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Jeffery A. Masters
University of Louisville

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INVASIVE PLANTS AS DRIVERS AND PASSENGERS OF COMMUNITY CHANGE IN A DISTURBED URBAN FOREST

By

Jeffery A. Masters
B.S. Angelo State University, 1994
M.S. Angelo State University, 2002

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A Dissertation Approved on

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by the Following Dissertation Committee:

Dissertation Director
Sarah M. Emery

James E. Alexander

Margaret C. Carreiro

Kendra A. Cipollini

Perri K. Eason

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ABSTRACT

INVASIVE PLANTS AS DRIVERS AND PASSENGERS OF COMMUNITY CHANGE IN A DISTURBED URBAN FOREST

Jeffery A. Masters

March 28, 2014

Invasive species can impact local ecosystems by decreasing biodiversity and local abundances of native species. Invasive species also frequently establish in disturbed habitats. An invasive species may dominate a habitat because the introduced species is a superior competitor (driver model) for resources or because the introduced species is more tolerant of noncompetitive processes such as anthropogenic disturbance that reduces the diversity and abundance of native species (passenger model).

Ranunculus ficaria (Ranunculaceae) is an invasive plant species in the northeastern United States, and can be especially dense in urban riparian habitats. It emerges early and forms thick mats of vegetation that may outcompete other plants for resources. It also produces an abundance of showy flowers that may impact local pollination service. The urban riparian habitats where this species occurs are also subject to intense flooding events that can alter the riparian corridor and eliminate plants not adapted to this disturbance. This work examines *R. ficaria*'s role in the community changes associated with a highly disturbed urban riparian habitat. I studied *R. ficaria* tolerance of leaf litter disturbance associated with flooding, as well as its direct competitive effects on other species. I also examined how *R. ficaria* alters pollinator services in invaded areas. To gain insight into how removal of an invasive species affects arthropod assemblages and associated ecosystem services, I also compared arthropod diversity, abundance, and decomposer and nectarivore functional groups in plots invaded with *Lonicera maackii* (bush honeysuckle) and removal plots.

I found that *R. ficaria* is tolerant of changes in leaf litter depth caused by flooding. It can also negatively impact the sprouting and growth of native species, probably through competition for space. I generally found positive impacts on pollination services in invaded areas, but I found low seed set in one native species, possibly due to the degraded habitat. Removal of *L. maackii* produced only small changes in arthropod abundance and diversity, suggesting either little initial impact of invasion, quick recovery of arthropod groups after biomass removal of *L. maackii*, or a shift to an alternative stable state following *L. maackii* invasion. Our results suggest that *R. ficaria* can act as a passenger, tolerating aspects of hydrological disturbance that other species cannot. However, this species can also drive low abundance and diversity through resource competition. *Lonicera maackii* appears to be acting as a passenger in this system with little impacts on native arthropod communities. These results have ecosystem management implications for both of these invasive species. While removal of *L. maackii* would likely have little impact on arthropod ecosystem services, removal of *R. ficaria* would negatively impact pollination services in an already degraded habitat.

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CHAPTER I

INTRODUCTION

As globalization and awareness of its environmental consequences have increased, more attention has been given to the spread and impacts of invasive species. Invasive species are important economic and environment pests, affecting everything from agriculture and medicine to recreation. Invasive species can also act as vectors of disease and parasites, and their impacts on agriculture and human health are estimated to cost $138 billion annually just in the United States (Pimentel et al. 2005). Invasive species are of great interest to evolutionary biologists and ecologists because they represent examples of dramatic evolutionary and ecological change. Invasive exotic species pose threats to endangered species (80% of endangered species are at risk due to interactions with invasive species), threaten native habitats, decrease biodiversity, contribute to genetic degradation, and facilitate the establishment of other invasive species (Pimentel et al. 2005). These are concerns that cross many disciplines and political views, making management of invasive species an environmental issue of primary importance.

Most invasive species have one or more specific traits that account for their success in the invading habitat. Invasive plants occur in greater numbers and in denser populations than the native plants, exhibiting larger size and faster growth rates (Wolfe 2002). Many invasive plant species are r-selected and produce numerous offspring that can quickly dominate local habitats (Rejmanek and Richardson 1996). Another common explanation for invasives' success is that they lack the biotic constraints they had to confront in their native environment (enemy release hypothesis) (Keane and Crawley 2002). The evolution of increased competitive ability (EICA) which predicts that invasive plant species which have escaped their specialized enemies in their native habitat can evolve with a decrease in investment in anti-herbivore chemical defenses is another related hypothesis (Blossey and Notzold 1995). Invasive plants also frequently establish in disturbed areas (Hobbs and Huenneke 1992, Jia et al. 2009). In some situations, invasive dominance occurs because the invading species is able to thrive in areas that native species can no longer tolerate due to anthropogenic disturbance (Price et al. 2011).

According to the driver-passenger model of species invasions outlined by MacDougall and Turkington (2005), invasive species dominance can occur because the introduced species is a superior competitor (driver model) or because the introduced species is less susceptible to noncompetitive processes that negatively affect other species (passenger model). Some passengers, although dominant, may actually provide facilitative effects for native species or ecosystem services (facilitative passenger). On the other hand, invasive species can interact with disturbance to further reduce native species through positive feedbacks (back-seat driver model) (Bauer 2012). Management of invasive plants usually involves removal as a first step, but if the invasive plant is a passenger of ecosystem change, removal may not help to restore degraded habitats. It would be helpful for managers to determine if invasive species are the "drivers," "passengers," "facilitative passengers," or "back-seat drivers" of ecosystem change in heavily invaded areas in order to optimize management (MacDougall and Turkington 2005, Bauer 2012).

ORGANIZATION OF DISSERTATION

In this dissertation, we examine how *Ranunculus ficaria* interacts with leaf litter depth, native plants, and sympatric species in an urban riparian habitat. We looked at direct competitive effects of invasion as well as the impacts on local pollination services. In particular, we ask whether *R. ficaria* is a "driver" of low species diversity and abundance; or a "passenger" taking advantage of a highly disturbed habitat. We also discuss the management implications of our results. In a complementary study, we examined how management of an invasive species affects arthropod assemblages by comparing plots invaded by *Lonicera maackii* (bush honeysuckle) to removal plots.

In chapter two of this dissertation, we consider the "passenger" characteristics of *R. ficaria* by examining its response to different leaf litter depths associated with urban flooding. The study was conducted in the riparian corridor along Beargrass Creek in Cherokee park located in Louisville, KY. We manipulated leaf litter depths (bare ground to 20 cm) in *R. ficaria* monocultures, and then recorded biomass and the reproductive output of *R. ficaria*. Only very deep leaf litter negatively affected *R. ficaria* biomass and propagule production. *Ranunculus ficaria* was able to tolerate leaf litter depths that other species cannot tolerate, suggesting that *R. ficaria* acts partly as a passenger in this system.

Chapter three of this dissertation focuses on competitive (driver) effects of *R. ficaria* invasion through a removal experiment in the riparian corridor along Beargrass Creek. In two factorial field experiments, we examined nutrient competition, allelopathy, and space/light competition effects of *R. ficaria* invasion by examining how *R. ficaria* removal affects early season sprout species richness and abundance, as well as the growth of an added native riparian grass, *Elymus riparius*. We found no effects on species diversity, but recruited sprout abundance and *E. riparius* biomass were both significantly higher in all removal plots. There was no evidence for nutrient competition or allelopathy, indicating that *R. ficaria* partly relies on being a superior competitor for space and light to dominate local habitats. Our results show that *R. ficaria* has some role as a driver of lower species diversity in heavily invaded areas.

In the fourth chapter, we determined the impacts of *R. ficaria* invasion on local pollination services. We observed pollinator behavior to compare visitation rates to natives in invaded and uninvaded areas. In addition, we collected stigma from native ephemerals in each habitat to determine heterospecific and conspecific pollen deposition amounts. Mature fruits from the native ephemerals were also collected in both habitats. We found that *R. ficaria* invasions increase pollinator visitation rates and conspecific pollen deposition on native ephemerals, with very low heterospecific pollen deposition. However, seed set in one native species was reduced. Management should consider the facilitative effects of this species on pollination services, but also the possible negative effects.

In chapter five, we explored how the management of invasive species affects arthropod assemblages and associated ecosystem services by comparing plots invaded with *L. maackii* with removal plots. We discovered that *L. maackii* removal has only a small effect on arthropod assemblages in the first year after removal. No differences between plots were detected after three years. Our study's results indicate that managers may not need to be concerned about the effect of honeysuckle removal on arthropods and associated decomposition and pollination services.

Chapter six is a general summary of the dissertation research. We also present future research directions which include expanding the *R. ficaria* removal experiment to include direct measurements of effects of disturbance. We also describe an experiment to explore how increases in distribution of *R. ficaria* can alter plant communities through shifts in pollinators.

SITE DESCRIPTIONS

We conducted our *R. ficaria* studies along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301, longitude -85.698220), Beargrass Greenway (latitude 38.245939, longitude -85.700499), and Seneca Park (38.235°; -85.668°), part of the Olmsted Parks and Metro Parks systems in Louisville, Kentucky. The dominant trees in these woodlands were *Acer saccharum*, *Fraxinus americana*, and *Celtis occidentalis* with a mean tree basal area within the plots of 25.7 ± 3.1 m^2 ha^{-1}. The unmanaged understory had few saplings and consisted mostly of *Lonicera* shrubs with the exotic shrub *Ligustrum sinense* (Chinese privet) being co-dominant in some locations. The mull soils in these woodlands were silt loams in the Crider and Caneyville soil series, supported exotic earthworms (mostly *Lumbricus terrestris*; Pipal and Carreiro, unpublished) and were characterized by a circumneutral pH (6.39 ± 0.17).

The catchment in this area is urbanized and strongly channelized (~33% impervious surface (Beargrass Creek Watershed Council, 2005) and most study sites were subject to flooding throughout the year. At the sites designated as invaded in the *R.*

ficaria study, the riparian corridor was heavily invaded with *R. ficaria* (>90% cover), and very few native spring ephemerals grew directly along the creek. However, several invasive and weedy species grew in the riparian corridor. Violets (*Viola sororia*), dead nettle (*Lamium purpurea*), penny cress (*Thlaspi arvense*), dandelion (*Taraxacum officinale*), and invasive garlic mustard (*Alliaria petiolata*) were all in flower at the time of our *R. ficaria* studies. There were several native ephemerals in flower in areas directly adjacent to the riparian corridor which included spring beauty (*Claytonia virginica*), toothwort (*Cardamine concatenata*), sessile trillium (*Trillium sessile*), trout lily (*Erythronium americanum*), and Dutchman's breeches (*Dicentra cucullaria*). These adjacent areas were also designated as invaded for our *R. ficaria* study. The uninvaded sites were picked to approximate the same topography, canopy cover, and native flower density as the invaded sites. The uninvaded areas were dominated by *C. virginica*, *C. concatenata*, and false anemone (*Enemion biternatum*) in spring. Sessile trillium, trout lily, and Dutchman's breeches were also in flower in uninvaded sites at the time of the *R. ficaria* studies. The dominant trees at the uninvaded sites were oak (*Quercus* sp.), *A. saccharum*, and *F. americana*.

CHAPTER II

DOES LEAF LITTER DEPTH INFLUENCE *RANUNCULUS FICARIA* (RANUNCULACEAE) INVASIONS?

Summary-*Ranunculus ficaria* is an invasive plant species in the northeastern United States, especially in urban riparian habitats. Changes in the frequency and intensity of flooding events in these urban riparian corridors create patches of heavy litter and patches of bare ground where native species either cannot penetrate or are exposed to freezing temperatures and drying conditions. These changes can result in competitive advantages for invasive species that are adapted to these disturbances. We conducted a field experiment to test the effects of leaf litter depth on *R. ficaria* biomass, bulbil production, flower production, and seed production under deep (20 cm) litter, intermediate (10 cm) litter, shallow (5 cm) litter, and bare ground along an urban stream in Louisville, KY. Deep litter and lack of litter decreased plant biomass compared with shallow litter. Bulbil production was not significantly different across treatments. Flower and seed production were only reduced in deep litter. *Ranunculus ficaria*'s ability to maintain production across a large range of litter depths may provide a competitive advantage over plant species not adapted to varying litter depths.

INTRODUCTION

Invasive plant species are important economic and environmental pests, posing threats to endangered species, altering native habitats, decreasing biodiversity, and facilitating the establishment of other invasive species (Pimentel et al. 2005). Several mechanisms have been proposed to explain invasive plants' success, including occurring in densities great enough to monopolize resources and outcompete native species (Wolfe 2002). Other invasive species have unique allelopathic properties that inhibit growth of native species (Callaway and Ridenour 2004). In many cases, anthropogenic disturbance plays a driving role in the establishment of invasive plant species (Lozon and MacIsaac 1997, Schooler et al. 2010). Anthropogenic disturbance can facilitate invasion directly by eliminating less tolerant species or indirectly by altering resources or habitat traits (Price et al. 2011). Invasive species and disturbance are both associated with ecosystem change, including changes in species diversity. In invaded areas that are also regularly disturbed, it is important to determine if invasive species are the cause of ecological changes (drivers), taking advantage of an ecological niche created by the disturbance (passengers), or benefitting from disturbance in addition to directly contributing to ecosystem changes (MacDougall and Turkington 2005, Bauer 2012). For an example, if an invasive is known to be a passenger, it may be possible for land managers to manipulate disturbance regimes, rather than the plants directly, to most effectively reduce invasion (Jia et al. 2009, Menuz and Kettenring 2013).

Urbanization and altered hydrology in urban riparian drainages is a major cause of disturbance to adjacent natural habitats. Sheet erosion and poor water quality associated with catchment urbanization of streams can greatly reduce populations of native species along riparian areas either by directly washing away plants or by altering the habitat (Walsh et al. 2005). The change in hydrology can also facilitate the establishment of tolerant invasive species which may further alter the riparian habitat (Stromberg et al. 2007).

One aspect of habitat alteration associated with urban stream flooding is the redistribution of leaf litter in the riparian corridor and the expanded flood plain. Flooding in riparian areas creates some areas of very deep leaf litter deposition and other areas with no leaf litter (Nilsson et al. 1999). This variation affects local community structure because deep leaf litter and flotsam drifts suppress the growth of riparian plant species not adapted to this disturbance, whereas species that are sensitive to cold temperatures or desiccation are inhibited in areas scoured free of leaf litter (Facelli and Pickett 1991a, Xiong et al. 2003, Sayer 2006). Invasive species that can tolerate different leaf litter depths may have a competitive advantage in these habitats over native species not adapted to varying leaf litter depths (Baker and Murray 2010).

Ranunculus ficaria var. *bulbifera* (formerly *Ranunculus ficaria* var. *bulbifera*) is an invasive species in riparian areas of temperate deciduous forests in the northeastern United States, and it can be especially dense in urban riparian habitats. A perennial native to Europe and western Asia, it was first reported in the United States in 1867, and was probably introduced as an ornamental (Axtell et al. 2010). *Ranunculus ficaria* is now present in low-lying wet areas in many temperate deciduous forests. It emerges as early as September, overwinters, and then forms thick mats of vegetation and produces an abundance of showy flowers in late winter and spring (Sakai et al. 2001). Invasive populations of *R. ficaria* have three modes of reproduction: seeds, bulbils, and tubers.

Seeds generally show low viability, and population growth mostly depends on vegetative propagation through bulbils and tubers (Marsden-Jones 1935, Verheyen and Hermy 2001). Whereas the success of this species in native European populations is positively correlated to the previous year's humidity and rainfall (Tyler 2001), almost nothing is known about factors influencing North American population success. A better understanding of what makes this species so successful will lead to better control efforts.

This species has traits which may make it particularly adapted to severe hydrological disturbance associated with urbanization. During flooding events, waxy cuticles and thick tuber clumps provide *R. ficaria* with some amount of resistance to high velocity water flow (pers. obs.). Flooding also disperses bulbils, seeds, and loose tubers. Combined with early emergence, flooding may allow *R. ficaria* to dominate the riparian corridor and adjacent areas. Whereas little is known about the ecology of *R. ficaria* in flood-prone habitats, other invasive plants in urban riparian areas are tolerant of flooding and effectively disperse via flooding (Johansson and Nilsson 1993, Thomas et al. 2005).

Effective dispersal is probably the most important result of flooding for *R. ficaria*, but this disturbance also redistributes leaf litter, exposing overwintering sprouts to cold and dry conditions, or creating a physical barrier by burying sprouts in deep leaf litter. The objective of this study was to examine impacts of varying leaf litter depths on *Ranunculus ficaria* growth and reproduction in a replicated field experiment. We expect that *R. ficaria* will be tolerant to a wide range of leaf litter depths, partly explaining its success as an invasive in this habitat.

METHODS

We conducted our study along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301, longitude -85.698220) and Beargrass Greenway (latitude 38.245939, longitude -85.700499), which are part of the Olmsted Parks and Metro Parks systems in Louisville, Kentucky. The catchment in this area is urbanized and strongly channelized (~33% impervious surface (Beargrass Creek Watershed Council, 2005)) and the study sites are subject to flooding throughout the year. The riparian corridor is heavily invaded with *R. ficaria* (>90% cover), forming large monoculture patches at both sites. The Greenway site is also heavily invaded by amur honeysuckle (*Lonicera maackii*).

In fall 2011, we collected approximately 60 kg of fallen leaf litter from properties near our study site, which was then mixed thoroughly and air-dried. This litter was a mix of oak (*Quercus spp*.) and maple (*Acer spp*.) leaves, which represented the two dominant tree genera in our invaded sites. Other common tree species in our study sites included sycamore (*Platanus occidentalis*) and box elder (*Acer negundo*).

