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To What Extent do Non-native Shrubs Support Higher Trophic Levels?

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TO WHAT EXTENT DO NON-NATIVE SHRUBS SUPPORT HIGHER TROPHIC LEVELS?

A thesis submitted in partial fulfillment of the
requirements for the degree of
Master of Science

by

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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY ARI ZAKROFF ENTITLED TO WHAT EXTENT DO NON-NATIVE SHRUBS SUPPORT HIGHER TROPHIC LEVELS? BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT

Zakroff, Ari. M.S. Department of Biology, Wright State University, 2023. To what extent do non-native shrubs support higher trophic levels?

Invasive species threaten ecosystems and economies. Globally, biological invasions are estimated to have cost over $2.1 trillion since 1970. In Eastern North American woodlands, invasive plants are rapidly displacing natives. This is concerning, because invasive plants may not support the diverse and abundant arthropod communities essential to ecosystem function. Despite the conceptual understanding of invasive shrubs' potential to transform forest communities, scant research has focused on the effect of invasive plants on higher trophic levels here in Ohio. To address this gap, I examined the diversity and abundance of arthropod communities, caterpillar performance, and caterpillar predation on two invasive shrubs, Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum obtusifolium*), relative to native counterparts. *Lo. maackii* supported a depauperate community; however, *Li. obtusifolium* hosted a surprisingly robust community. Nevertheless, both invasives proved poor hosts for caterpillars and were less preferred for foraging insectivores.

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Thesis Introduction

Biological invasions are a growing threat to global biodiversity and broader ecosystem function (Mack et al. 2000). Furthermore, the economic costs of invasives, in terms of the damage they cause and control efforts, were estimated to have tripled every decade since 1970—totaling an estimated US$47 billion to US$163 billion globally in 2017 (Diagne et al. 2021). Unfortunately, the rate of human-mediated spread of alien species continues to grow with no sign of plateauing (Seebens et al. 2017). Furthermore, invasive species are the most frequently cited contributing factor to extinctions in the modern era, ahead of both exploitation of biological resources and agriculture (Bellard et al. 2016). Invasive species threaten multiple trophic levels, all of which are needed to maintain current ecosystem functions (Soliveres et al. 2016). Climate change is predicted to increase the rate of biological invasions in the coming years, likely making the northeastern United States an invasion hotspot (Bellard et al. 2013). In particular, climate change is expected to facilitate invasion by exotic plants. This is because rising temperature, nitrogen, and CO_2 levels appear to favor invasive plants over native counterparts (Liu et al. 2017).

Ecological importance of invasive plants

Plants form the base trophic level in most terrestrial ecosystems and make up ~80% of Earth's biomass (Bar-On et al. 2018). If one were to remove plants from the ecosystem, all higher trophic levels would promptly collapse (Hunter & Price 1992). In the woodlands of eastern North America, invasive exotic plants are outcompeting native plants and reducing biodiversity (Ritters et al. 2018; Webster et al. 2006). Not only do invasive plants often displace native plant species and threaten floral communities they may also contribute little to local food webs (Liebhold 2017). The replacement of native flora by non-native, invasive plants may lead to wholesale ecological transformation (Vilà et al. 2011). This is partially due to the effects of invasive plants on arthropods essential to ecosystem function (Bauer et al. 2012).

The ecological importance of arthropods

There are upwards of 7 million species of insects and other arthropods, representing the majority of animal biodiversity (Stork 2018). Additionally, arthropods are the largest constituent of animal biomass (Bar-On et al. 2018)—surpassing the combined biomass of all wild vertebrates by approximately 20 to 1 (Tuma et al. 2020). Furthermore, insects and other arthropods provide a host of essential ecosystem services, such as pollination, pest control, and decomposition—valued at over $57 billion annually in the United States alone (Losey & Vaughan 2006). Consequently, the severe global decline of insects all the more worrisome (Wagner 2020; Sánchez & Wyckhuys 2021). This decline is widespread—even arthropod populations in protected areas are dwindling (Hallmann et al. 2017; Salcido et al. 2020). Many factors are likely to blame, from climate change to ever-growing rates of pesticide application (Sánchez-Bayo & Wyckhuys 2019). However, invasive plants likely contribute by reducing habitat quality and homogenizing plant communities (Tallamy & Narango 2021; Qian & Ricklefs 2006). If insect populations continue to decline, many ecosystem functions will deteriorate, such as pollination (Klein et al. 2007), nutrient cycling (Mattson & Addy 1975; Nichols et al. 2008; Woodman et al. 2021), and the maintenance of overall biodiversity (Ollerton 2017;

Lister & Garcia 2018). Notably, alien plants may not negatively affect all arthropods—some may benefit from the increased structural complexity offered by some invasive plants (Landsman et al. 2021).

Based on current estimates, herbivores constitute approximately half of global insect diversity (Stork 2018). Concerningly, native herbivore communities are especially sensitive to invasive plants (Scherber et al., 2010). Insect herbivores, such as caterpillars, tend to be highly-host specific (Loxdale et al. 2011; Forister et al. 2015). These plants may be unrecognizable as food, nutritionally inferior, or have novel defenses to which native herbivores are unadapted (Bezemer et al. 2014). Additionally, many predatory arthropods rely on these herbivorous insects. Therefore, the replacement of native plants by invasives could trigger a collapse in arthropod communities (Simao et al. 2010). If this occurs, the effects will ripple across trophic levels, reducing biodiversity (Wagner 2020).

Plant-animal interactions

Plants feed herbivorous arthropods that are a food source for higher trophic levels—thereby supporting biodiversity (Narango et al. 2017). Arthropods are a critical food source for many bird species, both in and out of the breeding season (García-Navas 2013; Smallwood & Wood 2023). Among arthropods on plants, caterpillars of Lepidoptera are especially important food resources for birds (Newell et al. 2014; Kleintjes & Dahlsten 1994). Perhaps unsurprisingly, birds preferentially forage on tree species that host diverse caterpillar assemblages (Piel et al. 2021). Declines in insectivorous bird abundance in North America are associated with declines in local arthropod populations (Tallamy & Shriver 2021). Invasive plants may contribute to declines in arthropods and associated declines in birds (Fig. 0-1).

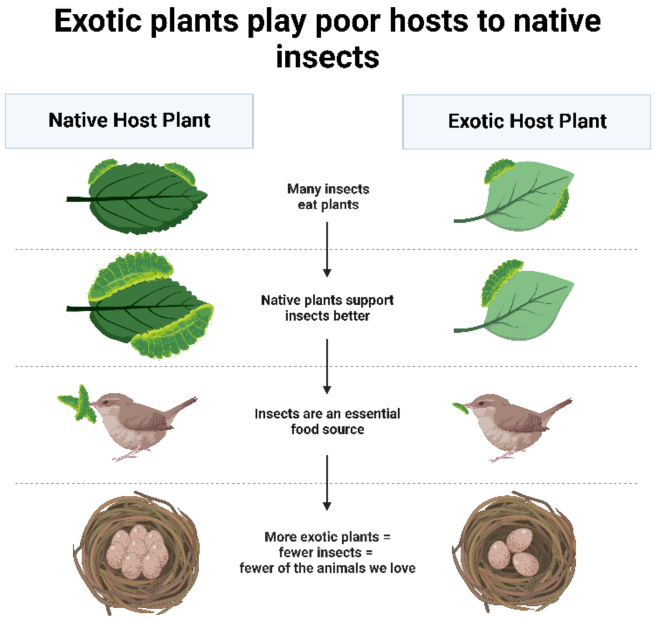

Figure 0-1 As primary producers, plants profoundly affect ecosystems. If exotic plants host fewer or lower quality (e.g., smaller) arthropods, fewer resources will be passed on to higher trophic levels.

Specialist herbivores and their obligate predators are most clearly vulnerable to decline from plant invasions, as specialist herbivores are heavily reliant on a narrow range of hosts (Schirmel et al. 2016). Generalist herbivores may face a smaller hurdle in terms of switching to novel hosts (Keane & Crawley 2002). However, if an invader is phylogenetically close to a native plant taxon, specialists of that native may be far more successful than generalists on the novel invasive host (Castells et al. 2014). Because invasive plants represent an abundant food source, they would be a boon to any herbivores able to make the switch (Rodríguez et al. 2019).

When a plant invades a region beyond its natural range, it often leaves its natural enemies (i.e., herbivores and pathogens) behind (Keane & Crawley 2002). This could provide a strong advantage to non-native plants competing with native flora (Keane & Crawley). Exotic plants often suffer reduced herbivory relative to co-occurring natives, especially for woody invaders (Bodawatta et al. 2019; Xu et al. 2021). This reduced herbivory likely helps non-native plants outcompete native species in some instances (Carpenter & Cappuccino 2005). Nevertheless, relative herbivory is not universally lower on non-native plants (Ivison 2022). Ultimately, herbivory is likely only one of many factors contributing to the invasiveness of non-native plants.

Because ecological restoration aims to enhance ecosystem functions and services, removing these plants is often central to ecological restoration projects (Kettenring & Adams 2011). Removing invasive plants could bolster local biodiversity by providing space for native plants and indirectly providing resources for higher trophic levels. However, it is unfeasible to actively control all invasive plant species, given the limited resources. Rather, restorationists can only effectively manage a few taxa. To realize the greatest ecological reward, we must evaluate the relative impacts of key invaders on local ecosystems.

Thesis Objectives

The driving question of my thesis is to what extent exotic plants support arthropods and higher trophic levels relative to native plants. Although we know invasive plants can reduce biodiversity and alter ecosystem function, there is scant research into the specific arthropod communities supported by invasive plants and how they compare to those supported by native plants (Pyšek et al. 2012). Considering the importance of arthropods to ecosystem function and the growing prevalence of exotic plants (Yang & Gratton 2014; Seebens et al. 2017), it is important to assess how well exotic plants support arthropod communities and the contributions of these communities to higher trophic levels, including insectivorous birds. To examine these issues, I conducted three studies. First, I conducted rapid field surveys to assess arthropod community abundance, richness, and diversity on focal invasive plants and native counterparts. Second, I undertook a combined field survey and rearing project to assess the abundance, richness, community overlap, and success of caterpillars on native and invasive hosts, as well as compare herbivory levels among invasives and natives. Last, I used model caterpillars to investigate the potential contribution of focal invasive plants to higher trophic levels by comparing attack rates of caterpillars on invasive and native plants in the field.

Focal Study Species

For each of my research objectives, I focused on two invasive shrubs from Asia—border privet (*Ligustrum obtusifolium*) and Amur honeysuckle (*Lonicera maackii*) (Braun 1989). These shrubs have swept through Ohio woodlands in recent decades, out-competing native plants and reducing habitat quality (Miller 2006; Collier et al. 2002). Both *Lo. maackii* and *Li. obtusifolium* are associated with declining populations of native trees and forbs in American woodlands (Shannon-Firestone and Firestone 2015; Gorchov and Trisel 2003; Hartman and McCarthy 2007). I compared *Lo. maackii* and *Li. obtusifolium* to two ecologically similar and phylogenetically close native woody plants: blackhaw (*Viburnum prunifolium*) and ash (*Fraxinus* spp.).

Lonicera maackii

Amur honeysuckle (*Lonicera maackii*), a member of Caprifoliaceae, is a fast-growing deciduous shrub (Deering and Vankat 1999). Although this plant is native to East Asia, there are several members of the genus native to Ohio; however, none are locally abundant, and all have a vining as opposed to shrub-forming growth habit (Braun 1989). Therefore, I compared *Lo. maackii* to *V. prunifolium*. My justification for this is that *V. prunifolium* is related to *Lo. maackii*, relatively abundant in the same habitats, and is morphologically similar to *Lo. maackii*. *V. prunifolium* is a member of the family Adoxaceae (Zhang et al. 2003), which was somewhat recently separated from Caprifoliaceae (Donoghue et al. 2001). Adoxaceae and Caprifoliaceae are the only families in the order Dipscales (Bell & Donoghue 2005).

The horticultural industry introduced *Lo. maackii* to North America from Asia during the late 19th century as an ornamental plant (Luken and Thieret 1996). By the 1920s, the species escaped cultivation and spread to Ohio ecosystems by the early 1960s (Luken and Thieret 1996, Braun 1961). Since that time, *Lo. maackii* has invaded habitats across the eastern united states, southeastern Canada, and the Pacific Northwest (Kartesz 2015). *Lo. maackii* is associated with losses in the abundance and diversity of native plants. For example, *Lo. maackii* decimates tree seedling communities—reducing species richness by up to 41% and density by 68% (Collier et al. 2002).

Several factors likely promoted the invasion success of *Lo. maackii*: high dispersal rate, rapid seedling growth, long growing season, allelopathy, escape from natural enemies, and novel weapons against native herbivores. Mature plants yield heavy fruit loads, which are widely dispersed by both white-tailed deer and frugivorous birds (Casellano and Gorchov 2013, Bartuszevige and Gorchov 2006). *Lo. maackii* seedlings exhibit rapid growth and plants of all ages develop leaves earlier and keep them later than most native plants, shading out conspecific competitors (Deering and Vankat 1999, McKinney and Goodell 2010, McEwan et al. 2009). Beyond rapid growth, *Lo. maackii* relies on allelopathy to outcompete native plants—releasing compounds that inhibit the growth of competing species (Cipollini et al. 2008). In its native range, *Lo. maackii* undoubtedly faces a suite of coevolved herbivores; however, these species are mostly absent from North America (Lieurance and Cipollini 2013). Thus, the plants experience lower herbivory and may be able to shift resources from defense toward growth or reproduction (Lieurance and Cipollini 2012, Blossey and Notzold 1995). Furthermore, this species may have novel defensive compounds to which local herbivores have not had time to adapt (Lieurance et al. 2015).

Although it has recently been reported that as many as 91 native caterpillar species have been found on *Lo. maackii* (Stireman & Workman 2023), studies have also found that *Lo. maackii* presence in habitats is negatively correlated with caterpillar abundance Stireman et al. 2014). However, when comparing *Lo. maackii* to native plants, we know little about how arthropod communities, caterpillar performance, or predation differ. Clarifying these things will help us determine the degree to which *Lo. maackii* supports higher trophic levels.

