

Exploring indirect effects of biological invasions on native consumers and native seeds

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ABSTRACT

Invasive plants are important threats to biodiversity that impact natural ecosystems through both direct and indirect effects on communities. Although direct effects have been well-studied, little is known about the indirect effects of invasions. I hypothesized that invasive species may have indirect effects on native plants by impacting small mammal seed predators. I examined 1) the effect of an invasive shrub on changes in rodent foraging behavior due to changes in perceived predation risk by the rodent, and 2) the impact of rodent preference for invasive shrub cover on removal of native seed species in invaded areas. The first part of the study measured giving-up densities in foraging trays that varied in presence of an artificial cover in forest patches of high and low *L. maackii* density. I found significant changes in behavior and preference for artificial cover between high and low density habitats which co-varied with moon illumination, and concluded that rodents prefer to forage in areas with high *L. maackii* density because of lower perceived predation risk. This indicates that invasive shrubs do change rodent behavior. The second part of this study examined apparent competition effects between *L. maackii* and native plant species (*Cornus drummondii* and *Symporicarpus orbiculatus*) by measuring seed removal by rodents in the forest patches. I did not find a significant difference in seed removal rates across any of the effects that I examined. Slightly higher seed removal in high *L. maackii* plots might imply that rodents prefer those areas for protection from predation. However, native seed predation is not affected, possibly because the abundance of *L. maackii* seeds in the environment can supplement the rodents' diet. Instead of competitive interactions between native and invasive species, I concluded that *L. maackii* may provide a refuge for native seeds by supplying an alternative abundant food resource. I recommend further research be done to examine invasive plant and rodent seed predator interactions across different spatial and temporal scales so that indirect effects of invasions will be better understood.

CHAPTER 1: INTRODUCTION

Biological invasions

Invasive species can have important implications for the health of ecosystems. The invasion and spread of harmful species has increased in the past several decades because of human-caused introduction and disturbance (Elton 1958, Wilcove et al. 1998), and invasives are becoming key factors in global environmental change (Wilcove et al. 1998, Theoharides and Dukes 2007). Most biological invasions are detrimental, costing billions of dollars in repair and eradication (Pimentel et al. 2000) and causing unanticipated effects on native ecosystems (Elton 1958, Bazzaz 1984). A significant proportion of harmful invasives are plant species that escape from cultivation and become weeds, spreading at a rate of 680,000 ha each year in the United States (Babbitt 1998). Invasive plants can become established and spread throughout an ecosystem if they are repeatedly and intentionally introduced (Baker 1984, Sakai et al. 2001) or are favored by humans for their use as agricultural resources or for their aesthetic beauty (Pimentel et al. 2005). The effects of invasive plants are widespread. The establishment of an invasive plant species in an area can decrease plant diversity (Wilcove et al. 1998, Theoharides and Dukes 2007, Bazzaz 1984); inhibit forest regeneration; decrease agricultural yields; change the structure and function of communities and ecosystems; change the genetic, population, and community compositions of an area (Elton 1958, Bazzaz 1984, Vitousek 1984); and generally alter ecosystem properties (Vitousek 1990).

Direct and indirect effects of invasions

Ecosystem effects can be caused directly by the invasive species or indirectly, mediated through other species. Invasive plants can directly compete with native plants for nutrients, light, pollinators, seed dispersers, and space (Elton 1958). Many invasive species introduce “novel weapons” such as root exudates and toxins into ecosystems and compete by attacking native competitors (Theoharides

and Dukes 2007). These paths towards ecosystem domination can be complimented by natural advantages that make invasive species superior competitors, such as release from natural enemies that had co-evolved in their native habitats. Further success can come from indirect ecosystem effects, such as the development of new mutualisms with other native organisms that improve survival of the invading plant (Elton 1958, Theoharides and Dukes 2007, Vitousek 1984). The indirect effects of invasive plants on native species have been poorly studied in most systems.

Apparent competition

One example of an indirect interaction between invasive and native plants is apparent competition. Apparent competition is defined as the situation where the presence of one species leads to reduced density of another species, which includes competition, shared predation, and other indirect effects (Holt 1977). Apparent competition between native and invasive plants can occur if the invasive plant species changes predation pressure, reproductive allocation, or foraging behavior of consumers, resulting in larger effects on native plants (Holt 1977, Holt and Kotler 1987). This effect can occur because of structural changes in the forest that provide refuges for the consumer closer to the native plant (Meiners 2007, Orrock et al. 2008). This could lead to an increase in damage to native plants and could cause their eventual extirpation while providing the invasive species with an opportunity for range expansion (Meiners 2007). Apparent competition can vary in its effects on plant communities, and the effects can change over space. In one case involving a weevil introduced for biocontrol, native wavy-leaf thistles experienced more damage in closer proximity to the targeted invasive plant than when they were further away (Russell et al. 2007). This effect has also been demonstrated with native seed predators (Orrock et al. 2008). However, this could lead either to an overall decrease in population size of native plants and eventual extirpation, or to a regeneration opportunity due to the creation of a refuge for stands of native plants that are further

from the concentration of predators near the invasive plants (Meiners 2007). The magnitude and direction of the effect of apparent competition and its role in the facilitation of plant invasions is still unknown.

Rodent foraging behavior

Small mammal consumers can have far-reaching effects on ecosystems through interactions with seeds (Reichman 1979, Price and Reichman 1987). Consumers can have indirect effects on native plant communities that can help or hurt invasions (Pearson and Callaway 2008). Rodents in particular are well-known seed predators (Janzen 1971). Rodent seed predator abundance and distribution is highly dependent on food availability, but their foraging behavior is dependent on perceived risk of predation (Brown and Kotler 2004). Small mammals are at high risk of predation while foraging, so foragers often attempt to decrease direct and indirect predation costs to maximize fitness by minimizing risk per reward. This is often reflected in rodents through changes in microhabitat choice to adjust risk and returns (Brown and Kotler 2004, Manson and Stiles 1998, Stankowich and Blumstein 2005). Understanding these aspects of seed predator foraging behavior allows me to examine the effects of consumers on plant communities and invasions through apparent competition.

This paper

In this paper, I use the invasive shrub *Lonicera maackii* and the generalist seed predator *Peromyscus leucopus* to answer two questions: 1) does the invasive species alter rodent foraging behavior by providing a refuge from predators and 2) does seed removal differ between invaded and un-invaded areas in a manner that is consistent with the idea of apparent competition. Such studies on the indirect impacts of invasions are rare and therefore are not well-used in ecosystem

management (Theoharides and Dukes 2007, Pearson and Callaway 2008). By expanding knowledge of consumer and community interactions and developing a better understanding of the ways that invasive species alter natural habitats, there is a higher chance of detecting, preventing, or stopping negative effects of invasion before they become too detrimental.

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CHAPTER 2: *Lonicera maackii* alters *Peromyscus leucopus* foraging behavior by changing perceived risk of predation

Abstract: Invasive plants are important threats to biodiversity that affect communities through both direct and indirect effects. Indirect effects can be mediated through changes in the behavior of key consumers. I examined the effect of an invasive shrub, *Lonicera maackii*, on rodent seed predator foraging behavior due to changes in the risk of predation perceived by the rodent. I measured giving-up densities in foraging trays in forest patches of high and low *L. maackii* density. I experimentally manipulated the presence or absence of an artificial cover on foraging trays and predicted that rodents would have less of a preference for artificial cover in sites with high invasive shrub cover. I found significant changes in behavior and preference for artificial cover between high and low density habitats which co-varied with moon illumination. I concluded that rodents prefer to forage in areas with high *L. maackii* density because of lower perceived predation risk, indicating that the invasive shrub does change rodent behavior and may result in apparent competition effects with other species. I recommend that the causes and effects of changes in rodent foraging behavior be further examined in light of habitat modification by invasive species to uncover other potential interactions between these effects.

INTRODUCTION

Invasive plants

Invasive species are becoming increasingly prevalent in natural areas due to human disturbance and introduction (Elton 1958). In order to protect these areas we need to understand the direct and indirect mechanisms by which they affect native communities. Invasive plants are responsible for a significant amount of ecosystem damage caused by invasive species (Pimentel et al. 2005). Once established, invasive plants can compete directly with native plants for nutrients, light, pollinators, seed dispersers and space; or they can compete indirectly, for example, by causing structural changes to the environment or by forming novel relationships with other native organisms (Elton 1958, Vitousek 1984, Theoharides and Dukes 2007). For example, invasive plants can affect rodent behavior by changing forest structure and food availability in invaded areas (Meiners 2007, Orrock et al. 2008). This interaction could be significant if it led to changes in rodent abundance and altered

their impact on native plants as a result, an effect known as apparent competition (Holt 1977). Recent work suggests that apparent competition might be a mechanism through which invasive plants affect native plant communities (Meiners 2007, Orrock et al. 2008), but the link between invasive plants and rodents has not been well-studied.

Invasions and consumer behavior

Consumers can cause significant changes to community composition and are important for understanding plant communities (Meiners 2007, Pearson and Callaway 2008). Seed predators especially can decrease plant population sizes and viability and alter plant spatial distribution (Janzen 1971). Rodents are important seed predators in many ecosystems and have demonstrated top-down control of plant communities through seed consumption (Reichman 1979, Brown and Heske 1990, Heske et al. 1993). Consumers are also important prey for a variety of higher-level consumers. Higher-level consumers affect their prey by direct population reduction (consumption) or indirect trait-mediated interactions, with the latter usually having a higher impact on predator-prey interactions (Preisser et al. 2005). Rodents exhibit indirect trait-mediated interactions by changing foraging behavior to avoid high-risk situations (Stankowich and Blumstein 2005, Verdolin 2006). Since changes in foraging behavior have implications for rates of seed predation, these changes can affect plant communities (Janzen 1971).