In December 2011, we constructed 50 1 m x 1 m treatment plots grouped into 10 blocks of 5 plots each in the *R. ficaria* monoculture patches along the riparian corridor. Five blocks (25 plots) were in the Beargrass Greenway site and 5 blocks (25 plots) were located in the Cherokee Park site. The plots in each block were not continuous, but all plots in the block were within 3 meters of each other. Chicken wire cages (2-inch mesh, approximately 30 cm tall) anchored with rebar stakes and landscaping pins were constructed around and over each plot to keep each litter manipulation in place. The chicken wire cage also limited access by large herbivores such as deer. Each block contained one plot each with the following treatments: deep litter (20 cm), intermediate litter depth (10 cm), shallow litter (5 cm), no leaf litter with cage in place, and an ambient control with no cage and no litter manipulation. Ambient litter had a slightly different composition and depth across blocks. Deep litter treatments approximated extreme litter deposition after a flooding event, and the removal of all leaf litter in a cage represented scouring effects also associated with flooding events.

We monitored plots weekly to remove litter from the top of the cages, as well as to repair damage from weather, wildlife, and vandalism. We collected data on initial sprouting propagules, final biomass of *R. ficaria,* and final reproductive output (bulbils, flowers, seeds) from 0.5 m x 0.5 m subplots in the center of each plot to limit edge effects. Initial sprouts were counted in January 2012. Final biomass of *R. ficaria* in plots was harvested in April 2012 by clipping plants at ground level, drying at 60°C for 48 hours and weighing. Final reproductive output per plant was also counted in April 2012. We collected environmental data weekly within each plot without disturbing the sampling subplot. These data included surface soil temperature (2 cm depth), surface soil moisture (2 cm depth using General DSMM500 soil moisture meter), and light penetration through the litter to the top of the emerging plants (Extech EasyView 30 light meter).

We performed general linear model analyses on each response variable to evaluate the effects of litter depth on *R. ficaria* reproduction, survival, and growth. Block, soil temperature, soil moisture, and light penetration were covariates. Bulbil, flower, and seed data were transformed (ln(x +1)) to meet test normality assumptions. Spearman’s rank correlation was used to determine correlations between biomass and bulbils, and between flowers and seeds. All analyses were performed in SYSTAT v. 12 (SYSTATv12 2007).

RESULTS

Ranunculus ficaria plants in shallow (5 cm) litter produced 63.6% more biomass than plants with no leaf litter cover, and plants in ambient litter conditions produced 38.1% more biomass than plants with no leaf litter (Fig. 1, Table 1). No other significant differences in biomass were detected between treatments. There was a trend for decreasing biomass under increasing leaf litter depths with an observable difference in biomass production between deep (20 cm) and shallow (5 cm) leaf litter plots (Fig. 1). However, this difference was not significant in the full statistical model. Increasing light levels below the litter had a positive effect on biomass (Table 1). Although there was a positive correlation between final *R. ficaria* biomass and bulbil production (ρ=0.506, p=<0.001), there were no significant differences in bulbil production detected between treatments (Fig. 2, Table 1). As with biomass, there was a trend showing decreasing bulbil production in deeper litter (Fig. 2). None of the environmental factors significantly impacted bulbil production, and there were no block effects on biomass or bulbil production (Table 1).

Flower production was very sensitive to deep leaf litter depth, and deep litter (20 cm) plots produced very few flowers. Flower production in deep leaf litter (20 cm) was significantly different than all other depths. Flower production was 1703.5 % higher in ambient litter depths than deep (20 cm) leaf litter depth. There were 1931.6% more flowers produced on bare ground plots than in deep (20 cm) litter plots. Flower production in shallow (5 cm) litter was 1464.9% higher than deep (20 cm) leaf litter, and plots with 10 cm of litter produced 561.4% more flowers than in 20 cm (Fig. 3). There were no other significant differences between treatments. There were block effects detected for flower production (Table 1), most likely due to differences in tree canopy coverage in the different sites.

There was a significant correlation between flower and seed production (ρ=0.939, p=<0.001), and the average seeds per flower produced were lower in Greenway plots (p=0.022, df=1, F=5.674). Significant differences in seed production were detected between deep litter (20 cm) and all other treatments. Compared to deep litter (20 cm), seed production was 1692.5% higher in ambient litter depths, 1628.0% higher in bare ground plots, 1585.0% higher than in shallow (5 cm) litter, and 725.2% higher in10cm depths (Fig. 4, Table 1). There were block effects on seed production (Table 1).

Despite litter effects, propagules were still produced in large numbers across treatments. An estimated 789 bulbils per square meter were produced in the most productive plots (5 cm depth). Although deep litter plots (20 cm) were the least productive for bulbils, there was still an estimated 262 bulbils per square meter (Fig. 2). Ambient plots produced an average of 686 bulbils per square meter. Seeds were produced in large numbers in all treatments but deep litter. Bare ground, shallow litter (5 cm), and ambient plots were the most productive for seeds, and all produced close to the same average amount of seeds (~740 seeds per square meter) (Fig. 4).

DISCUSSION

Redistribution of leaf litter by flooding is a regular process for most rivers (Nilsson et al. 1999). This process may be especially profound in urban areas where storm runoff is efficiently channeled into the riparian corridor causing flash flooding. This redistribution of leaf litter can have varying effects on the riparian plant community which may respond to leaf litter mass and chemical properties (Nilsson et al. 1999). In our study, leaf litter was mixed to control for varying decomposition rate and nutrient content of the litter species, and the differences detected between treatments should be due to leaf litter depth acting as a physical barrier to sprouting propagules. Shallow leaf litter depths can aid in seedling establishment (Facelli and Pickett 1991b, Hovstad and Ohlson 2008), but frequently any leaf litter has an overall negative effect on sprout and seedling survival (Xiong and Nilsson 1999, Hovstad and Ohlson 2008). Plant species that can tolerate a wide spectrum of leaf litter depths are expected to have a competitive advantage over species that are inhibited by leaf litter in areas where depth varies greatly (Facelli and Pickett 1991a, Benitez-Malvido and Kossmann-Ferraz 1999).

Ranunculus ficaria reproduction was not hindered by leaf litter, except for seed production in very deep litter. The strong correlation between flower and seed production suggests very little pollen limitation in this self-incompatible entomophilic species (Metcalfe 1939, Taylor and Markham 1978). The average seeds per flower produced were lower in Greenway plots, probably due to interactions with honeysuckle. Shading by honeysuckle can reduce pollinator visitation rates (Goodell et al. 2010). Overall, the differences that were observed between treatments were not due to variation in micro-environmental factors (covariates of temperature, moisture, and light) usually influenced by leaf litter. Instead, these differences were likely due to leaf litter acting as a physical barrier to smaller vegetative sprouts and seedlings. Deep litter can inhibit sprouts, especially herbs and other species with small seeds (Facelli and Pickett, 1991; Sayer, 2006; Baker and Murray, 2010). Vegetative reproduction may provide *R. ficaria* one strategy to deal with the physical barrier of deep litter. Reliance on tubers may give new growth sufficient energy to penetrate deep litter, and to tolerate low light conditions when buried. Bulbils also provide more energy for sprouts than seeds, reducing the impact of deep litter as a physical barrier.

Ranunculus ficaria may have a competitive advantage in being able to penetrate and reproduce effectively across litter depths that many other herbs cannot penetrate. Deep leaf litter generally has a negative effect on native seedling sprouting and survival; however, varying litter depths can create habitat patchiness that could increase plant diversity, even in the presence of aggressive invaders (Facelli and Pickett 1991a, Schramm and Ehrenfeld 2010). The plots in this study were placed in *R. ficaria* monocultures that were disturbed by flooding during the study period. No other herb species emerged in any of the treatment plots during the experiment; therefore we were unable to separate the effects of leaf litter depth, *R. ficaria* density, and disturbance on native species in this study.

Ranunculus ficaria appears to act as a passenger (*sensu* (MacDougall and Turkington 2005), tolerating flooding disturbance that other species cannot. Once established, this species may act as a driver, emerging early and outcompeting other species for light and other resources, or negatively affecting some species through allelopathy (Cipollini and Schradin 2011). Managing flooding disturbances may prevent this species from establishing and becoming problematic. Current management practices for *R. ficaria* focus mostly on herbicide use to control populations in early spring (Czarapata 2005). However, this method has had only partial success. Some management techniques may actually facilitate invasion. For example, mowing is shown to increase vegetative spread in *Alternanthera philoxeroides* (Jia et al. 2009). A similar response to mowing has been suggested from genetic studies on *R. ficaria* (Reisch and Scheitler 2009), and control methods for this species should be considered carefully.

High fecundity and dispersal by flooding are likely driving the invasions of *R. ficaria*. Our results suggest that varying leaf litter depths caused by flooding disturbance do not affect *R. ficaria*, even at depths expected to negatively affect growth and reproduction of other species. In addition, flooding associated with urban hydrology is expected to further reduce numbers of native species not adapted to this disturbance. Urban flooding appears to facilitate *R. ficaria*, while negatively affecting local species, and flood mitigation in urban riparian corridors may be effective in controlling this species.

Tables

Table 1.—Results of GLM for effects of leaf litter depth and environmental factors on biomass, bulbils, flowers, and seeds. Statistically significant results ($p < 0.05$) are bolded.

	Biomass			*Bulbils*			*Flowers*			*Seeds*		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Treatment	4	5.042	**0.003**	4	1.607	0.196	4	12.315	**0.000**	4	12.586	**0.000**
Block	9	1.405	0.226	9	1.001	0.459	9	2.557	**0.024**	9	5.420	**0.000**
Soil Temperature	1	0.734	0.398	1	0.650	0.426	1	0.618	0.438	1	0.383	0.541
Soil Moisture	1	0.590	0.448	1	1.370	0.250	1	0.331	0.569	1	0.446	0.509
Light	1	4.309	**0.046**	1	0.005	0.945	1	0.541	0.467	1	0.346	0.561

Figure Legends

Fig. 1.—Average final biomass of *R. ficaria* produced in each litter depth. Letters indicate significant differences in post-hoc Tukey pairwise comparisons determined from full model, and error bars indicate one (±) SE

Fig. 2.—Average number of *R. ficaria* bulbils produced in each leaf litter depth. Letters indicate significant differences in post-hoc Tukey pairwise comparisons determined from full model, and error bars indicate one (±) SE

Fig. 3.—Average number of *R. ficaria* flowers produced in each leaf litter depth. Letters indicate significant differences in post-hoc Tukey pairwise comparisons determined from full model, and error bars indicate one (±) SE

Fig. 4.—Average number of *R. ficaria* seeds produced in each leaf litter depth. Letters indicate significant differences in post-hoc Tukey pairwise comparisons determined from full model, and error bars indicate one (±) SE

Figures

Figure 1

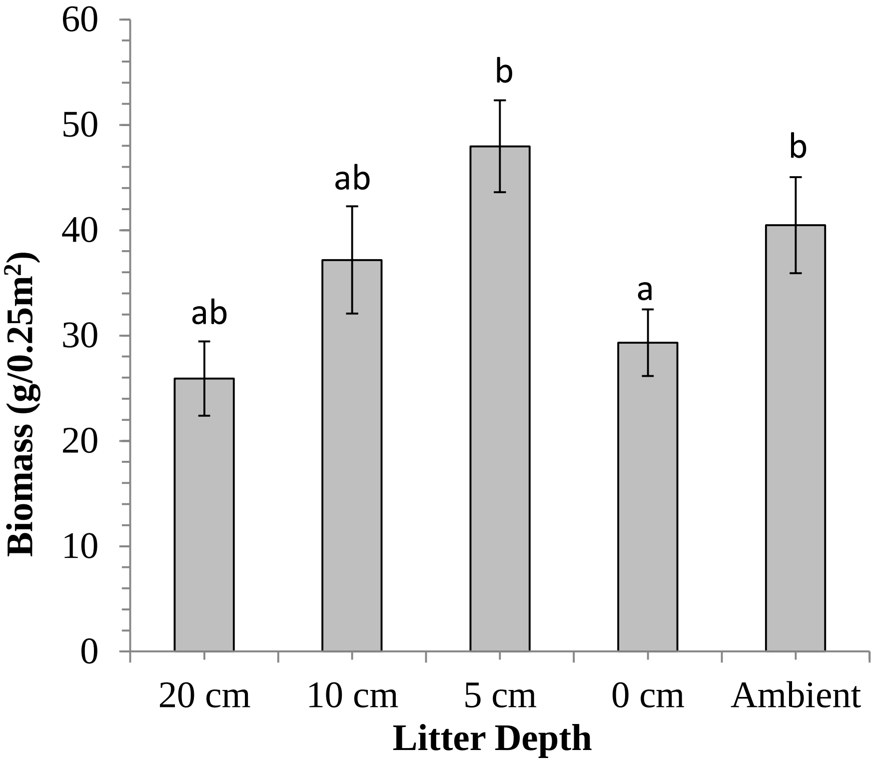


Figure 2

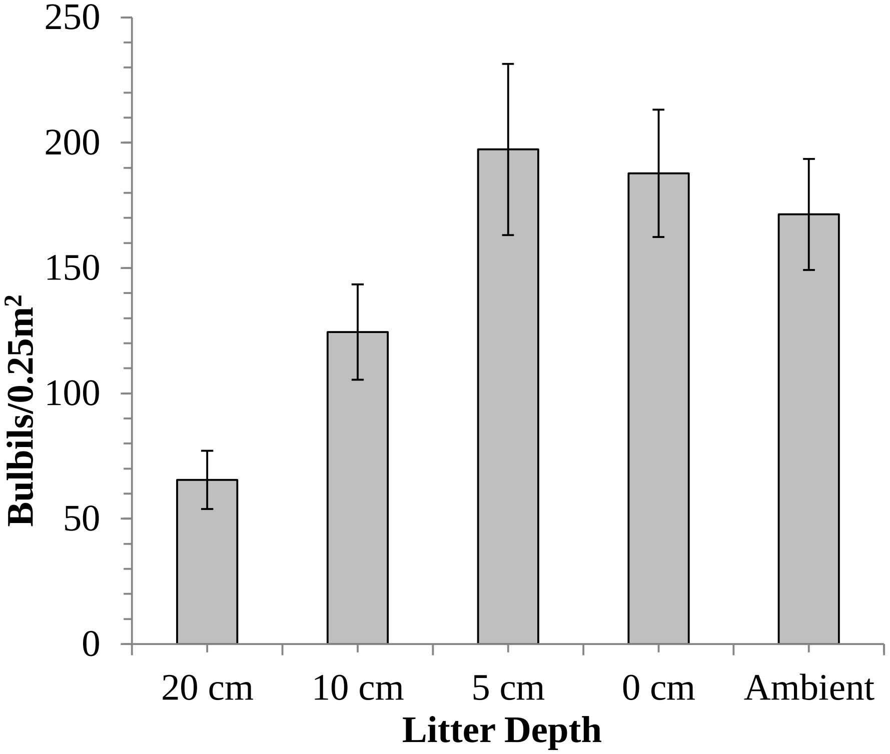

250
200
150
100
50
0
Bulbils/0.25m^2
20 cm
10 cm
5 cm
0 cm
Ambient
Litter Depth

Figure 3

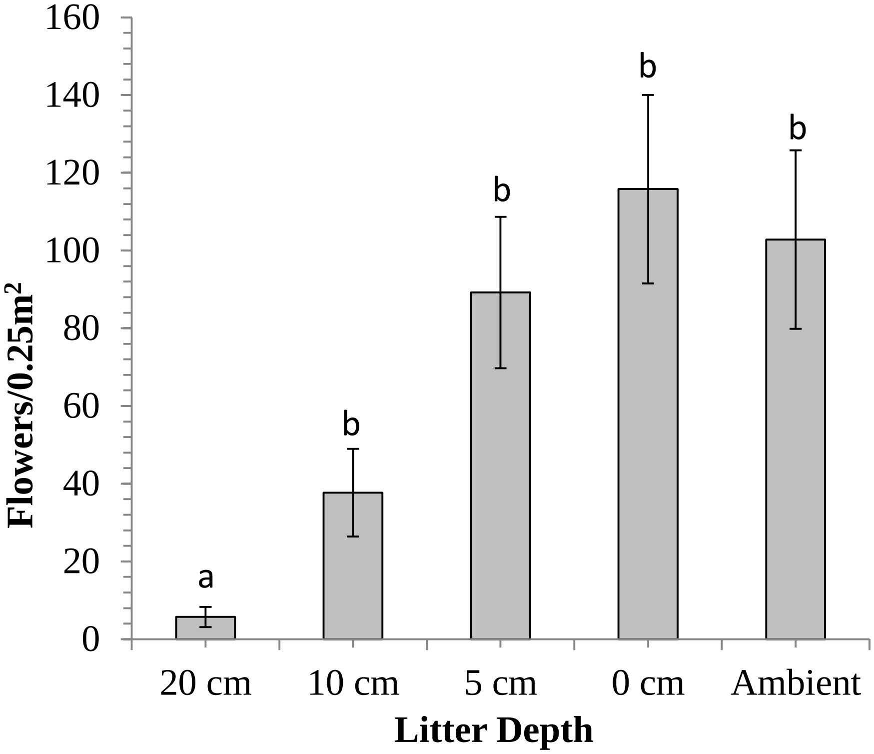
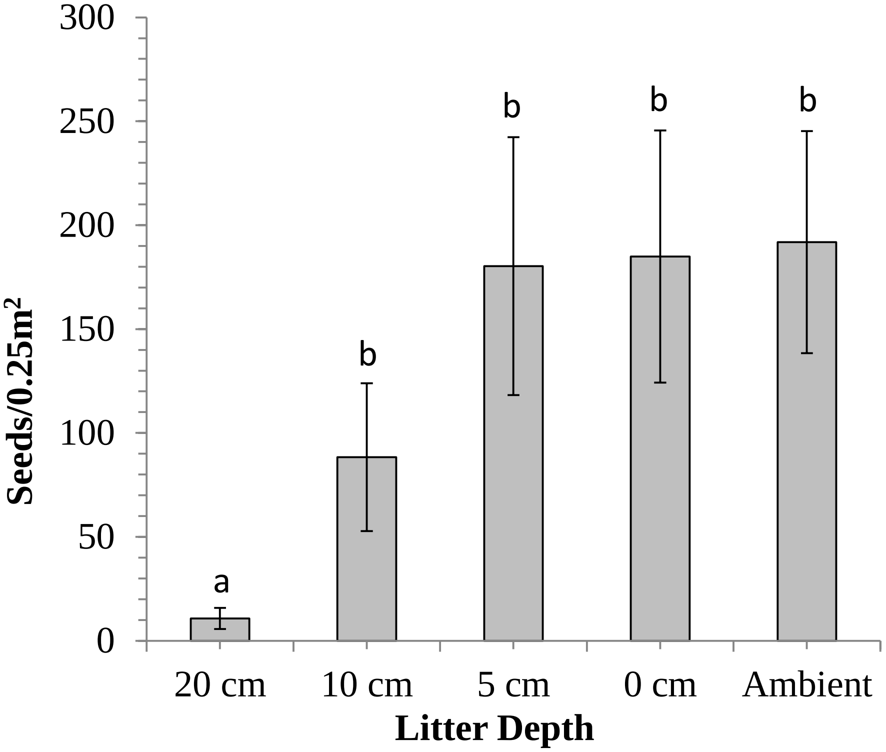

160
140
120
100
80
60
40
20
0
Flowers/0.25m²
a
b
b
b
b
20 cm
10 cm
5 cm
0 cm
Ambient
Litter Depth

Figure 4


300
250
200
150
100
50
0
Seeds/0.25m²
a
b
b
b
b
20 cm
10 cm
5 cm
0 cm
Ambient
Litter Depth

CHAPTER III

ARE THERE MULTIPLE MECHANISMS OF COMPETITION BETWEEN THE INVASIVE PLANT *RANUNCULUS FICARIA* AND NATIVE SPECIES ALONG AN URBAN STREAM?