Ligustrum obtusifolium

Border privet (*Ligustrum obtusifolium*), like *Lo. maackii*, was imported in the 19th century as an ornamental shrub (Cothran 2003). Over the past century, *Li. obtusifolium* has invaded most of Eastern North America, through the eastern United States and into Canada (United States Department of Agriculture 2014). The species is fast-growing and tolerant of both poor light and low nutrient conditions (Maddox et al. 2010). Additionally, *Ligustrum* displays remarkably high fecundity. Mature plants of a close relative, common privet (*Ligustrum vulgare*), can produce over 10,000 fruits per season, potentially yielding tens of thousands of seeds (Obeso and Grubb 1993). Frugivorous birds may then disperse these seeds long distances to new habitat patches (Debussche and Isenmann 1994). *Li. obtusifolium*, likely shares these remarkable reproductive dispersal traits, potentially contributing to its success as an invader.

Unlike *Lonicera*, there are no members of the genus *Ligustrum* native to Ohio—nor to anywhere else in the New World (Braun 1989, Wallander and Albert 2000). Additionally, no members of the genus' subtribe to which it belongs, Ligustrinae, are native to the Americas (Wallander & Albert 2000). In short, the species is a phylogenetic novelty in Ohio ecosystems. This may contribute to its recent invasive success, as successful invasion by exotic plants is associated with their phylogenetic isolation (Parker et al. 2012).

Ash (*Fraxinus* spp.), like *Ligustrum*, is a member of the family Oleaceae (Wallander & Albert 2000). Currently, *Fraxinus* spp. are in severe decline throughout much of Eastern North America and may soon face functional extirpation in many regions (Herms & McCullough 2014). This is largely due to the emerald ash borer (*Agrilus planipennis*) an invasive beetle that feeds on the phloem of *Fraxinus* trees, eventually killing even large, healthy individuals (Poland & McCullough 2006). *Fraxinus* spp. mortality often nears 100% in heavily affected stands (Klooster et al. 2014). The loss of

Fraxinus spp. in North America threatens the hundreds of arthropod species it supports, including over 100 species of Lepidoptera representing 20 families (Gandhi & Herms 2010; Robinson et al. 2023). As *Fraxinus* populations dwindle and *Li. obtusifolium* spreads, *Li. obtusifolium* may partially replace ash saplings in the understory of eastern North American woodlands. As a member of Oleacea, some of the arthropod community of *Fraxinus* spp. may switch to this novel host. However, early assessments indicate poor performance by *Fraxinus* spp. specialists on close relatives of *Li. obtusifolium*, *Li. sinense* and *Li. vulgare* (Kalina et al. 2017; Horne 2023). Therefore, it is uncertain whether *Li. obtusifolium* could realistically offer refuge to the herbivores of *Fraxinus* spp.

Key findings

My thesis work assesses to what extent exotic *Lo. maackii* and *Li. obtusifolium* support higher trophic levels relative to native *V. prunifolium* and *Fraxinus* spp. I organized my findings into three chapters. In Chapter 1, I present the results of my arthropod surveys. Key results include the following: (1) *Lo. maackii* hosts a depauperate arthropod community relative to *V. prunifolium*—primarily driven by herbivores, (2) The ratio of predators to herbivores is approximately four times greater on *Lo. maackii* than on *V. prunifolium*, (3) *Li. obtusifolium* supports an arthropod community with a greater or similar abundance and diversity as *Fraxinus spp*. Chapter 2 relates the findings of my surveys of caterpillar abundance, diversity, and herbivory, as well as the success and growth of caterpillars in my rearing experiment. There were several interesting findings from that work: (1) *Lo. maackii* hosts a far lower density of caterpillars than *V. prunifolium*; however, (2) the extrapolation of caterpillar richness from *Lo. maackii* appears similar to or greater than *V. prunifolium*, (3) *Lo. maackii* experienced only ~1/3 the herbivory from chewing arthropods as *V. prunifolium*, (4) caterpillar performance trended lower on *Lo. maackii* than *V. prunifolium*, (5) *Li. obtusifolium* hosts a density of caterpillars comparable to *Fraxinus* spp.; furthermore, (6) *Li. obtusifolium* hosts a rarefied richness of caterpillars similar to or greater than *Fraxinus* spp., (7) chewing herbivory is similar between *Li. obtusifolium* and *Fraxinus* spp., (8) caterpillar performance trended lower on *Li. obtusifolium* with significantly lower growth rates than *Fraxinus* spp. My third and final chapter reports the results of my spring and summer model caterpillar experiment. In the spring, the overall attack rate trended lower on *Lo. maackii* than *V. prunifolium*; however, attack rates did not significantly differ between *Li. obtusifolium* and *Fraxinus* spp. In the fall, there were significant differences. Specifically, there were differences in attack rates between aggregated native and non-native plants as well as between *Lo. maackii* and *V. prunifolium*. The attack rate was significantly higher on native than non-native hosts. Also, birds attacked caterpillars less frequently on *Lo. maackii* than *V. prunifolium*, yet arthropod attack rates trended higher on the invasive plant.

Broader significance of this work

The findings of these studies increase our understanding of how and to what degree *Li. obtusifolium* and *Lo. maackii* support native insects and the potential effects of these invasive plants on higher trophic levels. These results will help inform land managers to evaluate the long-term threat posed by *Li. obtusifolium* and *Lo. maackii* to the health of Ohio forests and wildlife. This may also ease the challenge of determining how best to allocate the limited resources available for ecological restoration.

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Chapter 1 How do arthropod communities on invasive shrubs compare to those on natives?

Abstract

Invasive species threaten ecosystems and economies. Invasive plants are economically harmful because they diminish agricultural output and are expensive to control. The U.S. alone loses about $9.6 billion annually due to invasive plants. In eastern North American woodlands, exotic shrubs are displacing native plants and transforming understory communities. The displacement of native plants by these non-natives may reduce the resources available to higher trophic levels by not supporting arthropod communities as well as native plants do. Invasive plants may either be unrecognizable to native herbivores or possess defenses to which these herbivores are poorly adapted. Despite the conceptual understanding of invasive shrubs' potential to transform forest communities, remarkably little research effort has focused on characterizing the arthropod communities they support or their impact on higher trophic levels. To address this gap, I compared arthropod community diversity, abundance, and composition on two invasive shrubs in southwestern Ohio: Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum obtusifolium*), to two native plant taxa: blackhaw (*Viburnum prunifolium*) and ash saplings (*Fraxinus* spp.). I assessed the abundance, diversity, and structure of arthropod communities hosted by each plant species over a growing season in 11 forested sites in southwestern Ohio. There were significant differences in terms of the abundance and diversity of arthropod

communities hosted by these plants. *Lo. maackii* hosted a depauperate arthropod community, with fewer individuals and species per cubic meter of foliage than its native counterpart, *V. prunifolium*. Primarily, this was driven by the poor herbivore community on *Lo. maackii*. Contrary to expectations, *Li. obtusifolium* hosted a larger and more diverse community than *Fraxinus* spp. Surprisingly, the herbivore community on *Li. obtusifolium* was similar or greater in abundance and diversity than that of *Fraxinus* spp. This suggests *Li. obtusifolium* may not contribute to arthropod community decline in the short term. Additionally, there was a significant, albeit small, effect of host species on the family-level arthropod community composition for both native-invasive pairs. Invasive plants may suppress community diversity and ecosystem services, but the degree likely varies based on the invasive species in question and on which natives they displace.

Introduction

Globalization is rapidly introducing exotic species to terrestrial ecosystems. Some of these species exhibit characteristics that allow them to displace native species (Hayes & Barry 2008). When this occurs, it can transform the local ecology, creating novel ecosystems with never-before-seen species combinations (Hobbs et al. 2006). These biological invasions threaten ecosystems and economies. The costs associated with lost economic output and the control of invasive species have increased every decade since 1970—reaching a mean annual global loss of about $163 billion in 2017 (Diagne et al. 2021). In 2022, the total cost of biological invasions since 1970 surpassed $2 trillion (Diagne et al. 2022). In addition to economic costs, invasive species are the most frequently cited factor to extinctions in the modern era, contributing to over 32% of all IUCN recognized extinctions between 1500 CE and 2017 CE (Bellard et al. 2016). The rate of these economically and ecologically disastrous invasions appears to only be increasing (Seebens et al. 2017), likely hastened by globalization and climate change (Early et al. 2016; Bellard et al. 2013).

Plants form the first trophic level in nearly all terrestrial ecosystems; without plants, terrestrial ecosystems as we know them could not exist (Hunter & Price 1992). It is alarming that invasive plants tend to suppress native plant abundance and diversity (Qian & Ricklefs; Vilà 2011) while often simultaneously contributing less to ecosystem functions than native plants (Milanović 2020). In particular, invasive plants may contribute less to local food webs than native plants. One reason for this is that non-native plants often do not support as abundant or as diverse of arthropod communities as natives (Simao et al. 2010; Bezemer et al. 2014).

Arthropods both make up the largest component of animal biomass and the vast majority of biodiversity (Stork 2018; Bar-On et al. 2018). Unsurprisingly, these hugely diverse and abundant organisms are essential to a plethora of ecosystem functions (Yang & Gratton 2014). From cycling nutrients (Chapman et al. 2003; Nichols et al. 2008) and pollinating plants (Ollerton 2017) to regulating primary production (Mattson & Addy 1975), insects affect nearly every aspect of terrestrial ecosystems. Furthermore, insects are an essential food source for many organisms (Baxter et al. 2005; Nyffeler & Birkhofer 2017). Unfortunately, insect abundance and diversity is plummeting globally (Hallmann et al., 2017; Wagner 2020; Cardoso et al 2020). Invasive plants are already associated with declines in insects (Tallamy et al. 2021), which are in turn linked to mirroring declines in insectivorous bird communities (Tallamy & Shriver 2021).

When species are transported to new locations, they may escape their natural enemies. This is what the enemy-free space hypothesis proposes (Jeffries and Lawton 1984). Exotic plants may host lower abundances and diversities of herbivorous arthropods due to being “released” from their coevolved herbivorous enemies (Keane & Crawley 2002). There are several barriers to colonization of exotic plants by native arthropods. Perhaps most importantly, native arthropods may not recognize exotic plants as food (Pearse et al. 2013). Alternatively, exotic plants may have defensive compounds to which native arthropods are not adapted (Callaway and Ridenour 2004). Also, exotic plants may offer inferior nutrition to native arthropods (Newman 2001). Even if these factors do not kill herbivores, they can slow growth and maturation—increasing the predation risk for these arthropods (Pearse et al. 2013). Exotic shrubs may host lower abundances and diversities of herbivorous arthropods due to “escape” from their coevolved herbivorous enemies.

Phylogenetic isolation appears to contribute to successful invasion by exotic plants (Parker et al. 2012). It is possible that phylogenetic novelty shields some exotic plants from colonization by insect herbivores due to circumventing coevolution with herbivores (Roques et al. 2006). This would cause these exotics to face lower herbivory pressure than do native counterparts. In turn, this would allow these invasive plants to invest less in defense and more into growth or reproduction (Herms & Mattson 1992). Consequently, the probability of an exotic plant successfully invading a habitat may be closely linked to the initial local floral diversity (Levine et al. 2014). This is supported by the observed positive correlation between the diversity of native plants in a community and the rate of herbivory on exotic plants—possibly because greater diversity increases the likelihood that some local native plants will be phylogenetically similar to a given invader (Pearse and Hipp 2014).

Surprisingly and despite the clear importance, little literature exists that compares the arthropod communities on native and non-native plants in North America. Consequently, much of the assumed effects of invasive plants on local ecosystems remain speculative. Although existing research suggests invasive plants are associated with declining arthropod abundance in forests of northeastern North America, we know little about how arthropod communities on exotic plants differ from those on native species (Fickenscher 2014). This is in spite of the vital role arthropods play in ecosystem function. To understand the broader implications of exotic plant invasions, we need a greater understanding of the arthropod communities that they support. With rapid field surveys, I was able to compare the abundance, diversity, and community composition of arthropods on ecologically similar and phylogenetically close invasive and native plants.

Focal Invasive Taxa

My study compared two invasive shrubs from Asia—border privet (*Ligustrum obtusifolium*) and Amur honeysuckle (*Lonicera maackii*) to two native taxa, blackhaw (*Viburnum prunifolium*) and ash (*Fraxinus* spp.) (Braun 1989). These exotic shrubs are sweeping through Ohio woodlands, out-competing native plants and reducing habitat quality (Miller 2006; Collier et al. 2002). Botanical surveys link both *Lo. maackii* and *Li. obtusifolium* to declining populations of native trees and forbs in American woodlands (Shannon-Firestone & Firestone 2015; Gorchov & Trisel 2003; Hartman & McCarthy 2007). These species are likely contributing to wholesale ecological transformation of the floral landscape of Ohio.

Amur Honeysuckle (Lonicera maackii)

Lo. maackii is one of several highly invasive *Lonicera* in eastern North America (Miller 2006). It is a fast-growing deciduous shrub (Deering and Vankat 1999) that was imported horticultural industry during the late 19th century as an ornamental plant (Luken and Thieret 1996).

Figure 1-1 This early April photo displays *Lo. maackii* leafing out before most native plants in the Wright State Biological Preserve in Dayton, OH.

By the 1920s, the species had escaped cultivation, spreading to natural areas during the early 1960s (Luken and Thieret 1996, Braun 1961).

Lo. maackii is a member of the family Caprifoliaceae native to East Asia, there are local congeners; however, none are locally abundant, and all have a vining as opposed to shrub-forming growth habit (Braun 1989). However, there is a native shrub that is related and ecologically similar shrub: blackhaw (*Viburnum prunifolium*). Although *V. prunifolium* is not in Caprifoliacea, it is in the sister family Adoxaceae (Zhang et al. 2003). This family is one of only two in the order Dipscales (Bell & Donoghue 2005). Historically, *V. prunifolium* and the rest Adoxaceae were part of Caprifoliaceae; however, the families were separated in the early 2000s (Donoghue et al. 2001). This woodland shrub occupies many of the habitats invaded by *Lo. maackii* and exhibits a similar growth form (Braun 1989). These phylogenetic and ecological factors could translate to *V. prunifolium* supporting a similar arthropod community to *Lo. maackii*.

