

Apparent competition: an impact of exotic shrub invasion on tree regeneration

Scott J. Meiners

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Abstract Invasion of habitats by exotic shrubs is often associated with a decrease in the abundance of native species, particularly trees. This is typically interpreted as evidence for direct resource competition between the invader and native species. However, this may also reflect indirect impacts of the exotic shrubs through harboring high densities of seed predators—known as apparent competition. Here I present data from separate seed predation experiments conducted with two shrub species exotic to North America; *Rosa multiflora*, an invader of abandoned agricultural land, and *Lonicera maackii*, an invader of disturbed or secondary forest habitats. Both experiments showed significantly greater risks of seed predation for tree seeds located under shrub canopies when compared to open microhabitats within the same site. These results indicate the potential importance of indirect impacts of exotic species invasions on native biota in addition to the direct impacts that are typically the focus of research.

Keywords Exotic shrubs · Habitat selectivity · *Lonicera maackii* · North America · *Rosa multiflora* · Seed predation · Survival analysis

S. J. Meiners (✉)
Department of Biological Sciences, Eastern Illinois
University, 600 Lincoln Avenue, Charleston, IL
61920-3099, USA
e-mail: sjmeiners@eiu.edu

Abbreviations

DHNC Douglas-Hart Nature Center
HMFC Hutcheson Memorial Forest
Center

L. maackii *Lonicera maackii*
P. leucopus *Peromyscus leucopus*
R. multiflora *Rosa multiflora*

Introduction

The introduction and spread of exotic plant species is a major concern from both the perspectives of conservation and ecological theory. The spread of exotic plants is often associated with (1) declines in local plant diversity (Woods 1993; Hutchinson and Vankat 1997), (2) inhibition of forest regeneration (Woods 1993; Hutchinson and Vankat 1997) and (3) reductions in the productivity of agricultural land (Pimentel et al. 2000). In addition, invasions often accrue the financial costs of biological or chemical control (Pimentel et al. 2000). Despite the importance of invasions, ecologists have struggled to understand the impacts of these invasions on community structure and dynamics (Parker et al. 1999; Byers et al. 2002).

The impacts of plant invasions on communities are typically interpreted as the result of

competitive interactions (Fig. 1). Exotic species, particularly problematic invaders, are often very competitive and can lead to decreased populations of native species (D'Antonio and Mahall 1991; Hutchinson and Vankat 1997; Gould and Gorchov 2000). Experimental studies between mature plants often show the invading species to be competitively superior to natives, allowing many of these invaders to develop large, essentially monospecific stands (D'Antonio and Mahall 1991; Collins and Wein 1993; Hamilton et al. 1999).

However, not all interactions between exotic plant species and resident native species need be competitive. There is a growing body of evidence for indirect interactions between invaders and recipient communities, often mediated through the soil (Marler et al. 1999; Bever 2003). Food web theory provides another mechanism through which two species may develop a negative interaction mediated by a shared predator, known as apparent competition (Holt and Lawton 1994; Holt 1997). This interaction is possible whenever two plant species share common predators, herbivores or pathogens (Fig. 1). Typically, this is generated when the prey species together support a larger predator population than either alone, though effects on the two species may be quite asymmetric. Apparent competition is a common feature of food web studies (Holt and Lawton 1994), but also occurs among plants (e.g., Veech 2000; Sessions and Kelly 2002). The presence of apparent competition does not rule out the potential for direct competitive interactions between species, and both direct and indirect processes may function simultaneously to generate community structure.

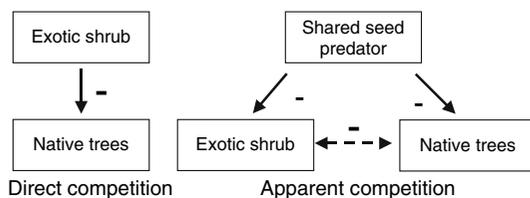


Fig. 1 Schematic drawing of the net interactions between exotic shrub invasion and native trees through direct resource competition (left) and apparent competition mediated by shared seed predators (right). Direct interactions are shown in solid lines and indirect in dashed

Seed predation commonly has strong impacts on the composition and dynamics of plant communities (Crawley 1992; Hulme 1993; George and Bazzaz 1999). As seed predators typically forage on a broad range of available seeds, many plants within the community share the same predators and therefore have the potential to exhibit apparent competition. However, seed predators do not typically utilize all available habitats and often selectively forage in areas which provide more food resources (Herrera et al. 1994) or which provide relatively safe environments in which to forage (Holl 2002). For these reasons, shrub cover, whether native or exotic, is often associated with increased levels of seed predation when in a more open matrix, (Hulme 1993; Hulme 1996; McCormick and Meiners 2000). In systems that have become heavily invaded by exotic shrubs, selective use of shrub cover may create areas of intense seed predation. This is particularly true when invasions occur in systems that typically lack a well-developed shrub layer. The compounding impacts of competition between trees and invading shrubs with reduced seed regeneration may together generate the declines in tree regeneration commonly seen in systems invaded by exotic shrub species.