Summary-Invasive species are believed to decrease biodiversity and local abundances of native species, but few studies have been able to establish direct causation between invasive species and negative effects. Some invasive species may simply be more tolerant of ecosystem change. Determining invasive species role in ecosystem change, including competitive interactions, may help direct restoration efforts. Several hypotheses have been presented to explain mechanisms of invasion, and species that can employ multiple mechanisms can be expected to be more competitive in any environment. *Ranunculus ficaria* is an invasive species in many temperate deciduous forests in the northeastern United States, and is especially dense in urban riparian habitats. In two experiments, we determined competitive effects (nutrient competition, allelopathy, and space/light competition) of *R. ficaria* invasion by examining the effect of *R. ficaria* removal on early season sprout species richness and abundance, as well as the growth of an added native riparian grass, *Elymus riparius*. In Experiment 1, there were 63.3% more sprouts in removal plots than in invaded plots, but removal had no effect on species diversity. There was no evidence for nutrient competition or allelopathy in Experiment 1. In Experiment 2, biomass of *E. riparius* was 50.3% greater in removal

plots, but removal had no effect on *E. riparius* sprouts counted in the plots after one month. There were 493.4% more sprouts from other species in removal plots versus invaded plots. There was again no evidence for nutrient competition or allelopathy in Experiment 2. *Ranunculus ficaria* partly relies on being a superior competitor for space and light to dominate local habitats, and has some role in reducing species diversity in invaded areas.

INTRODUCTION

Invasive species are widely believed to decrease biodiversity (Pimentel et al. 2005). However, few studies have been able to establish direct causation between invasive species dominance and reduced species diversity, in part because multiple factors can contribute to the success of introduced species (Gurevitch and Padilla 2004, Didham et al. 2005, MacDougall and Turkington 2005). The driver-passenger model of species invasions outlined by MacDougall and Turkington (2005) compares two ways that introduced species can become dominant in a habitat. Dominance can occur because the introduced species is a superior competitor (driver model) or because the introduced species is less susceptible to noncompetitive processes that may limit other species (passenger model). Invasive plants frequently establish in disturbed habitats (Hobbs and Huenneke 1992, Jia et al. 2009), and in some cases, invasive dominance is due to the ability of the invading species to establish in areas that native species can no longer inhabit because of anthropogenic disturbance (Price et al. 2011).

Under this framework, invasive species may not be responsible for losses in native diversity. Some passengers, although dominant, may actually provide facilitative effects for native species survival or other ecosystem services (facilitative passenger). For example, in areas susceptible to erosion, an abundant invasive species may serve to stabilize the soil and preserve some ecosystem services (Eviner et al. 2012). Alternatively, invasive species can interact with noncompetitive processes such as disturbance to further reduce native species (back-seat driver model) (Bauer 2012). For many invasive species, the mechanism of invasion is not clearly understood. Management of invasive plants usually involves removal as a first step, but if the invasive plant is simply a passenger of ecosystem change, removal will do little to restore habitats damaged due to some other mechanism. From this perspective, it may be useful for managers to distinguish whether invasive species are the “drivers,” “passengers,” “facilitative passengers,” or “back-seat drivers” of ecosystem change in heavily invaded areas in order to best control spread of problematic species (MacDougall and Turkington 2005, Bauer 2012).

The process of determining whether an invasive plant is driving ecosystem change or passively benefitting from ecosystem change can begin by examining its competitive effects on other plant species. There are numerous hypotheses to explain the competitive advantages of invasive plants. Most invasive plants have r-selected life history strategies (Rejmanek and Richardson 1996), and can occur in greater numbers and denser populations than native plant species (Wolfe 2002). This can result in invasive species outcompeting native species for resources such as nutrients and light (Woods 1993, Cipollini et al. 2008b). Many invasive plants also have novel allelopathic properties, allowing them to directly inhibit native plant growth (Callaway and Ridenour 2004, Callaway and Vivanco 2007). Another common explanation for invasive success is that invasives no longer face the biotic constraints they had to confront in their native environment. Many invasive plant species produce more biomass than native plants because they have escaped herbivores that suppress biomass in the plant's native range (enemy release hypothesis) (Keane and Crawley 2002). Another closely related hypothesis is the evolution of increased competitive ability (EICA). This theory predicts that invasive plant species that have escaped specialized herbivores in their introduced range can evolve with a decreased investment in chemical defenses and more energy invested into production relative to native plants (Blossey and Notzold 1995). While individually these characteristics have been shown to impart advantages to particular species, invasive plants that can employ multiple mechanisms of competition are likely to have an advantage over other species.

Ranunculus ficaria var. *bulbifera* (formerly *Ranunculus ficaria* L.) is an invasive species of low-lying wet areas in many temperate deciduous forests in the northeastern United States, and can be especially dense in urban riparian habitats. A perennial native to Europe and western Asia, it was first reported in the United States in 1867, and was probably introduced as an ornamental (Axtell et al. 2010). Invasive populations of *R. ficaria* have three modes of reproduction: seeds, bulbils, and tubers. Vegetative sprouts can emerge as early as September. In spring, it forms thick mats of vegetation that appear to prevent establishment of other species in invaded areas through resource occlusion. It has also been shown to have some allelopathic properties (Cipollini and Schradin 2011). These characteristics suggest that multiple competitive advantages could drive ecosystem change in invaded areas. However, many of the riparian habitats dominated by *R. ficaria* are highly disturbed due to urbanization. Flash flooding and contaminant inundation from street run-off are frequent in these areas (Walsh et al. 2005), and its dominance may be due to the ability to tolerate this disturbance, rather than any inherent competitive advantage.

In this study, we examined *R. ficaria*'s role as a driver or passenger of ecosystem change, testing for multiple mechanisms of competition (superior competitor for nutrients, allelopathy, or superior competitor for space/light) by examining the effects of *R. ficaria* removal on early-season herbaceous species richness and abundance, as well as the growth of a native riparian grass phytometer, *Elymus riparius*. We predicted that presence of *R. ficaria* would have a negative effect on native species due to allelopathy and competition for space. Because urban flooding often increases soil nutrients (MacDougall and Turkington 2005), we did not expect any effects of competition for soil resources.

METHODS

Study site

We conducted our studies along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301, longitude -85.698220) which is part of the Olmstead Parks system in Louisville, Kentucky. The catchment in this area is urbanized and strongly channelized (~33% impervious surface (Council 2005)), and the study sites are subject to flooding throughout the year, including street drainage and raw sewage overflow. The riparian corridor is heavily invaded with *R. ficaria* (>90% cover), which forms large monoculture patches at the study site.

Experiment 1

In early February 2012, we constructed 5 experimental blocks along a 25 m stretch of Beargrass Creek. Eight 25 cm x 25 cm plots were constructed within each block, and blocks were 3-10 m apart. Our treatment application followed a fully factorial block design with the following factors: 2 *R. ficaria* removal levels (presence/absence) x 2 carbon levels (added/control) x 2 nutrient levels (added/control). Removal treatments tested whether *R. ficaria* presence inhibited native plant species. The carbon treatment evaluated whether allelopathy was a mechanism regulating diversity, and the nutrient addition treatment tested whether competition for soil resources was a mechanism reducing diversity. We applied each treatment combination to the central 10 cm x 10 cm area within each plot. The remaining plot area acted as buffer area between treatments.

For the removal treatment, we removed *R. ficaria* from the entire plot with careful digging. The soil in each control (presence) plot was also disturbed, but *R. ficaria* was not removed, in order to control for any unintentional effects of digging. For the carbon addition treatment, we mixed 40 ml of activated carbon (dry measure) (Aquarium Pharmaceuticals) into the top 8 cm of soil. Activated carbon can absorb allelochemicals, and is frequently used in studies on allelopathy (Inderjit and Callaway 2003, Cipollini and Schradin 2011). For the nutrient addition treatment, we mixed 30 grams of Osmocote (Scotts-Sierra Horticulture Products) into the top 8 cm of soil. In late March, we counted and identified all sprouts in the center 10 cm x 10 cm area of each plot, and calculated species diversity (Shannon index, H') and total herb sprout abundance (excluding *R. ficaria* sprouts) based on individual species abundances. The data were analyzed with a three-way ANCOVA (SYSTATv12 2007) with *Ranunculus ficaria* removal, carbon addition, and nutrient addition as the main factors and block as a random covariate. All data were transformed (ln (x+1)) as needed to meet test parameters.

We evaluated whether nutrient competition or allelopathy were mechanisms explaining the success of *Ranunculus ficaria* by examining the responses of the native plant community. If *R. ficaria* removal itself increased plant diversity, we would interpret this as evidence for direct competition between the invasive and native plants (i.e., *R. ficaria* as a driver). If *R. ficaria* removal did nothing to alter plant diversity, this would be evidence of other factors such as flooding or a depauperate seed bank having overriding effects on the plant community (i.e., *R. ficaria* as passenger). If nutrient competition was important invaded plots with nutrient addition should show a positive response of other plants relative to controls. If carbon addition in invaded plots had a positive effect on diversity, then allelopathy may be an important competitive mechanism. Activated carbon may also have additional N and leak P, depending on the brand (Lau et al. 2008), and so nutrient addition also served as a control for the possible fertilization effects of carbon addition. If neither nutrient addition nor carbon addition had any effect, but *R. ficaria* removal did, we would take this as evidence that direct competition for space (light) was the main effect.

Experiment 2

In Experiment 1, there were no interactions detected between treatments in the fully factorial model, so we simplified the treatment application and the statistical model for Experiment 2 performed the following year in order to allow us to more directly test for the effects of removal while still accounting for the possible effects of nutrient limitation and allelopathy. We designed a 2 x 3 factorial experiment where *Ranunculus* *ficaria* presence or absence was crossed with three treatments to isolate potential competitive mechanisms (fertilized, allelopathic extract, or control). Because of a possible confounding effect of activated carbon on nutrient availability in Experiment 1, we also changed the method for testing allelopathic effects in Experiment 2 using a tea made from *R. ficaria* leaves as a treatment.

In February 2013, 10 new blocks were established perpendicular to stream flow in areas where *R. ficaria* densities exceeded 90% ground cover. Blocks were 1.25 m x 0.75 m and contained six 25 cm x 25 cm treatment plots separated by 25 cm buffer zones. *Ranunculus ficaria* individuals were removed from 3 randomly chosen plots in each block with careful digging. The soil in the 3 remaining plots was disturbed to mimic the removal plots. To test whether nutrient competition was important, 75 g of Osmocote were mixed into the top 8 cm of soil of one removal treatment plot and one invaded plot in each block. To test whether allelopathy was important, concentrated extract "tea" made by soaking 400 g of dried *R. ficaria* leaves in 2 L of distilled water for 48 hrs. Two-hundred ml of this tea was added to two treatment plots (one each of removal and invaded). The biomass used to create the concentration and final volume of extract applied to each plot approximated double the average dry weight biomass produced in 25 cm x 25 cm reference plots. This treatment was repeated later in the season as the plants began to flower. However, 1000 g of fresh plant material per 2 L of water were prepared for the second application. To standardize for the effect of watering the allelopathy plots, 200 ml of distilled water were added to the other treatment plots at the time of both field applications. The last two plots in each block were controls with no additional mechanism treatments beyond *R. ficaria* removal or presence.

In late February, approximately 1,000 (determined by weight) riverbank wild rye (*Elymus riparius*) seeds (source-Prairie Moon Nursery, www.prairiemoon.com) were added to each plot as a phytometer. This is a native grass species common in riparian areas and damp woodlands in Kentucky, but was not present at our study sites. In March 2013, we counted *E. riparius* seedlings and all sprouts other than *R. ficaria* and *E. riparius*. Sprouts at this time were too immature to identify, so species diversity of sprouts was not estimated in this experiment. We harvested surviving *E. riparius* individuals in May 2013 for dry weight measurement. The response data were analyzed with a two-way ANCOVA using SYSTAT v.12, with *Ranunculus ficaria* removal and mechanism treatment as the main factors, and block as a random covariate. The *E. riparius* biomass and other sprout abundance data were transformed (ln (x+1)) to meet test parameters. We elucidated mechanisms of competition by comparing germination and growth of *E. riparius* and other native plants in different plots. If soil resources were important, then invaded nutrient addition plots should show a positive response from *E. riparius* and the native community relative to controls. If the extract addition has a negative effect, then allelopathy may be an important factor. Direct competition for space (light) was assumed if *E. riparius* and native plants were more successful in *R. ficaria* in removal plots compared to invaded plots.

RESULTS

Experiment 1

In 2012 *R. ficaria* removal was the only significant factor influencing native plant abundance, with 63.3% more sprouts in removal plots than invaded plots (Fig. 1, Table

1). Removal had no effect on species diversity (Table 1), but carbon treated plots showed 43.9% lower species diversity than plots with no carbon added (Fig. 1, Table 1). There were also significant block effects for both response variables in 2012 (Table 1). No other significant effects from carbon addition, nutrient addition, or their interaction were detected (Table 1).

Experiment 2

In the 2013 experiment, *R. ficaria* removal was the only significant factor influencing final biomass of *E. riparius*, which was 98.9% greater in removal plots (Fig. 2, Table 2). However, removal had no effect on *E. riparius* sprouts counted in the plots after one month (Table 2). *Ranunculus ficaria* removal also significantly increased other native plant abundance, with an average of 493.4% more sprouts from other species in removal plots versus invaded plots in 2013 (Fig. 2, Table 2). There were no significant effects detected from nutrient and extract additions on *E. riparius* biomass or sprout number, and no significant effects detected on other sprouts (Table 2). There were significant block effects on all response variables in 2013 (Table 2).

DISCUSSION

Our results suggest that *Ranunculus ficaria* has a negative effect on native plant communities mainly through competition for soil space or light. Invasive species in other systems have been shown to be good competitors for space and light by shading out native plants (Smith 2013). For example, bush honeysuckle is known to reduce native understory plant diversity via shading (McKinney and Goodell 2010). Norway maple (*Acer platanoides*) can also outcompete native saplings and inhibit their growth in forest understory (Galbraith-Kent and Handel 2008). Competition for space and light can be especially important if invasives emerge earlier in the growing season than native plants (Rejmanek 2013, Wainwright and Cleland 2013). For example, invasive *Eragrostis curvula* (African lovegrass) in Australia relies on early emergence to outcompete native grasses (Firn et al. 2010). Early emergence in garlic mustard also contributes to a competitive advantage over native plants, and increased reproductive success (Engelhardt and Anderson 2011). *Ranunculus ficaria* emerges much earlier than native spring ephemerals and forms thick monocultures that likely crowd other species for soil space and light. Therefore, this early emergence may be a significant factor explaining this species success. The significant block effects in our results are likely due variation in canopy cover.

Nutrient additions did not have an effect on any response variable in either experiment, suggesting that nutrient competition is not important in this system. A previous study showed nutrient additions had significant effects on *Impatiens capensis* success, but not in the presence of *R. ficaria* (Cipollini and Schradin 2011). However, the study site in that experiment was not subject to the same urban flooding conditions (lawn/golf course run-off, sewage, etc.) as in our study and was likely more nutrient limited. There may have be some slight evidence for nutrient limitation in Experiment 1, as activated carbon addition may have reduced nutrient availability for some sprouts (Lau et al. 2008). Carbon addition is known to have unintended effects such as disrupting mycorrhizal associations (Wurst et al. 2010), and so the reduction of species diversity in carbon addition plots may be partly explained by this effect. However, the study area is also highly disturbed from frequent urban flooding. This disturbance can cause an influx of nutrients (Walsh et al. 2005) which may result in little nutrient limitation even in very dense populations. Our sites had consistent levels of nutrients and organic matter between invaded and removal plots (0.287-0.311% total N, 5.8-6.05% SOM) with fertilizer addition having minimal effects (see Appendix I).