Several factors likely influence this species' invasion success: high dispersal rate, rapid seedling growth, long growing season, allelopathy, escape from natural enemies, and novel weapons against native herbivores. Mature plants yield heavy fruit loads, which are widely dispersed by both white-tailed deer and frugivorous birds (Casellano and Gorchov 2013, Bartuszevige and Gorchov 2006). *Lo. maackii* seedlings exhibit rapid growth and plants of all ages develop leaves earlier and keep them later than most native plants, shading out conspecific competitors (Deering and Vankat 1999, McKinney and Goodell 2010, McEwan et al. 2009). Beyond rapid growth, *Lo. maackii* is allelopathic—it releases compounds that inhibit the growth of competing plants (Cipollini et al. 2008). In its native range, *Lo. maackii* undoubtedly faces a suite of coevolved herbivores; however, these species are mostly absent from North America (Lieurance & Cipollini 2013). Thus, possibly as a result, reported herbivory rates on *Lo. maackii* are quite low—only 1.8% to 3.09% per leaf (Lieurance & Cipollini 2012). Due to the minimal threat posed by herbivores, *Lo maackii* may shift resources from defense toward growth or reproduction (Blossey & Notzold 1995).

Lo. maackii population density is associated with low abundance and richness of forbs and trees (Sena et al. 2021, Shields et al. 2015). For example, *Lo. maackii* has been shown to decimate tree seedling communities—reducing species richness by up to 41% and density by 68% (Collier et al. 2002). Also, the presence of *Lo. maackii* appears to depress arthropod populations. One study in Kentucky parklands found terrestrial arthropod communities increased 46% in abundance and 31% in taxon richness three years after vs before *Lo. maackii* removal in test plots (Masters et al. 2017). We know little about how arthropod communities on *Lo. maackii* differs from the communities on co-occurring native plants. Currently, we do not know the trophic consequences of the widespread displacement of native plants by these invasives.

Figure 1-2 *Li. obtusifolium* often forms dense thickets that crowd out other plants, as pictured here in Englewood MetroPark.

Border privet (Ligustrum obtusifolium)

Like *Lo. maackii*, *Li. obtusifolium* is fast-growing and tolerant of both poor light and nutrient conditions (Webster et al. 2006). *Li. obtusifolium* has invaded most of eastern North America, including both the eastern United States and into southeastern Canada (United States Department of Agriculture 2014). Also, like *Lo. maackii*, border privet was imported in the 19th century as an ornamental shrub (Cothran 2003).

Li. obtusifolium appears to suppress a range of native plant species (Maynard-Bean & Kaye 2019). Additionally, this plant exhibits incredible fecundity. Mature plants of a close relative, *Ligustrum vulgare*, can produce over 10,000 fruits per season, yielding extraordinary numbers of seeds (Obeso and Grubb 1993). In turn, frugivorous birds disperse these seeds (Debussche and Isenmann 1994). It is likely *Li. obtusifolium* disperses similarly. *Li. obtusifolium* appears to be well defended chemically, with high concentrations of a phenotic secoiridoid glycoside, oleuropein, in its leaf tissue (Konno et al. 1999). When tissue is damaged by herbivory, oleuropein activates, working as a powerful protein denaturant (Konno et al. 1999). In its native range, it seems some specialist Lepidoptera have adapted to produce high levels of glycine in their gut, which is extremely effective at suppressing the harmful effects of oleuropein (Konno et al. 1998). Although relatively few studies have assessed herbivory on *Li. obtusifolium*, one study found that *Li. vulgare* is often preferred by white-tailed deer (*Odocoileus virginianus*) over native options in controlled preference trials (Averill et al. 2016). This indicates that at least some native herbivores find Ligustrum palatable, despite its defenses.

Unlike *Lonicera*, there are no members of *Ligustrum* native to Ohio—nor to anywhere else in the New World (Braun 1989, Wallander and Albert 2000). Additionally, there are not even any members of the genus' subtribe, Ligustrinae, native to this hemisphere

(Wallander and Albert 2000). The species is somewhat of a phylogenetic novelty in Ohio ecosystems, possibly contributing to its invasive success. However, there is a fairly common, albeit declining, related taxa in eastern North America: Ash (*Fraxinus* spp.)

Like *Li. obtusifolium*, *Fraxinus* is a member of the family Oleacea (Wallander & Albert 2000). Unlike *Li. obtusifolium*, *Fraxinus* spp. populations are crashing across much of North America. In large part, this is due to another invasive species: the emerald ash borer (Poland & McCullough 2006). This phloem-feeding beetle is killing *Fraxinus* old and young in droves, with mortality often nearing 100% in heavily affected areas (Klooster et al. 2014). The dwindling *Fraxinus* spp. populations clearly threaten its herbivore community (Gandhi & Herms 2010). Potentially, some of this community is or will switch to *Li. obtusifolium*; however, preliminary studies suggest *Fraxinus* spp. specialists may not perform well on *Ligustrum*. In trials with two related *Ligustrum* species, *Li. sinense* and *Li. vulgare*, a hemipteran and a selection of Lepidopterans did not perform well on these novel hosts (Kalina et al. 2017; Horne 2023). The Hemipteran was somewhat successful, but less so than when reared on native hosts; the Lepidopterans were largely unsuccessful. Therefore, it is unclear whether *Li. obtusifolium* represents a viable host for *Fraxinus* spp. arthropods.

Motivation for study

Although one might expect non-native plants to universally provide poorer resources for arthropods than native plants, this is not always the case. For example, in the Netherlands, exotic black cherry (*Prunus serotina*) supports a more diverse community of arthropods than does the native bird cherry (*Prunus padus*). Clearly, invasive species are at least sometimes able to support diverse arthropod assemblages.

In this study, I compared the abundance, diversity, and community structure of arthropod communities on *Lo. maackii* and *Li. obtusifolium* to that of corresponding native woody plants: blackhaw (*Viburnum prunifolium*) and ash saplings (*Fraxinus* spp.). My goal was to understand the larger consequences of plant invasions.

Research Methods

My surveys focused on comparing the arthropod communities on *Lo. maackii* and *Li. obtusifolium* relative to two natives, *Viburnum prunifolium* and *Fraxinus* spp. I compared privet (*Li. obtusifolium*) to ash (*Fraxinus* spp.) and honeysuckle (*Lo. maackii*) to blackhaw (*V. prunifolium*). Each exotic species is phylogenetically and ecologically related to the reference native species (Braun 1989). Although there are *Lonicera* species native to Ohio, they exhibit a drastically different growth structure—vining—and are relatively rare on the landscape (Braun 1989). Therefore, I selected *V. prunifolium*, an abundant shrub from the sister family Adoxaceae with a growth structure similar to *Lo. maackii* would be a good native counterpart.

Sites

I surveyed arthropod communities on the focal on native and invasive shrubs in moderate to high quality woodlands in the Miami-Valley region of Southwest Ohio. To broadly capture variation in local woodland habitats, I sampled arthropods from eleven sites (Table 1-1).

Sites	**GPS Coordinates**
Carriage Hill MetroPark	39.88°N, 84.09°W
German Town MetroPark	39.38°N, 84.25°W
Possum Creek MetroPark	39.42°N, 84.16°W
Twin Creek MetroPark	39.35°N, 84.21°W
Englewood MetroPark	39.52°N, 84.17°W
Glen Helen Nature Reserve	39.48°N, 83.53°W
Huffman MetroPark	39.48°N, 84.05°W
Medlar Conservation Area	39.36°N, 84.16°W
Sugar Creek MetroPark	39.37°N, 84.05°W
Taylorsville MetroPark	39.52°N, 84.10°W
Wright State Biological Preserve	39.47°N, 84.03°W

Table 1-1 All sites in which arthropod surveys were conducted.

Sampling arthropod communities

I surveyed arthropod communities on plants from May through mid-September. To do this, I used a beat sheet to survey arthropods from the focal plant species of 1 m^3 or greater in volume. I selected plants haphazardly along trails, as true random sampling would have been logistically challenging, slower, and have resulted in a far smaller sample size. However, I minimized habitat variation between samples in several ways. First, I recorded the dimensions of each plant for later volume-based standardization. Second, nearly all of my samples came from woodland interiors, mitigating edge effects. Third, for each native/exotic plant pair, I sampled native and exotic individuals from the same sites. Fourth, I typically sampled members of each native/exotic plant pair for any given day of sampling.

During surveys, I recorded all arthropods that were ≥ 3mm in length, which is near the minimum field identifiable size. I categorized arthropods by family, morphospecies, and feeding guild (e.g., predacious or herbivorous). This approach greatly reduced the time needed for identification, allowing me to record a far greater number of samples than if I had collected and identified all specimens in a laboratory. Although I was usually able to identify to the family level, this was not always possible. Additionally, I was occasionally unable to determine feeding guild. In these instances, I excluded those arthropods from family or feeding guild based analyses. Of note, I collected and reared in the lab all caterpillars that were ≥ 3mm in length (see Chapter 2).

Statistical Analysis and Interpretation

I conducted all of my analyses in RStudio v4.2.2 (R Core Team 2022). To compare arthropod abundance, richness, and guild composition between my focal plant taxa, I used quasi-Poisson generalized linear models (GLM). In my models, plant species and *Lo. maackii* density were fixed effects, and site and date were random effects. I constructed a separate model for each variable of interest. I assessed community wide variables of interest, such as mean overall abundance, richness, and diversity (e^H) of arthropods per m^3 of foliage. Additionally, I compared the mean abundance and richness of predators and herbivores. Furthermore, I evaluated differences in abundances of ants, spiders, hemimetabolous herbivores, and of caterpillars. I combined abundances of larval Lepidopterans and Symphytans as caterpillars due to their similar ecological functions.

Additionally, I examined differences in community structure through ordination. I used morphospecies during my field surveys, so I was limited to family level analysis—the finest taxonomic level that was consistent across all samples. To compare the communities, I constructed an NMDS model based on the Sørensen index in the Vegan package in R (Oksanen et al. 2022). To do this, I constructed a matrix in which I pooled family level abundances on a per site, per date, per host plant species basis. Because many taxa were rare and a few were highly abundant, I used a Hellinger transformation on these data. Additionally, I used the adonis2 function of Vegan to run a PMANOVA to test for differences in community compositions based on host species and site.

Results

During the 2022 field season, I surveyed ~912 m^3 of foliage from 345 individual plants. From this, I classified 4579 individual arthropods into morphospecies, families, and feeding guild. Arthropod communities differed markedly between host plants in terms of richness and abundance by foliar volume. These differences were greatest between *Lo. maackii* and *V. prunifolium*. The effect of site was significant for most models, as was the effect of date. *Lo. maackii* stem density only had a significant effect in one model: ant abundance on *Li. obtusifolium* and *Fraxinus* spp. (Table 1-6).

Abundance and richness of arthropods

Based on single factor deletions from the GLMs for *Lo. maackii* and *V. prunifolium*, there were significant effects of host plant species, site, and date of sampling, on the abundance, richness, and diversity of the overall arthropod community per cubic meter of foliage sampled (Table 1-2). In the GLM with all factors and levels, *V. prunifolium*, the native shrub, hosted a much greater abundance (Std. error = 0.123; $p = 0.012$) and richness of arthropods (Std. error = 0.112; $p = 0.005$) than the invasive *Lo. maackii*. In terms of Shannon diversity, *V. prunifolium* also exhibited a greater mean number of effective species than *Lo. maackii* (Std. error = 0.116; $p = 0.006$). In short, *Lo. maackii* hosted a depauperate arthropod community relative to *V. prunifolium* (Fig. 1-2).

The differences between *Lo. maackii* and *V. prunifolium* were even more striking when considering only herbivores (Fig. 1-3). GLMs indicated that *V. prunifolium* hosted a greater richness (Std. error = 0.175; $p = 1.93e^{-05}$) and abundance of herbivores (Std. error = 0.233; $p = 1.49e^{-06}$) per cubic meter. Although hemimetabolous herbivores were more abundant (Std. error = 0.218; $p = 0.046$) on *V. prunifolium*, the abundance of caterpillars was about 10 times greater on *V. prunifolium* than *Lo. maackii* (Std. error = 0.643; $p = 1.61e^{-05}$).

In contrast to herbivores the abundance and richness of predators were largely similar between *Lo. maackii* and *V. prunifolium* (Fig. 1-4) with no significant differences overall (Table 1-5). Notably, however, ant abundance trended higher on *Lo. maackii* than *V. prunifolium* (Table 1-6).

The patterns between native and non-native hosts were reversed for *Li. obtusifolium* and *Fraxinus* spp. overall (Fig. 1-2). *Li. obtusifolium*, the exotic, hosted a greater richness of arthropods (Std. error = 0.109; $p = 0.002$), diversity (Std. error = 0.110; $p < 0.001$), and abundance of arthropods than the native *Fraxinus* spp. (Std. error = 0.134; *p*

= 0.04). The abundance and richness of herbivores differed between *Li. obtusifolium* and *Fraxinus* spp. (Fig. 1-3). *Li. obtusifolium* hosted a greater richness (Std. error = 0.154; *p* = 0.028) and abundance (Std. error = 0.169; *p* = 0.031) of herbivores per cubic meter of foliage volume than native *Fraxinus* spp. GLMs indicated that hemimetabolous herbivores drove this disparity. Hemimetabolous herbivores were significantly more abundant on *Li. obtusifolium* than on *Fraxinus* spp. (Std. error = 0.184; *p* = 0.012); however, holometabolous caterpillars were not (Std. error = 0.370; *p* = 0.436). Additionally, there were significant differences between the predator communities on *Li. obtusifolium* and *Fraxinus* spp. (Table 1-4). Specifically, predator richness (Std. error = 0.124; *p* = 0.002), though not abundance (Std. error = 0.154; *p* = 0.283), was significantly higher on *Li. obtusifolium*. In particular, *Li. obtusifolium* hosted a greater abundance of ants than did *Fraxinus* spp. (Std. error = 0.315; *p* = 0.008).

	Overall Abundance						**Overall Diversity (e^H)**						**Overall Richness**					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus spp.*			*Lo. maackii / V. prunifolium*			*Li. obtusifolium / Fraxinus spp.*			*Lo. maackii / V. prunifolium*			*Li. obtusifolium / Fraxinus spp.*		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	34.043	0.0118	1	27.462	0.0443	1	21.471	0.0041	1	30.005	0.0005	1	22.758	0.0042	1	28.09	0.0016
Site	10	229.576	5.50E-06	8	151.658	4.30E-03	10	166.215	7.45E-10	8	41.006	3.63E-02	10	175.08	9.35E-10	8	45.017	4.34E-02
Date	1	76.276	0.0002	1	9.709	0.2316	1	46.6	2.41E-05	1	29.321	6.00E-04	1	53.138	1.21E-05	1	15.637	1.86E-02
Lo. maackii density	1	3.876	0.3955	1	0.281	0.8386	1	2.263	0.352	1	0.795	0.5721	1	0.676	0.6217	1	0.074	0.8719

Table 1-2 Analysis of Deviance table showing the effects of single factor deletions from the GLM models comparing overall arthropod abundance, diversity, and richness between focal plant species. Summary of deviance values, degrees of freedom, and *p*-values.