Rodents often attempt to minimize predation risk by changing microhabitat choice and foraging in areas with dense shrub cover where they are more protected from mammal or avian predators (Verdolin 2006, Brown and Kotler 2004, Matlack et al. 2008). Indirect cues of predation risk, such as moon illumination, have also been shown to have significant effects on rodent foraging due to increases in perceived (Longland 1994, Orrock et al. 2004, Vasquez 1994) and actual predation risk

(Kotler et al. 1991). Perceived predation risk can be assessed by giving-up densities (GUDs) which measure the seed density at the point at which the reward for searching for the next food item in a patch with diminishing returns is not worth the risk of staying in the patch for the time required to find it. For rodent seed predators, this translates to lower GUDs in habitats near shrub cover (Brown and Kotler 2004). I hypothesized that rodents would treat habitats invaded by shrubs as refuges and forage to low GUDs due to lower perceived predation risk. This would suggest that invasive shrubs can change consumer foraging behavior by providing safety refuges from predators, which may result in increased predation pressure on native plants.

My study investigated how seed predator foraging behavior changes in environments invaded by shrubs. I compared giving-up densities of *P. leucopus* in un-invaded deciduous forest plots to those in plots that were invaded by *L. maackii* to determine whether *L. maackii* provides sufficient cover to change foraging behavior. At both high *L. maackii* density sites and non-invaded sites, I examined rodent choice between artificially covered protected trays and openly exposed trays. *Peromyscus leucopus* has demonstrated a strong preference for shrubby covered habitats during foraging in other studies (Meiners 2007, Matlack et al. 2008, Williams et al. 1992, Mason et al. 2001, Morris and Davidson 2000, Wolf and Batzli 2004) suggesting that they would prefer the artificially covered trays in open environments. I predicted that the mice would have less of a preference for artificial cover in densely-invaded sites that have high shrub cover.

METHODS

Study species

Lonicera maackii, or Amur honeysuckle, is a bush honeysuckle of the Caprifoliaceae family. It is native to China but has been established globally since the early 1900s as an ornamental plant and

food resource for many types of wildlife. It first appeared in the United States in 1897 and has been documented in 24 states in the eastern US (Trisel and Gorchov 1994, Luken and Thieret 1995). It is among the most abundant shrubs in many Midwest forests and invades forests that previously had no understory shrub layer (Collier et al. 2002). Presence of *L. maackii* has been correlated with decreased diversity, decreased growth of forest plant species (Collier et al. 2002, Hutchinson and Vankat 1997, Gould and Gorchov 2000, Gorchov and Trisel 2003, Miller and Gorchov 2004, Hartman and McCarthy 2007), and changes in forest structure (McEvoy and Durtsche 2004). *Lonicera maackii* has also been observed to have effects on herpetofauna (McEvoy and Durtsche 2004) and avifauna (Schmidt and Whelan 1999, Bartuszevige and Gorchov 2006). Its diverse effects on many species in the community and its competitive superiority make it a good study species for investigating indirect effects of invasions.

The white-footed mouse (*Peromyscus leucopus*) is an important prey, predator, and host for parasites in forests and old fields in the United States. Although *P. leucopus* relies on various food sources, tree and understory plant seeds comprise their main diet (Lackey et al. 1985). Studies examining fear and foraging behavior have established that rodents use many indirect cues to assess predation risk and make foraging decisions, including moonlight, weather, ground cover, canopy cover, and distance from vegetation (Manson and Stiles 1998). Further studies show that *P. leucopus*, among other species, seek refuge during and after foraging in shrubby rather than in exposed areas (Matlack et al. 2008), resulting in lower GUDs under cover (Meiners 2007, Brown and Kotler 2004, Matlack et al. 2008, Morris and Davidson 2000, Wolf and Batzli 2004, Manson and Stiles 1998). Invasive shrubs can 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). While predation of *L. maackii* seeds by *P. leucopus* has

never been examined, *Peromyscus maniculatus* has been shown to consume *L. maackii* seeds, but not with any significant effect on the invader itself due to the large quantity of seeds produced (Williams et al. 1992). This system may have significant consequences for native plant survival and biodiversity if *L. maackii* facilitates increased native seed predation by *P. leucopus* without being negatively affected itself.

Study sites

This study took place at August A. Busch Memorial Conservation Area, a multiple use wildlife reserve in St. Charles, Missouri, USA adjacent to the intersection of Interstate 64/40 and Highway 94. Twelve sites of mixed hickory-oak deciduous forest evenly distributed through the conservation area with variable densities of *L. maackii* were used in this study (figure 1). Six sites had very low *L. maackii* presence while the other six sites were naturally invaded by high densities of *L. maackii*. There were no signs of use of different management practices between sites that could introduce confounding variables into my analysis. Because all sites were used and managed similarly and because of observations of an advancing invasion front, I concluded that *L. maackii* was only absent from un-invaded sites because of its limited dispersal range, and it was likely to reach these sites in future years.

A 30 m by 30 m plot marked in the middle of each site was used for all observations. Plots were separated by a distance of at least 300 m. This distance is smaller than the approximate home range of *P. leucopus* (Lackey et al. 1985), so mice may have foraged at more than one site. To reconcile this, I compared trays within sites, instead of just between sites, to examine rodent choice. Habitat data included photosynthetic photon flux in micromoles/m²/sec as measured with an Apogee Quantum sensor held approximately 1 m above the ground, a second light measurement with the

sensor held at ground level, leaf litter quantified as the number of leaves pierced by a metal dissecting probe stuck into the ground, and number of *L. maackii* individuals greater than 1 m in height in a 1 m radius (table 1); these data were collected at twelve points in each plot.

Data collection

On 16 October 2008 two foraging trays were placed approximately one meter apart at each of the twelve study sites. Tray placement within the site was determined during a three-week pilot study in which areas with consistent foraging were identified. Trays were translucent white plastic buckets of height 16 cm and diameter 18 cm with two 5 cm by 5 cm holes cut opposite one another on the sides, approximately 3.5 cm from the bottom of the bucket to allow rodent access. Each bucket was filled with one liter of dried and sifted playground sand with one dram (~3.6 g) of shelled millet mixed homogenously throughout. A translucent white plastic lid was placed on each bucket to prevent seed predation by birds or seed loss from adverse weather conditions. One randomly chosen tray in each pair was then covered with a 95 L black plastic container to provide artificial protection to rodents foraging in that tray. The container was propped 5-7 cm off the ground with logs under the long side of the container closest to the other tray in the pair to allow rodent access to the tray.

Trays were left out overnight and checked for rodent foraging activity each morning. During each visit, seeds were sieved from the sand and collected for processing in the lab. Data was collected over two 4-day periods: 31 October-3 November, and 7-10 November 2008. On 3 November trays were recharged with millet to maintain rodent interest in the buckets when data was not being collected. Each time the trays were checked, signs of feces, digging, seeds on the surface, mold, spillage, and insects in the tray were recorded. The sand was returned to the tray and reloaded with millet thoroughly mixed into the sand.

In the lab, seeds were placed in a drying oven on 50°C for 12-16 hours, and then sifted again through window screening to remove any remaining sand. Any rocks or inorganic matter remaining were removed and discarded. Organic material, including arthropods, plant matter, and feces was removed. The remaining millet sample was massed on a scale to measure amount remaining after trays were open to rodent foraging. Ten control sample measurements were taken in the lab of the mass of 1 dram vials of millet for comparison purposes.

Government monitoring stations provided data on weather conditions and moon phase. Climate data including temperature maximum, minimum and average; total precipitation; cloud cover and weather conditions for each day were collected from the St. Charles, Missouri weather station operated by NOAA and obtained through the National Weather Service website (<http://www.weather.gov/climate/>). Data on moon phases and fraction of moon illuminated was obtained from the NOAA website (<http://tidesandcurrents.noaa.gov/astronomical.html>) and the US Navy website (http://aa.usno.navy.mil/cgi-bin/aa_moonill2.pl) respectively to examine covariance of moonlight on foraging activity.

Data analysis

Foraging tray data were examined using a repeated-measures mixed-model analysis of covariance (SAS Institute Inc. 2000-2004). The model treated presence or absence of artificial cover, *L*, *maackii* treatment, and week as fixed effects, and moonlight was evaluated as a covariate. Each experimental site was modeled as a random effect, treating site as the subject in a repeated-measures design and using compound symmetry as the structure for modeling covariance among observations taken at a site on different days. I only used sites with evidence of foraging activity for

analysis, excluding two high and four low *L. maackii* density sites with no activity at any point during the study. Analysis began using the most complex model (i.e. 4-way interaction of cover, *L. maackii*, week, and moonlight), removing interaction terms from the model if they were not significant at p-value > 0.15 (Littell et al. 1996). Weather and habitat data were analyzed by t-tests comparing variables over time (for weather) and *L. maackii* density (for habitat).

RESULTS

Characterizing foraging activity

I collected data on 192 observations from 12 sites over 8 non-consecutive days. The presence of foraging activity was determined by the observation of two out of three tray characteristics: 1) presence of rodent feces in the tray, 2) evidence of digging in the sand inside the tray, and/or 3) lack of seeds on the surface of the sand. Based on these criteria, there were 51 samples that experienced foraging activity and 141 that did not. A one-way ANOVA (R Development Core Team 2008) between the mean masses of foraged, non-foraged and 10 control samples showed a significant difference between the three groups ($df = 2$; $F = 203.12$; p-value < 0.001). Further t-tests showed a significant difference between the control and foraged groups ($df = 96.57$; $t = -13.68$; p-value < 0.001) and between the foraged and non-foraged groups ($df = 98.29$; $t = 13.46$; p-value < 0.001), but not between the control and non-foraged groups ($df = 30.20$; $t = -0.84$; p-value = 0.410). This indicates that judgment of presence or absence of foraging was accurate. Some foraging was observed on all eight days but spanned only six of the twelve original study sites (four high density sites and two with low *L. maackii* density). Fifteen out of 51 of the foraged trays were uncovered and 36 out of 51 were artificially covered.