Because most previous work has focused on direct interactions between exotic shrubs and tree establishment, I specifically focus here on assessing indirect interactions mediated through shared seed predators. In this study, I use seed predation experiments from two separate systems, a forest and a successional old field, invaded by different species of exotic shrubs to evaluate the potential for apparent competition between invading shrubs and tree seedlings.

Materials and methods

To test for an association between exotic shrub invasion and seed predation intensity, two separate seed predation experiments conducted in North America were analyzed. One experiment was carried out in a mid-successional old field in the Piedmont region of New Jersey invaded by *Rosa multiflora* (Meiners and LoGiudice 2003). The other was conducted in a young, closed-

canopy forest in east-central Illinois that was invaded by *Lonicera maackii*. Both of these shrubs are natives of western Asia which were actively introduced into North America and have become spread throughout a broad region (Hindal and Wong 1988; Luken and Thieret 1996). In areas of heavy invasion, both of these species form large monospecific stands which appear to inhibit tree regeneration.

Seed removal in open vs. shrub-dominated microsites was monitored in both experiments. These data were analyzed with Cox regression using SPSS 11.1 (SPSS Inc, Chicago, IL) to determine the impacts of shrubs on the relative risk of seed predation. Details of each study design are outlined below.

Rosa multiflora experiment

This study was conducted at the Hutcheson Memorial Forest Center (HMFC) near East-Millstone, NJ, USA (40°30' N, 74°34' W). The study site was a 1-ha portion of an abandoned agricultural field and the adjacent young forest. Herbaceous cover in the field was dominated by several species of *Solidago*, *Aster* spp. and *Fragaria virginiana* and contained scattered trees and shrubs including a few large *Juniperus virginiana* trees (Meiners and Pickett 1999). This site was invaded by scattered individuals and clumps of *Rosa multiflora*. The data presented here are a re-analysis of a portion of the data originally published in Meiners and LoGiudice (2003). To avoid confounding influences of changing habitat types, only the portion of the site within the abandoned agricultural field was used here. The dominant seed predators in fields of the HMFC are white-footed mice, *Peromyscus leucopus* (Manson and Stiles 1998; Meiners and LoGiudice 2003).

Acer rubrum was used as a test species for seed predation intensity. *Acer rubrum* is a common, wind-dispersed tree species in successional old fields of the area and a dominant species within second growth forest stands at HMFC. While *A. rubrum* is a spring-dispersing species, we used it as a prey item in the fall. Seeds of this species can be found on the ground and under leaf litter in the fall and are readily taken by predators at

that time (Myster and Pickett 1993; Meiners and LoGiudice 2003). The phenological difference allowed experimental seeds to be clearly identified without contamination from naturally dispersing seeds.

A 60 × 90 m grid was set up from the forest-old field edge towards the center of the field. Within this grid, seventy 1 m² plots were arranged in a regular pattern at 10 m intervals. This spacing of plots should ensure that predators were responding to local vegetation structure and not the presence of adjacent seed dishes. Also, patches of *R. multiflora* were relatively small, typically containing only one seed dish. Within each plot, a 90 mm petri dish was placed that contained 15 *Acer rubrum* samaras. Seeds were collected in the previous spring and stored under refrigeration until needed. The experiment was initiated in late October of 1996 and dishes were monitored on days 5, 10, 15, 20, 30, 40, and 50 to determine seed removal. To minimize seed loss from wind, rain and animal activity, a 30 cm radius around each dish was searched for missing seeds, and any located seed replaced. Seeds not found as remains or located within 30 cm of the dish were designated as removed by seed predators, which often cache seeds.