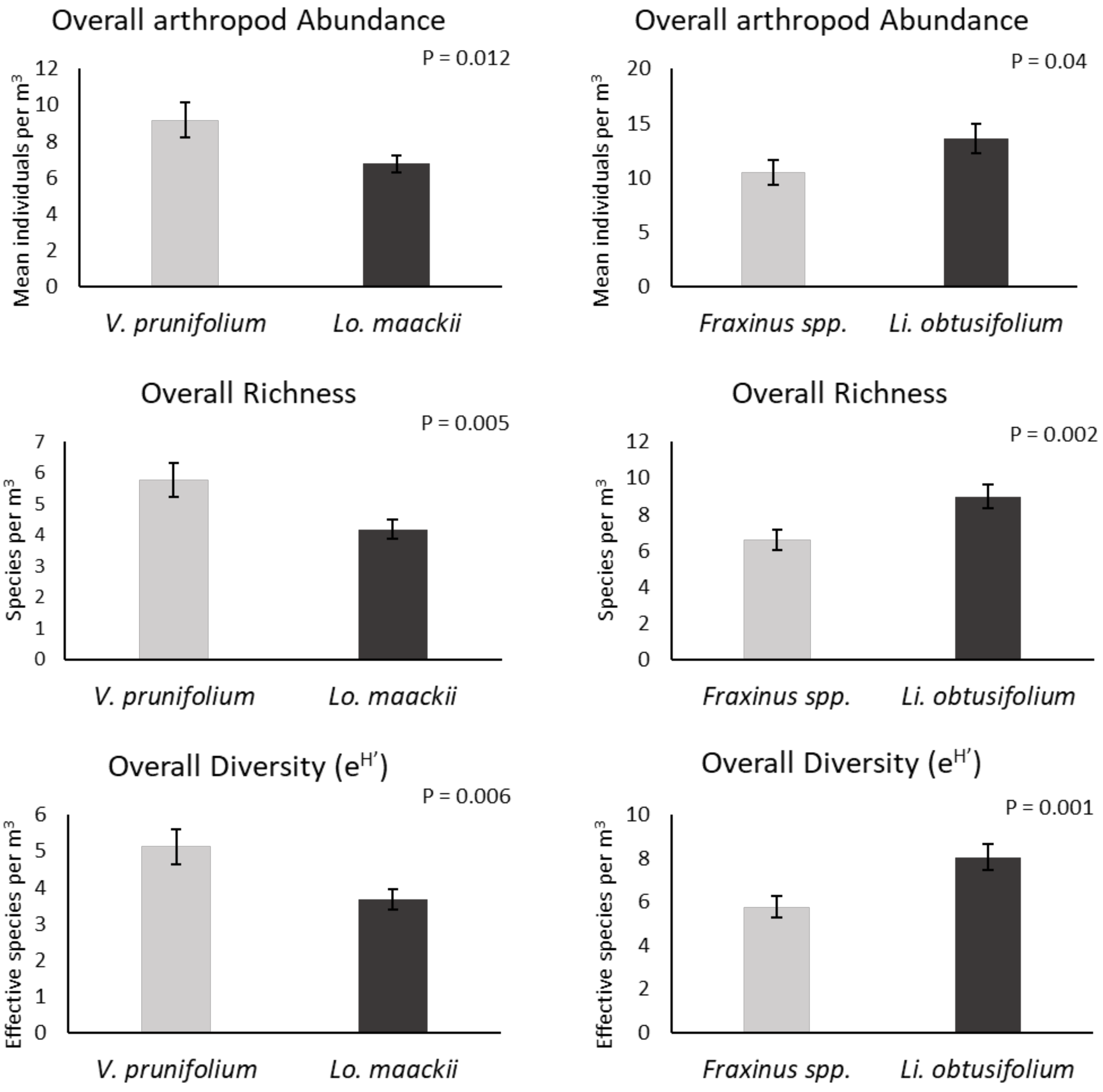

Figure 1-2 Comparisons of overall community composition between focal plants.

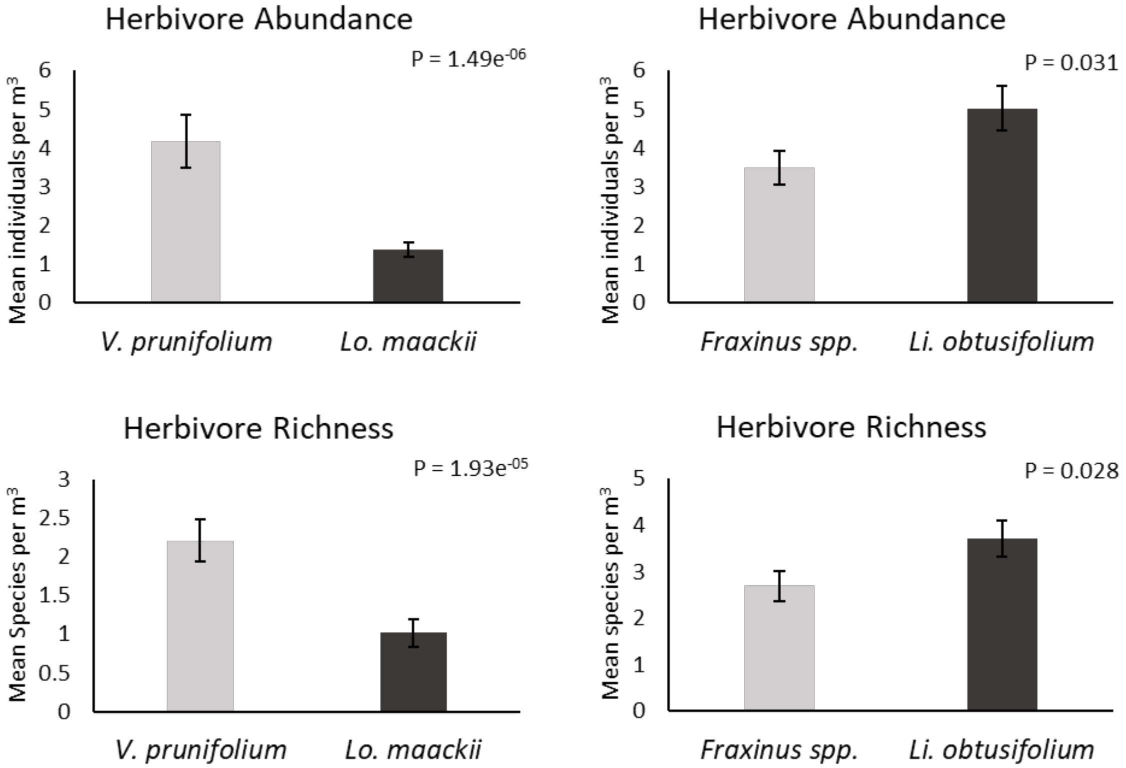

Figure 1-3 Comparisons of abundance and richness herbivores on focal plants.

	Herbivore Abundance						Herbivore Richness					
	Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.			Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	153.092	2.03E-08	1	18.734	2.54E-02	1	44.833	9.74E-07	1	11.925	2.42E-02
Site	10	128.109	0.0033	8	82.053	0.0051	10	61.263	0.0003	8	56.873	0.0021
Date	1	118.162	8.29E-07	1	1.963	4.69E-01	1	3.05	0.2015	1	4.779	0.1537
Lo. maackii density	1	14.484	0.0844	1	0.196	0.8191	1	34.392	1.80E-05	1	0.013	9.42E-01

Table 1-3 Significance of individual explanatory variables from GLM comparing the abundance and richness of herbivores on focal plant species. Summary of deviance values, degrees of freedom, and p-values.

	Hemimetabolous Herbivore Abundance						Caterpillar Abundance					
	Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.			Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	3.577	1.79E-01	1	20.928	1.12E-02	1	275.145	2.11E-13	1	1.7885	3.37E-01
Site	10	79.161	1.71E-05	8	103.463	0.0001	10	103.248	0.0272	8	30.9285	0.043
Date	1	48.733	7.00E-07	1	0.664	0.6516	1	69.925	0.0002	1	5.0587	1.06E-01
Lo. maackii density	1	0.823	5.19E-01	1	0.175	8.17E-01	1	24.791	0.0275	1	0.552	0.5936

Table 1-4 Significance of individual explanatory variables from GLM comparing the abundances of hemimetabolous herbivores and caterpillars on focal plant species. Summary of deviance values, degrees of freedom, and p-values.

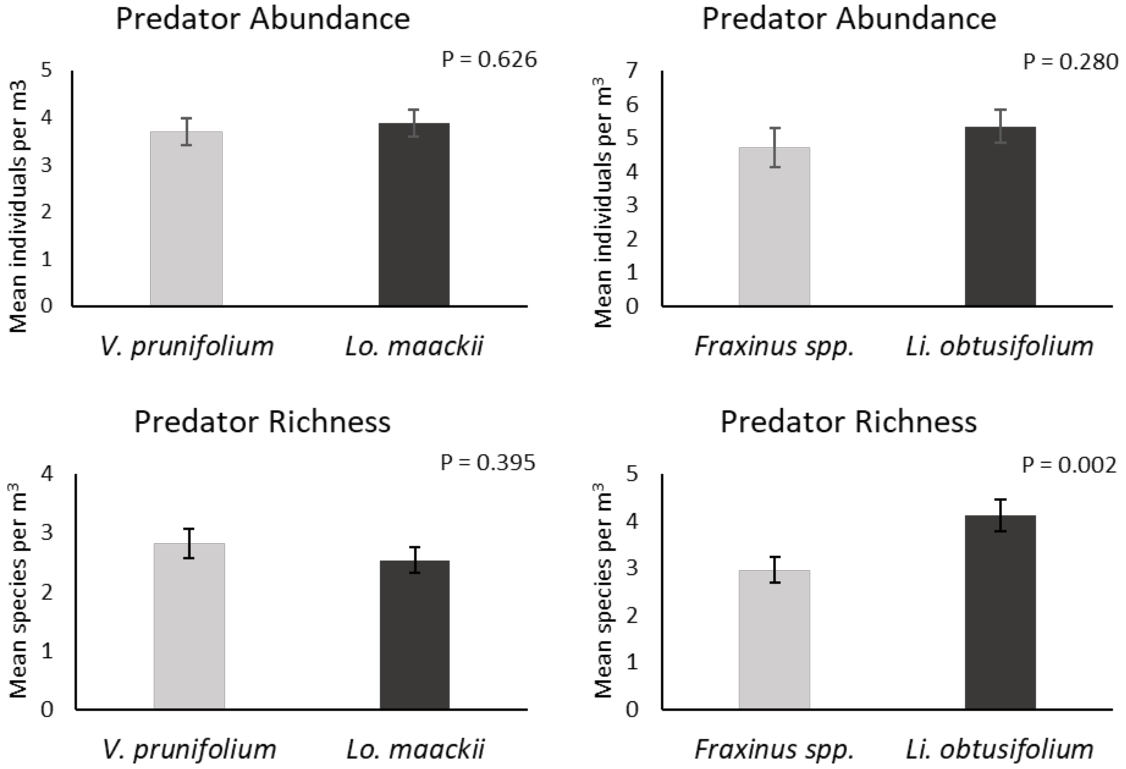

Figure 1-4 Comparisons of abundance and richness predators on focal plants.

	Predator Abundance						Predator Richness					
	Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.			Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.		
Predictor	df	Deviance	P (>Chi)	df	Deviance	P (>Chi)	df	Deviance	P (>Chi)	df	Deviance	P (>Chi)
Host	1	1.663	3.70E-01	1	4.927	2.45E-01	1	0.76	4.73E-01	1	16.9862	1.10E-03
Site	10	62.202	0.0008	8	47.628	0.1094	10	82.572	2.17E-08	8	13.4056	0.3938
Date	1	13.339	0.0111	1	5.591	2.15E-01	1	24.81	4.18E-05	1	20.5084	0.0003
Lo. maackii density	1	1.198	0.4464	1	1.552	0.514	1	0.039	8.71E-01	1	0.5599	5.53E-01

Table 1-5 Significance of individual explanatory variables from GLM comparing the abundance and richness of predators on focal plant species. Summary of deviance values, degrees of freedom, and p-values.

	Ant Abundance						Spider Abundance					
	Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.			Lo. maackii / V. prunifolium			Li. obtusifolium / Fraxinus spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	11.3386	2.69E-02	1	23.273	1.47E-02	1	0.334	6.35E-01	1	17.714	5.30E-03
Site	10	30.0575	0.2246	8	74.448	0.01463	10	72.78	3.69E-07	8	35.963	0.0458
Date	1	5.3444	0.1287	1	28.279	7.15E-03	1	20.214	0.0002	1	23.918	1.20E-03
Lo. maackii density	1	4.5636	0.1603	1	25.541	0.0106	1	0.082	0.8137	1	2.035	0.3449

Table 1-6 Significance of individual explanatory variables from GLM comparing the abundances of ants and spiders on focal plant species. Summary of deviance values, degrees of freedom, and p-values.

Family level Community Ordination

NMDS at the family level revealed that the arthropod communities overlapped to a high degree between host plant species. The stress level was moderately high (0.291), suggesting the model may be unsuitable for depicting these data. Nevertheless, a PMANOVA found a significant effect of host plant species ($p = 0.001$). That said, only a small degree of variance ($r^2 = 0.057$) between community compositions was explained by host plant species.

When comparing the communities on *Lo. maackii* and *V. prunifolium*, a PMANOVA (Table 1-7) also revealed a significant effect of host on community composition (p = 0.001). However, host identity explained a slight degree of variance (r^2 = 0.046) between in community compositions (Table 1-7). As for the previous ordination, the stress level was moderately high (0.283).

Based on a PMANOVA (Table 1-7), the communities of *Li. obtusifolium* and *Fraxinus* spp. significantly differed (p = 0.033); however, there is only a small portion of variance was explained by host (r^2 = 0.026) between the host plants and community compositions. Furthermore, the stress level was moderately high (0.257), albeit lower than in the other tests.