Foraging behavior and L. maackii

Performing type three tests of fixed effects (SAS Institute Inc. 2000-2004) of the variables *L. maackii* density, tray cover, and week with moonlight as a covariant among only sites with foraging activity showed that none of these effects were significant on their own, but all were significant when tested as interactions with other variables (table 2). The interaction among *L. maackii* density, cover, and week ($F_{2, 23.6} = 3.08$, p-value = 0.065) appeared significant (alpha = 0.10) in the tests of fixed effects but showed almost no difference in trends between low and high *L. maackii* density plots, with the exception that the difference between covered and uncovered trays in week 2 was smaller in the low density plots than in the high density plots (figure 2). There were significant differences between weeks in average temperature (week 1 avg. = 13.48°C, week 2 avg. = 4.12°C, p-value < 0.001) and cloudiness (measured as proportion of night described as “overcast”; week 1 avg. = 0, week 2 avg. = 0.32, p-value = 0.003).

The interaction among *L. maackii* density, cover, and moonlight was significant in determining rodent preference for covered and uncovered trays ($F_{2, 26.8} = 3.71$, p-value = 0.038). I found no interaction between covered and uncovered trays as moonlight increased in the high density *L. maackii* plots, but there was an interaction in the low density plots (figure 3). In high density plots, *P. leucopus* foraged to lower GUDs in the covered trays, but their preference did not change with increasing moon illumination. In the low density plots, however, the uncovered trays showed the reverse trend, with GUDs increasing with moonlight, while covered trays showed decreasing GUDs as moonlight increased, as were seen in the high density *L. maackii* plots. For low density plots at lowest moon illumination, GUDs were slightly lower in uncovered trays; but at highest levels of moonlight, uncovered trays were essentially untouched while covered trays were foraged heavily.

Moonlight was also significant as a covariate in affecting foraging. In low (% illuminated = 0.13, df = 5.38, t-value = 0.52, p-value = 0.622) and medium (% illuminated = 0.43, df = 1.86, t-value = -2.04, p-value = 0.188) illumination, there was no significant difference between covered and uncovered tray GUDs. In high levels of moonlight (0.76), however, there was a strong preference for covered trays (mean GUD = 0.70) over uncovered trays (mean GUD = 2.61; df = 4.29, t-value = -3.18, p-value < 0.031). The adjusted means for the *L. maackii* treatment by cover interactions showed that mean GUDs varied from 1.70 to 2.70 for each combination of variables when moonlight is constantly low (0.13). When moonlight was high (0.76), the GUDs ranged from 0.5 across covered trays in high *L. maackii* density plots, and up to 3.46 for uncovered trays in low *L. maackii* density plots.

DISCUSSION

Invasive species have strong effects on ecosystems and are the second largest threat to endangered and threatened species in the United States (Wilcove et al. 1998). Despite an emphasis in the scientific literature on the direct effects that invasive plants have on ecosystems, indirect interactions between invaders and native species may also be important. I examined the effect of invasive shrub cover on rodent foraging behavior to see if invasive plants can have significant effects on animal behavior. My study showed that *L. maackii* does have an effect on rodent perceived predation risk and foraging behavior, which is mediated by other well-known anti-predator behavior cues.

Observed interactions

The interaction of *L. maackii* density and artificial tray cover on rodent foraging behavior was significant when coupled with other variables that were measured, though I did not find the two-

way interaction alone to have significant effects. In particular, I detected two separate foraging constraints that affected the rodents' perceived risk of predation: week and moonlight. Further analysis of week attributed its effects to temperature and cloudiness, suggesting that these factors were important in determining rodent choice between the covered and uncovered foraging trays in my plots of differing *L. maackii* density. I expect that the effect of temperature is stronger, resulting in lower foraging in week two, which was colder. This effect may also have interacted with cloudiness, as has been documented in other studies ((Orrock and Danielson *in press*) **in press**).

Moonlight had a strong affect on *P. leucopus* foraging patterns as has been documented for other rodent species in many other studies (Longland 1994, Orrock et al. 2004, Vasquez 1994, Kotler et al. 1991). Rodents in areas with high densities of *L. maackii* did not take the presence of an artificial refuge into account when calculating changing predation risk as it related to moonlight, while the rodents in areas with low *L. maackii* relied heavily on the presence of artificial cover in order to decrease predation risk when there was more moonlight. My data suggest that moonlight has a disproportionately large effect on rodent foraging choices, and that it interacts with habitat to affect foraging, consistent with the findings of other studies (Longland 1994, Orrock et al. 2004, Kotler et al. 1991, Mandelik et al. 2003). However, moonlight is a constantly varying effect for foraging rodents, while the structure of the forest habitat is less cyclical. Rodents are likely to be more adept at managing changing risk due to moonlight because it is a recurring pattern, and they have fluid behavioral patterns that allow them to adjust to that risk. Alternatively, drastic changes in habitat could imply gradual directional changes in rodent fitness by permanently altering anti-predator behavior as forest structure changed. Such effects would not only have effects on rodents themselves, but also higher-level predators that must respond to prey adjustments.

I estimate that the effect I observed is conservative because the lack of rodent foraging activity across sites resulted in small sample sizes and low statistical power of my tests. However, at sites where I did observe significant rodent foraging activity, the patterns verified my hypothesis that rodents would prefer artificial refuges more in areas without invasive shrub cover than in areas with shrub cover. I also observed a trend of decreasing GUDs over time, which may have been related to temperature or other abiotic factors which, along with moon illumination, were covariates in my model. I would expect the interactions between the effects measured to change depending on the time of the year when the study was conducted and other temporal factors. For example, rodents have been observed to have less consideration for predation risk when food resources are scarce (McCormick and Meiners 2000). Since my study was conducted in the late fall when natural food sources may have been less abundant, the mice may have been more willing to forage in riskier areas as long as they would be able to acquire food (White and Geluso 2007), which may have minimized the existing effect of *L. maackii* cover on rodent foraging patterns. Despite these other considerations, the significance of the interactions between the variables measured suggests that the invasive shrub does change rodent foraging behavior, making this system intriguing for further research.

Implications for rodents and invasions

Plants have been demonstrated to affect rodent behavior in past studies because of varying foliage profile structure (M'Closkey and Lajoie 1975) and diverse structural habitats (Mandelik et al. 2003, Veech 2001), which alter perceived and actual risk of predation during foraging (Price and Reichman 1987). Rodents have likewise been shown to affect plants, through seed predation (Brown and Heske 1990, Heske et al. 1993) which can result in apparent competition between plants (Veech 2001). I found that an invasive plant can affect the behavior of rodent seed predators

by confounding cues that lead to anti-predator behavior and affecting perceived risk of predation. This study is unique because I observed that moonlight, a feature commonly recorded to have an impact on rodent foraging, was affected by an uncommon feature, the presence or absence of an invasive plant. Based on my results, I conclude that *L. maackii* creates a novel shrub layer in forest ecosystems that serves as a refuge to decrease the rodents' perceived risk of predation while foraging.

The impact that *L. maackii* has on *P. leucopus* foraging patterns may be an indirect pathway through which *L. maackii* competes with native plants in forests that lack a native shrub layer. Since *L. maackii* can serve as a refuge that decreases perceived predation risk of *P. leucopus*, the mice may forage in disproportionately high densities under *L. maackii* cover, which may result in increased predation pressure on the native seeds that occur in invaded areas, the effect known as apparent competition (Meiners 2007, Orrock et al. 2008, Holt and Kotler 1987). By facilitating the suppression of native plant seed populations by local consumers, *L. maackii* could more easily invade further into ecosystems. My study supports other observations that rodent seed predators may have important impacts in invaded areas through apparent competition (Meiners 2007, Orrock et al. 2008). These and other indirect effects may be important in other ecosystems invaded by *L. maackii* or other invasive species that create new structural complexities.

Future studies

These effects may become increasingly important over time because of the increasing impact that human interactions are having on forest ecosystems and shrub cover. Habitat loss and degradation is currently the leading cause of the endangerment of species in the United States, affecting 85% of threatened or endangered species. Invasive species are the second biggest cause of species

endangerment (Wilcove et al. 1998). Research has further indicated that habitat degradation and invasive species have synergistic effects on biodiversity in a variety of different systems (Didham et al. 2007). If rodent foraging behavior is truly linked to plant invasions, as has been established in this and other studies (e.g. Meiners 2007), then rodents have the potential to affect or be affected by this interaction. As habitat degradation and invasions change forest structure, rodent foraging behavior is likely to change. Furthermore, as rodent foraging behavior changes, forest structure may be affected, which could lead to further invasion or habitat degradation. Continued study on rodent foraging patterns in light of changing landscapes can help quantify the net effects of these interactions on various factors of environmental change.

Further research into invasive shrub and consumer interactions is necessary to understand the indirect effects of invasive plants on natural ecosystems. Little research has been done on secondary effects of invasive species, though consumer-mediated competition with native plants has the potential to cause drastic changes in an ecosystem (Meiners 2007). Direct and indirect effects may have an additive impact on native areas, which would have important implications for the speed and extent of biological invasions. If the causes and effects of invasions can be determined, advances can be made to improve prevention and eradication techniques.

I also recommend that similar experiments with different focal species be repeated in a variety of microhabitats throughout different times of the year, as food availability, predation risk, habitat structure, human disturbance, degree of invasion and relative effect size could vary based on location and timing of these experiments. For example, *L. maackii* is considerably more noticeable in deciduous forests in the late fall when most other plants have lost their foliage but the honeysuckle still retains its leaves. Additionally, rodents may be more sensitive to changes in

predation risk if food resources are more abundant (McCormick and Meiners 2000). Temporally-variable effects are likely to be observed in other species as well, especially in temperate zones. Future studies could assess the effect of invasive species on higher level predators as well, to determine if there are more indirect interactions to be observed throughout various trophic levels. This study established a novel link between habitat, invasion and rodent behavior that would also be useful to examine in other ecosystems where plant invasion or rodents are persistent, for example, grasslands and deserts. Since control and management efforts for invasive species need to be habitat-specific (Luken and Mattimiro 1991), amassing more information about changes in ecosystem dynamics due to shrub invasion in a variety of different habitats will be practical for maintaining or restoring native plant communities.

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Table 1: Average differences in habitat characteristics in plots with high or low densities of *Lonicera maackii*. Six high and six low density sites were used. Values are mean \pm one standard deviation; p-values from a two sample t-test with df = 10. *** Indicates a significant difference between high and low density sites.