We found no evidence for allelopathy as a mechanism of competition in our study. Addition of carbon did not affect sprout numbers in Experiment 1, and the addition of the extract did not affect any response variable in Experiment 2. We found a significant effect of carbon on native plant diversity in Experiment 1, but in the opposite direction as predicted. The addition of carbon actually decreased native plant diversity, possibly due to the unintended effects on soil nutrients and mycorrhizae. Other studies have shown that *Ranunculus ficaria* can negatively impact growth and reproduction of native plants through allelopathy, but this effect varies by target species (Cipollini and Schradin 2011), and the species used as a response variable in our experiment may be tolerant to these allelochemicals. Alternatively, we only applied the alleopathic tea twice, and the frequent urban flooding at our site could prevent the buildup of allelopathic chemicals. Additionally, we only used above-ground biomass to make the tea. The alleopathic properties of this species merit additional study.

Invasive plants can be classified as drivers of ecosystem change or passengers benefitting from disturbance (MacDougall and Turkington 2005, Wilson and Pinno 2013). From a management perspective, invasive species that are passengers or drivers require different approaches for control. Directly reducing populations of invasive plants is important for species that are drivers, while controlling disturbance is more important for invasive plants that are passengers. Our results establish *R. ficaria* as a superior competitor for light or soil space, indicating a role in driving ecosystem change and suggesting that direct management of these populations should help restore native diversity. However, the specific role of disturbance in this system was not explored in our study. Some of our results (no nutrient competition or allelopathic effects detected) could be explained by the effects of urban flooding. In addition, many native species are known to be intolerant to the flash flooding associated with urban hydrology (Meyer et al. 2005, Walsh et al. 2005). Because this system exhibits some aspects of a passenger model of ecosystem change, management of this species should also consider the effects of urban hydrology to be successful.

TABLES

Table 1 Results of ANCOVA for treatment effects on sprout abundance and diversity (H'), 2012

	Sprout Abundance			***Sprout Species Diversity***		
Source	*df*	*F*	*p*	*df*	*F*	*p*
Removal	1	6.930	**0.011**	1	1.960	0.167
Carbon	1	0.092	0.763	1	6.139	**0.016**
Nutrient	1	0.561	0.457	1	0.901	0.347
Removal × Carbon	1	0.033	0.856	1	0.290	0.592
Removal × Nutrient	1	3.699	0.060	1	0.548	0.462
Carbon × Nutrient	1	1.619	0.209	1	2.417	0.126
Removal × Carbon × Nutrient	1	0.090	0.766	1	1.428	0.237
Block	1	48.942	**0.000**	1	17.772	**0.000**

Statistically significant results ($p < 0.05$) are bolded.

Table 2 Results of ANCOVA for *Ranunculus ficaria* removal and treatment effects on *Elymus riparius* sprout abundance, *Elymus riparius* biomass, and other sprout abundance, 2013

	E. riparius sprouts			***E. riparius biomass***			***Other sprout abundance***		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Removal	1	1.178	0.283	1	7.814	**0.007**	1	71.561	**0.000**
Treatment	2	2.914	0.063	2	0.717	0.493	2	2.217	0.119
Removal × Treatment	2	2.437	0.097	2	0.380	0.686	2	0.707	0.498
Block	1	20.143	**0.000**	1	4.564	**0.037**	1	0.955	0.333

Statistically significant results ($p < 0.05$) are bolded.

Figure Legends

Figure 1- Effects of *Ranunculus ficaria* removal on average sprout abundance, and species diversity (H') comparisons of carbon addition plots, 2012. Error bars represent +/-1SE.

Figure 2- Effects of *Ranunculus ficaria* removal on *Elymus riparius* biomass, and average sprout (other than *E. riparius*) abundance per plot in 2013. Error bars represent +/-1SE.

Figures

Figure 1

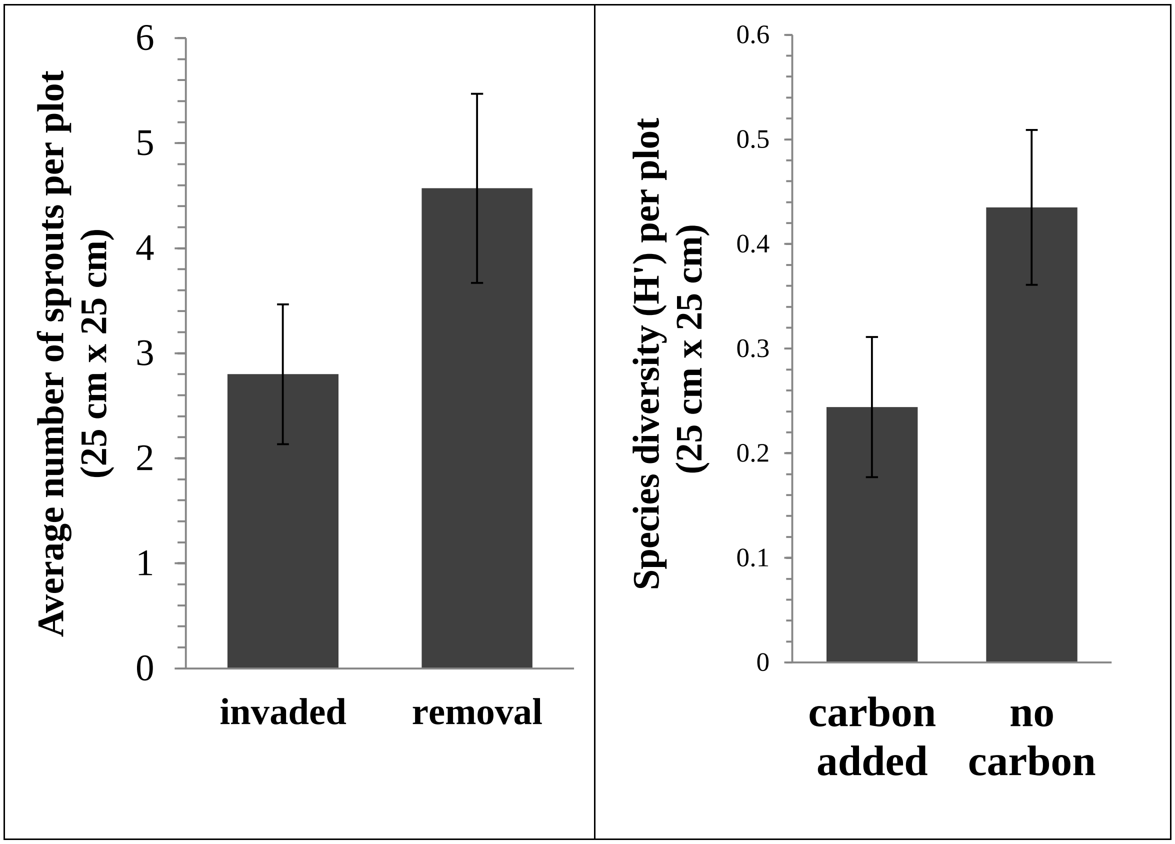
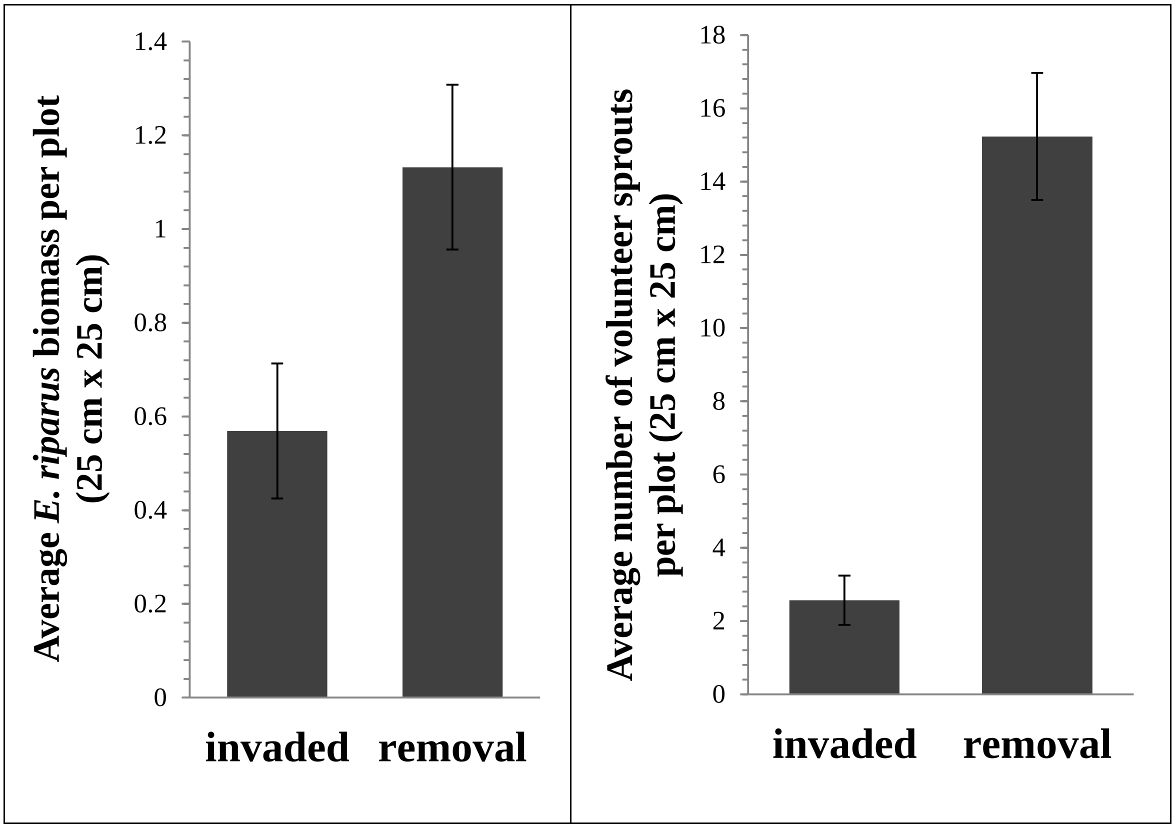


Figure 2



1.4
1.2
1
0.8
0.6
0.4
0.2
0
Average *E. riparus* biomass per plot (25 cm x 25 cm)
invaded
removal
18
16
14
12
10
8
6
4
2
0
Average number of volunteer sprouts per plot (25 cm x 25 cm)
invaded
removal

CHAPTER IV

THE SHOWY INVASIVE PLANT *RANUNCULUS FICARIA* DIFFERENTIALLY AFFECTS POLLINATOR ACTIVITY, POLLEN DEPOSITION, AND SEED PRODUCTION FOR TWO NATIVE SPRING EPHEMERAL PLANTS

Summary- Many invasive plant species have stronger floral attractants than native plants. Relatively lower floral attractiveness can reduce pollinator visitation to native plants, which can result in a reduction of seed-set in entomophilous species. Alternatively, additional floral resources provided by invasive plants may increase pollinator activity, which can facilitate pollination of native species. If pollinators are shared between native and invasive plants, foreign pollen can clog stigma of native plants, reducing seed set. *Ranunculus ficaria* (Ranunculaceae) is a showy perennial invading low-lying wet areas in temperate, deciduous forests of the eastern United States. To determine the impact of *R. ficaria* on native pollination services, we compared pollinator visitation rates, stigma pollen loads, and seed production of two sympatrically flowering, entomophilous native species (*Claytonia virginica* and *Cardamine concatenata*) between habitats invaded by *R. ficaria* and uninvaded habitats. We found significantly higher (240.4%) visitation rates to natives in invaded plots but no differences in pollinator diversity between invaded and uninvaded plots. We also found significantly higher (342.3%) per flower visitation rates to *C. virginica* in invaded plots. *Claytonia virginica* stigmas from invaded habitats had 155.3% more conspecific pollen resulting in 58.3% more seeds per capsule in invaded areas. There was 280.3% more conspecific pollen on *C. concatenata* stigmas in invaded compared to uninvaded habitats, but there were 104.6% more seeds per silique in uninvaded habitats. Our results indicated that this invasive species increases pollinator activity and conspecific pollen deposition on sympatrically flowering native ephemerals, but may have differential effects on native seed production. Management options should consider the facilitative effects of this species on pollination services, as well as the possible negative competitive effects.

INTRODUCTION

Invasive species are known to alter native habitats, and pose threats to biodiversity (Pimentel et al. 2001). Many invasive species also act as pests and disease vectors, resulting in a substantial cost to agriculture and human health (Pimentel et al. 2005). Consequently, determining the types of impacts of exotic species on native ecosystems is a major concern for conservation scientists and land managers. Invasive plant species usually impact native plants negatively through resource occlusion, acting as superior competitors for nutrients, water, space, and sunlight (Levine et al. 2003). Invasive plant species can also disrupt local pollination services resulting in reduced seed set in native species (Chittka and Schurkens 2001, Bjerknes et al. 2007). Reduced seed production can occur because pollinators prefer the exotic invaders over the natives, decreasing visitation rate and conspecific pollen deposition to natives, or because increased heterospecific pollen deposition on native plant stigmas interferes with fertilization (Chittka and Schurkens 2001). Alternatively, additional floral resources (nectar, pollen, etc.) provided by prolifically flowering invasive plants can increase overall pollinator abundance and activity, resulting in more pollination and higher seed set in co-flowering native species compared to the same species in uninvaded habitats (Moeller 2004).

Many alien plants were introduced as ornamentals, and often have a strong scent and showy flowers, making them very attractive to pollinators. Native plants growing near these species may experience reduced pollinator visitation and pollen limitation due to relatively lower floral attractiveness (Brown et al. 2002). Invasive plants that are taxonomically similar to native species can also have a significant impact on pollination services because of similarities in flower morphologies (Memmott and Waser 2002). For example in Japan, pollinator visitation and seed set were reduced in the native dandelion *Taraxacum japonicum* when grown with the invasive congener *T. officinale*, probably because *T. officinale* produced more nectar (Kandori et al. 2009). Allogamous plants that rely on specific pollinators may be especially sensitive to invasive plant species, if that species is able to monopolize pollinators in the local habitat. However, reproductive success may be reduced even in generalist native plants, if the invasive plant population is dense enough (Dietzsch et al. 2011). For example, *T. officinale* has showy flowers and only outcompeted *Hypochaeris thrincioides* and *Perezia carthamoides* for pollinators when growing in high abundances in the central Chilean Andes populations (Munoz and Cavieres 2008).

Alternatively, prolifically flowering invasive species may provide facilitative effects for native species pollination (Moeller 2004). The additional floral resources provided by these invasive species can increase pollinator abundance and diversity as well as foraging range and duration (Memmott and Waser 2002, Feldman et al. 2004, Tepedino et al. 2008, Tscheulin et al. 2009). Some invasive plant species that produce very attractive flowers may also act as “magnet species”, attracting more pollinators and increasing pollination in sympatric co-flowering native plants even for those species with lower floral attractiveness (Thomson 1978, Molina-Montenegro et al. 2008). If the flowers from different species in the community have the same relative attractiveness then adding more flowers of any species is expected to increase pollinator activity (Mitchell et al. 2009) suggesting that invasive species can act as magnet species even without superior floral attractants per individual flower.

Even if pollinator visitation rates increase in the presence of invasive plants, reproductive output in native plants may be reduced by heterospecific pollen deposition (Morales and Traveset 2008). Fertilization and seed production can be disrupted by heterospecific pollen through several mechanisms including stigma clogging, stylar clogging, and pollen allelopathy (Brown and Mitchell 2001, Holland and Chamberlain 2007, Tscheulin et al. 2009). Determining which specific mechanisms causes low seed set due to heterospecific pollen can be difficult, and usually the mechanism depends on the density of the hetrospecific pollen (Murphy 2000). However, native stigmas do not have to be completely occluded from conspecific pollen to affect reproduction. For example, seed set in native *Decodon verticillatus* was reduced by 33.3% when pollen from invasive *Lythrum salicaria* was added to stigma in a 1:1 mixture with conspecific pollen in a greenhouse study (Da Silva and Sargent 2011).

Ranunculus ficaria var. *bulbifera* (formerly *Ranunculus ficaria* var. *bulbifera*) is an invasive species in riparian areas of temperate deciduous forests in the northeastern

United States. A perennial native to Europe and western Asia, it was first reported in the United States in 1867, and was probably introduced as an ornamental due to its large yellow flowers (Axtell et al. 2010). This species can emerge as early as September, and forms thick mats of vegetation. It begins flowering in late winter, peaks by mid-spring, and often covers invaded areas with a collectively large floral display.

This study examines *R. ficaria* impacts on pollination services by comparing pollinator visitation rates, heterospecific pollen deposition, and seed production in two native entomophilous co-flowering species in invaded and uninvaded habitats. This study addressed three main questions: 1. Are pollinator visitation rates to native plants reduced in areas heavily invaded with *Ranunculus ficaria*? 2. If pollinators are shared, is there potential for *R. ficaria* pollen to clog stigmas in sympatric, co-flowering native species? 3. Is seed production reduced in native plants located in areas heavily invaded by *R. ficaria*?

METHODS

Study site

We conducted our study along Beargrass Creek (Middle Fork) in Cherokee Park (latitude 38.243301, longitude -85.698220) which is part of the Olmsted Parks in Louisville, Kentucky. The catchment in this area is urbanized and strongly channelized (~33% impervious surface (Council 2005)), and the study sites are subject to flooding throughout the year. The dominant trees in these woodlands are *Acer saccharum*, *Fraxinus americana*, and *Celtis occidentalis*.   The riparian corridor is heavily invaded with *R. ficaria* (>90% cover), and very few native spring ephemerals are present.