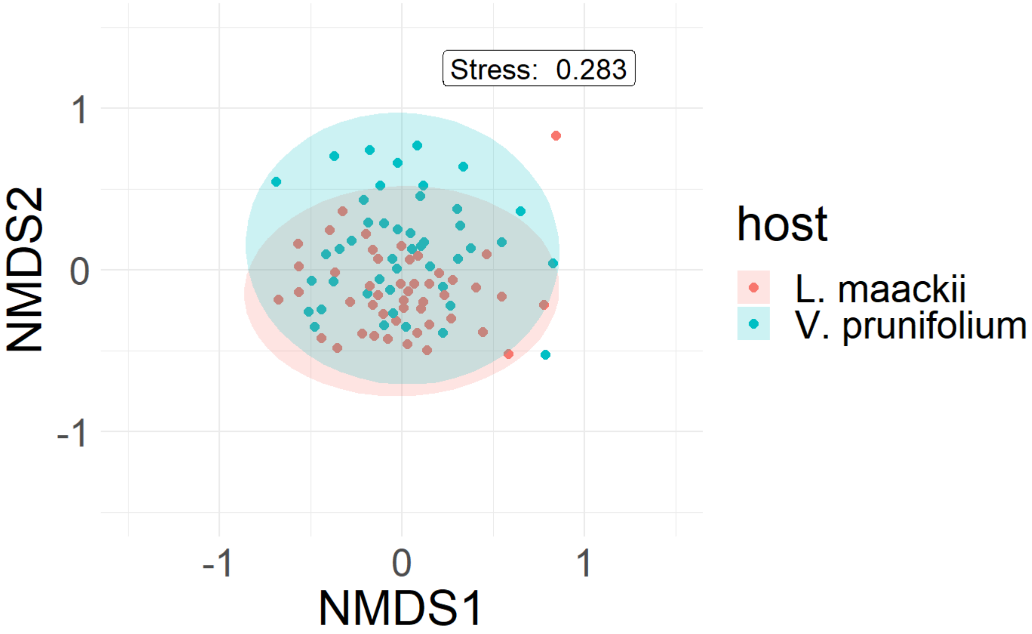

Figure 1-5 Plotted results of NMDS comparing the community composition of *Lo. maackii* and *V. prunifolium* using Hellinger transformed abundances at the family level.

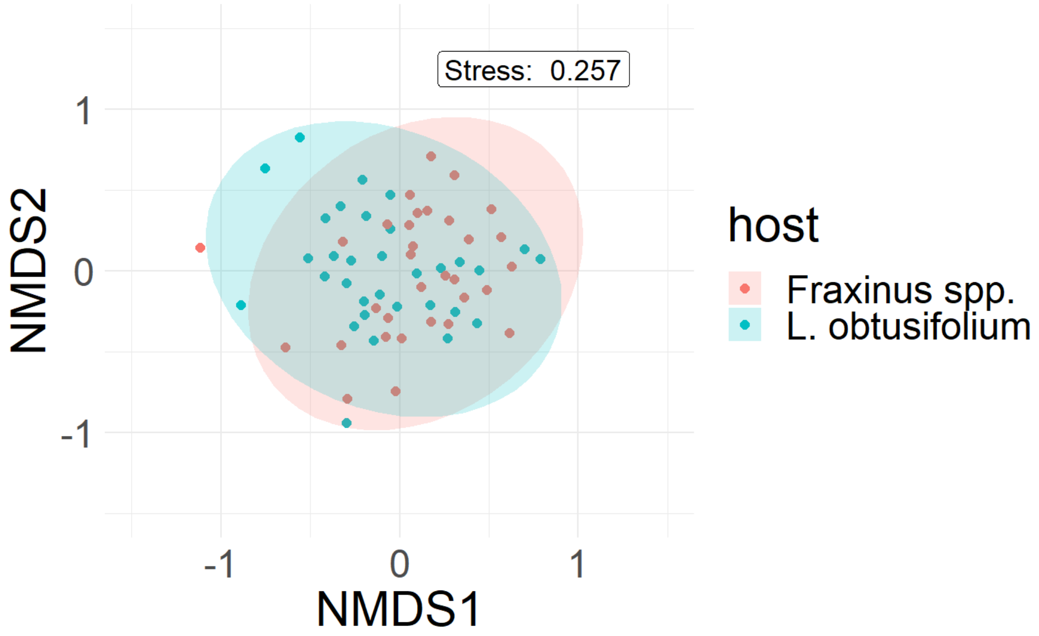

Figure 1-6 Plotted results of NMDS comparing the community composition of *Li. obtusifolium* and *Lo. maackii* using Hellinger transformed abundances at the family level.

Community Composition										
	Lo. maackii / V. prunifolium					Li. obtusifolium / Fraxinus spp.				
Predictor	*df*	*Sum of Sq.*	*R^2*	*F*	*P (>F)*	*df*	*Sum of sq.*	*R^2*	*F*	*P (>F)*
Host	1	1.1052	0.04587	4.5474	0.001	1	0.4505	0.02614	1.8168	0.025
Site	10	3.5434	1.47E-01	1.458	0.001	8.00E+00	3.3905	0.19678	1.7093	0.001
Residual	80	19.4423	0.80704			54	13.389	0.77708		
Total	91	24.0908	1			63	17.2299	1		

Table 1-7 Significance of individual explanatory variables from a PMNOVA that tested differences in family level arthropod community composition. Summary of degrees of freedom, sum of squares, F-value, and p-value. The test was run with 999 permutations.

Discussion

The results for *Lo. maackii* were as I expected based on its non-native status and lack of coevolved relationships with native arthropods. This invasive hosted a depauperate arthropod community relative to the native counterpart *V. prunifolium*. This pattern appears to have been driven by the herbivore community. *Lo. maackii* only hosted about one-third as many individual herbivores by volume as *V. prunifolium*. Furthermore, less than half as many species were typically found on honeysuckle as on its native counterpart. Fittingly based on its paucity of herbivores, *Lo. maackii* also experienced significantly less herbivory than *V. prunifolium*. This aligns with common garden experiments that found *Lo. maackii* receives less herbivory damage than do native *Lonicera* species (Lieurance et al. 2015). Although it remains unclear why *Lo. maackii* may suffer less herbivory than comparable native plants, some researchers suggest high levels of phenolic compounds, such as luteolin-7-glucoside, may make the plant particularly unpalatable to many herbivores (Lieurance et al. 2015). Notably, the ratio of predators to herbivores was approximately four times greater on the invasive *Lo. maackii* as on the native *V. prunifolium*. This skewed predator to herbivore ratio may present yet another obstacle to colonization of *Lo. maackii* by herbivores.

Unlike herbivores, predators did not significantly differ in abundance or diversity on *Lo. maackii* compared to *V. prunifolium*. This aligns with previous studies investigating trends in arthropod communities on exotic plants (Scherber et al. 2010). As predators do not feed on plants, it follows that their communities would vary less between plant species. Counterintuitively, predatory arthropods may actually be more sensitive to plant diversity than herbivores. One study found that over the long term, the loss of plant diversity can make arthropod communities become dramatically less rich and heavily skewed from predator to herbivore dominated (Haddad et al. 2009). The reason for the surprisingly strong negative effect of invasive plants on herbivores may partially be a result of predators not following prey onto novel hosts (Grosman et al. 2009). This is an idea I tested in Chapter 3.

The abundance and diversity of arthropod communities on *Li. obtusifolium* and *Fraxinus* spp. ran counter to our expectations. Relative to native *Fraxinus* spp., *Li. obtusifolium* hosted a similar herbivore community and a more diverse predator community. So, if *Li. obtusifolium* replaces *Fraxinus* spp. in woodlands as *Fraxinus* spp. continue to decline, the diversity and abundance of arthropods may remain similar for the short term. Additionally, as *Li. obtusifolium* is confamilial with *Fraxinus* spp., some herbivorous arthropods may be able to switch to this novel host. Although the arthropod communities of *Li. obtusifolium* and *Fraxinus* spp. may be comparable in terms of arthropod abundance and richness, *Li. obtusifolium* appears to suppress a range of native plant species (Maynard-Bean & Kaye 2019), which may suppress arthropod communities in the ecosystem. Furthermore, *Li. obtusifolium* hosts a greater abundance of predators but a similar abundance of herbivores as *Fraxinus* spp. This shifts the ratio of predators to herbivores higher, potentially increasing predation on herbivores. Eventually, this could suppress the herbivore community—potentially reducing resource availability to higher trophic levels.

Although *Fraxinus* spp. as a whole appear to be poorer hosts than *Li. obtusifolium*, this may be an incomplete picture. One species of *Fraxinus* included in this study, *F. quadrangulata*, may be more strongly defended chemically than other local *Fraxinus* species. This could explain both its resistance to the emerald ash borer (*Agrilus planipennis*) and its poor herbivore community in this study (Tanis & Mccullough 2015). Therefore, I reanalyzed the data with *F. quadrangulata* excluded. This reduced the sample size for *Fraxinus* spp. from N = 70 to N = 60. Despite this relatively small reduction in sample size, there were key differences in the results. Although *Li. obtusifolium* still hosted greater arthropod richness ($p = 0.0042$) and diversity ($p = 0.0013$), the difference between it and *Fraxinus* were no longer significant for overall arthropod abundance ($p = 0.141$), herbivore abundance ($p = 0.6315$) and herbivore richness ($p = 0.0652$).

Conclusion

The depauperate herbivore community on *Lo. maackii* relative to native *V. prunifolium* may partially explain this invasive plant's remarkable success in Eastern North America. Fewer herbivores should equal lower herbivory, which appears to be the case here (see Chapter 2). This could signal both more competition for plants and less food for higher trophic levels. *Lo. maackii* supports a smaller, less diverse herbivore community than co-occurring natives, such as *V. prunifolium*. This likely partially shields it from herbivory, possibly allowing it to invest more in growth and reproduction. Furthermore, herbivorous arthropods are vital for passing resources from primary producers to higher trophic levels (Yang & Gratton 2014). If invasive *Lo. maackii* supports fewer herbivorous arthropods, less energy will be made available for consumers in the ecosystem (Lister & Garcia 2018). The paucity of caterpillars is particularly threatening to songbirds, as many rely on these larvae to feed chicks and refuel during migration (Piel et al. 2021).

There are a few caveats to this study. Of note, all sampling occurred over a single season. The effect of non-native plants on arthropod biodiversity is likely highly variable (Landsman et al. 2021), and community compositions can vary considerably between years (Haddad et al. 2009). Additionally, although the rapid, morphospecies identifications facilitated collecting a large sample size, it did make it impossible to determine how the specific, species-level compositions differed between focal plant communities. Considering the high level of specialization among insects (Loxdale et al. 2011), it is possible and even likely that community compositions significantly varied beyond what I could ascertain.

Although many arthropods are highly host specific, utilizing only a handful of plant taxa (Loxdale & Harvey 2011), it may be worth taking a step back. It seems true that specialization is the rule, not the exception among arthropods, particularly herbivorous insects (Forister et al. 2015). Nevertheless, when considering overall arthropod biodiversity, individual plant taxa may be less important than overall plant diversity. In support of this, plant species composition and land cover may be the greatest determiners of insect community compositions across all major functional groups, from parasitoids and detritivores to predators and herbivores (Tobisch et al. 2023). Furthermore, declining plant diversity is closely associated with cratering arthropod richness (Haddad et al. 2009). Invasive plants are among the greatest threats to the native plant diversity on which arthropods depend (Qian & Ricklefs 2006). Therefore, if we hope to preserve the crucial functions and services provided by arthropods, we should find ways to control invasive plants and slow the rate of new invasions.

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Chapter 2 How well do invasive woody plants support caterpillars relative to native plants?

Abstract

Caterpillars (the larvae of Lepidoptera) are the dominant arthropod herbivores in many ecosystems, including the woodlands of eastern North America. These abundant and diverse insects are crucial to ecosystem functions—providing top-down control on plants and as a vital food source for higher trophic levels. Throughout their shared history, caterpillars and plants have been locked in an evolutionary arms race. However, native caterpillars and exotic invasive plants lack a shared history; therefore, they have not had the opportunity to coevolve. The motivation of this study was to assess the support provided by invasive plants to caterpillars. I did so by comparing the caterpillar abundance and herbivory in the field in Ohio and their performance in the lab on invasive Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum obtusifolium*) to those on phylogenetically and ecological counterparts—blackhaw (*Viburnum prunifolium*) and ash (*Fraxinus* spp.). Herbivory and caterpillar abundance were far lower on *Lo. maackii* than *V. prunifolium*; however, both metrics were similar between *Li. obtusifolium* and *Fraxinus spp*. The probability of pupation trended higher for caterpillars on native plants overall and was significantly higher on *Fraxinus* spp. than on *Li. obtusifolium*. Additionally, there was a non-significant, but suggestive, trend toward lower growth in caterpillars on the exotic host plants. These results suggest that relative to natives, exotic plants are inferior hosts and contribute less to supporting

higher trophic levels. Consequently, the continued spread of these exotic plants could erode ecosystem function in eastern North American woodlands.

Introduction

As few as 14% of native plant species support as much as 90% of Lepidoptera diversity (Narango et al. 2017). The larvae of Lepidoptera (hereafter referred to as caterpillars) tend to be specialists (Forister et al. 2015). Caterpillars are essential to woodland ecosystems. These herbivorous insects consume vast quantities of foliage in these ecosystems. In some forests, caterpillars consume more plant material than all other herbivores combined (Janzen 1988). In turn, caterpillars are a vital food source for an array of vertebrate and invertebrate taxa (Müller et al. 2006; Kalka & Kalko 2006). For example, most songbirds depend on caterpillars, particularly while rearing chicks and during fall migration (Newell et al. 2014).

Non-native plants often do not support as abundant or as diverse of arthropod communities as natives (Bezemer et al. 2014; Litt et al. 2014). Furthermore, invasive plants may dramatically alter the composition of arthropod communities. Specifically, invasives may favor generalist herbivores (Rodríguez et al. 2019) and shift the ratio of herbivores to predators (Simao et al. 2010). It seems that the structural complexity of invasive plants significantly affects predator communities. Invasive plants with low structural complexity, such as grasses, are associated with depauperate predator communities (Simao et al. 2010). Conversely, invasive plants with high complexity are associated with high abundance and diversity of at least one major group of predators: spiders (Loomis et al. 2014). Curiously, spider diversity is more strongly associated with plant structural complexity than with prey availability (Greenstone 1984). This relationship may be due to the importance of three-dimensional habitat for web-building spiders (Pearson 2009). Unlike predators, herbivores need more from plants than a place to live—they need to be fed. The invasive plants offer several obstacles to colonization by herbivores: novel weapons, unrecognizability, and potentially poor nutritional value.