Table 2: Type 3 tests of fixed effects for rodent GUDs in foraging trays at sites that experienced foraging activity only (four high and two low *L. maackii* sites), n = 73 foraged tray-nights. * Indicates interaction between two effects.

Figure 1: Map of August A. Busch Memorial Conservation Area in St. Charles, Missouri, USA. White squares mark 30 m by 30 m plots with low *L. maackii* density and black squares mark plots with high *L. maackii* density. Shaded areas correspond to *L. maackii* density in forest patches with darker areas representing higher density.

Figure 2: Effects of week and artificial cover on giving-up densities in foraging trays in high and low *L. maackii* density plots. Week 2 had more cloud cover and lower temperatures. Results are based on mixed model analysis of covariance (table 2). Means and standard errors are shown.

Figure 3: Effects of moon illumination and artificial cover on giving-up densities in foraging trays in high and low *L. maackii* density plots. Results are based on mixed model analysis of covariance (table 2). Means and standard errors are shown.

Table 1

	High density (n=6)	Low density (n=6)	p-value
Average # of <i>L. maackii</i> stems in a 1m radius	2.64 ± 0.96	0.03 ± 0.07	0.001***
Average light intensity at 1m above ground (μmoles/m ² /sec)	81.46 ± 58.12	93.94 ± 41.42	0.678
Average light intensity at ground level (μmoles/m ² /sec)	37.81 ± 14.75	68.46 ± 54.99	0.238
Average number of leaf layers on ground (litter)	0.81 ± 0.33	1.10 ± 0.30	0.139

Table 2

Effect	Num DF	Den DF	F-value	p-value
<i>Lonicera maackii</i> treatment	1	8.32	0.24	0.638
cover	1	11.3	1.53	0.241
week	1	2.91	0.22	0.673
moonlight	1	11.0	2.34	0.154
<i>Lon.</i> treatment*cover	1	11.3	4.19	0.065
cover*week	1	22.4	9.48	0.005
moonlight*cover	1	26.5	8.82	0.006
moonlight*week	1	10.1	2.85	0.122
<i>Lon.</i> treatment*cover*week	2	23.6	3.08	0.065
moonlight* <i>Lon.</i> treatment*cover	2	26.8	3.71	0.038

Figure 1

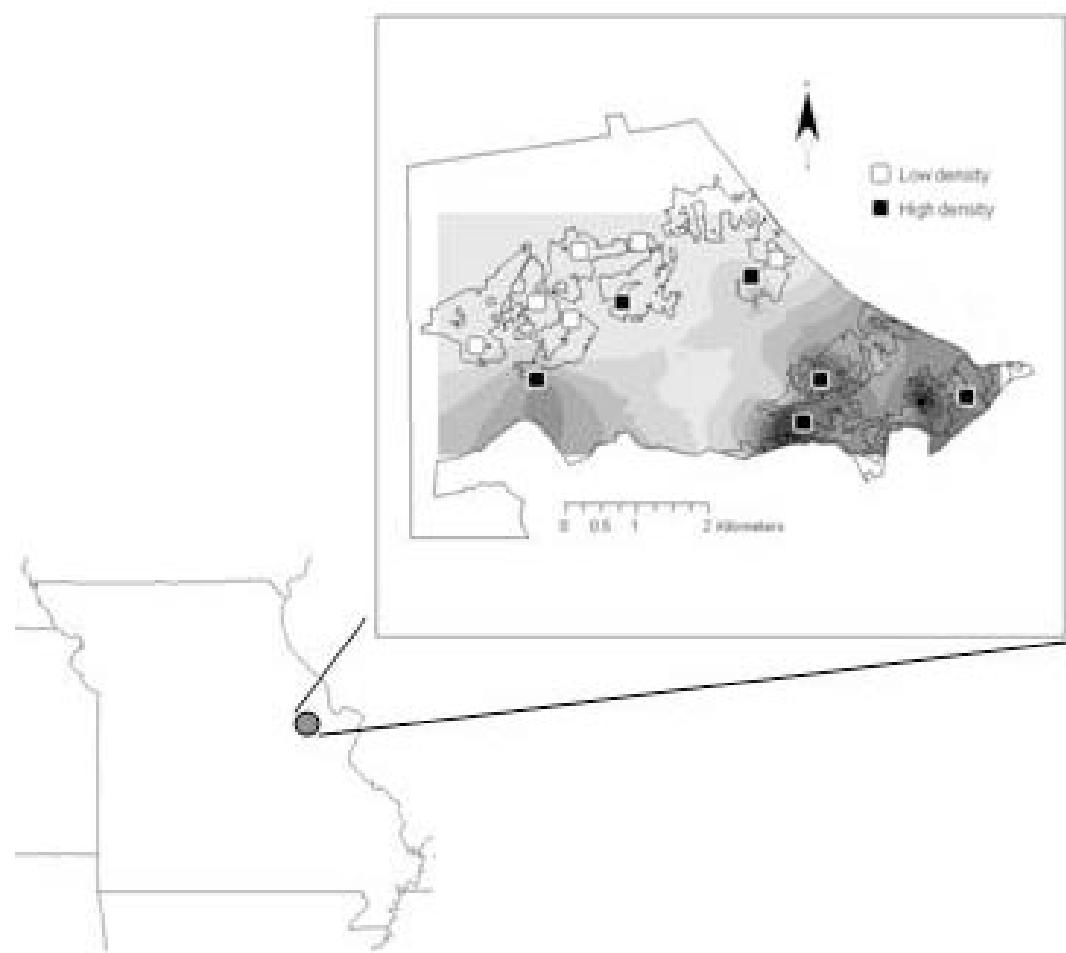


Figure 2

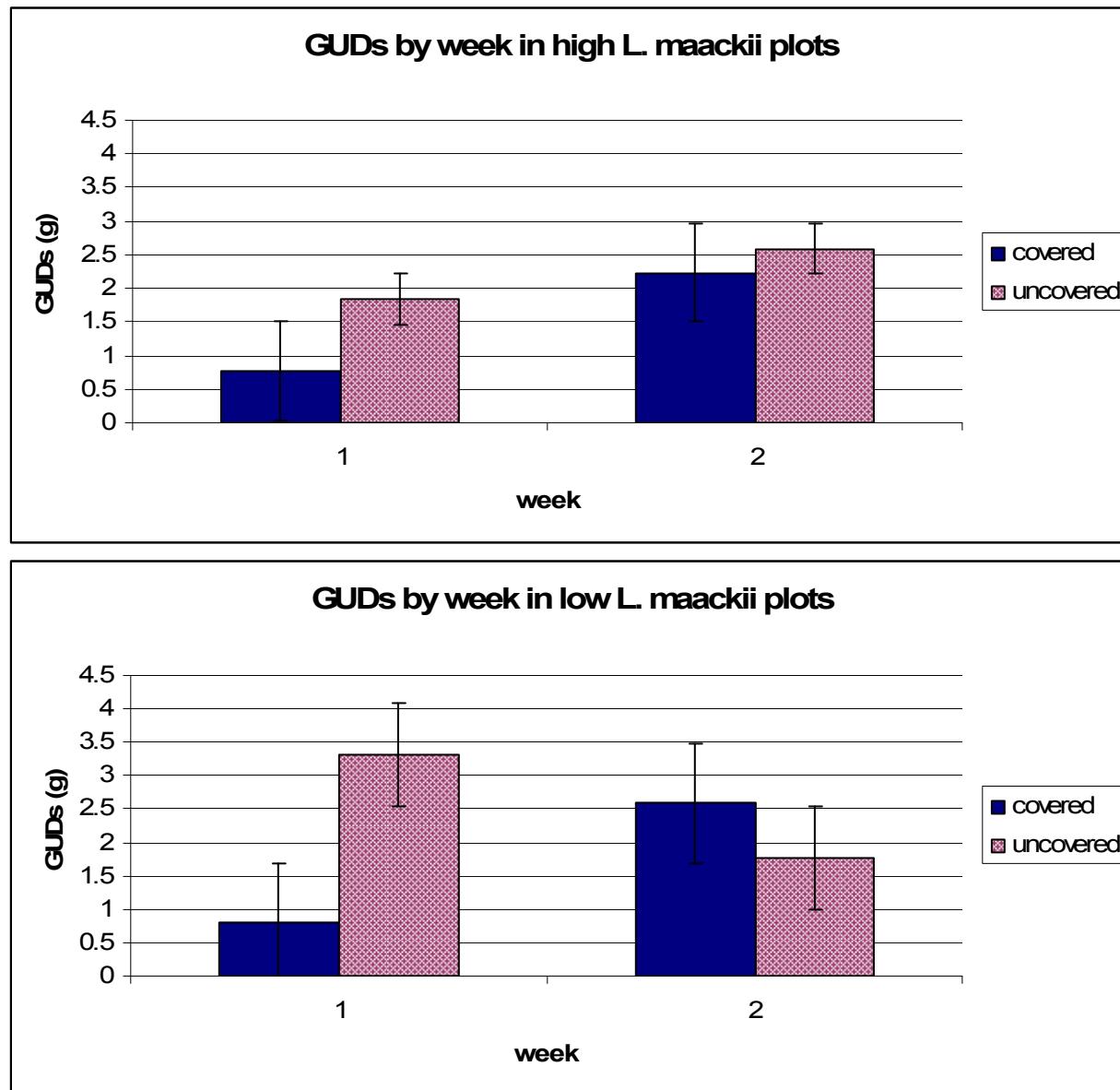
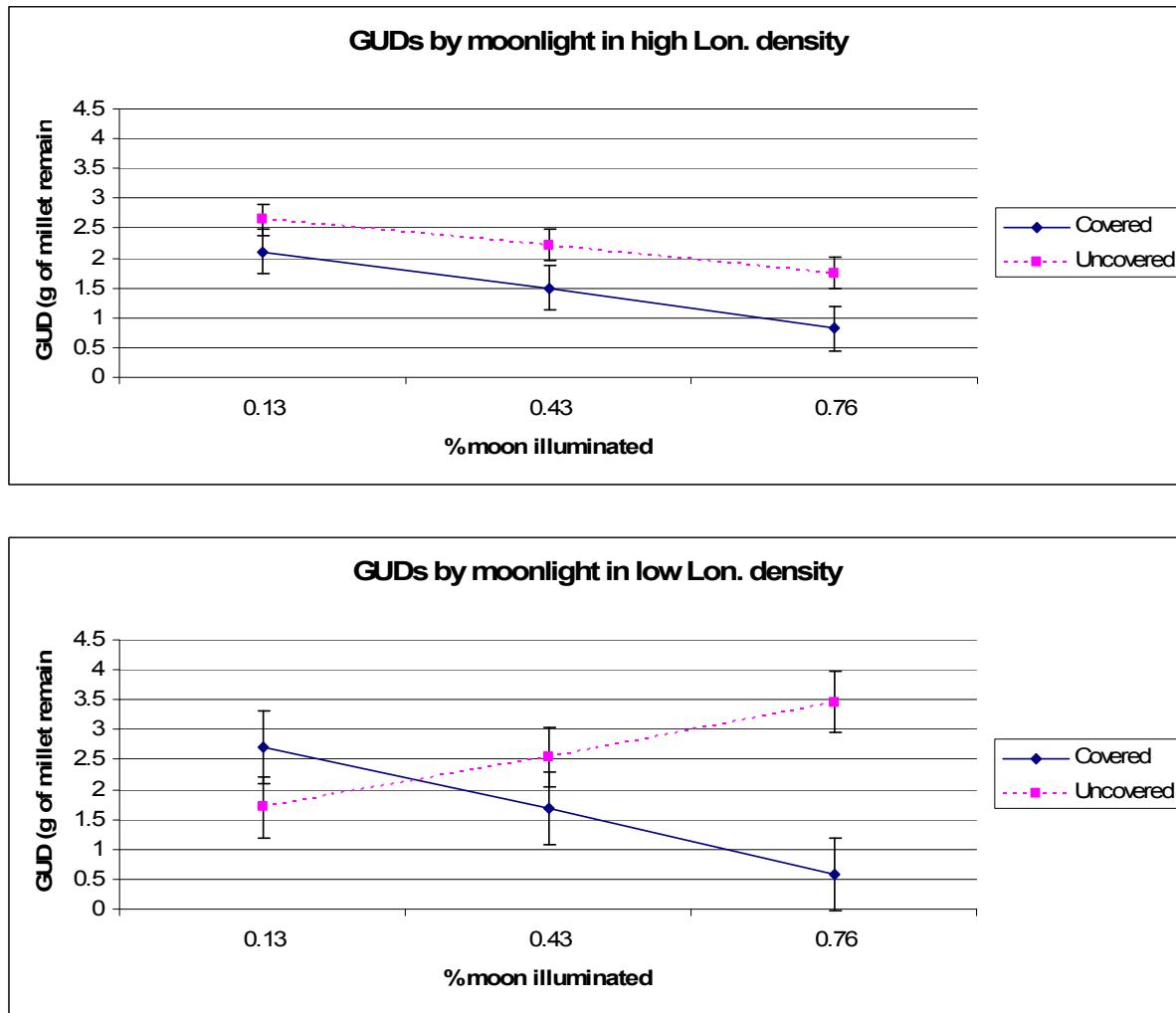


