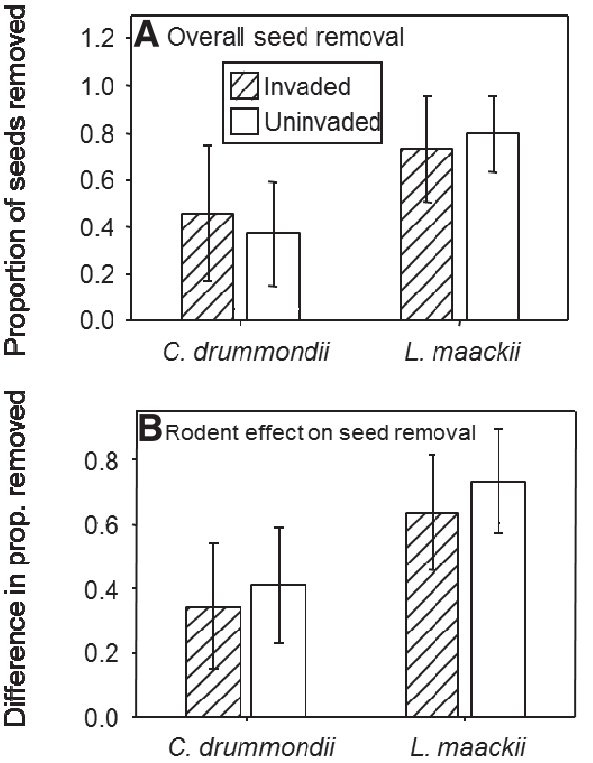


FIG. 2.—Proportion of seeds removed after exposure to rodents and arthropods in spring (28 d in invaded and uninvaded areas **(A)** and the difference in proportion removed between trays with both rodent and arthropod access and trays with only arthropod access (representing removal by rodents; **(B)** Bars illustrate means +/− one standard error

of habitat and rodent exclosure (*S. orbiculatus*: $F_{1.8.44} = 0.43$, $P = 0.53$; *L. maackii*: $F_{1,\ 8.14} = 0.05$, $P = 0.82$; *C. drummondii*: $F_{1,\ 16} = 0.20$, $P = 0.66$).

### SPRING SEED REMOVAL

Seed removal occurred at 28 of the 44 depots used in the spring period (excluding one raccoon-disturbed site), 14 in uninvaded plots and 14 in invaded plots. When seeds were removed in rodent-access trays, direct evidence of seed mortality was found in 21% of foraged trays. Overall seed removal was higher in the spring than in the winter, with average proportions removed in the spring ranging from 0.37 to 0.79 across treatments (Fig. 2).

There were significant differences in overall seed removal in trays open to both arthropods and rodents between the different species offered ($F_{1,\ 9.98} = 6.61$, $P = 0.03$), with higher removal of *Lonicera maackii* ($0.76 \pm 0.14$) than of *Cornus drummondii* ($0.41 \pm 0.18$). There were no significant differences between habitats when overall seed removal was analyzed ($F_{1,\ 8.06} = 0.00$, $P = 0.99$), and there was no significant interaction between the two effects ($F_{1,\ 9.98} = 0.35$, $P = 0.57$, Fig. 2A).

When analyzing each species individually for the contribution of rodents to seed removal, both species showed significantly higher removal in depots with rodent and arthropod access than in depots with only arthropod access (*Lonicera maackii*: mean proportion of seeds removed in rodent and arthropod access = 0.72 ± 0.14, mean in arthropod only access = 0.03 ± 0.02, $F_{1, 17} = 17.07$, $P < 0.001$; *Cornus drummondii*: mean in rodent and arthropod access = 0.40 ± 0.18, mean in arthropod only access = 0.02 ± 0.02, $F_{1, 18} = 8.50$, $P = 0.01$; Figure 2B). The effect of habitat was not significant (*L. maackii*: $F_{1, 17} = 0.02$, $P = 0.90$; *C. drummondii*: $F_{1, 18} = 0.58$, $P = 0.46$) nor was the interaction of habitat and rodent exclosure (*L. maackii*: $F_{1, 17} = 0.08$, $P = 0.78$; *C. drummondii*: $F_{1, 18} = 0.18$, $P = 0.68$).