Herbivores are locked in an arms race with their plant hosts, continuously adapting to myriad physical and chemical defenses. Often, this leads to extreme specialization in arthropod herbivores, allowing them to be highly successful on a narrow range of hosts (Jones et al. 2022). Among arthropod herbivores, specialization is likely the norm (Forister et al. 2015). Furthermore, even many purported generalists are likely to exhibit local specialization (Loxdale et al. 2011). Consequently, invasive plants likely experience lower herbivory in their introduced range (Keane & Crawley 2002). This could grant invasive plants a competitive advantage over native competitors.

There are two major obstacles to colonization of invasive plants by native herbivores: unrecognizability and unpalatability. Plants constantly produce volatile compounds; however, this production is strongly associated with biotic and abiotic stressors, such as high temperature and herbivore attack (Dong et al. 2016). Arthropods cue in on these compounds to locate suitable host plants (Carroll et al. 2008; Knolhoff & Heckel 2014). Exotic plants produce volatiles that are novel to local arthropod herbivores; consequently, these herbivores may not recognize these volatiles as a signal of potential food (Bezemer et al. 2014). Some herbivores may jump this hurdle, but this does not guarantee success on invasive hosts. Invasive plants that recently colonized an ecosystem may have a suite of chemical and physical defenses to which native herbivores are not adapted (Gruntman et al. 2017). Additionally, invasive plants may simply be inordinately well defended (Hierro et al. 2022). Even generalist herbivores may struggle to colonize invasive plants (Lankau et al. 2004; Schaffner et al. 2011).

Despite the challenges presented by exotic host plants to native arthropod herbivores, at least some are able to make the jump. For example, in the Netherlands, a robust community of arthropods has colonized non-native black cherry (*Prunus serotina*) since its intentional introduction to Europe in the 1600s (Schilthuizen et al. 2016; Starfinger et al. 2003). In fact, *P. serotina* hosts a more diverse community of herbivorous arthropods than its local native congener, bird cherry (*Prunus podus*) (Schilthuizen et al. 2016). Some native herbivores may be able to switch to novel, invasive hosts due to ecological fitting. This describes organisms that may be pre-adapted to fit a new niche (Janzen 1985). For example, herbivores adapted to feeding on hosts phylogenetically close to an invader may already be adapted to a suite of defenses similar to the novel invader's (Agosta 2006). In contrast to *P. serotina*, which has native congeners in its invaded range, Douglas-fir (*Pseudotsuga menziesii*), does not (Roques et al. 2006). *P. menziessi* has only accumulated about a third as many herbivore species in Europe as in its native range (Roques et al. 2006), possibly due to its phylogenetic isolation, Ecological fitting may partially explain the success of certain invasive plants. Overall, the invasive plant success seems to correlate with phylogenetic isolation in invaded ranges (Parker et al. 2012).

Although some studies have found caterpillars on invasive plants (Stireman & Workman 2023), there studies have found invasive plants to be poor hosts for at least some native generalist and specialist caterpillars (Tallamy et al. 2010; Horne et al. 2023). Therefore, it remains unclear if invasive exotics will affect native caterpillar abundance and diversity over the long term. Furthermore, there have been few direct comparisons of caterpillar performance on invasive plants relative to native counterparts. Answering these questions would both help us understand how invasive plants are affecting this aspect of biodiversity and infer the trophic contributions of these plants in terms of supporting caterpillars, which are essential prey items for many insectivores.

Study System

This study focused on two non-native woody plants: Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum obtusifolium*). Although these taxa are not closely related, they pose similar ecological concerns for woodland ecosystems. Both species have invaded vast swaths of eastern North America, where they are associated with plummeting native floral diversity (Collier et al. 2002; Maynard-Bean & Kaye 2019). These invasive shrubs appear to be transforming forest ecosystems in many regions of eastern North America (Webster et al. 2006). Consequently, both species are invasive plants of concern in the eastern United States (Maddox et al. 2010; Buerger et al. 2016).

Lo. maackii was introduced to North America as an ornamental plant in the late 1800s (Luken & Thieret 1996). Since then, it has colonized nearly all of the eastern United States, the Pacific Northwest, and southeastern Canada (Kartesz 2015). Several traits likely contribute to this shrub's invasion success. These include phenotypic plasticity, rapid growth, allelopathy, and phenology (McNeish & McEwan 2016). *Lo. maackii* performs well under a wide range of light conditions, helping it colonize a wide range of habitats (Luken et al. 1997; Lieurance & Landsbergen 2016). Additionally, it is able to maintain extremely rapid growth, even in high competition conditions (Deering & Vankat 1999). Furthermore, it directly inhibits the growth of co-occurring plants by releasing chemicals into the soil (Cippollini & Bohrer 2016). Lastly, *Lo. maackii* begins leafing out earlier and keeps its leaves later in the season than do almost any native plants—granting it a longer growing season and potentially allowing it to shade out co-occurring plants (McEwan et al. 2009). Of particular relevance to my study, herbivore release may also contribute to *Lo. maackii*'s success. *Lo. maackii* has a diverse array of defensive compounds (Cipollini et al. 2008). These may be novel to native herbivores, which would explain low rates of herbivory previously observed on *Lo. maackii* relative to native *Lonicera* in a common garden (Lieurance et al. 2015).

Although it is less studied than *Lo. maackii*, *Li. obtusifolium* appears to share many characteristics that contribute to its invasiveness. It too was introduced as an ornamental plant during the 1800s, later escaping cultivation (Cothran 2003). Since then, it has spread across much of North America (Kartesz 2015), partially due to its tolerance for low light and nutrient conditions (Webster et al. 2006). Although untested in *Li. obtusifolium*, two related invasive species, *Ligustrum vulgare* and *Ligustrum sinense* exhibit allelopathy (Shannon-Firestone & Firestone 2015). The allelopathy of these plants is associated with decreased growth and increased mortality in neighboring plants (Greene & Blossey 2012). It is likely *Li. obtusifolium* similarly suppresses competing native plants. Another competitive advantage of *Li. obtusifolium* is its remarkable fecundity, which is likely similar to the related *Ligustrum vulgare*, which can produce tens of thousands of seeds from a single mature plant annually (Obeso and

Grubb 1993). In turn, frugivorous birds disperse these seeds (Debussche and Isenmann 1994), likely facilitating the rapid spread of this invader.

The rate of exotic plant invasions is increasing across the globe (Seebens et al. 2017). Much of this spread of exotic plants is driven by globalization (van Kleunen et al. 2015). In coming decades, climate change will likely favor many invasive plants over native counterparts (Liu et al. 2017). This may facilitate a range expansion of many invasive plants in North America (Bradley et al. 2010) and other temperate ecosystems (Seebens et al. 2015). To fully assess the ecological threat posed by more frequent and expanding invasions, we need to assess the trophic effects of invasive plants. The major question of this study is how well *Lo. maackii* and *Li. obtusifolium support diverse and abundant caterpillar communities* compared to native plants. Answering this question would build a clearer understanding of how these invasive shrubs are interacting with the ecosystem.

Methods

Caterpillar field surveys

I surveyed caterpillars over the growing season from May 2022 to October 2022. I collected specimens via beat sheet from woodlands in the Miami-Valley region of Southwest Ohio. To gather a dataset representative of the region, I collected from at eight sites in the Dayton Metro Area, including the Wright State University Biological Preserve, Sugarcreek MetroPark, Englewood MetroPark, Germantown MetroPark, Twin Creek MetroPark, Carriage Hill Metropark, Medlar Conservation Area, Glen Helen Nature Preserve. To account for sampling effort, I recorded the approximate cubic volume of each plant sampled. I assigned each caterpillar I collected to a morpho species and took photos of some specimens to aid later, more specific identification. I collected every caterpillar that survived the beating and was at least 3mm in length.

I transferred all of the caterpillars I collected to the laboratory at Wright State University. My rearing protocol was as follows. Upon reaching the lab, I assigned each caterpillar a unique identifier that incorporated collection date and site, then recorded the length with a ruler and mass with a balance for each caterpillar. I photographed some individuals for future reference. Caterpillars were housed singly in labeled transparent plastic containers lined with paper towels for ease of cleaning and to maintain humidity levels and provisioned with foliage from the host plant species from which the caterpillar was collected. These cups were under CFL lighting with a 12-hour L:D cycle at ambient temperature (21°C-25°C). Every two days, I weighed the caterpillars, fed them fresh foliage of the plant taxa from which I collected them, replaced their paper towel substrate, and lightly wetted their cups with a spray bottle of water. I recorded the final fates of each caterpillar—death, parasitism, pupation, and adult eclosion. If a caterpillar died, I noted the cause of death, so far as it could be discerned (e.g., starvation or parasitism).

Identification

I identified host plants in the field with the aid of field guides (Braun 1989; Maddox et al. 2010). About half of the total caterpillars died before pupation. These were identified to the narrowest taxonomic level possible based on larval morphology (Wagner 2005). Caterpillars that successfully developed into adult moths were mounted and further identified based on external morphology (i.e., none were dissected). I used a range of field guides (Covell 2005) and online sources to help identify these, including The North American Moth Photographer's Group (http://mothphotographersgroup.msstate.edu), BugGuide (https://bugguide.net), and iNatralist (https://www.inaturalist.org). All specimens are housed in the Stireman insect collection (JOSC) at Wright State University.

Herbivory Assessment

I assessed leaf damage to compare herbivory rates across the study plants in woodland sites in southwestern Ohio. My motivation for this was to compare utilization of these plants by herbivorous insects, herbivory is an essential step in the transfer of energy between trophic levels. I used eight wooded sites in or near Dayton, OH for this study: Carriage Hill MetroPark, George Rogers Clark Park, the Glen Helen Nature Preserve, John Bryan State Park, Green County Park's Narrows Reserve, and Wright State University's Biological Preserve. Leaves were collected by members of the lab. Plants were haphazardly sampled along trails at survey sites in September and October (end-of-season herbivory), with at least 5m between sampled plants and an attempt to intersperse plant species surveyed. 2-5 branches (leaves in the case of ash) were blindly selected per plant, by haphazardly grabbing a branch with closed eyes, and 5-10 leaves (or ash leaflets) were collected as a group from each selected branch. Subsequently, 10-30 of these leaves were selected per plant with a random number generator for measurement. Although not completely random, these methods were adopted to introduce as little bias as possible into the selection of leaves for herbivory measurement. Percent chewing leaf damage was measured with the Leafbyte application or visually estimated after training with LeafByte (Getman-Pickering et al., 2020). Low (1-3%) and high (>50%) levels were estimated visually, as using Leafbyte results in little or no improvement in accuracy in these cases.

Analysis

I conducted all of the analyses for this study in RStudio v4.2.2 (R Core Team 2022). To compare caterpillar abundance and richness across my focal plant taxa, I used quasi-Poisson generalized linear models (GLM) for each plant species pair. In my models, host plant species and *Lo. maackii* density were fixed effects, and site and date were covariates. I constructed separate models to quantify the effect of host on the mean overall abundance and richness of caterpillars per m^3 of foliage. I combined abundances of larval Lepidopterans and Symphytans as caterpillars due to their similar ecological functions.

I was also interested in the effect of host plant species on the success and growth of caterpillars. Unfortunately, there was minimal overlap in the caterpillar species found and reared on my focal plants, which generally precluded intraspecific comparisons of caterpillar performance across plants. Instead, my comparisons of performance were at the family level. Additionally, many caterpillars require exacting, often poorly understood conditions to successfully overwinter. Therefore, I used pupation, not eclosion, as the threshold of developmental success. It was also unclear whether parasitized caterpillars should count as successful. Although they died, they did feed and at least partially develop on their host plant. Furthermore, many parasitized individuals reached pupation. Therefore, I ran models including parasitism as developmental success and models that excluded parasitized caterpillars. These were binomial models that assessed the probability of success (1) and failure (0). The factors included in the model were host plant species, caterpillar family, initial mass at collection. I included family to account for any families that consistently exhibit higher survival rates. Initial mass served as a proxy for caterpillar age, as mortality tends to be extremely high in early instars (Zalucki et al 2002).

To compare the richness of caterpillars on each focal plant, I computed individual-based rarefaction curves using (Chao et al. 2016). This is an online, interactive version of the iNext package for R. It allows analysis of species diversity based on Hill numbers through a mixture of interpolation and extrapolation with random bootstrap regeneration (Chao et al. 2016). I identified 329 caterpillars with an adequate specificity for individual-based rarefaction in *iNext*. To facilitate comparison between focal plants, I extrapolated richness on each host. For the comparison between *Lo. maackii* and *V. prunifolium*, the sample size was much smaller for *Lo. maackii* (n = 26), so I only extrapolated *Lo. maackii*'s richness out to the sample size I collected from *V. prunifolium* (n = 264). This allowed me to estimate the richness I would have observed on *Lo. maackii* had I sampled it more intensively. The sample size *Li. obtusifolium* (n = 22) and *Fraxinus* spp. (n = 16), were much more similar to one another. Therefore, I extrapolated to twice the sample size of *Li. obtusifolium* for both, in an effort to estimate the richnesses of both had I collected larger samples. For both rarefactions, I used 1000 bootstraps and a CI of 0.95.

To compare growth of caterpillars across host plants, I constructed a quasi-Poisson GLM with growth as a response of host species and caterpillar family. I limited my sample set to caterpillars that displayed growth over time—excluding those that died before their second weighing or declined in mass between every weighing. Also, many caterpillars gained mass to a point, then leveled off or declined in mass until pupation. To account for this, I only included weighing up to the peak mass of each caterpillar. After filtering the data in this way, I converted the natural log of the masses and then regressed the log-transformed masses and the corresponding Julian dates for each caterpillar species and estimated the slope of the best fit line.

To compare leaf herbivory between hostplants, I calculated the mean percentage of missing leaf area for the leaves collected from each plant, treating individual plants, not leaves, as the sample unit. I tested the effect of host and site on mean herbivory with a quasi-Poisson Generalized Linear Model (GLM).

Results

Caterpillar field surveys

Between May 2022 and October 2022, I surveyed 383 larval Lepidoptera and Symphyta from my focal plant species. The difference between the caterpillar communities on the native *V. prunifolium* and the exotic *Lo. maackii* was dramatic and highly significant (Table 2-1 and 2-2). *Lo. maackii* only hosted about a tenth as many individual caterpillars (Fig. 2-1; Std. error = 0.643; $p < 0.001$) and a fifth as many species (Fig. 2-2, Std. error = 0.389; $p < 0.001$) per m^3 foliage as *V. prunifolium*. In contrast *Li. obtusifolium* a similar abundance (Fig. 2-1; Std. error = 0.37; $p = 0.44$) and richness of caterpillars per m^3 of foliage as *Fraxinus* spp. (Fig. 2-1, Std. error = 0.377; $p = 0.198$).