Figure 3



CHAPTER 3: Seed removal of native and invasive species and evidence for invasive-mediated apparent competition

Abstract: Invasive plants threaten biodiversity and impact natural ecosystems through both direct and indirect effects on communities. Although direct effects have been well-studied, little is known about the indirect effects of invasions. This study looked at the indirect effect of apparent competition, when one species changes the survival and recruitment of another by changing pressure of predation by a key consumer. I examined apparent competition effects between the invasive shrub *Lonicera maackii* and native plant species (*Cornus drummondii* and *Symporicarpos orbiculatus*) by measuring seed removal by rodents in forest plots that had low or high densities of *L. maackii*. I did not find a significant difference in seed removal rates across any of the effects that I examined, although seed removal was slightly higher in high *L. maackii* plots. *C. drummondii* experienced twice as much predation in high *L. maackii* density plots, but the difference was not significant. Since mouse behavior has been found to change with the presence of *L. maackii*, this may mean that more mice are foraging in invaded areas but their effects on native seeds have been offset by their effects on the invasive seeds in the environment. Instead of competitive interactions between native and invasive species, I concluded that *L. maackii* may provide a refuge for native seeds by supplying an alternative abundant food resource to the rodents that it attracts by providing shelter. Low predation was observed overall due to a large variance in predation across sites. This study demonstrated the spatial heterogeneity of seed predation that may be influenced by habitat characteristics such as the presence of an invasive species. The indirect effects of invasions and the density-dependent effects of seed removal may have important implications in other ecosystems. We recommend that further seed removal studies be conducted that span longer time periods to account for predation risk throughout the period of vulnerability for the seed and to measure temporally varying interactions between invasive species and seed predators.

INTRODUCTION

Biological invasions

Understanding the ecosystem implications of invasive species is important because of increases in human-caused introduction and spread of a variety of invasive organisms (Elton 1958) and because of the connections that invasive species have with global environmental change (Wilcove et al. 1998, Theoharides and Dukes 2007). Harmful invasive species can cost billions of dollars worth of

damage and environmental effects (Pimentel et al. 2005), and their impacts on ecosystems are widespread and possibly underestimated (Vitousek 1990). For example, in the United States, over 50% of species classified as endangered and threatened are at risk because of the effects of invasive species (Wilcove et al. 1998). Invaders can have direct or indirect impacts on native plant species (Elton 1958). While direct effects, such as resource competition, are well-documented and better understood, indirect effects have rarely been examined. One indirect effect, the presence of one species leading to a reduced density and population size of another species through shared predator effects, is termed apparent competition (Holt 1977). The role of apparent competition in plant invasions is not well known.

Seed limitation and predation

Invaders can affect native ecosystems through apparent competition by changing the predation pressure by consumers, and therefore decreasing native plant recruitment by increasing relative rates of seed loss (Meiners 2007, Orrock et al. 2008). Quantifying seed loss is important because seeds have a direct effect on plant recruitment, and plants exposed to seed predators can be extirpated quickly compared to those that face threats at other stages in their life cycle (Janzen 1971, Hulme 1998). Many seed limitation studies (reviewed in Turnbull et al. 2000) have found that seed additions do not lead to higher seedling densities, suggesting that plant recruitment is not always limited by low seed arrival at a site, but by post-arrival mortality. This may indicate that seed predators have a high influence on seed mortality and could decrease seedling abundance (Orrock et al. 2006), especially in populations that are not at the carrying capacity of the microhabitat (Clark et al. 2007). Therefore, if the density of seed predators changes over time or space, relative plant abundances are also likely to change (Janzen 1971). Invasive plants, especially

shrubs, have the ability to increase seed predator density by providing refuges that decrease the consumers' risk of predation while they forage (Meiners 2007, Orrock et al. 2008).

In this paper, I evaluate apparent competition as an indirect mechanism that decreases native plant recruitment and facilitates plant invasions. I examined the removal of seeds of native and invasive plant species by white-footed mice (*P. leucopus*) in areas that were differentially invaded by the shrub, *Lonicera maackii*. *Lonicera maackii* is a Eurasian invasive shrub that is present throughout the eastern United States (Luken and Thieret 1996). Previous studies on the indirect effects of *L. maackii* suggest that apparent competition may be an important mechanism by which *L. maackii* invades ecosystems due to differential predation of native seeds in invaded areas (Meiners 2007). However, apparent competition assumes differential removal of native and invasive seeds, and the removal of *L. maackii* seeds by rodent seed predators has never been quantified in this context. In order to determine the effect of apparent competition in invasions, seed removal studies must show that higher rates of predation occur in invaded areas for native seeds only, while invasive seeds do not experience increased consumption. The study described below filled this gap by quantifying removal of native (*Cornus drummondii* and *Symporicarpos orbiculatus*) and invasive (*L. maackii*) seeds in habitats that have and have not been invaded by the shrub to understand the role that apparent competition plays in decreasing native plant recruitment.

METHODS

Study species

Lonicera maackii, or Amur honeysuckle, is a bush honeysuckle of the Caprifoliaceae family. It is native to China but was established globally by the early 1900s as an ornamental plant and food resource for many types of wildlife. It first appeared in the United States in 1897 and has been

documented in 24 states in the eastern US (Trisel and Gorchov 1994, Luken and Thieret 1995). It is among the most abundant shrubs in many Midwest forests and invades forests that previously had no understory shrub layer (Collier et al. 2002). Presence of *L. maackii* has been correlated with decreased diversity and growth of a variety of forest plant species (Collier et al. 2002, Hutchinson and Vankat 1997, Gould and Gorchov 2000, Gorchov and Trisel 2003, Miller and Gorchov 2004, Hartman and McCarthy 2007) and changes in forest structure (McEvoy and Durtsche 2004). *L. maackii* has also been observed to have effects on herpetofauna (McEvoy and Durtsche 2004) and avifauna (Schmidt and Whelan 1999, Bartuszevige and Gorchov 2006). Its diverse ecosystem impacts and competitive superiority make it a good study species for studying indirect effects of invasions.

Cornus drummondii (rough-leaved dogwood) and *S. orbiculatus* (coralberry) are both forest shrubs that occur naturally in my study area. These species were chosen because they were similar in structure to *L. maackii*, and they were fruiting at the same time as the invasive species.

Symporicarpos orbiculatus is a member of the honeysuckle family Caprifoliaceae, along with *L. maackii*, although their seed morphologies are very different. *Lonicera maackii* seeds are thin and flat while *S. orbiculatus* seeds are much smaller and rounder. No previous seed removal studies were found using *S. orbiculatus*. *Cornus florida* has been the subject of prior seed removal studies (e.g. (Myster and Pickett 1993, Kwit et al. 2004)), though very few studies examine removal of *C. drummondii*. This study was the first of its kind to examine rodent predation of these two important shrub species.