However, several invasive and weedy species shared the riparian corridor with *R. ficaria*. Violets (*Viola sororia*), dead nettle (*Lamium purpurea*), penny cress (*Thlaspi arvense*), dandelion (*Taraxacum officinale*), and invasive garlic mustard (*Alliaria petiolata*) were all in flower at the time of our study. There were several native ephemerals in flower in areas directly adjacent to the riparian corridor, including spring beauty (*Claytonia virginica*), toothwort (*Cardamine concatenata*), sessile trillium (*Trillium sessile*), trout lily (*Erythronium americanum*), and Dutchman's breeches (*Dicentra cucullaria*). These areas adjacent to *R. ficaria* monocultures were designated as "invaded" for our study. Nearby uninvaded sites were picked with approximately the same topography, canopy cover, and native flower density as the invaded sites. However, the intensity of seasonal flooding was much lower at the uninvaded sites, with some areas not flooding at all. The uninvaded areas were dominated by *C. virginica*, *C. concatenata*, and false anemone (*Enemion biternatum*). Sessile trillium, trout lily, and Dutchman's breeches were also in flower in uninvaded sites. The dominant trees at the uninvaded sites were oak (*Quercus* sp.), *A. saccharum*, and *F. americana*. The two most abundant native spring ephemerals that were observed co-flowering with *R. ficaria* were spring beauty (*C. virginica*) and toothwort (*C. concatenata)*. Both species require pollinator visitation for seed production under natural conditions (Schemske 1977, Spooner 1984).

Pollinator Observations

In March 2012, we conducted a study that examined how the relative abundance of *R. ficaria* affected overall pollinator activity. We established 25 1 m by 1 m observation plots which contained different densities of *R. ficaria* (range of 0 to 281 flowers per plot). We observed and recorded all floral visitors to each plot during 15 min periods. In 2012, we also followed 25 individual pollinators in the invaded sites to observe visitation fidelity of pollinators by recording flowers species visited by each pollinator for as long as possible. From these observations we determined if plots with the same floral density had differences in visitation rates due to the relative amount of *R. ficaria* flowers. We also determined if pollinators preferred *R. ficaria* over other flowers by examining two invaded plots where the abundance of *R. ficaria* flowers were equal and double the *C. virginica* flowers.

In March 2013, we established 38 1 m by 1 m observation plots in invaded sites and 15 in uninvaded sites to evaluate the impacts of *R. ficaria* on pollinator visits to the native ephemeral, *C. virginica*. Many plots also contained other co-flowering species. *Claytonia virginica* was the most abundant flower in all uninvaded plots but one, where the most abundant was *E. biternatum*. The numbers of open flowers were counted in each plot. We recorded all floral visitors to the plots during the 15 min observation periods. From this data we calculated overall totals visits, and visits per *C. virginica* flower per 15 minutes in both invaded and uninvaded sites. *Claytonia virginica* observation data were taken from 10 invaded and 14 uninvaded plots and were square root transformed to meet normality assumptions. All pollinator observations in both habitats were made between 11 am and 3 pm on mild (> 16 °C, little wind), sunny/partly cloudy days.

To examine local scale (plot level) effects of *R. ficaria* density on pollinator activity, we performed a linear regression between the relative abundance of *R. ficaria* and pollinator visitation rates in plots for both 2012 and 2013. If *R. ficaria* is preferred or is a magnet species, visitation rates are expected to rise with relative abundance of *R.*

ficaria. To get an estimate of pollinator activity on a landscape scale, we compared overall pollinator visitation rates and visits to *C. virginica* between invaded and uninvaded areas using Student's t-test on 2013 data after data transformation (ln (x+1)) to meet test assumptions. In this analysis, higher visitation rates are expected in invaded areas if *R. ficaria* is acting as a magnet species.

Stigma clogging

In March 2013, we collected 15 stigmas each from *C. concatenata* and *C. virginica* in invaded sites and 15 stigmas each from uninvaded sites. We collected stigmas after 3 pm on mild (> 16° C), sunny/partly cloudy days. Stigmas were collected with forceps and dissecting scissors and each was placed in a vial with 70% ethanol for transport back to the lab. For pollen identification and counting, we treated stigmas with aniline blue to stain pollen grains. The numbers of pollen grains on each of the native species' stigmas were counted in 3 categories: *R. ficaria* pollen, conspecific pollen, and other heterospecific pollen. Larger depositions of heterospecific pollen were expected to increase the likelihood of stigma clogging. Student's t-tests were used to compare pollen loads in invaded and uninvaded sites after data transformation (ln (x+1)).

Seed set

To compare the average number of seeds per flower for the two native species in invaded and uninvaded areas, we returned to the field sites two weeks after our pollinator observations and stigma collection in 2013 to collect mature fruit. We collected one silique each from 50 haphazardly chosen *C. concatenata* plants in both invaded and uninvaded sites. We also collected 50 mature capsules each from haphazardly chosen *C. virginica* plants in both invaded and uninvaded sites. We estimated reproductive output by determining the average number of seeds produced per fruit for each species. Student's t-tests were used to compare average seed per fruit in invaded to uninvaded sites after data transformation (ln (x+1)).

RESULTS

In 2012, regression analysis showed no effect of the relative abundance of *R. ficaria* flowers (F=0.469, p=0.500; data not shown) on pollinator activity (visitation rates to plots). Regression analysis on 2013 data also showed no effect of the relative abundance of *R. ficaria* flowers (F=3.007 p=0.091) on visitation rates. Total flower abundance was also not significant in either year at the plot level (2012, F=0.203, p=0.657; 2013, F=3.365, p=0.075). However, we found significantly higher (240.4%) overall visitation rates (F=18.205, p= <0.001) in invaded plots compared to uninvaded plots in 2013 (Fig. 1). We also found significantly higher (342.3%) per flower visitation rates to *C. virginica* (F=7.061, p= 0.014) in invaded plots (Fig. 1). In plots where the abundance of *R. ficaria* flowers were equal to or greater than the *C. virginica* flowers, 78% of the visits were to *C. virginica* (n=33 visits; data not shown). The primary pollinators visiting plants in both invaded and uninvaded areas in both years were syrphid flies and halictid bees. We observed very little pollinator sharing. In 2012, only one syrphid fly of the 25 pollinators followed was observed visiting both *C. virginica* and *R. ficaria*. The other 24 pollinators were loyal to single species during observations.

Claytonia virginica stigmas from uninvaded habitats had 155.3% more conspecific pollen (F=7.181, p=0.012) resulting in 58.3% more seeds per capsule in invaded areas (F=25.546, p= <0.001) (Fig. 1, Fig 3). There was 280.3% more conspecific pollen (F=27.765, p= <0.001) on *C. concatenata* stigmas in invaded compared to uninvaded habitats, but there were 104.6% more seeds per silique (F=19.853, p= <0.001) in uninvaded habitats (Fig. 2, Fig. 3). There was very little *R. ficaria* pollen on stigmas from both species in invaded areas (mean=2.13 grains per stigma for *C. virginica*, mean=6.80 grains per stigma for *C. concatenata*) (Fig.1, Fig. 2). There was also small amounts of *R. ficaria* pollen detected on *C. virginica* stigmas in uninvaded areas but it was significantly less than pollen on stigmas in invaded areas (F=4.984, p=0.034) (Fig. 1). There was no *R. ficaria* pollen detected on *C. concatenata* stigmas from uninvaded areas (Fig. 2).

DISCUSSION

Invasive species that contribute additional floral resources to a community can increase overall pollinator abundance, diversity, and activity resulting in more conspecific pollen deposition and higher reproductive output by native plants (Memmott and Waser 2002, Feldman et al. 2004, Tepedino et al. 2008, Tscheulin et al. 2009). Overall higher pollinator visitation rates in our invaded plots and more conspecific pollen deposition on sympatric native species indicated that *R. ficaria* has a positive effect on pollinator activity in our study system. However, this corresponded to an increase in seed set for only one of the two native species examined.

The relative density of invasive plants and flowers often determines the invasive species' impacts on pollinator behavior and on native plant reproduction (Munoz and Cavieres 2008, Dietzsch et al. 2011). In our study, overall pollinator visits were higher in invaded areas, but the relative abundance of *R. ficaria* within plots had no effect on visitation rates and pollinators showed no preference for *R. ficaria*, suggesting that simple presence of the invasive plant may be a more important influence on pollinator activity than species ratios in this system. While we did not directly observe pollinator visits to *C. concatenata*, pollen deposition data indicated that visits were higher in invaded areas for this species as well. It appears that *R. ficaria* is a strong magnet species for pollinators in this system on a landscape scale.

The low amounts of *R. ficaria* pollen and the large amounts of conspecific pollen found on both native species suggest that reduced fitness due to heterospecific pollination was low or non-existent. Our individual pollinator observations suggested that pollinators are generally loyal visitors to only one species at a time, as has been reported in other studies. The small amount of *R. ficaria* pollen found on native stigmas in both invaded uninvaded plots may actually be due to wind dispersal. *Ranunculus ficaria* pollen was produced in high enough amounts that wind could easily disperse pollen to native plants. *Claytonia virginica* and *C. concatenata* are both entomophilous, so observing seed set in these species gives a good indication of the fitness impacts of *R. ficaria* due to mechanisms associated with pollinators. *Claytonia virginica* had significantly higher seed set as expected from higher visitation rates and conspecific pollen deposition in the invaded sites. However, seed set in *C. concatenata* was lower despite higher conspecific pollen deposition in invaded sites. *C. concatenata* had no heterospecific pollen deposition in uninvaded sites, while *C. virginica* had small amounts of *R. ficaria* pollen in both invaded and uninvaded sites. The simple presence of *R. ficaria* pollen on *C. concatenata* stigmas in invaded sites may have interfered with seed production due to pollen allelopathy (Gaur et al. 2007, El-Ayeb et al. 2009). However, pollen allelopathy has never been reported in the Ranunculaceae. Most pollen allelopathy has been reported in the families Poaceae, Asteraceae, and Brassicaeae (Murphy 2001, Murphy et al. 2009a, Murphy et al. 2009b, Matsumoto et al. 2010). It is still unclear exactly why seed set was reduced in *C. concatenata* but not in *C. virginica* and further work is needed to tease apart possible mechanisms.

Many management protocols call for the removal of invasive species as the first step in restoration. However, in many cases reduced biodiversity and low occurrence of native species are due to disturbance, and presence of the invasive species is just a symptom of a degraded habitat (MacDougall and Turkington 2005). In some situations, invasive species may have the potential to maintain ecosystem function lost due to habitat disturbance or degraded habitat. For example, invasive *Oxalis pes-caprae* in the Mediterranean basin has some facilitative effects on native pollination, and removal of this species decreased pollinator efficiency and reproductive output in native plants (Ferrero et al. 2013). The invaded sites in our study are highly disturbed by frequent flooding and urban run-off, and no native ephemerals occur directly in the riparian area with *R. ficaria*. In areas directly adjacent to *R. ficaria* invasions, pollinator activity and conspecific pollen deposition were increased compared to uninvaded areas. Disturbance from urban flooding may be the main driver of low diversity in our study system, and counter to conventional wisdom, removal of the invasive species may further damage ecosystem services or inhibit restoration, especially for native plants dependent on insect pollinators. Our results indicate that competitive and facilitative effects of invasive plants can be species-specific, and so a better understanding of whole community responses to invasion is needed to make sound management decisions.

Figure Legends

Figure 1 Overall average visitation rates per plot per hour in invaded and uninvaded plots and average visitation rates to *Claytonia virginica* per flower per hour

Figure 2 Average number of pollen grains per stigma for *Claytonia virginica* and *Cardamine concatenata*

Figure 3 Average number of seeds per fruit for *Claytonia virginica* and *Cardamine concatenata*