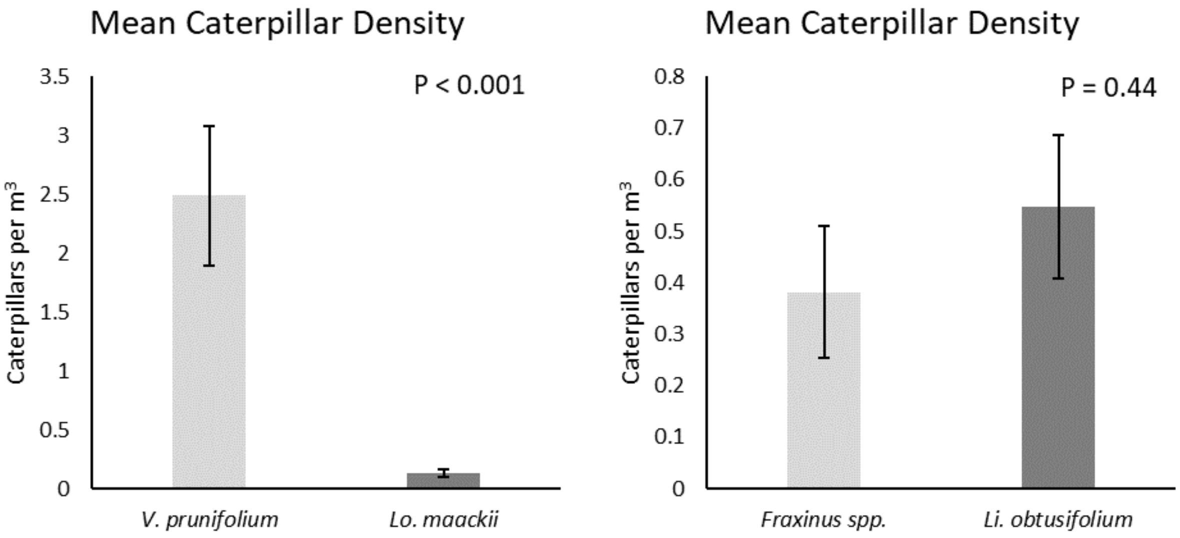

Figure 2-1 Mean abundance of caterpillars per cubic meter of foliage sampled. P-values of the effect of host from quasipoisson GLM that included site, *Lo. maackii* density within a 3 m radius of samples, and date as covariates.

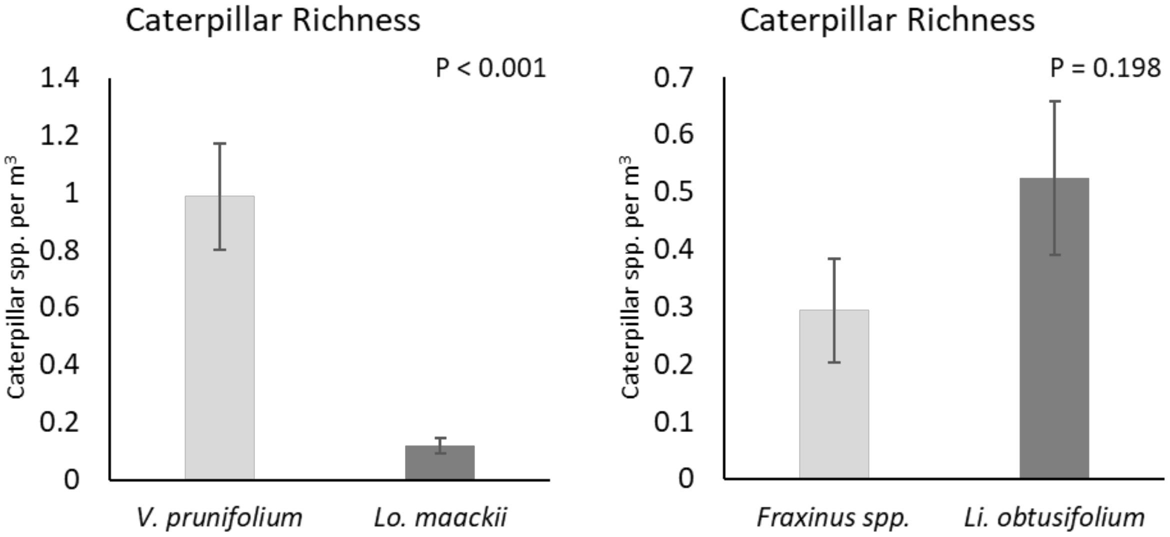

Figure 2-2 Mean richness of caterpillars per cubic meter of foliage sampled. P-values of the effect of host from quasipoisson GLM that included site, *Lo. maackii* density within a 3 m radius of samples, and date as covariates.

	Caterpillar Abundance					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	275.145	2.11E-13	1	1.7885	3.37E-01
Site	10	103.248	0.0272	8	30.9285	0.043
Date	1	69.925	0.0002	1	5.0587	1.06E-01
Lo. maackii density	1	24.791	0.0275	1	0.552	0.5936

Table 2-1 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on the mean abundance of caterpillars per cubic meter of foliage.

	Caterpillar Richness					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	81.24	3.58E-13	1	4.2598	1.10E-01
Site	10	40.728	0.003122	8	25.1666	0.05671
Date	1	10.624	0.1733	1	3.1539	0.16855
Lo. maackii density	1	2.85	0.008558	1	1.174	4.01E-01

Table 2-2 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on the mean caterpillar species per cubic meter of foliage.

Based on rarefactions in *iNext*, it appears *Lo. maackii* may host a caterpillar community of similar or greater richness than their *V. prunifolium* (Fig. 2-3). These results come with the caveat that the sample set was overwhelmingly represented by *V. prunifolium* (n = 264). Similarly, *Li. obtusifolium* appears to host a richer caterpillar community than *Fraxinus* spp. (Fig. 2-4). Notably, *Lo. maackii* and *Li. obtusifolium* appear to support similar caterpillar richness, despite being unrelated and invasive.

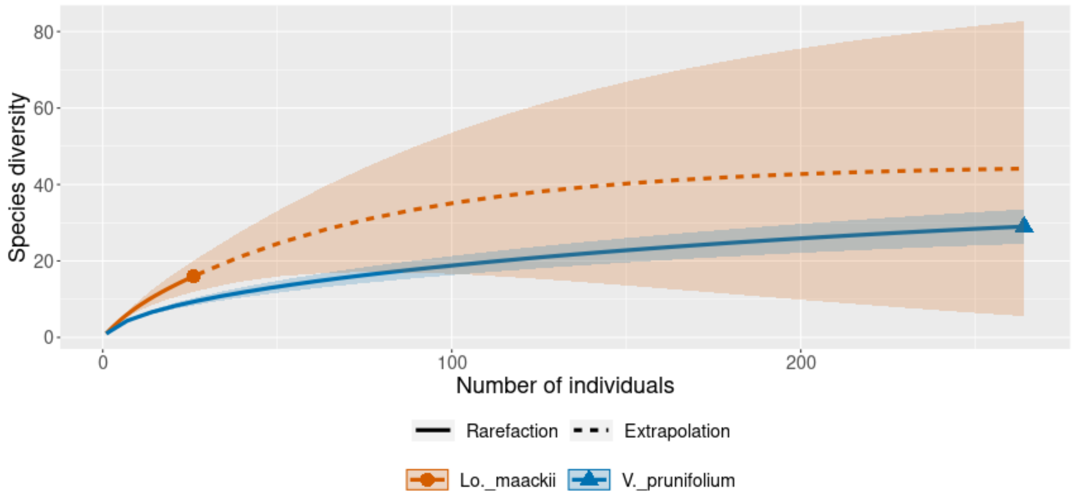

Figure 2-3 Individual based rarefaction curves for caterpillars on *Lo. maackii* and *V. prunifolium*. Dashed lines indicate extrapolated species accumulation to a sample of n = 264. Background colors represent 95% CI.

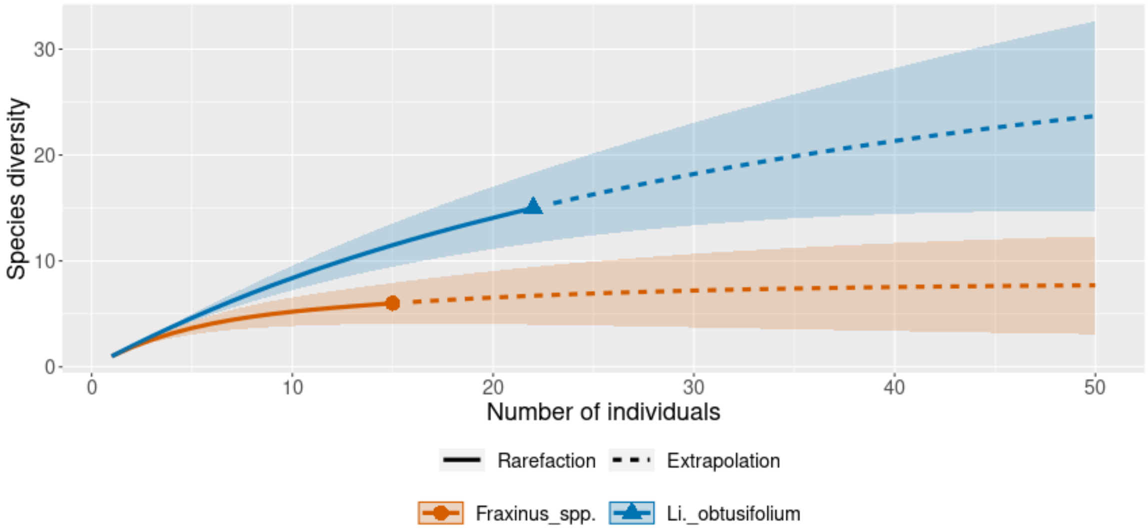

Figure 2-4 Individual based rarefaction curves for caterpillars on *Li. obtusifolium* and *Fraxinus* spp. Dashed lines indicate extrapolated species accumulation to a sample of n=50. Background colors represent 95% CI.

Herbivory

Levels of herbivory mirrored caterpillar abundance trends across host plants. *V. prunifolium* experienced far greater herbivory than *Lo. maackii*—approximately 12.1% compared to about 4.3% (Fig. 2-4; Std. errors of 0.978 and 0.768, $p < 0.00001$). There was also a significant effect of site on herbivory (Table 2-3). In contrast, herbivory rates on *Li. obtusifolium* and *Fraxinus* spp. were within 0.2% of one another and did not appreciably differ (Fig. 2-5, $p = 0.903$). For this pair, the effect of site was nonsignificant (Table 2-3).

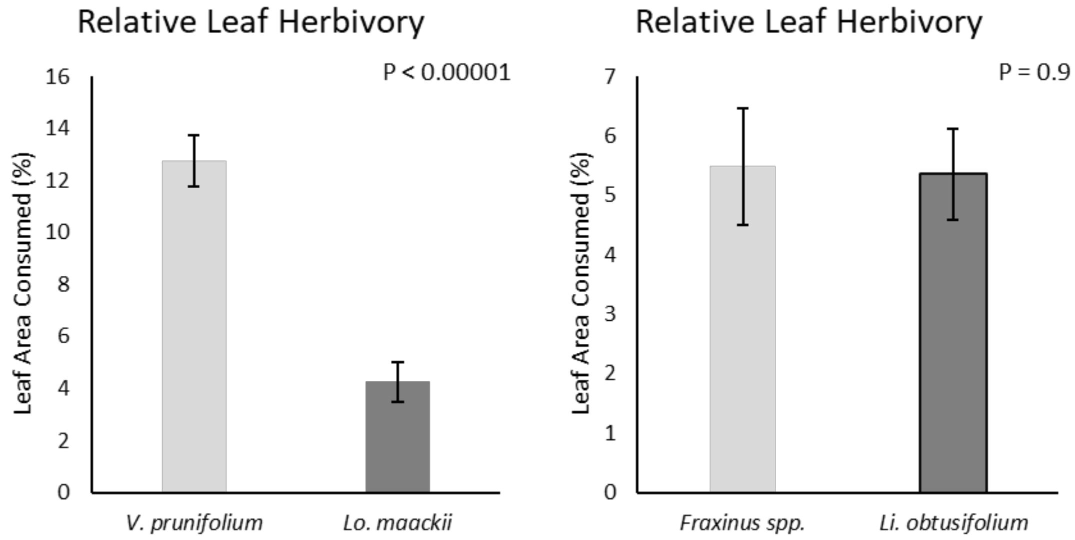

Figure 2-5 Mean observed leaf damage from chewing herbivores across focal plant species.

	Herbivory Damage					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	109.641	1.94E-08	1	0.074	8.77E-01
Site	8	75.313	0.005558	8	40.473	0.1055

Table 2-3 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on chewing herbivory damage observed on plant leaves.

Caterpillar performance

In total, I collected and attempted to rear 346 caterpillars. Of these, 74 were Symphyta; however, no Symphyta reached pupation. Therefore, I excluded these from most analyses, except where noted. Of the remaining 252 lepidopteran caterpillars reared in this study, 84 died, 28 were parasitized, 96 pupated but failed to eclose, and 44 eclosed as adults (Table 2-4).

Host	*Total Caterpillars*	*Parasitism Rate*	*Success Rate*
V. prunifolium	*193*	*12.4%*	*64.1%*
Lo. maackii	*25*	*8.0%*	*43.5%*
Fraxinus spp.	*12*	*8.3%*	*100%*
Li. obtusifolium	*22*	*4.6%*	*52.4%*
Total	*252*	*11.1%*	*62.5%*

Table 2-4 Summary of Lepidoptera fates across host plants in rearing experiment.