Study sites

This study took place at August A. Busch Memorial Conservation Area, a multiple use wildlife reserve in St. Charles, Missouri, USA adjacent to the intersection of Interstate 64/40 and Highway

94. Twelve sites of mixed hickory-oak deciduous forest evenly distributed through the conservation area with variable densities of *L. maackii* were used in this study (figure 1). Six sites had very low *L. maackii* presence while the other six sites were naturally invaded by high densities of *L. maackii*. There were no signs of use of different management practices between sites that could introduce confounding variables into my analysis. Because all sites were used and managed similarly and because of observations of an advancing invasion front, I concluded that *L. maackii* was only absent from un-invaded sites because of its limited dispersal range, and it was likely to reach these sites in future years.

A 30 m by 30 m plot was marked in the middle of each site and all observations took place within this plot. Plots were separated by a distance of at least 300 m. Habitat data included photosynthetic photon flux in micromoles/m²/sec as measured with an Apogee Quantum sensor held approximately 1 m above the ground, a second light measurement with the sensor held at ground level, leaf litter quantified as the number of leaves pierced by a metal dissecting probe stuck into the ground, and number of *L. maackii* individuals greater than 1 m in height in a 1 m radius (table 1); these data were collected at twelve points in each plot.

Seed collection

Seeds of *L. maackii*, *C. drummondii*, and *S. orbiculatus* were used in this experiment. All seeds were collected from fruits of naturally occurring plants from throughout August A. Busch Memorial Conservation Area in October and November 2008. Seeds were removed from the fruits, washed clean of pulp and allowed to air-dry for several days. Seeds were stored at room temperature until placed out in the field.

Data collection

On 17 November 2008 six seed removal trays were placed in three pairs at each of the twelve study sites. Each seed removal tray was a translucent white plastic bucket measuring 18 cm in diameter and 12 cm high with two 5 cm by 5 cm holes cut opposite one another on the sides approximately 2 cm from the bottom of the bucket to allow rodent access. Both access holes on one bucket of each pair were fixed with one 8 cm by 8 cm piece of 1 cm metal hardware cloth on the inside and outside of the bucket connected by a metal wire twisted to secure the hardware cloth. These served as rodent excluders so that the effect of rodent seed removal could be quantified and isolated from total seed removal which included arthropod activity. The other bucket had access holes that allowed both arthropod and rodent entrance. Each bucket was filled with 400 g of dried, sifted fine sand; 10 *L. maackii* seeds, 10 *C. drummondii* seeds, and 10 *S. orbiculatus* seeds were placed on the surface of the sand. A white plastic lid was placed on each bucket to prevent seed predation by birds or seed loss from adverse weather conditions.

The three pairs of trays were placed in a triangle in the center of the each plot approximately 6 m apart, with less than 1 m between each tray in a pair. Trays were left out for thirty days to allow consumer access to seeds. This duration is comparable to some seed removal studies (Meiners 2007, Plucinski and Hunter 2001, Meiners and LoGuidice 2003) but longer than many studies (Myster and Pickett 1993, Mittelbach and Gross 1984, Webb and Willson 1985, Willson and Whelan 1990, Hulme and Hunt 1999). The sites were checked twice during this period, on 24 November and 5 December to record raccoon disturbance. If trays were disturbed they were set upright and any sand and seeds that could be located were replaced. The disturbance was also recorded for reference during data analysis.

On 17 December 2008 the seed removal trays were collected from the field sites. In the lab, the sand/seed samples were dried in a drying oven at 30°C for 24 hours. The six samples that were still wet were left for approximately 24 more hours. The samples were then sifted through window screening to separate the sand from the seed samples. Any remaining rocks or inorganic material was discarded and any arthropods, feces, plant debris or other organic material was collected and preserved for future analysis. Seed predation at each tray was then quantified into number of seeds of each species that were left intact in the tray and approximate number of depredated seeds represented by remains. Notes were made if arthropods, rodent feces or non-study species of seeds or berries were in the tray.

Data analysis

Data were analyzed using SAS software (SAS Institute Inc. 2000-2004) to examine seed removal in areas with high or low *L. maackii* invasion using an analysis of variance general linear model. The model treated exclusion of rodents, *L. maackii* cover, and seed species as fixed effects and each of the twelve sites as a random effect. Proportion of seed removed by rodents was calculated by subtracting the number of seeds left in trays where both arthropods and rodents had access from the number of seeds left in trays where only arthropods had access and dividing by ten. Data from one high and one low density site were discarded because of severe raccoon disturbance at the sites.

RESULTS

Seed removal including rodents and arthropods

Of the 72 trays that were used in this experiment, 41 experienced some kind of foraging activity. Twenty-one of the foraged trays were in high *L. maackii* plots and nineteen were in low *L. maackii* plots. When seed removal in all trays was analyzed (table 2), only seed species identity had a

significant effect on determining amount of removal ($F_{2,32} = 3.55$, p-value = 0.041) with *C. drummondii* having higher proportions remaining (mean = 0.90) than both *S. orbiculatus* (mean = 0.85) and *L. maackii* (mean = 0.85). Proportion of seeds remaining was approximately equal across *L. maackii* treatments (high *L. maackii* mean = 0.84, low *L. maackii* mean = 0.89, $F_{1,8} = 0.31$, p-value = 0.590). Although the interaction of *L. maackii* treatment and species was not significant ($F_{2,32} = 1.37$, p-value = 0.268), there was an effect of species on removal when the low *L. maackii* treatment trays were examined alone (linear contrast, *L. maackii* treatment by species, treatment = low, $F_{2,32} = 4.48$, p-value = 0.019). The effect of species was also found to be significant in the interaction of rodent exclusion and *L. maackii* treatment in low *L. maackii* densities only when both mice and arthropods had access to the trays ($F_{2,32} = 6.06$, p-value = 0.006). The effect of rodent exclusion was not significant ($F_{1,8} = 4.05$, p-value = 0.079), though a much higher proportion of seeds remained in trays with arthropod access only (mean = 0.96) than in trays with rodent and arthropod access (mean = 0.77). I explored this effect further by examining seed removal by rodents alone after accounting for and removing arthropod removal effects.

Rodent seed removal alone

Despite observed differences in proportions of seeds removed by rodents in the high and low *L. maackii* density plots, there was no statistically significant difference in rodent seed removal between the two treatments ($F_{1,8} = 0.09$, p-value = 0.776, table 3). A higher proportion of seeds was removed by rodents in high density *L. maackii* plots than in low density plots (proportion removed in high density = 0.24, proportion removed in low density = 0.18), but the difference was not significant. Although *Lonicera maackii* and *S. orbiculatus* still appeared to have slightly higher proportions of seeds removed than *C. drummondii* overall (*L. maackii* = 0.22.0, *S. orbiculatus* = 0.22, *C. drummondii* = 0.19), the proportions of each species removed were not statistically

significant ($F_{2,16} = 0.51$, p-value = 0.608), and the interaction of *L. maackii* density and species was not significant ($F_{2,16} = 1.68$, p-value = 0.217). However, I note that *Cornus drummondii* experienced removal rates that were on average twice as great in high density plots (proportion removed = 0.26) than in low density plots (proportion removed = 0.12; figure 2). The lack of statistical significance in removal rates across species is the result of large variation in removal between sites (as shown by the error bars, figure 2).

DISCUSSION

Apparent competition is one indirect interaction between plant species that may have a role in promoting biological invasions. This effect has the potential to devastate native plant communities by causing seed predators to focus on areas under invasive shrub cover, destroying seed banks and recruitment opportunities of native plants. My study measured seed removal rates of native and invasive seed species to determine whether there was differential removal based on the state of invasion of the habitat where the rodents foraged. I did not find a significant difference in removal in invaded versus un-invaded habitats, which suggests that apparent competition between the study species is not taking place in the system I examined.

Invasive shrub effects on seed removal

Most of the removal I observed was due to rodent, and not arthropod, foraging; other measured effects, such as discrimination by seed species in low *L. maackii* habitats, were therefore considered in light of rodent effects. I observed slightly higher removal in high density plots although the results were not significant, suggesting that there is no effect of *L. maackii* density on seed removal by rodents overall. Individually, all three species experienced lower removal in the high *L. maackii* density plots, with *C. drummondii* experiencing the most drastic difference. Although *L. maackii*

specifically did not have a significant effect, I did observe general spatial heterogeneity in proportions of seed removal across sites.

My results indicate that seed removal may be slightly higher overall in high *L. maackii* density areas, although seed predators only appeared to discriminate by one species, *C. drummondii*.

Cornus drummondii was the largest of the three species that I used in my removals (approx. 0.4 cm compared to *L. maackii* = 0.2 cm and *S. orbiculatus* = 0.1 cm), which suggests that rodents may prefer it as a food source (Mittelbach and Gross 1984, Chambers and MacMahon 1994) and that arthropods may be less likely to choose it (Janzen 1971). Since removal of *C. drummondii* was twice as high in invaded areas as in un-invaded areas, it is possible that *L. maackii* does induce changes in rodent behavior and foraging patterns, with the increased seed predation pressure being focused on *C. drummondii*. I can conclude that *L. maackii* is having an impact on rodent consumption of different seed species, but removal is not higher for native seeds versus invasive seeds, so apparent competition is not occurring.

The presence of slightly higher foraging in trays in areas invaded by *L. maackii* may indicate rodent preference for these areas because they provide refuges from predation pressure. Since rodents generally prefer to forage under shrub cover, and un-invaded sites in my study have few natural shrubs, *L. maackii* may have provided the necessary habitat. However, I did not observe a significantly higher proportion of seeds consumed in invaded areas, suggesting that the invasive shrub may change rodent foraging patterns without having an effect on native or invasive seed species. This could be explained by the presence of food sources in the surrounding environment that could reduce the need for rodents to forage out of the trays. For example, *L. maackii* has been shown to have very high berry and seed output and be a good food source for rodents (Williams

1999). Although there may be more nutritious seed species available, the abundance of *L. maackii* seeds in invaded environments may compensate for its proposed lower nutritional value (Williams et al. 1992). Since my study was conducted in winter when other resources are scarce and rodents rely on seeds for a larger proportion of their diet (Kollmann et al. 1998), rodents may have been attracted to highly invaded areas for the abundant food sources, in addition to the predation refuge. More information about the distribution of rodents across my sites, the temporal variation in their foraging patterns, and naturally-occurring seed densities in invaded and un-invaded areas would help to better identify the effects I observed.