### RODENT ABUNDANCE IN INVADED AND UNINVADED HABITATS

We caught 54 rodents over 360 trap nights; *Peromyscus leucopus* was the only species captured. Twenty-eight mice were captured at invaded sites and 26 were captured at uninvaded sites. No individual was captured at more than one site. There was no significant difference in rodent abundance between invaded and uninvaded areas ($t = 0.29$, DF = 10, $P = 0.77$). There was a significant relationship between the number of rodent captures near seed removal depots (adjusted by excluding disturbed traps that were not available to capture *P. leucopus*) and the removal of seeds by rodents in the winter for all three species used (*Cornus drummondii*: $r^2 = 0.592$, $F_{1,8} = 11.6$, $P < 0.01$; *Lonicera maackii*: $r^2 = 0.708$, $F_{1,8} = 19.36$, $P < 0.01$; *Symphoricarpos orbiculatus*: $r^2 = 0.611$, $F_{1,8} = 12.56$, $P < 0.01$) and in the spring for both species used (*C. drummondii*: $r^2 = 0.659$, $F_{1,9} = 17.36$, $P < 0.01$ *L. maackii*: $r^2 = 0.520$, $F_{1,9} = 9.734$, $P = 0.01$).

## DISCUSSION

Our study provides two key findings: first, our data suggest that there is no consistent effect of *Lonicera maackii* shrub invasion on native seed removal in our forest plots. Second, our study highlights the role of rodents as seed predators in forests and the significant temporal and species-specific variation in seed predation experienced by shrubs in forested systems. Our work indicates that *L. maackii* seeds were preferentially removed over one native species (*Cornus drummondii*) species in both winter and spring seed removal studies (Figs. 1 and 2), while another native species (*Symphoricarpos orbiculatus*) was consumed as often as *L. maackii* in one season of trials. The preferential removal of *L. maackii* over *C. drummondii* was observed in both invaded and uninvaded habitats, although the effect was stronger in uninvaded habitats in both seasons. Differences between our results and other seed removal studies with closely related species suggest high variation in rodent seed predation and context-specific results based on the seed species available and a variety of environmental factors. These observations may have consequences for future studies of seed predation as well as for understanding the dynamics of forest shrub establishment.

Although *Lonicera maackii* can have far-reaching effects on native taxa (Hartman and McCarthy, 2007; Allan *et al.*, 2010; McKinney and Goodell, 2010; Conley *et al.*, 2011; Watling *et al.*, 2011) and may alter rodent behavior (Mattos and Orrock, 2010; Dutra *et al.*, 2011), our results suggest that apparent competition mediated by rodent and arthropod granivores may not be an important pathway through which the shrub interacts with native shrubs in our region in the seasons that we studied. This study adds to a growing body of research examining the interactions between native consumers and *L.* maackii from this region, such as Mattos and Orrock (2010) and Dutra *et al.* (2011), which both documented increases in rodent activity under dense shrub cover. Dutra *et al.* (2011) demonstrated through a factorial design manipulating shrub cover and berry presence that the mechanism of

increased activity was the presence of protective cover and not necessarily the presence of increased food resources (*L. maackii* berries). Our study builds on this literature by asking whether increased activity under shrub cover necessarily has consequences for the fate of food sources being foraged, and examines *L. maackii* seeds (rather than fruits) and native seeds as other food resources that are accessed by consumers in invaded and uninvaded forests. We predicted that we would detect apparent competition by observing higher removal of native seeds than invasive seeds in invaded areas, since foraging activity is higher there. However, our results suggest that instead of fostering apparent competition, seed predators may prefer to consume seeds of *L. maackii* more than native seeds, with the strength of this preference varying with season (Figs. 1–2).