Figures

Figure 1

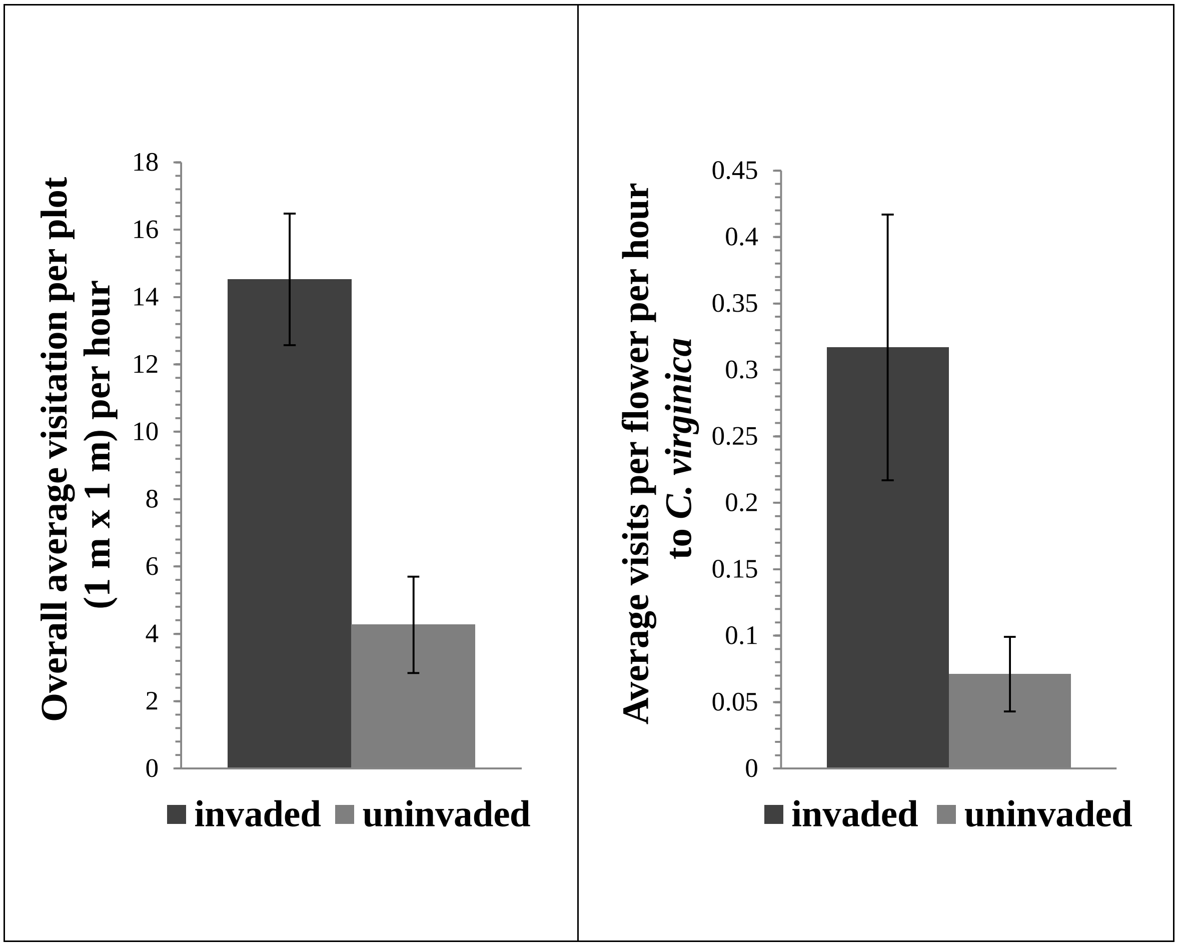


Figure 2

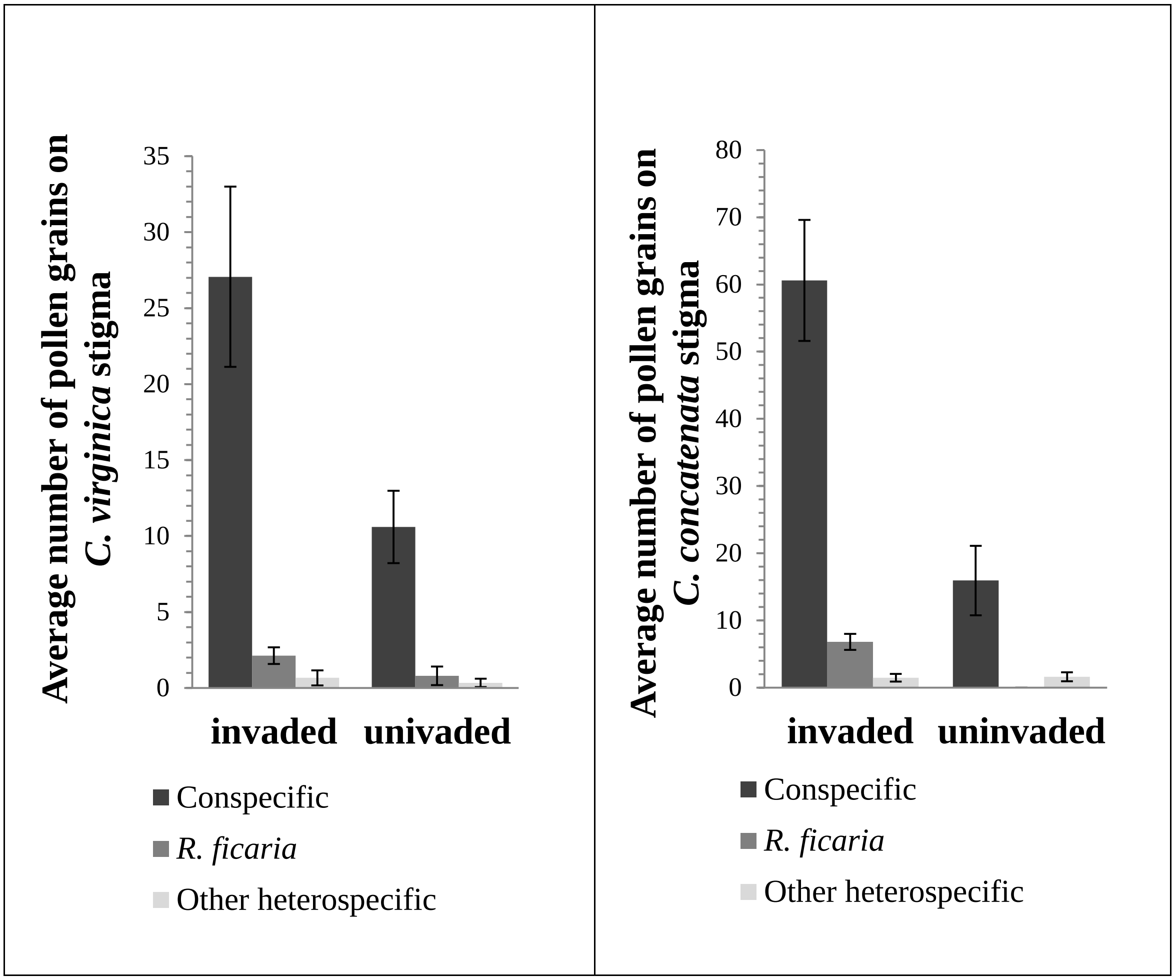
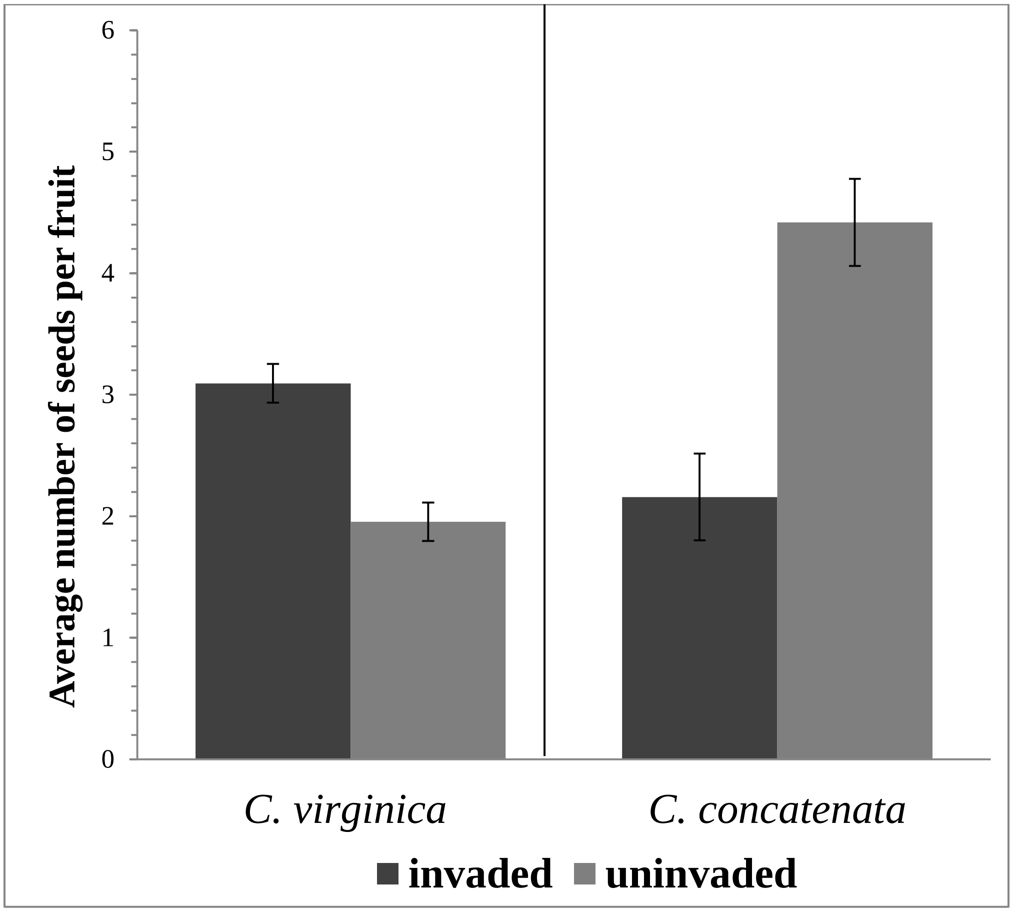

Average number of pollen grains on *C. virginica* stigma
35
30
25
20
15
10
5
0
invaded
univaded
Conspecific
R. ficaria
Other heterospecific
Average number of pollen grains on *C. concatenata* stigma
80
70
60
50
40
30
20
10
0
invaded
uninvaded
Conspecific
R. ficaria
Other heterospecific

Figure 3



6
5
4
3
2
1
0
Average number of seeds per fruit
C. virginica
C. concatenata
■ invaded
■ uninvaded

CHAPTER V

FEW IMPACTS OF INVASIVE BUSH HONEYSUCKLE (*LONICERA MAACKII*) REMOVAL ON ARTHROPOD COMMUNITIES

Summary- Invasive plant species are often associated with low biodiversity across multiple trophic levels, and management of invasive species often seeks to restore biodiversity. However, few studies have evaluated arthropod response to invasive plant removal, despite the important roles that arthropods play in ecosystems. To determine the impacts of invasive bush honeysuckle (*Lonicera maackii*) removal on arthropod communities, we conducted a management experiment by removing *L. maackii* from half of ten paired plots located in heavily invaded areas of parkland in Louisville, Kentucky. We sampled arthropods in managed and unmanaged plots using pitfall and sticky traps in the spring, summer, and fall of the first and third years after shrub removal to determine differences in arthropod abundance and morphospecies richness and arthropod decomposer and nectarivore functional groups in removal and invaded plots. Overall abundance and morphospecies richness detected from pitfall trap were not different in either year. Sticky traps detected 5.6% higher arthropod abundance and 14.1% higher morphospecies richness in removal plots one year after removal plots, but no differences in abundance or morphospecies richness were detected in the third year. Decomposer arthropods were not different between removal and invaded plots in either year. In the first year post-removal, nectarivore abundance was 2.1% higher in invaded plots and nectarivore morphospecies richness was 12.2% higher in removal plots. Nectarivores also showed significant seasonal variation one year after removal, with nectarivore abundance 67.2% higher in removal plots in fall. Our results suggest that arthropods show little sensitivity to removal of this invasive species in forest understories after one year.

INTRODUCTION

Invasive plant species are often associated with low biodiversity across multiple trophic levels and ecosystems (Levine et al. 2003, Gaertner et al. 2009, Hejda et al. 2009). For example, many invasive plants are associated with lower arthropod diversity (van Hengstum et al. 2014). Invasive plants can affect arthropod communities directly by altering habitat structure and food availability (Chittka and Schurkens 2001), and indirectly, by reducing native plant species richness and diversity (Toft et al. 2001, Gerber et al. 2008). Because arthropods play vital roles in ecosystem processes (e.g., pollination) increasing arthropod diversity through invasive plant removal may be of interest to land managers. Frequently, evaluations of invasive species removal efforts only focus on the response of the target species, or perhaps the plant community as a whole, which may not be sufficient to fully assess the effectiveness of invasive plant management (Temperton et al. 2004, Heleno et al. 2010). The examination of arthropod community responses, especially for those groups that provide key ecosystem services to management, may give land managers a better evaluation of ecosystem-level repercussions of their restoration efforts.

Despite the importance of understanding whole-community responses to invasive species management, only a small number of studies have evaluated impacts of invasive plant removal on arthropod communities (Reid et al. 2009, van Hengstum et al. 2014). The few studies on arthropod responses to invasive plant removal have exhibited conflicting results. For example, arthropod food webs were reestablished following removal of *Phragmites australis* in *Spartina* salt marshes (Gratton and Denno 2005). In another study, removal of the invasive plant,*Ligustrum sinense* increased native bee diversity (Hanula and Horn 2011). However, *Gypsophila paniculata* invasion appears to increase arthropod activity, and removal decreased abundances and diversity in Michigan sand dunes (Emery and Doran 2013). Often the direction of these patterns depends on environmental conditions and the species involved. Therefore, because of the possibility for complex interactions, it becomes important when managing invasive plant species to consider impacts of restoration efforts on arthropod communities on a case-by-case basis.

Lonicera maackii (bush honeysuckle) is an invasive shrub from East Asia, introduced into the United States for erosion control and landscaping as early as 1898 (Luken and Thieret 1996). *Lonicera maackii* is now established in 24 states in the eastern U.S. and has extended its range into Ontario, Canada (Runkle et al. 2007). The success of this species may be attributed to several characteristics. *Lonicera maackii* is allelopathic, inhibiting the growth of native seedlings, and decreasing reproduction in sympatric plants (Cipollini et al. 2008a). Spring leaf emergence for *L. maackii* occurs before native shrubs and trees, providing early access to resources, and further inhibiting native seedling growth and establishment (Miller and Gorchov 2004). In addition, *L. maackii* aggressively fills gaps in the forest canopy throughout the season, preventing the growth of mid-successional trees, and possibly limiting water and nutrients for even shade-tolerant species (Hutchinson and Vankat 1997, Luken et al. 1997). It also produces many large flowers that are mostly entomophilous (Goodell et al. 2010). Prolific production of large fruit, coupled with bird dispersal, may additionally aid the success of this invasive species (Luken and Thieret 1996).

Removal of *L. maackii* in invaded areas has been shown to increase tree seedling survival, herb establishment, and vine recovery (Luken et al. 1997, Hartman and McCarthy 2004). Because it has been shown to affect plant communities, *L. maackii* removal may also affect arthropod communities and their ecosystem services. Decomposer groups may be affected by honeysuckle invasion and removal because this species has an extended phenology, and produces a large foliar biomass with leaf litter that decomposes more rapidly than native tree leaf litter (Trammell et al. 2012). Pollinator groups may also be affected by invasive honeysuckle due to its floral characteristics. While the white color and long floral tube of *L. maackii* flowers are typical of moth pollination syndromes, many small bees and other pollinators have also been observed on the flowers (Goodell et al. 2010). These abundant, nectar-rich flowers may outcompete native flowers for pollinators, especially those native plants that rely on moths. Additionally, *L. maackii* has been shown to reduce pollinator activity and seed set in native plants due to shading (Goodell et al. 2010, McKinney and Goodell 2010), and so pollinators may show a positive response to removal. Alternatively, more floral resources can have facilitative effects on arthropods (Molina-Montenegro et al. 2008), so removal may decrease pollinator activity.

This study addressed two questions: 1) Does *L. mackii* removal alter arthropod abundances and species diversity? 2) Does *L. mackii* removal affect arthropod groups that provide key ecosystem services (pollination and decomposition)? We addressed these questions in a manipulative field experiment, in which we examined responses of arthropod communities to *L. mackii* removal in an eastern deciduous urban forest in north central Kentucky.

METHODS

To determine the impact of *L. maackii* management on arthropod communities, we established six haphazardly placed 10 m x 10 m paired plots (3 m buffer between pairs) in heavily invaded areas (100% understory cover; >100 stems plot^{-1}) of Cherokee (38.241°; -85.696°), and Seneca Parks (38.235°; -85.668°) which are part of the Olmsted Parks Conservancy in Louisville, Kentucky. The dominant trees in these woodlands were *Acer saccharum*, *Fraxinus americana*, and *Celtis occidentalis* with a mean tree basal area within the plots of 25.7 ± 3.1 m^2 ha^{-1}. The unmanaged understory had few saplings and consisted mostly of *Lonicera* shrubs with the exotic shrub, *Ligustrum sinense* (Chinese privet), being co-dominant in some locations. The mull soils in these woodlands were silt loams in the Crider and Caneyville soil series, supported exotic earthworms (mostly *Lumbricus terrestris*; Pipal and Carreiro, unpublished) and were characterized by a circumneutral pH (6.39 ± 0.17).

In January 2009, we removed all *L. maackii* from one plot in each pair. Stems were cut at the base of the shrub and an herbicide solution (25% N-(phosphonomethyl) glycine) was applied to the cut stems. Cut biomass was removed from the plots. To sample arthropod abundance and diversity, we divided all plots into sixteen 2.5 m x 2.5 m quadrats, and buried one pitfall trap (an empty 0.24 L plastic cup) flush with ground surface in each of the four central quadrats. Pitfall traps were assumed to trap decomposer groups and other ground dwelling arthropods. A yellow sticky trap (21 cm x 10 cm) was positioned approximately 8 cm above the soil in two diagonally opposite, center quadrats in each plot. Sticky traps were assumed to trap primarily flying insects including nectarivore and pollenivore functional groups. Sampling was conducted in April, July, and October of 2009 (the year immediately following management), and in May, July, and November of 2011 (third year after management). These sampling dates corresponded to seasonal differences between *L. maackii* and the associated tree canopy. The spring sampling occurred after *L. maackii* leaf emergence, but before the canopy leaves emerged. Summer sampling occurred after leaf production had peaked for both. Fall sampling occurred after canopy leaf senescence, but before *L. maackii* leaves fell. Samples were collected for 48 h, and transported in coolers back to the lab where they were stored at -20° C until processing. Arthropods were identified to family, and sorted by morphospecies and functional group (Marshall 2006).

We also quantified the stem density of other shrub species in each plot in the summers of 2009 and 2011 to account for the effects of vegetation shifts on arthropod abundances. These data were influenced heavily by the co-dominant shrub *Ligustrum sinense* in most plots.

Significant differences ($p \leq 0.05$) in total arthropod abundance and morphospecies richness, nectivore abundance and morphospecies richness, and decomposer abundance and morphospecies richness between removal and invaded plots were determined using mixed linear models in SYSTAT v.12 (SYSTATv12 2007) with honeysuckle removal and season as fixed effects and block (each plot pair) and shrub density as random covariates. All abundance data were transformed (ln +1) to meet test assumptions. Results from each trap type were analyzed separately, as the traps specialized in capturing different groups of arthropods. We also examined results from each year separately because different personnel processed the data for each year, and so sampler bias could artificially create differences between years. Strong climate differences between the sampling years could also mask treatment effects.

RESULTS

There were no differences in arthropod abundance or morphospecies richness detected between invaded and removal plots in any season in either year from pitfall traps. Sticky traps detected significantly higher (5.6%) arthropod abundance (Invaded, x=88.3, SE=18.6; Removal x=93.3, SE=17.9) and higher (14.1%) morphospecies richness (Invaded, x=17.9, SE=1.5; Removal x=20.5, SE=1.4) in removal plots in 2009, but no differences in abundance or morphospecies richness were detected in 2011 (Table 1, Table 2). There were also block effects detected on arthropod abundance measures in 2009 sticky traps and 2011 pitfall traps (Table 1).

There were no differences in decomposer abundance or morphospecies richness between invaded and removal plots in either year (Table 3, Table 4). The most abundant decomposer groups caught in pitfall traps in every season of each year were isopods (mostly Family Oniscidae). Camel crickets (Family Rhaphidophoridae) and springtails (several families) were also abundant decomposer groups across all sampling dates

(Appendix II). In addition to decomposer groups, pitfall traps caught a number of predators, with ground beetles (Family Carabidae) being the most abundant group (Appendix III). Sticky traps also caught a large number of herbivores, mostly the leaf hoppers (Family Cicadellidae) and aphids (Family Aphidae) (Appendix III). There were also no removal effects on these groups.

In 2009, nectarivore abundance was 2.1% higher in invaded plots (Invaded, x=66.8, SE=14.1; Removal x=65.4, SE=12.9) but nectarivore morphospecies richness was higher (12.2%) in uninvaded plots (Invaded, x=10.3, SE=0.5; Removal x=11.5, SE=0.6) (Tables 3 and 4). There were no differences in nectarivore abundance or morphospecies richness in 2011. In 2009, nectarivore abundances were also significantly affected by the interaction of removal and season (Table 3). In fall, nectarivore abundance was 67.2% higher in removal plots (Fig. 1). There were also block effects detected in 2009 nectarivore abundance measures (Table 3). The most abundant groups classified as nectarivores were midges (several families) and parasitoid wasps (several families), and taxa were consistent between removal and invaded plots across all sampling dates in both years (Appendix II).

There were seasonal (sampling date) effects detected across all tests except for 2009 decomposer morphospecies richness, and 2011 nectarivore abundance and morphospecies richness (Tables 1 - 4). The number of shrub stems (other than honeysuckle) occurring in plots also had significant effects on total arthropod abundance and morphospecies richness, and decomposer morphospecies richness in 2011 (Tables 1, 2, and 4**)**.

DISCUSSION

Our results indicate that bush honeysuckle removal has only a small impact on arthropod communities. Sticky traps detected higher arthropod abundance in invaded plots and morphospecies richness in removal plots in 2009, but no differences in abundance or morphospecies richness were detected in 2011. The morphospecies richness differences may be due to a reduction in the physical barriers presented by thick *Lonicera* growth, making sticky traps more visible to more species of flying insects. In 2009, immediately after removal, the structural complexity of vegetation in removal plots was low compared to invaded plots, especially in the spring when honeysuckle is usually the only actively growing species. As annual understory plant species colonized removal plots, the physical structural complexity of the understory increased, possibly making sticky traps more obscured by 2011. The higher abundances in invaded plots in 2009 were likely due to a few densely occurring species taking refuge in stands of *L. mackii*. This effect also dissipated when the physical structural complexity of the understory increased in removal plots. Overall, the differences were small and removal of *Lonicera* appears to have little effect on arthropod abundance and morphospecies richness three years after management.