Spatial heterogeneity of removal

My results indicated general spatial heterogeneity in seed predation which may have reduced the significance of measured effects. Spatial variation in rodent foraging activity and seed predation is frequently observed and can be attributed to micro-habitat (e.g. Matlack et al. 2008), macro-habitat (Verdolin 2006), geographic area (e.g. Hulme 1998), seed density, seed distance from parent plants (Janzen 1971), and interactions with other species (e.g. Orrock and Danielson 2004). While I did not find that *L. maackii* contributes significantly to the observed spatial heterogeneity, there are likely to be other variables that this study did not measure that are causing or confounding my results. Further analysis of the surrounding habitat that examines other site characteristics would be useful for further analysis.

Implications for seed survival

This analysis contrasts with the conclusions of Meiners' 2007 study on apparent competition by rodents in areas invaded by *L. maackii* (Meiners 2007). Meiners found that rodent predation of a single native tree species increased under *L. maackii* cover, concluding that *L. maackii* caused

asymmetric apparent competition that impacted the native but not the invasive species. My research concurs with Williams' 1999 study that shows that rodents will consume *L. maackii* (Williams 1999), indicating that the interaction is not asymmetric. This could suggest that rodent choice is based on the encounter rate of different food items. Density-dependent seed predation effects have been observed by Martinez-Garza et al. in 2004 where the presence of small mammal or bird seed predators obscured the effects of inter- and intra-specific competition between plants because predators chose one seed species to preferentially consume (Martinez-Garza et al. 2004). My data imply that, contrary to the competitive interactions I hypothesized, *L. maackii* presence may provide a refuge for native seeds by supplying an abundant alternative food source. Although this implies higher pressure and lower recruitment for *L. maackii* itself, studies of seed removal of other species have shown that plants can have high seed and seedling survival (Beckage and Clark 2005) and colonization (Boman and Casper 1995) despite predation pressures, and *L. maackii* has proven to be a superior competitor in many ecosystems (Collier et al. 2002, Luken and Goessling 1995). Further work indicates that seeds dispersed near conspecifics have a low likelihood of survival due to intra-specific competition (Kwit et al. 2004), so rodents may be focusing predation pressure on seeds that were already unlikely to survive. This hypothesis can also hold true for heterospecific seeds that share predators and resource demands, but this may, again, depend on relative densities (Kwit et al. 2004).

This study observed very low levels of seed removal when compared to relative rates of removal from other studies, which resulted in the low power for my tests. Many studies in similar forest systems lost 90% of seeds over the entire experiment (Meiners 2007, Plucinski and Hunter 2001, Moore et al. 2007). Removal for *Cornus florida* in other studies has ranged from 40-95% over the life of the study (Myster and Pickett 1993, Kwit et al. 2004). Seed removal in my study may have

been low because of the weather and cold temperatures experienced during the study, including several snowfalls. Rodents consume the smallest number of seeds in the winter (Kollmann et al. 1998); therefore, if rodents had already adjusted energy requirements to prepare for the winter, seed removal would be low overall. Alternatively, if rodents were still active but food resources were becoming scarce as the season progressed, the foragers may have shown less of a preference for particular seed types or foraging site characteristics in order to consume any available food source. Rodent populations and distributions may also fluctuate seasonally. Since most seed removal studies in similar ecosystems occurred in summer (Kwit et al. 2004, Webb and Willson 1985, Moore et al. 2007), my removal rates are unlikely to be comparable to those observed in other studies. The period of study should span the entire period of risk for the seed, from when trees fruit until the following spring. I examined part of this window by quantifying seed removal soon after initial dispersal during the early period of risk. As one of the few studies on winter rates of seed removal, my research fills a void in the scientific literature.

Further study

This study is unique among seed removal manipulations because the duration was longer than most studies, which take place in 1-2 weeks (Myster and Pickett 1993, Mittelbach and Gross 1984, Webb and Willson 1985, Willson and Whelan 1990). This gave me the advantage of a large window during which seed removal could have occurred had the rodents been actively foraging in the environment. However, my time frame was not long enough to observe seasonal variation in seed removal patterns. Future studies conducted over longer time frames and across multiple seasons may pick up on very different patterns due to changes in rodent diet and seed preferences (Boman and Casper 1995, McCormick and Meiners 2000), which could link *L. maackii* cover to differential seed predation. Seed removals of longer duration would also increase the ecological relevance of

the determined effect by allowing predation risk to be quantified over the entire period when the seed is vulnerable: from dispersal until germination (Chambers and MacMahon 1994). The age of invasion, size of the invaded area, and changes in the predator population over time or across habitats could also have strong effects on the relationship between the invasive species and seed predation (Boman and Casper 1995).

Despite my own past research indicating that the present of shrubby cover like *L. maackii* does change rodent foraging patterns by decreasing perceived predation risk, this study suggests that the interaction does not have an actual impact on the predation of native seeds in forests that are or are not invaded by the honeysuckle. This seems to indicate that *L. maackii* can have far-reaching effects on an ecosystem, but apparent competition with native plants through rodent foraging habits does not appear to be an important pathway through which the shrub competes with native plants. Since this particular indirect effect of an invasive species does not seem to be important at this time, it is likely that *L. maackii* has become a successful invader through other direct or indirect pathways.

Rodents have proven to be important consumers in many ecosystems (Kwit et al. 2004, Reichman 1979, Price and Reichman 1987, Brown and Heske 1990) and further research into their interactions with invasive plants in general may identify unnoticed causes or effects of community modifications. This study also emphasizes the importance of understanding the heterogeneity of post-dispersal seed predation and its related density-dependent effects to fully comprehend consumer and habitat dynamics (Kwit et al. 2004). Further research into the direct and indirect effects that invasive species have on ecosystems will help ecologists to better understand ecosystem interactions and help wildlife resource managers to more ably prevent and control biological invasions.

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Table 1: Average differences in habitat characteristics in plots with high or low *Lonicera maackii* densities. Six high and six low density sites were used in the study. Values are average ± one

standard deviation; p-values from two sample t-test with df = 10. *** Indicates a significant difference between high and low density sites.

Table 2: ANOVA table of fixed effects for seed removals (including arthropod removals) at ten sites (excluding two with raccoon disturbance), n = 60 trays. *Indicates interaction between two effects.

Table 3: ANOVA table of fixed effects for seed removal of rodents only (arthropod removal excluded) at ten sites (excluding two with raccoon disturbance), n = 30 trays. *Indicated interaction between two effects.

Figure 1: Map of August A. Busch Memorial Conservation Area in St. Charles, Missouri, USA. White squares mark 30 m by 30 m plots with low *L. maackii* density and black squares mark plots with high *L. maackii* density. Shaded areas correspond to *L. maackii* density in forest patches with darker areas representing higher density.

Figure 2: Effects of *L. maackii* density treatment on proportion of seeds removed by rodents only by species. Results are based on analysis of covariance (table 3). Means and standard errors are shown.

Table 1

	High density (n=6)	Low density (n=6)	p-value
Average # of <i>L. maackii</i> stems in a 1m radius	2.64 ± 0.96	0.03 ± 0.07	0.001***
Average light intensity at 1m above ground ($\mu\text{moles}/\text{m}^2/\text{sec}$)	81.46 ± 58.12	93.94 ± 41.42	0.678
Average light intensity at ground level ($\mu\text{moles}/\text{m}^2/\text{sec}$)	37.81 ± 14.75	68.46 ± 54.99	0.238
Average number of leaf layers on ground (litter)	0.81 ± 0.33	1.10 ± 0.30	0.139

Table 2

Effect	Num df	Denom df	F value	Pr > F
<i>L. maackii</i> trt	1	8	0.31	0.590
Excluder	1	8	4.05	0.079
Excluder* <i>L. maackii</i> trt	1	8	0.02	0.881
Species	2	32	3.55	0.041
<i>L. maackii</i> trt*species	2	32	1.37	0.268
Excluder*species	2	32	0.19	0.826
Excluder <i>L. maackii</i> trt*species	2	32	2.41	0.106

Table 3

Effect	Num. df	Denom. df	F value	Pr > F
<i>L. maackii</i> trt	1	8	0.09	0.776
Species	2	16	0.51	0.608
<i>L. maackii</i> trt*species	2	16	1.68	0.217