Our findings contrast with previous studies that suggest the potential for *Lonicera spp.* to generate apparent competition via seed predators (Meiners, 2007; Shahid *et al.*, 2008). Importantly, previous studies examined different ecological contexts. Meiners (2007) examined predation of *Fraxinus pennsylvanica* in autumn by rodents increased under *L. maackii* cover. Shahid *et al.* (2008) examined removal of three invasive species (*Lonicera morrowii*, *Rhamnus cathartica*, and *Rosa multiflora*) and two native shrubs (*Cornus amomum* and *Rubus idaeus*), finding that natives were preferentially consumed by rodents in autumn. Within the context of these studies, our results highlight how season of seed deployment and consumer preference for seed species play an important role in determining relative rates of seed removal.

We observed very low levels of seed removal when compared to relative rates of removal from other studies of seed removal in deciduous temperate forests (*e.g.,* >90% seeds removed in Plucinksi and Hunter, 2001; Meiners, 2007; Moore *et al.*, 2007; 40–95% *Cornus florida* removed in Myster and Pickett, 1993; Kwit *et al.*, 2004). However, most seed removal studies in similar ecosystems occurred in the summer when rodent and arthropod activity is likely to be greater. We would expect relative rates of seed predation to change across seasons as the availability and relative abundance of different seed species changes. Although documenting low rates of seed removal, our results reveal relevant information about seed survival after dispersal at the end of the summer and before seedling establishment the following spring. Our study fills a gap in the literature by mimicking seed exposure to granivores during a time when seeds would most likely be available for post-dispersal predation, during the winter and spring periods.

The importance of rodents as primary seed predators in our system is illustrated by significant differences between depots that did and did not allow rodent access (Figs. 1–2) and reinforced by our observations of depredated seeds inside the rodent-accessed depots. Significantly more seeds of all species were removed in trays that allowed rodents access in both our winter and spring studies, and greater than 20% of foraged, rodent-accessed depots contained seed fragments confirming seed predation by rodents. Rodents are key consumers in many ecosystems (*e.g.,* deserts, Reichman, 1979; Brown and Heske, 1990; coastal scrublands, Deveny and Fox, 2006; tropical forests, Velho *et al.*, 2009; temperate forests, Schnurr *et al.*, 2002); our research demonstrates their contribution to seed predation in invaded forests, which are now common throughout much of the Eastern and Midwestern United States. In illustrating the substantial rates of seed predation caused by *Peromyscus leucopus* on some species (*e.g., Lonicera maackii*), our results suggest that ecological factors that affect the abundance of rodents (*e.g.,* mesopredator release, Crooks and Soule, 1999), habitat fragmentation (Nupp and Swihart, 2000) and species invasion (Didham *et al.*, 2007; Theoharides and Dukes, 2007) may also have implications for changes in the nature and strength of seed predation and indirect effects. Importantly though, *P. leucopus* have

been shown to be flexible with food sources and foraging habitats in different environments and when food is scarce, which may explain why Dutra *et al.* (2011) and Mattos and Orrock (2010) found habitat-related differences in foraging activity even though we did not find habitat-related changes in seed removal. If *P. leucopus* were frequently consuming a food source that our study did not examine (*e.g.,* arthropods), then we would not have detected a strong signal of seed removal effects, suggesting that a more complete examination of possible food sources for omnivorous consumers will be necessary in order to determine habitat-related patterns.

## CONCLUSIONS AND FUTURE DIRECTIONS

Our results suggest that native seed predators do not mediate apparent competition that promotes *Lonicera maackii* invasion. However, comparison of our work with other studies of *L. maackii* suggests that the role of seed predators may change with food availability and preference and across seasons and habitats. More concrete links need to be established between consumer presence/foraging activity, seed predation, and plant recruitment. Future studies that combine experimental seed additions with experimental manipulation of consumers, structure and food in habitats invaded by *L. maackii* to measure the full effects of mice on *L. maackii* and native plant recruitment would add valuable insight into understanding this system. Moreover, studies that explicitly evaluate the role of seed traits (*e.g.,* seed tissue quality) in affecting granivore preference would be useful for providing mechanisms capable of producing the strong species-specific differences we observed. Most importantly, our results suggest that the role of consumer-mediated interactions in the context of biological invasions may be highly context-dependent. Future studies capable of distinguishing the importance of ecological context in affecting consumer-mediated effects will be critical for gaining insight into the likelihood and severity of biological invasions.

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