The percent cover of *Rosa multiflora* present in each 1 m² plot was recorded in June 1996 with the aid of a sampling frame. Plots were defined as being either open or shrub dominated when *R. multiflora* cover exceeded 25%. While the research site was still being invaded by *R. multiflora*, it was adjacent to extensive areas which had developed into dense monospecific thickets. Details of the vegetation of the site are presented in Meiners and Pickett (1999).

Lonicera maackii experiment

This study was conducted at the Douglas-Hart Nature Center (DHNC), Mattoon, IL, USA (39°29' N; 88°17' W). The site was a 13.4-ha mesic forest planted for conservation purposes in the late 1960s. Shortly after the center was established, *Lonicera maackii* was planted around the margins of the forest as food and cover for birds. The exotic shrub then expanded to dominate the forest understory. At the time of the

study, approximately 9 ha of the site were dominated by *L. maackii*. The site also contained populations of the native shrubs *Sambucus canadensis* and *Viburnum dentatum* in low densities. Similar to the NJ site, the dominant seed predators were white-footed mice, *Peromyscus leucopus*, but also included eastern chipmunks, *Tamias striatus* (T. A. Nelson, unpublished data).

In a heavily invaded, 20 × 50 m portion of the site, a series of ten, 5 × 5 m plots were established in the fall of 2001. A 2 m buffer area surrounded each experimental plot. Half of the plots were randomly assigned to have all *L. maackii* plants removed. The other five remained in *L. maackii* cover as control plots. Stems of all *L. maackii* within removal plots were cut and placed outside of the experimental area in September, 2001.

The influence of *L. maackii* on seed predation intensity was assessed 2–30 October, 2001. Dishes made of aluminum screening were placed on the soil surface and anchored with a galvanized nail. Five of these dishes were placed into each plot within the central 3 × 3 m of the plot. Into each dish, 10 *Fraxinus pennsylvanica* seeds were placed and monitored on days 2, 7, 14, 21, and 28 for seed removal as described above. This species was abundant in the forest canopy of the site and would represent a common food resource for foraging seed predators. The wing of each samara was clipped to reduce the likelihood of blowing out of the dish and to separate experimental seeds from those naturally dispersing.

Results

Despite being conducted in different systems invaded by different shrub species, these two experiments generated remarkably similar results. Both experiments indicated increased rates of predation in microsites dominated by exotic shrubs (Fig. 2). In both experiments a large proportion (56 and 31% for *Rosa* and *Lonicera*, respectively) of removed seeds were recovered as depredated remains, verifying predator activity. In all cases damage appeared consistent with small mammal predation (bite marks, fecal matter) though many seeds appeared to have been cached and removed whole.

In the *Rosa multiflora* experiment, 86% of all *Acer rubrum* seeds were removed by the end of 50 days. Cox regression indicated that the risk of predation in shrub-dominated plots was 64% higher than that of open plots (Wald Chi-square 44.2, 1 df, $P < 0.001$). The majority of predation occurred at the beginning of the experiment, suggesting that surviving seeds may have escaped predation. Predator behavior also differed between shrub and non-shrub plots. Seed dishes placed under shrub canopies tended to have complete seed removal during one sampling interval while seeds dishes placed in open microsites had seeds removed over an extended period of time.

Overall, predation intensity was much higher in the *Lonicera maackii* experiment than seen with *Rosa multiflora*. This area consistently had high population densities of *P. leucopus* (T.A. Nelson, personal communication). In the *L. maackii* dominated site, 74% of all *Fraxinus pennsylvanica* seeds were removed by the end of 28 days. The risk of predation in plots with intact exotic shrub canopies was 59% higher than in plots where

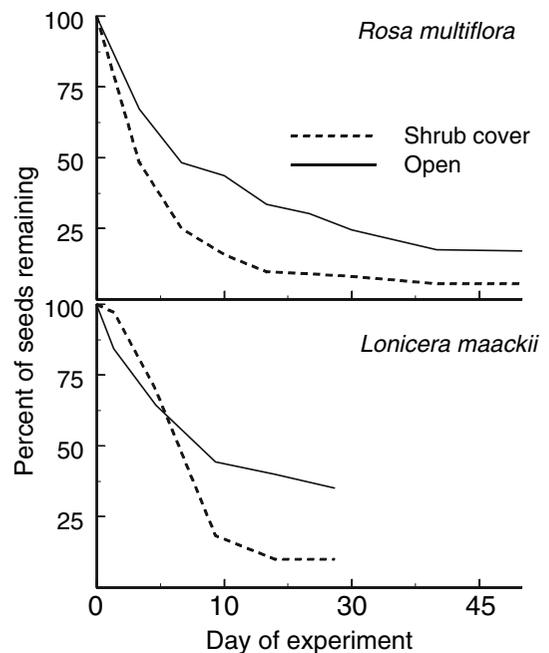


Fig. 2 Survival of tree seeds in shrub-dominated and open microsites in systems invaded by *Rosa multiflora* and *Lonicera maackii*

exotic shrubs had been removed (Wald Chi-square 19.4, 1 df, $P < 0.001$).