While it is often expected that removal of an invasive species should restore affected communities (Gratton and Denno 2005, 2006), severely degraded habitats may be unable to “bounce back” simply by removing the invasive species (Suding et al. 2004, Reid et al. 2009). It is also possible that there is a delay in a community’s response to management. Habitats degraded by *L. maackii* can take as long as seven years after removal to recover plant species richness and cover (Runkle et al. 2007). Our results from one year and three years after removal may not have captured the recovery time needed. In other cases, plant invasions may have little or no impact on arthropod abundance and species diversity (Hartley et al. 2010), and so arthropod assemblages would be expected to show little response to management. For example, *L. maackii* may provide similar resources for arthropods as displaced native plants (e.g., spicebush). In this case, arthropods would show little response to invasion (and removal) despite large changes in the plant community. Scale may be another complicating factor. Our study plots were 10 m x 10 m placed within large invaded areas several ha in size, so the relatively small scale of the removal may have had little effect relative to the insects' foraging and dispersal flight distances, which can often range several km (Pasquet et al. 2008). In addition, the surrounding forest matrix had changed between sampling years due to management. This could have also altered expected arthropod responses to honeysuckle removal.

Invasive honeysuckle is known to have effects on leaf litter decomposition and soil biota (Arthur et al. 2012, Trammell et al. 2012), but arthropod decomposer groups were unaffected by honeysuckle removal in our study. These results support other work on arthropod decomposer abundances and bush honeysuckle removal. Christopher and Cameron (2012) found no difference in total leaf litter arthropod abundance and diversity between removal and invaded plots sampled over a year, and suggested that the microclimate changes caused by invasion have little effect on litter arthropods (Christopher and Cameron 2012).

In spring 2009, nectarivore abundance was higher in invaded plots, but in fall 2009 nectarivore abundance was higher in removal plots. These differences may be due to resource availability associated with the plant community. While shading is shown to reduce nectarivore activity in honeysuckle stands, the large floral display can also increase pollinator activity in invaded areas to compensate for this effect (McKinney and Goodell 2011). It is likely that in spring 2009, immediately after removal, structural complexity of vegetation and floral display in removal plots were very low, discouraging nectarivore presence. As the year progressed, some late-flowering annual understory plant species colonized the removal plots, possibly reversing this effect. Honeysuckle flowering peaks in spring at our study site, and the largest floral display for other understory species in removal plots occurred in summer (e.g., *Alliaria petiolata*, *Impatiens capensis*, *Hydrophyllum canadense*, *Phytolacca americanum*; M. Carreiro, unpub. data), so this may explain the observed nectarivore activity. In 2009, overall nectarivore morphospecies richness was higher in removal plots, but nectarivore abundances were higher in invaded plots. By 2011, we found no differences in nectarivores between invaded and removal plots, possibly because more perennial understory plant species had established in removal plots, effectively replacing the physical structure and floral display previously provided by honeysuckle. Our results also showed that whereas overall nectarivore abundances were high across all treatments, very few pollinators such as bees and Lepidoptera were collected. This may be due to a sampling bias associated with yellow sticky traps, but these traps are known to capture pollinators in other studies (Nielsen et al. 2008). It is more likely that these pollinator groups are just not very common in our study area. Our results suggest that managers concerned about pollinator services for native plants should not expect the decrease in potential pollinators associated with honeysuckle removal to be long-lasting.

We found significant seasonal and block effects in this study. There were large differences in moisture and temperature between sampling dates in each year (data not shown) that could account for the seasonal differences in arthropods. We only sampled once per season, and sampling dates may not represent weather pattern effects of the entire season. However, seasonal and weather effects on arthropod activity are expected (Honek and Kocourek 1988, Briers et al. 2003). Even ground arthropod activity is very sensitive to temperature which can affect pitfall sampling results (Saska et al. 2013). Block design and consistency in sampling dates limit these concerns in our experiment. The block effects detected in our results were mostly likely due to differences in slope, light penetration from the tree canopy, other shrubs (*Ligustrum sp.*) and winter creeper (*Euonymus fortunei*) ground cover between plot pairs (data not shown). Our results suggest that season and plot characteristics had more influence on arthropod communities than invasive species removal.

Removal of invasive species can often have unpredictable results, and studies on the impacts of invasive plant species management on multiple trophic levels can help direct restoration efforts (Reid et al. 2009, Heleno et al. 2010). In our study, *L. maackii* removal had little effect on arthropod abundance and diversity. Time since removal and the scale of the removal may be important considerations. Even so, our results suggest that managers may not need to be concerned with the effect of honeysuckle removal on arthropods and associated decomposition and pollination services.

Tables

Table 1 Linear mixed model analysis for effects of honeysuckle removal on arthropod abundance

	2009 pitfall			*2009 sticky*			*2011 pitfall*			*2011 sticky*		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Treatment	1	2.383	0.136	1	10.475	**0.004**	1	2.328	0.140	1	0.655	0.426
Season	2	6.611	**0.005**	2	130.279	**0.000**	2	43.941	**0.000**	2	5.391	**0.012**
Treatment × Season	2	0.042	0.959	2	2.351	0.118	2	0.781	0.469	2	0.711	0.501
Block	5	0.889	0.504	5	4.689	**0.004**	5	5.154	**0.002**	5	0.375	0.860
Other Shrub Stems	1	2.397	0.135	1	4.130	0.054	1	4.899	**0.037**	1	1.102	0.304

Statistically significant results ($p < 0.05$) are bolded.

Table 2 Linear mixed model analysis for effects of honeysuckle removal on arthropod morphospecies richness

	2009 pitfall			*2009 sticky*			*2011 pitfall*			*2011 sticky*		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Treatment	1	1.272	0.270	1	6.626	**0.017**	1	2.659	0.116	1	0.024	0.879
Season	2	4.490	**0.022**	2	28.048	**0.000**	2	18.453	**0.000**	2	5.630	**0.010**
Treatment × Season	2	1.497	0.244	2	0.187	0.831	2	0.556	0.580	2	1.762	0.193
Block	5	1.079	0.397	5	1.353	0.278	5	1.272	0.308	5	0.935	0.476
Other Shrub Stems	1	0.486	0.493	1	1.631	0.214	1	4.307	**0.049**	1	1.609	0.217

Statistically significant results ($p < 0.05$) are bolded.

Table 3 Linear mixed model analysis for effects of honeysuckle removal on decomposer and nectarivore abundance

	2009 decomposers			*2009 nectarivores*			*2011decomposers*			*2011 nectarivores*		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Treatment	1	3.771	0.064	1	4.991	**0.035**	1	1.426	0.244	1	0.469	0.500
Season	2	5.172	**0.014**	2	74.095	**0.000**	2	25.387	**0.000**	2	2.821	0.079
Treatment × Season	2	0.426	0.658	2	3.846	**0.036**	2	0.106	0.900	2	0.130	0.879
Block	5	0.177	0.969	5	3.419	**0.019**	5	3.307	0.021	5	1.383	0.266
Other Shrub Stems	1	1.855	0.186	1	3.058	0.094	1	1.149	0.294	1	0.784	0.385

Statistically significant results (*p* < 0.05) are bolded.

Table 4 Linear mixed model analysis for effects of honeysuckle removal on decomposer and nectarivore morphospecies richness

	2009 decomposers			*2009 nectarivores*			*2011 decomposers*			*2011 nectarivores*		
Source	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*	*df*	*F*	*p*
Treatment	1	1.398	0.249	1	10.645	**0.003**	1	0.192	0.665	1	0.010	0.921
Season	2	1.511	0.241	2	15.758	**0.000**	2	15.834	**0.000**	2	1.565	0.230
Treatment × Season	2	2.053	0.150	2	1.321	0.286	2	1.426	0.260	2	0.549	0.585
Block	5	0.317	0.898	5	1.694	0.176	5	1.789	0.153	5	1.074	0.399
Other Shrub Stems	1	0.156	0.696	1	3.397	0.078	1	5.463	**0.028**	1	1.729	0.201

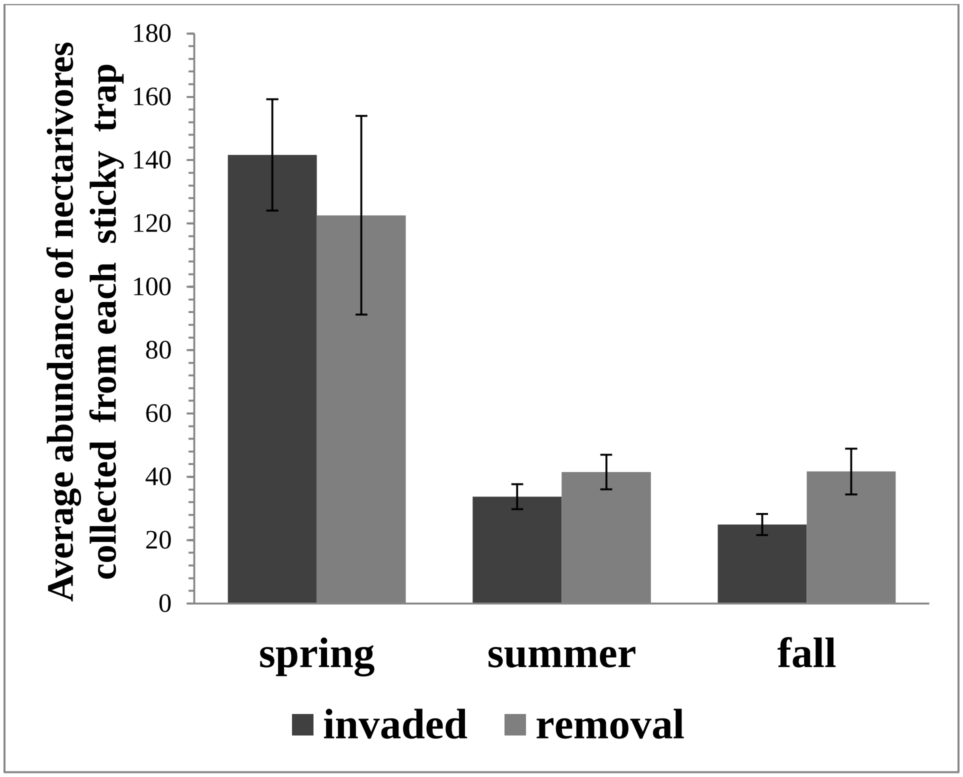
Statistically significant results ($p < 0.05$) are bolded.

Figure Legend

Figure 1 Average abundances per plot of nectarivores in 2009 by season

Figures

Figure 1



CHAPTER VI

SUMMARY AND FUTURE DIRECTIONS

Summary

This dissertation investigated *Ranunculus ficaria*'s impacts on species diversity and native plant populations in a disturbed urban riparian habitat. Specifically, the work determines *R. ficaria*'s roles as a passenger and as a driver of lower diversity and native species abundance. Chapter two shows that *R. ficaria* can act as a "passenger" by tolerating varying leaf litter depths caused by flash flooding. The removal study in chapter three shows how *R. ficaria* can act as "driver" by outcompeting other species for space and light. The pollination study shows that the additional floral resource provided by *R. ficaria* invasion can increase pollinator activity resulting in higher seed set in some native species. These results suggest that for pollination services *R. ficaria* can act as a "facilitative passenger" increasing conspecific pollination and seed-set. This has management implications because these facilitative effects may be lost if *R. ficaria* is completely removed. In contrast, chapter five showed that removal of another invasive species, *L. maackii,* had only a small effect on arthropod diversity and abundance, and arthropod assemblages were no different in *L. maackii* removal plots after three years.

While the *R. ficaria* removal study shows that this invasive species can be a "driver," the leaf litter study only partly illuminates *R. ficaria*'s passenger characteristics.

More work is needed to determine the how flooding disturbance impacts native species plant diversity. In addition, the *L. maackii* study in chapter five illustrates how removal of invasive species itself can have positive, negative, or neutral effects depending on species or local environmental conditions. Considering the results of the pollination study in chapter four, additional work is needed to determine if spread or removal of *R. ficaria* would affect pollination services and native species plant diversity at the community scale.

Future Directions

In this dissertation, I illustrated that *R. ficaria* can act as a "driver" by decreasing other species diversity and abundance through competition for space. *Ranunculus ficaria* also showed some characteristics of a passenger by tolerating aspects of disturbance that are expected to negatively affect other species. However, our study did not directly measure other aspects of disturbance and their impacts on native species. Erosion and contamination from street run-off are likely the primary drivers of low diversity in this habitat. The next step for this study would be to expand the competition study to include these disturbance effects on native plant species diversity and local abundances. Our study also showed that *R. ficaria* invasion can increase pollinator activity. Future studies on this system would determine how changes in pollinator assemblages and local pollination services can drive long term changes in the local plant community.

1. How does disturbance caused by urban flooding influence plant community assemblages and *R. ficaria* invasion?

I would like to continue to examine how invasive species and disturbance act to reduce native plant abundance and diversity. The main research questions can be answered with an expansion of the removal experiments. If there is a positive response from native plants after large scale removal of the invasive species, then the invasive species was likely driving the negative effects on native plants. However, in the expanded study I would also take measures of flooding intensity and soil degradation. I would collect data from a gradient down a single stream (such as Beargrass Creek) that has invaded and uninvaded areas. I would collect the same data from several same-aged streams across an urban to rural gradient. This would give an indication of how urbanization and flooding disturbance may be affecting local plant species across several streams, as well as an indication of the interaction between *R. ficaria* invasion and flooding disturbance.

For measures of the physical effects of flooding on plant communities, I would compare the velocity, depth, and time of inundation for floods in invaded and uninvaded areas. Sampling points would be staked out across the floodplain of an invaded stream. A flow rate sensor would be used to measure flow rate at each point during flooding events. At the same time, I would record the water depth at each point. The duration of inundation for each point would also be recorded. These flooding statistics would then be compared to *R. ficaria* densities, as well as the abundance and diversity of other plants around each point (5 m x 5 m plots). This design can help explain how flooding intensity might facilitate invasion by reducing the diversity and abundances of competitors. The results from other streams could be correlated with the results from *R. ficaria* invaded streams to answer comparative questions about how flooding affects plant communities.

For example, do other invasive or weedy plant species dominate stream floodplains with similar flooding statistics as floodplains invaded with *R. ficaria*?

I would also examine how soil composition and depth are affected by street run-off and flooding velocity during flooding events. Soil in the sampling points would be tested for heavy metals as an estimate of contamination. I would also employ a series of transplant experiments. First, I would transplant several native plants into areas where *R. ficaria* has been removed. In greenhouse experiments, native plants would also be potted in soil from invaded habitats. Additionally, I would add a control treatment in the field with native plants in anchored pots. This treatment would help isolate the effects of flooding velocity from other soil effects. Because high velocity flooding may significantly redistribute soil, top soil depth would be measured at random points along the invaded floodplain before and after flooding events as an additional explanatory variable.

This combination of treatments and observations could give information on the impacts of flooding disturbance, the competitive effects *R. ficaria*, and any possible interactions further separating its dual role as “driver” and “passenger”.

2. How will an expanding range of *Ranunculus ficaria* shift insect assemblages and what are the implications for pollinator-driven changes in plant community composition?

As *R. ficaria* expands its range it may encounter and disrupt novel pollinator syndromes in the new habitat, which could lead to the loss of some species and facilitation of other species due to altered pollinator behavior. Collectively, these interactions could lead to large scale changes in the plant community due to shifts in pollinator assemblages. I plan to implement several experiments to examine plant and pollinator interactions in sympatric species to determine patterns of community change due to pollinator interactions. The studies will include pollinator observations and distribution mapping of pollinators and plants.

The first step would be extensive sampling across a gradient of uninvaded habitats to invaded habitats similar to the one described above. Insects would be collected from a series of transects along the gradient in early to late spring. A variety of trapping methods would be utilized including sweep nets, pitfall traps, and pheromone traps. This data would give an indication of active insects in the areas at the time of sampling. Plants surveys would also be performed along the transects. At points along each transect, all plant species would be identified from a one meter square plot, specifying plants with open flowers. Three-dimensional structure of vegetation would also be estimated in these plots. This could be done economically by vertically placing a yardstick at random points in the plot and recording vegetation height at points where vegetation touches the yardstick. Each transect and sampling point (plot location) would be mapped.

Pollinator observations will also be made along the sampling transacts. The methods would be similar to those explained in chapter four. Observation plots (1 m x 1 m) would be constructed at random points along each transect along the invasion gradient. All open flowers in the plots would be counted by species. All pollinator visits to the plots would be recorded for fifteen minute observation periods. During observations, I would record pollinator species, species of the flower visited, and the time spent on each flower. I would also track individual pollinators following the methods described in chapter four. I would map each transect and plot location.

By comparing censoring data to observed behavior, I can determine if there are consistent differences in native plant communities as pollinator assemblages or pollinator behavior changes with invasion. I would correlate this data to other plant data including estimates of biomass and reproductive output for native species at the study sites. Geographic Information System (GIS) maps and niche modeling techniques could be used to predict future patterns of plant community change due to shifts in pollinator assemblages.