Figure 1

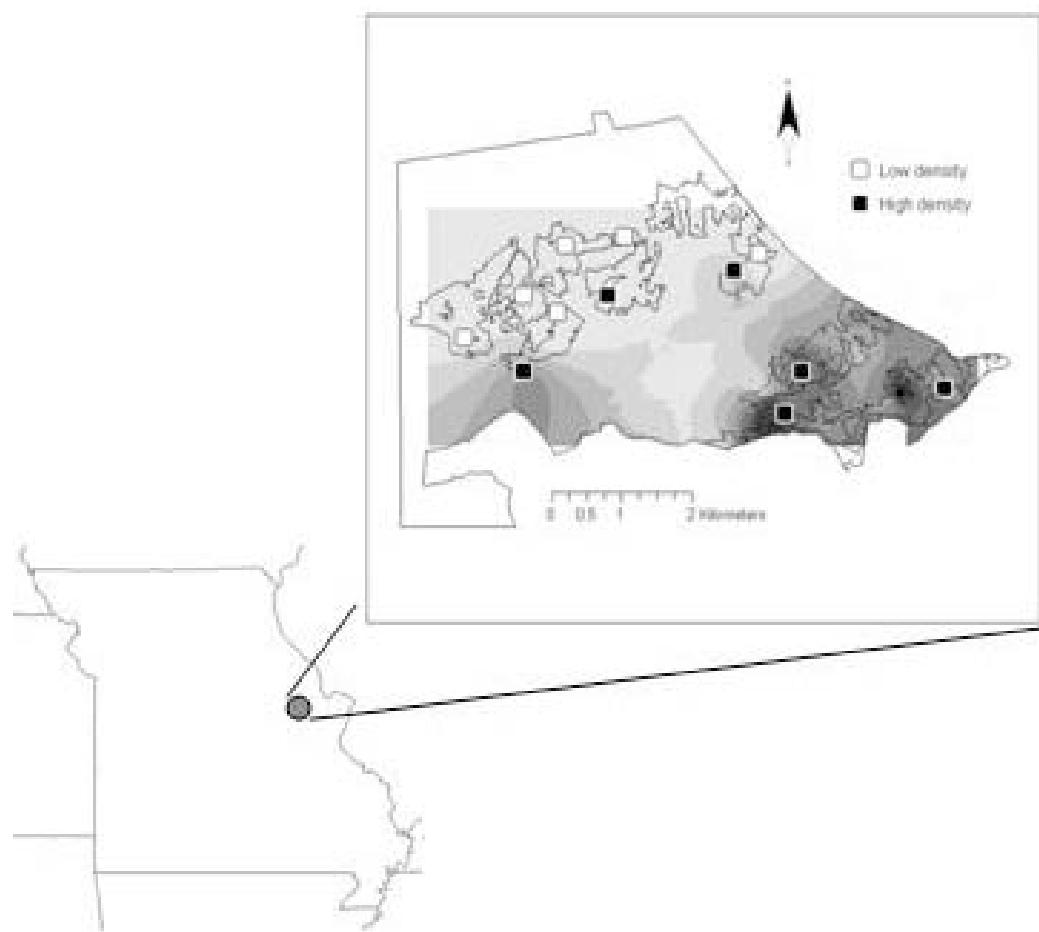
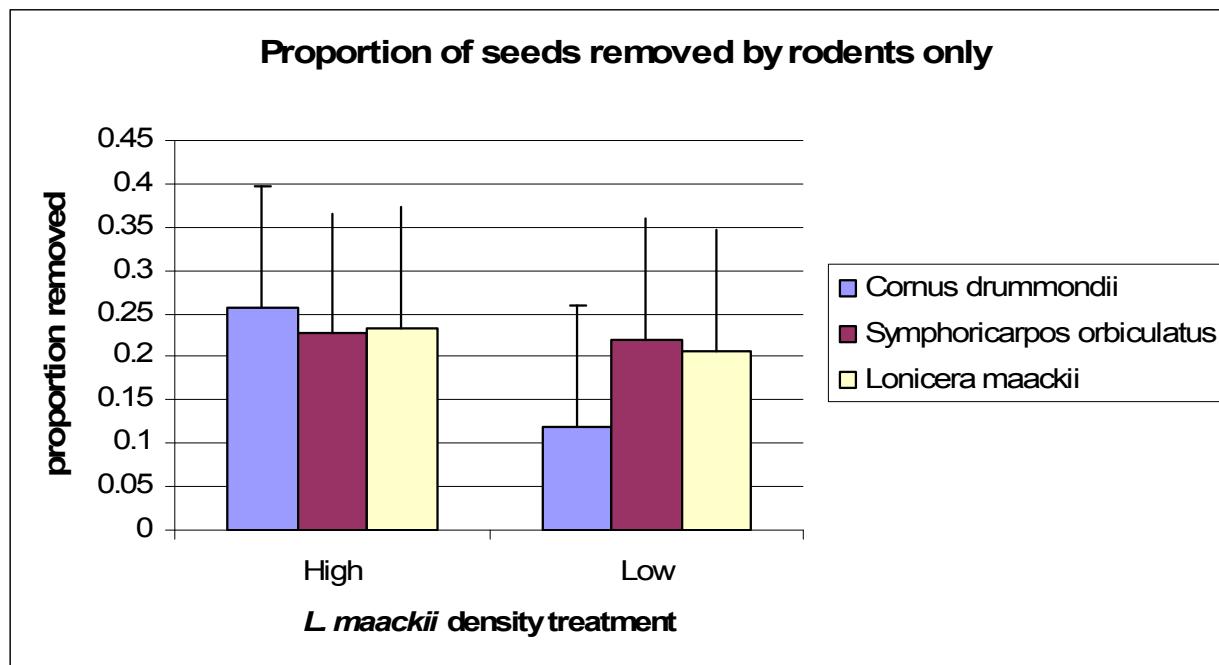


Figure 2



CHAPTER 4: CONCLUSION

Invasive species have demonstrated varied and intense effects on ecosystems in the past and threaten to become more prevalent and damaging in the future (Elton 1958, Bazzaz 1984, Wilcove et al. 1998, Theoharides and Dukes 2007). Invasive species cost time, energy, manpower and billions of dollars to control and eradicate (Pimentel et al. 2000), with much of the effort going into the management of plant species (Pimentel et al. 2005). Although invasive plants have many different mechanisms of establishing and spreading throughout native ecosystems, most research has examined the direct effects of plant-plant interactions, while the indirect secondary ecosystem interactions mediated through other trophic levels have been largely ignored. This paper has attempted to dissect the mechanism behind one such indirect effect: apparent competition between invasive and native plants due to rodent foraging behavior.

To do this I asked two questions. First, how does rodent foraging behavior change due to differences in perceived predation risk in the presence or absence of an invasive shrub? I hypothesized that perceived predation risk would decrease in areas where the shrub had established, causing rodents to forage less cautiously in invaded areas but demonstrate higher perceived risk and more cautious foraging behavior in relatively open habitats that had experienced no shrub invasion. This hypothesis was tested by measuring giving-up densities in artificially covered and uncovered pairs of trays left out overnight in six invaded and six native forest plots.

My second study attempted to translate the behavioral changes hypothesized in my first study into actual implications for survival of native seeds in the invaded and natural plots. I predicted that native seeds typically consumed by rodent seed predators would be at higher risk of predation in plots invaded by the shrub because the animals would be able to forage more with lower risk of

predation and have higher rates of consumption under the cover and protection of the shrub. This hypothesis was tested by measuring rates of seed removal by rodents in trays in both invaded and natural habitats left out for several weeks in the study plots.

The results of the first study indicated that *Lonicera maackii* shrub cover does have an effect on rodents' perceived predation risk, although the patterns interact with other abiotic conditions. Rodents were less sensitive to other factors that changed predation risk, such as moonlight or the presence of artificial refuges, in habitats with high *L. maackii* density. In low *L. maackii* habitats rodents decreased foraging activity when they perceived elevated risk from higher moon illumination and showed more of a preference to forage in artificially covered areas. My observation of the interaction between rodent foraging behavior and invasive honeysuckle allows for the possibility of a form of apparent competition between the invasive and native plants due to changes in *P. leucopus* behavior.

My second study showed that there was no significant difference in seed removals between high and low density plots, although slightly higher proportions of removal were observed in high density plots. This could indicate that rodents are altering foraging patterns to spend more time in the invaded patches due to a decrease in perceived predation risk, but since invaded patches offer a higher abundance of invasive seeds, rodents do not concentrate their predation on native seeds. I therefore conclude that, although rodents forage differently under shrub cover, the differences do not translate into increased predation of native plant seeds. Instead, I suggest that *L. maackii* may provide a refuge from predation for native seeds by swamping predators with its own seeds as a food source. Although *L. maackii* has proven to be a superior competitor and invader (Luken and

Goessling 1995, Collier et al. 2002), it does not seem to use apparent competition as a mechanism for invasion into forest habitats.

Due to low foraging activity and timing difficulties, I did not observe any significant effects in the seed removal study. As mentioned in my discussion, the results I observed could still indicate that *L. maackii* has an effect on seed predation that I did not detect due to spatial or temporal variation. In order to improve upon my dataset and draw more comprehensive conclusions about the interactions that I predicted, I will be collecting more data in the spring of this year. I will be repeating the seed removal study with more sites to observe differences across sites and compare results from the spring to the results from the winter that were analyzed here. I will also be trapping for rodents at the original sites used in the two studies described above in hope that abundance and distribution data will add insight into the foraging behavior and seed predation results that I observed in the fall and winter.

The results and conclusions from this study can be used to formulate conservation and management strategies. Invasive plants have important and diverse ecosystem effects (Elton 1958, Bazzaz 1984) which can directly or indirectly decrease the abundance and diversity of native species (Wilcove et al. 1998). Understanding these effects and species interactions is the key to eliminating threats using the most cost and time effective methods. For example, one common method for controlling *L. maackii* invasion and spread is to clip the branches to decrease growth and reproductive abilities (Luken and Mattimiro 1991, Williams et al. 1992), but clipping branches would not decrease use of the shrub as a refuge for safe foraging by small mammal seed predators. Clipping would therefore not be an effective management technique if seed predators have large impacts on decreasing native plant recruitment. My research indicates that rodent seed predators do use *L. maackii* as a refuge,

but that changes in seed removal across differing densities of *L. maackii* are not high enough for rodents to contribute significantly to apparent competition and invasion of this species. Therefore, management does not have to account specifically for rodent effects that are enhanced by *L. maackii* presence.

My studies have shown that rodent seed predators are dynamic components of forest communities that can change their behavior and react to changes in habitats caused by invasive plant species. My research also emphasizes the importance of examining indirect effects of ecosystem interactions. Because rodents are important consumers in many ecosystems (Janzen 1971, Reichman 1979, Brown and Heske 1990), their foraging behaviors and food preferences are likely to have a large effect on native or invasive species in various systems. The indirect interactions between species are rarely studied and poorly understood, but having an estimate of the magnitude of these effects can solve management and conservation problems. Applying the concepts of rodent foraging behavior and indirect ecosystem effects to invasions is quickly becoming a necessary task, as invasive species become ubiquitous throughout the world.

I recommend that further research concentrate on understanding the indirect effects of invasions and applying that understanding to management applications. In the case of *L. maackii*, the effect of apparent competition should be examined over a larger gradient of plant densities, using more sites and more species of native plant seeds. I would expect the direction and magnitude of the effect of apparent competition to change over seasons as well, depending on food availability, forest characteristics and abiotic conditions. Apparent competition, rodent foraging behavior and other indirect interactions can be measured in other invasive species as well (ex: *Rosa multiflora*, *Serica*

lespedeza, *Alliaria petiolata*) to better understand how these species invade and change the ecosystems where they occur.

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