Discussion

Both research sites shared the same dominant seed predator, *Peromyscus leucopus*. This species is well known to preferentially forage in areas of high structural complexity, particularly under woody cover (Manson and Stiles 1998), which provides protection from avian and mammalian predators. Selective use of habitat by *P. leucopus* is thought to be the dominant factor that determines the spatial pattern of seed predation at HMFC (Manson and Stiles 1998) and would also be expected at DHNC. Despite documented preferential use of available habitat, these predators often utilize a variety of habitats (Pearson 1959) and foraging preferences may disappear in times of low food availability (McCormick and Meiners 2000). This flexibility in foraging selectivity probably resulted in the moderate removal of seeds from non-preferred habitats.

While the dominant seed predator in both of the experiments presented here was *P. leucopus*, the apparent competition documented in this study may well be found in other systems with other predators. The concentration of seed predator activity under shrubs is a relatively common phenomenon across many systems with many different mammalian seed predators (Hulme 1993; Herrera et al. 1994; Hulme 1996; Manson and Stiles 1998). Apparent competition between shrub invaders and native taxa should occur whenever there is a generalist seed predator that behaviorally selects to forage under shrub cover. Shrubs that produce non-preferred seeds or which do not provide protection from the seed predators' natural enemies should only show competitive interactions with regenerating trees. It is quite possible that this is a common phenomenon wherever shrubs, native or exotic, form dense canopies that provide seed predators with cover. Therefore, these indirect effects of shrubs on tree regeneration may arise in any system, though they may be more common with invasive species that tend to generate large, continuous stands and produce abundant seed crops.

Shrubs as a life form often combine rapid growth with competitive traits that allow them to rapidly colonize newly available habitats (Grime 2001). While these traits enhance their ability to capitalize on ephemeral opportunities for establishment in forested systems (e.g. gaps) they often put shrubs in direct competition with trees that may also rely on canopy disturbances for regeneration. Local enhancement of seed predation intensity may be the first in a series of challenges to tree regeneration (George and Bazzaz 1999). Those seeds that survive predation and make it to germination must then establish and grow under an established shrub and face direct competitive interactions (Gorchov and Trisel 2003). While the abundance of these exotic shrubs is often greatly reduced in shaded forest understories (Robertson et al. 1994; Luken and Goessling 1995), sufficient numbers of tree seedlings may not survive under these shrubs to eventually outcompete the opportunistic invaders. At low densities, shrub cover may even facilitate tree establishment by concentrating seed predator activity within limited microsites, providing safe sites for regeneration. As shrub cover increases within a site, the area in which seeds may escape predation becomes smaller, potentially leading to reductions in tree regeneration over large areas. Shrub invasions such as those of *R. multiflora* and *L. maackii* often generate large monospecific stands, particularly near forest edges where tree regeneration would also be the greatest. Therefore, the net influence of shrub invasion on forest regeneration should be negative in heavily invaded sites.

The interactions described here appear to be an example of asymmetric apparent competition, with the impacts falling primarily on the seeds of tree species. While seed predators would be consuming seeds of the shrub species (Drickamer 1970), these seeds would be unlikely to establish under the shade of a mature shrub (Robertson et al. 1994; Luken and Goessling 1995). In contrast, shade-tolerant tree species would have the opportunity to become established if they escaped predation. Once established, tree seedlings would be subjected to direct resources competition with the shrub (Gorchov and Trisel 2003). However tree seedling growth may not be reduced by the presence of the exotic shrubs studied here

(Meiners and Martinkovic 2002), and may even benefit from the protection from deer afforded by these shrubs (Meiners and Martinkovic 2002; Gorchov and Trisel 2003).

This and other studies indicate the need for focus on the more subtle impacts of plant invasions. These effects may be just as important as competitive or other direct effects but may be more difficult to detect. Plant invasions may generate a complex suite of changes within a system that will result in the net impacts seen within plant communities.

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