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Appendices

Appendix I- Soil Analysis of invaded plots and control plot

	Control Plots (no Nutrients)	Nutrient Addition Plots
Organic matter	5.8%	6.05%
Nitrogen	0.287%	0.311%
Phosphorus	176	171
Potassium	280	319
Soil pH	7.6	7.4
Calcium	7600	6489
Magnesium	728	639
Zinc	58.3	51.1

Appendix II- Abundances for Taxa Classified as Decomposers and Nectarivore

Taxa	Functional Group	Abundance Invaded	Abundance Removal
Class Crustacea			
Order Isopoda	Decomposer	389	264
Class Diplopoda	Decomposer	14	17
Class Entognatha			
Order Collembola	Decomposer	150	253
Class Insecta			
Order Archaeognatha	Decomposer	2	0
Order Blattaria			
Family Blattellidae	Decomposer	4	2
Order Dermaptera	Decomposer	1	2
Order Orthoptera			
Family Gryllidae	Decomposer	19	54
Family Rhaphidophoridae	Decomposer	49	44
Order Lepidoptera			
Family Gracillariidae	Nectarivore	0	1
Family Sphingidae	Nectarivore	0	1
Unidentified Lepidoptera	Nectarivore	6	0
Order Diptera			
Family Blephariceridae	Nectarivore	3	3

Family Calliphoridae	Nectarivore	6	7
Family Cecidomyiidae	Nectarivore	441	360
Family Ceratopogonidae	Nectarivore	1	11
Family Chironomidae	Nectarivore	1136	1058
Family Chloropidae	Nectarivore	2	2
Family Clusiidae	Nectarivore	344	143
Family Culicidae	Nectarivore	48	24
Family Dixidae	Nectarivore	0	1
Family Dolichopodidae	Nectarivore	351	254
Family Empedidae	Nectarivore	24	12
Family Lauxaniidae	Nectarivore	5	4
Family Muscidae	Nectarivore	34	54
Family Mycetophilidae	Nectarivore	440	286
Family Phoridae	Nectarivore	285	323
Family Pipunculidae	Nectarivore	7	9
Family Rhagionidae	Nectarivore	0	1
Family Sciaridae	Nectarivore	447	307
Family Sciomyzidae	Nectarivore	6	10
Family Sepsidae	Nectarivore	1	0
Family Simulidae	Nectarivore	54	42
Family Stratiomyidae	Nectarivore	70	18
Family Syrphidae	Nectarivore	40	43
Family Tabinidae	Nectarivore	1	1

Family Tachinidae	Nectarivore	1	0
Family Tephritidae	Nectarivore	1	2
Family Tipulidae	Nectarivore	15	18
Unidentified Diptera	Nectarivore	231	211
Order Coleoptera			
Family Agyrtidae	Decomposer	1	0
Family Bostrichidae	Decomposer	3	0
Family Dermistidae	Decomposer	1	0
Family Lampyridae	Nectarivore	1	2
Family Scydmaenidae	Decomposer	1	0
Family Siphidae	Decomposer	0	1
Family Trogidae	Decomposer	0	1
Order Hymenoptera			
Family Argidae	Nectarivore	0	6
Family Bethylidae	Nectarivore	0	1
Family Braconidae	Nectarivore	301	251
Family Chrysididae	Nectarivore	1	6
Family Crabronidae	Nectarivore	38	0
Family Cynipidae	Nectarivore	2	2
Family Diapriidae	Nectarivore	2	0
Family Encyrtidae	Nectarivore	2	3
Family Eurytomididae	Nectarivore	0	2
Family Evaniidae	Nectarivore	5	7

Family Halictidae	Nectarivore	4	8
Family Ichneumonidae	Nectarivore	52	49
Family Megachilidae	Nectarivore	0	1
Family Papmphiliidae	Nectarivore	0	1
Family Proctotrpidae	Nectarivore	1	0
Family Sphecidae	Nectarivore	0	3
Family Tenthredinidae	Nectarivore	14	18
Family Vespidae	Nectarivore	1	0
Superfamily Chalcidoidea	Nectarivore	1445	993
Unidentified Parasitoid Wasps	Nectarivore	208	180

Appendix IIIa – All taxa and functional group classifications from invaded plots listed by abundance

Taxa	Total Collected	Functional Group
Superfamily Chalcidoidea	1445	nectarivore
Family Chironomidae	1136	nectarivore
Family Cicadellidae	1080	herbivore
Family Sciaridae	447	nectarivore
Family Cecidomyidae	441	nectarivore
Family Mycetophilidae	440	nectarivore
Family Aphidae	420	herbivore
Order Isopoda	389	decomposer
Family Dolichopodiae	351	nectarivore
Family Clusiidae	344	nectarivore
Family Braconidae	301	nectarivore
Family Phoridae	285	nectarivore
Order Diptera: unknown ID	231	nectarivore
unknown parasitoid wasp	208	nectarivore
Order Collembola	148	decomposer
Family Formicidae	141	omnivore
Family Carabidae	123	predator
Order Thysanoptera	123	herbivore
Family Chrysomelidae	76	herbivore

Family Membracidae	75	herbivore
Family Stratiomyidae	70	nectarivore
Order Opiliones	68	predator
Family Psylidae	62	herbivore
Order Coleoptera: unknown ID	61	other
Family Coccinellidae	58	predator
Family Lycosidae	58	predator
Family Staphylinidae	57	predator
Family Simulidae	54	nectarivore
Family Ichneumonidae	52	nectarivore
Family Scarabaeidae	51	herbivore
Family Trombidiidae	50	predator
Family Culicidae	48	nectarivore
Family Raphidophoridae	48	decomposer
Family Anthicidae	42	omnivore
Family Syrphidae	40	nectarivore
Family Crabronidae	38	nectarivore
Family Phlaeothripidae	36	herbivore
Family Muscidae	34	nectarivore
Family Elateridae	30	herbivore
Family Mordellidae	25	herbivore
Family Empedidae	24	nectarivore
Family Gryllidae	19	decomposer

Family Cantharidae	18	predator
Order Aranae: Unknown ID	16	predator
Family Tipulidae	15	nectarivore
Family Salticidae	14	predator
Family Tenthredinidae	14	nectarivore
Class Diplopoda	13	decomposer
Family Thomisidae	12	predator
Family Asilidae	8	predator
Family Bruchidae	8	herbivore
Family Araneidae	7	predator
Family Derbidae	7	herbivore
Family Miridae	7	predator
Family Pipunculidae	7	nectarivore
Family Calliphoridae	6	nectarivore
Family Hemerobiidae	6	predator
Family Sciomyzidae	6	nectarivore
Family Triozidae	6	herbivore
Subclass Acari	6	predator
Family Evaniidae	5	nectarivore
Family Lauxaniidae	5	nectarivore
Family Nitidulidae	5	herbivore
Order Lepidoptera: unknown ID	5	nectarivore
Family Blattellidae	4	decomposer

Family Cercopidae	4	herbivore
Family Halictidae	4	nectarivore
Family Muscidae	4	nectarivore
Family Belphariceridae	3	nectarivore
Family Bostrichidae	3	decomposer
Family Tingidae	3	predator
Order Mecoptera	3	other
Family Aleyrodidae	2	nectarivore
Family Chloropidae	2	nectarivore
Family Cynipidae	2	nectarivore
Family Delphacidae	2	herbivore
Family Diapriidae	2	nectarivore
Family Encyrtidae	2	nectarivore
Family Eulophidae	2	other
Family Machilidae	2	decomposer
Family Mutillidae	2	predator
Family Pentatomidae	2	predator
Family Poduridae	2	decomposer
Family Psocidae	2	herbivore
Order Pseudoscorpionida	2	predator
Order Salticidae	2	predator
Class Chilopoda	1	predator
Family Agyrtidae	1	decomposer

Family Ceratopogonidae	1	nectarivore
Family Chrysididae	1	nectarivore
Family Dermestidae	1	decomposer
Family Forficulidae	1	decomposer
Family Gelastocoridae	1	predator
Family Histeridae	1	predator
Family Isotomidae	1	decomposer
Family Issidae	1	herbivore
Family Lampyridae	1	nectarivore
Family Leiodidae	1	other
Family Phaphidophoridae	1	decomposer
Family Pisauridae	1	predator
Family Proctotrupidae	1	nectarivore
Family Rhinotermitidae	1	other
Family Rhinotermitidae	1	other
Family Scydmaenidae	1	decomposer
Family Sepsidae	1	nectarivore
Family Tabanidae	1	nectarivore
Family Tachinidae	1	nectarivore
Family Tenebrionidae	1	herbivore
Family Tephritidae	1	nectarivore
Family Tetrigidae	1	other
Family Tipulidae	1	other

Family Vespidae	1	nectarivore
Order Archaeognatha	1	decomposer
Order Lepidoptera: Larvae	1	herbivore
Order Polydesmida	1	decomposer
Order Reduvidae	1	predator

Appendix IIIb – All taxa and functional group classifications from removal plots listed by abundance

Taxa	Total Collected	Functional Group
Family Cicadelidae	1119	herbivore
Family Chironomidae	1058	nectarivore
Superfamily Chalcidoidea	993	nectarivore
Family Aphidae	419	herbivore
Family Cecidomyiidae	360	nectarivore
Family Phoridae	323	nectarivore
Family Sciaridae	307	nectarivore
Family Mycetophilidae	286	nectarivore
Order Isopoda	264	decomposer
Family Dolichopodidae	254	nectarivore
Order Collembola	252	decomposer
Family Braconidae	251	nectarivore
Order Diptera: unknown ID	211	nectarivore
unknown parasitoid wasp	180	nectarivore
Family Clusiidae	143	nectarivore
Order Thysanura	142	herbivore
Family Carabidae	136	predator
Family Formicidae	122	omnivore
Family Chrysomelidae	106	herbivore

Family Psyllidae	73	herbivore
Family Phlaeothripidae	69	herbivore
Family Trombidiidae	66	predator
Family Membracidae	55	herbivore
Family Gryllidae	54	decomposer
Family Muscidae	54	nectarivore
Family Simulidae	52	nectarivore
Family Crabronidae	52	predator
Order Coleoptera: unknown ID	51	other
Family Ichneumonidae	49	nectarivore
Family Curculionidae	48	herbivore
Family Staphylinidae	48	predator
Family Rhaphidophoridae	44	decomposer
Order Araneae: Family Lycosidae	44	predator
Family Syprhidae	43	nectarivore
Order Opiliones	36	predator
Family Mordellidae	32	herbivore
Family Coccinellidae	30	predator
Family Thomisidae	28	predator
Family Anthicidae	26	omnivore
Family Culicidae	24	nectarivore
Family Elateridae	21	herbivore
Family Scarabaeidae	20	herbivore

Order Aranae	20	predator
Family Stratiomyidae	18	nectarivore
Family Tenthredinidae	18	nectarivore
Family Tipulidae	18	nectarivore
Class Diplopoda	16	decomposer
Family Salticidae	16	predator
Family Cantharidae	15	predator
Family Triozidae	12	herbivore
Family Empedidae	12	nectarivore
Family Bostrichidae	11	herbivore
Family Ceratopogonidae	11	nectarivore
Order Araneae: Family Araneidae	11	predator
Family Sciomyzidae	10	nectarivore
Family Psocidae	9	herbivore
Family Pipunculidae	9	nectarivore
Family Bruchidae	8	herbivore
Family Halictidae	8	nectarivore
Family Derbidae	7	herbivore
Family Calliphoridae	7	nectarivore
Family Evaniidae	7	nectarivore
Family Argidae	6	nectarivore
Family Chrysididae	6	nectarivore
Family Lauxaniidae	4	nectarivore

Family Asilidae	4	predator
Family Miridae	4	predator
Family Pisauridae	4	predator
Family Reduvidae	4	predator
Family Tingidae	4	predator
Family Entomobryidae	3	decomposer
Family Cercopidae	3	herbivore
Order Lepidoptera: larvae	3	herbivore
Family Blephariceridae	3	nectarivore
Family Encyrtidae	3	nectarivore
Family Sphecidae	3	nectarivore
Family Leiodidae	3	other
Order Mecoptera	3	other
Order Psocoptera	3	other
Class Chilopoda	3	predator
Order Acari	3	predator
Family Blattellidae	2	decomposer
Order Dermaptera	2	decomposer
Family Delphacidae	2	herbivore
Family Tenebrionidae	2	herbivore
Family Chloropidae	2	nectarivore
Family Cynipidae	2	nectarivore
Family Eurytomidae	2	nectarivore

Family Lampyridae	2	nectarivore
Family Tephritidae	2	nectarivore
Family Scirtidae	2	other
Family Chrysopidae	2	predator
Family Tetragnathidae	2	predator
Order Hemiptera: Heteroptera	2	predator
Family Paradoxosomatidae	1	decomposer
Family Silphidae	1	decomposer
Family Trogidae	1	decomposer
Family Amphipsocidae	1	herbivore
Family Cerambycidae	1	herbivore
Family Cicadidae	1	herbivore
Family Tettigoniidae	1	herbivore
Family Bethylidae	1	nectarivore
Family Dixidae	1	nectarivore
Family Gracillariidae	1	nectarivore
Family Megachildae	1	nectarivore
Family Pamphiliidae	1	nectarivore
Family Rhagionidae	1	nectarivore
Family Sphingidae	1	nectarivore
Family Tabinidae	1	nectarivore
Family Poduridae	1	other
Family Rhinotermitidae	1	other

Order Isoptera	1	other
Family Gnaphosidae	1	predator
Family Hemerobiidae	1	predator
Order Lithobiomorpha	1	predator

CURRICULUM VITAE

Jeffery Alan Masters
1374 S. 2nd St. Apt. 5
Louisville, KY 40208
e-mail: jamast04@louisville.edu

EDUCATION:

University of Louisville	Biology	Ph.D. (May 2014)
Advisor: Dr. Sarah Emery; Dissertation title: *Invasion biology of Ranunculus ficaria*		
Angelo State University	Biology	M.S. 2002
Angelo State University	Biology/Chemistry	B.S. 1994

RESEARCH:

I primarily study plant population and community ecology with a focus on plant and insect interactions. I am concerned with how pollinator species interact with floral traits to influence plant distribution and community species assemblages. My other research interests include threats to native plant species and sensitive ecosystems.

Works published, in press, or under review

Masters, J.A. and S.M. Emery. 2014. Does leaf litter depth influence *Ranunculus ficaria* (Ranunculaceae) invasions? (under review *American Midland Naturalist*)

Emery, S.M., **J. A. Masters**, S.Benanti, and C. B. Gottshall. 2013. Patterns of trophic-level diversity across a primary successional gradient (under review *American Midland Naturalist*)

Dissertation

Invasion ecology of *Ranunculus ficaria* (Ranunculaceae).

Does leaf litter depth influence *Ranunculus ficaria* (Ranunculaceae) invasions?

Differential effects of an invasive species on pollination services.

Do multiple mechanisms of competition drive the dominance of an invasive plant along an urban stream?

Effects of honeysuckle (*Lonicera mackii)* removal on arthropod abundance and diversity.

Master's Thesis

Allozyme analysis of the Chisos Mountain hedgehog cactus (*Echinocereus chisoensis*).

Grants

University of Louisville, School of Interdisciplinary and Graduate Studies – Dissertation Completion Grant- Fall 2014
Marcia Athey Research Grant - Kentucky Academy of Science 2012
Beechmont Botancal Garden Club Grant-2010
Carr Graduate Research Scholarship -Angelo State University 2001-2002

Presentations at Scholarly Meetings

Allozyme analysis of the Chisos Mountain hedgehog cactus (*Echinocereus chisoensis*) - Texas Academy of Science Meeting 2002.
Genetic comparisons of the widespread Warnock cactus and the endemic Mariposa cactus (*Sclerocactus warnockii* and *Sclerocactus mariposensis*) - Carr Research Presentation Angelo State University.
Brine ion baselines for Redhead Ridge wetlands restoration project-22nd National Conference on Undergraduate Research, Salisbury University April 10-12, 2008
The impact of bush honeysuckle (*Lonicera maackii*) removal on arthropod diversity in an urban forest – Ecological Society of America 2011 (poster).
Effects of leaf litter depth on the reproductive output of *Ranunculus ficaria* (Ranunculaceae) – Kentucky Academy of Science 2012.

Honors

Second Place - Graduate Oral Presentation Competition - Kentucky Academy of Science 2012
Honorable Mention - Graduate Oral Presentation Competition - Texas Academy of Science 2003
Carr Scholarship (Undergraduate) - Angelo State University

Additional research experience

Population Mapping of *Argythamnia aphoroides* (Euphorbiaceae) GIS
Germination Ecology of *Argythamnia aphoroides* (Euphorbiaceae)
Germination Ecology of *Argythamnia simulans* (Euphorbiaceae)
Brine Ion Baselines for Redhead Ridge Wetlands Restoration Project-Texas Gulf Coast
Electrophoresis and Genetic Analysis on *Sclerocactus mariposensis* (Cactaceae)
Electrophoresis and Genetic Analysis on *Sclerocactus warnockii* (Cactaceae)
Assisting Reproductive Studies on *Echinocereus chisoensis* (Cactaceae), *Callirhoe* (Malvaceae), *Argythamnia aphoroides* (Euphorbiaceae) *Argythamnia simulans* (Euphorbiaceae)
Undergraduate Research – Germination Ecology of *Eriogonum nealleyii* (Polygonaceae)

TEACHING:

Teaching Assistant-University of Louisville- Anatomy and Physiology Lab Instructor 2010 -2013
Co-Instructor Plant Taxonomy – University of Louisville-2012
Part-Time Faculty Angelo State University - Anatomy and Physiology Lab Instructor 2007-2009
Adjunct Faculty - Howard Junior College - Anatomy and Physiology Instructor 2007-2009
Substitute Teaching-Primary Education Schools, San Angelo ISD, San Angelo, TX 2004-2008
Volunteer Lab Assistant in Entomology, Limnology, Invertebrate Zoology, and Plant Taxonomy, Angelo State University 2001-2002, 2004-2007

SERVICE:

Service to the Profession/University

University of Louisville Biology Graduate Student Association –vice-president, 2011-2013
Editing for the Texas Journal of Science - Indexing 2006-2010
Reviewer for Arkansas Journal of Science -2006

Service to the Community

Kentucky Native Plant Society- Instructor for Plant Taxonomy Workshop 2013
Interviewed for article published in Louisville Courier Journal newspaper, "Bully Buttercup" (*Ranunculus ficaria*) and interviewed for follow-up story on WDRB, local Fox affiliate 2013
Invited Professional Consultant at Louisville Metro Sewer District meeting to discuss the impacts of a proposed pipeline 2012
Science Days Presentations to Visiting Primary Schools, Angelo State University 2001-2002, 2004-2007

Professional Societies

Ecological Society of America
Kentucky Academy of Science
Texas Academy of Science