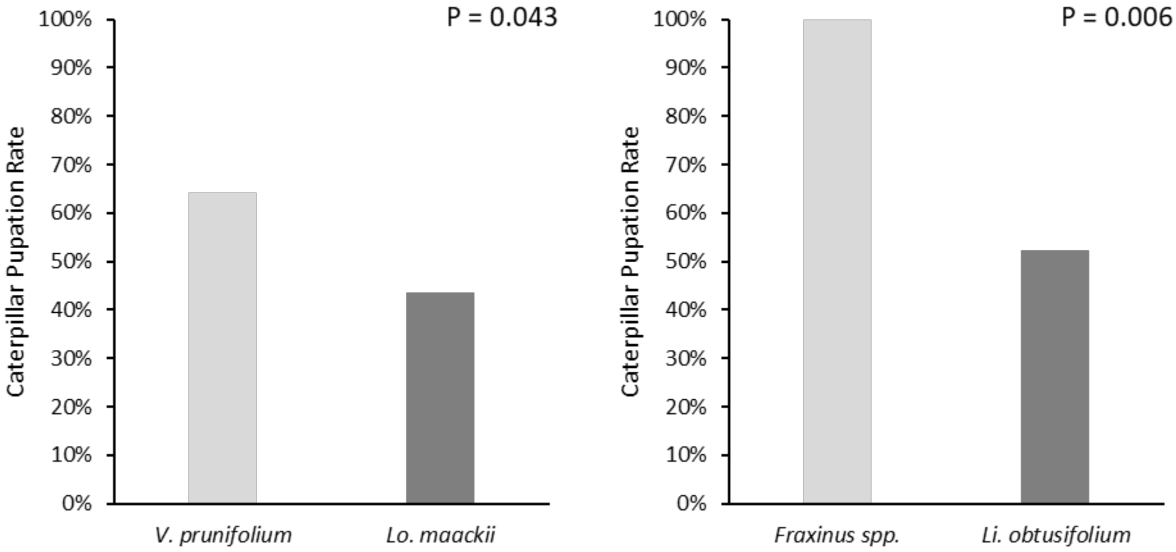

Figure 2-6 Percentage of caterpillars that reached pupation across host plant species. P-values are based on and ANOVA comparing GLMs with and without host plant species as a factor.

In each native-exotic host comparison, success rates trended lower on the exotic plants than on their native counterparts (Table 2-4). For *Lo. maackii* and *V. prunifolium*, this trend was significant (Table 2-5). Caterpillars reared on *Lo. maackii* had a lower likelihood of pupating; ~43% of caterpillars pupated on *Lo. maackii* as compared to ~64% of caterpillars reared on *V. prunifolium*. However, in the GLM model with all factors and levels, the effect of host was marginally non-significant (std. error = 0.5127; z = 1.872; *p* = 0.0612). Additionally, there was a significant effect of family, but not initial mass, on likelihood of pupation (Table 2-5). The mean slope of caterpillars on *Lo. maackii* was 0.15 (std. error = 0.017). In contrast, the mean slope for caterpillars on *V. prunifolium* was 0.23 (std. error = 0.007). Overall, caterpillar family had a significant effect on growth rates (Table 2-5). After accounting for phylogenetic effects of host family, growth rates trended lower on *Lo. maackii* than *V. prunifolium* (p = 0.072).

	Caterpillar Success					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	4.094	4.30E-02	1	3.4656	6.27E-02
Family	7	8.0264	3.30E-01	7	13.4562	0.06174
Initial Mass	1	2.6608	0.10285	1	0.0076	0.93059

Table 2-5 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on the likelihood of caterpillar pupation.

When comparing *Li. obtusifolium* and *Fraxinus* spp., caterpillars reared on the invasive plant tended to perform poorly. All of the caterpillars on *Fraxinus* spp. pupated but only ~52% of caterpillars reared on *Li. obtusifolium* did the same (Table 2-3). However, the difference in success between *Li. obtusifolium* and *Fraxinus* spp. was marginally non-significant (Table 2-4), perhaps due to the small sample size (n = 34). Nevertheless, the change in the transformed masses of caterpillars reared on *Li. obtusifolium* had a lower slope (estimate = 0.13, std. error = 0.024) than caterpillars reared on *Fraxinus* spp. (estimate = 0.18, std. error = 0.026). As for *Lo. maackii* and *V. prunifolium*, caterpillar family had a significant effect on growth rates (p = < 0.00001).

	Caterpillar Growth Curves					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	0.86263	2.19E-05	1	0.12448	4.82E-02
Family	10	1.91039	1.77E-05	8	1.62101	2.86E-08

Table 2-6 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on caterpillar growth rates.

The proportion of parasitized caterpillars collected from *V. prunifolium* was about 50% higher than those from *Lo. maackii* (Table 2-4). However, in the GLM incorporating all factors and levels, the effect of host was not significant (Std. error = 7.91; p = 0.448). Despite this, an ANOVA showing the effects of single factor deletions from the GLM models on caterpillar parasitism rates found the model incorporating both host plant species and caterpillar family to significantly differ from the model that used caterpillar family alone (Table 2-7). In contrast, there were no significant differences in parasitism rates between *Li. obtusifolium* and *Fraxinus* spp.—unsurprising in light of the negligible sample size.

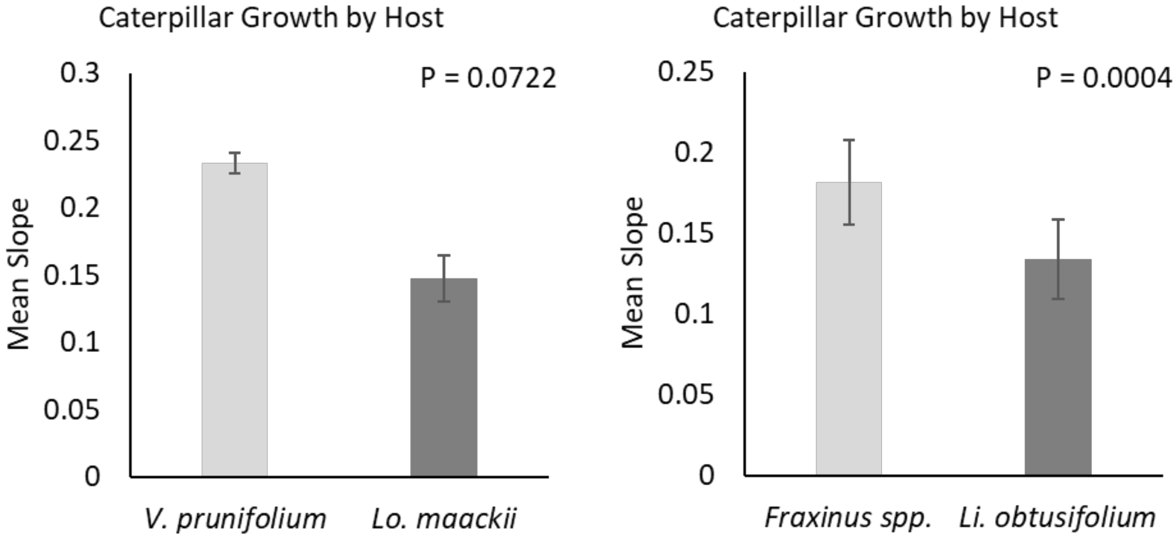

Figure 2-7 Mean slope of the log-transformed masses over time was lower for caterpillars reared on invasive than for those on native plants. P-values are from a GLM assessing the effect of host plant species on growth while controlling for caterpillar family.

	Caterpillar Parasitism Rates					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*df*	*Deviance*	*P (>Chi)*	*df*	*Deviance*	*P (>Chi)*
Host	1	4.5906	3.22E-02	1	0.045442	8.31E-01
Family	7	3.4494	8.41E-01	8	0.197719	1.00E+00

Table 2-7 Analysis of Deviance table showing the effects of single factor deletions from the GLM models on caterpillar parasitism rates.

Discussion

My surveys indicated that caterpillars were far less abundant per cubic meter of foliage on some exotic hosts than native hosts (see *Lo. maackii* and *V. prunifolium*), but not universally (see *Li. obtusifolium* and *Fraxinus* spp.). However, the richness of caterpillar communities was similar or even greater on the exotic hosts, mirroring results from past studies on *Lo. maackii* (Stireman & Workman 2023). The low abundance / high richness pattern was particularly stark for *Lo. maackii* relative to *V. prunifolium*. Although it only hosted a tenth of the density of caterpillars as *V. prunifolium*, the rarefaction suggests the community on *Lo. maackii* may be far more diverse. However, the small sample size resulted in an extremely wide CI, leaving the question of richness open for interpretation and in need of further research.

The lack of coevolved relationships between invasive plants and native arthropods may be something of a double-edged sword—releasing them from specialist herbivores but leaving them vulnerable to generalists (Fan et al. 2013). The novelty of invasive plants makes it unlikely that specialists have had time to adapt to these potential hosts; however, it also means that invasive plants have had little time to develop defenses targeted at local generalist herbivores. This seems to be supported by the literature.

Invasive plants can support robust communities of arthropod herbivores, but these communities are dominated by generalists (Rodríguez et al. 2019). Among caterpillars of Californian skippers, species with wide diet breadth and ranges are more likely to jump to exotic host plants (Jahner et al. 2011). Interestingly, populations of some generalists may be buoyed by invasive plants; however, the primary generalists benefiting from invasive plants may be invasive herbivorous insects (Rodríguez et al. 2019). Despite the potential colonization of invasive plants by generalist arthropods, it seems that generalist caterpillars may perform poorly on these novel hosts (Tallamy et al. 2010). Furthermore, there is evidence that some Lepidoptera preferentially oviposit on invasive plants on which their larvae perform poorly (Davis et al. 2015; Sun et al. 2020). If native Lepidoptera frequently oviposit on exotic plants that are unsuitable hosts, invasive plants may represent an ecological trap for native generalist caterpillars.

In line with past studies (Lieurance & Cipollini 2012), I found *Lo. maackii* to suffer less than 5% leaf herbivory. This was only a third of the herbivory I observed on *V. prunifolium*. This aligns with past studies, which found *V. prunifolium* to experience significantly greater herbivory rates than both *Lo. maackii* and many other native plants (Lieurance & Cipollini 2013; Bodawatta et al. 2019). However, it is not universally true that exotic plants experience reduced herbivory (Allen et al. 2021). Some studies have even found greater herbivory and herbivore diversity on exotic than native plants—suggesting that other factors, such as rapid growth, are more important to their success than enemy release (Allen et al. 2021). It is possible *V. prunifolium* is particularly palatable to herbivores rather than that *Lo. maackii* hosts an especially small herbivore community. This is supported by the high levels of herbivory which I observed. It is possible this affects both herbivory rates and caterpillar success; however, I did not factor this into my study. Further comparisons of herbivory across *Lo. maackii* and native plant taxa could clarify this issue.

Caterpillars reared on invasive plants exhibited similarly low success rates—about 43.5% on *Lo. maackii* and approximately 52% on *Li. obtusifolium*. Additionally, the mean slope of the log-transformed masses over time was lower for caterpillars reared on invasive than for those on native plants, even when factoring in the effect of caterpillar family. This suggests that these invasive plants are poor hosts for local caterpillars. This aligns with past studies that observed poor performance of both generalist and specialist caterpillars on invasive plants in Eastern North America (Tallamy et al. 2010; Horne et al. 2023). If these invasives are unsuitable hosts for native caterpillars, then the replacement of native plants by these exotic invaders threatens local caterpillar populations.

Considering the relatively poor performance of caterpillars on invasive hosts, it is curious that parasitism rates were nearly twice as high for caterpillars reared on native host plants. Although the sample sizes were too low to determine if this pattern was ecologically or statistically significant, past research suggests parasitism is highly dependent on host plant species (Lill et al. 2002). In part, it seems host plant quality plays an important role in caterpillar resistance to parasitism (Vyas & Murphy 2022). Additionally, host plant phytochemistry plays a major role in parasitoid prey detection (Whitman & Eller 1990). Both the quantity and quality of plant volatiles likely influence visitation by parasitoids (Hoballah et al. 2002). Furthermore, parasitoids provide a major source of top-down control on caterpillars (Hawkins et al. 1997). Consequently, if caterpillars on invasive plants are less likely to be targeted by parasitoids, this could provide a selective advantage to any species able to colonize novel host plants. Further research is required to determine whether this represents a significant driver of long-term herbivore recruitment in invasive plants.

Many factors affect caterpillar performance that could not be assessed in this study. For example, the probability of predation for a given caterpillar is partially dependent on the host plant on which caterpillars feed. In part, this is due to the chemical composition of hostplants affecting the vulnerability of caterpillars to predation (Coley et al. 2006). A primary predator of caterpillars, birds, foraging preferences are associated with the chemical compositions of caterpillar host plants (Müller et al. 2006). Consequently, caterpillars can sometimes be more successful on heavily defended plants—even if the caterpillars' growth is slowed.

Ash trees are rapidly declining in the eastern United States due to emerald ash borer (*Agrilus planipennis*), putting their specialist herbivores at risk (Gandhi & Herms 2010). While ash declines, border privet (*Ligustrum obtusifolium*) continues to spread (United States Department of Agriculture 2014). *Li. obtusifolium*, like *Fraxinus*, is a member of the family Oleacea (Wallander & Albert 2000). So, it may be a viable (and abundant) host to some herbivores of *Fraxinus*. However, *Li. obtusifolium* may be a poor-quality host, as *Fraxinus* spp. specialist hawkmoths (Sphingidae) performed poorly on a close relative, European privet (*Ligustrum vulgare*) (Horne et al. 2023).

If exotic plants are primarily attacked by generalist caterpillars, as suggested by past research (Zhang et al. 2018), this could affect the contribution of invasive exotics to supporting higher trophic levels and diverse food webs. Some studies have found generalists to have poorer chemical defenses than specialists (Dyer 1995), which may explain why generalists tend to experience higher predation (Singer et al. 2014; Dyer & Floyd 1993). Furthermore, although invasive plants may represent an abundant and growing resource for generalist caterpillars, this will not necessarily translate to more caterpillars on the landscape. This is because generalist caterpillars tend to have substantially lower population densities than specialists. One study found that caterpillars that feed on 10 plant taxa exhibit 36% lower population density than monophagous caterpillars (Sudta et al. 2022). Therefore, the spread of invasive plants may depress broad scale caterpillar populations—thereby reducing food resources available for higher trophic levels. The uncertainty of the trophic implications of shifting ratios of generalist to specialist herbivores in arthropod communities warrants further research.

Conclusions

Overall, caterpillar abundance and herbivory are far lower on *Lo. maackii* than *V. prunifolium*; however, both metrics were similar between *Li. obtusifolium* and *Fraxinus* spp. Additionally, rarefaction suggests caterpillar diversity may be similar or even greater on the invasive than native focal plants. This suggests invasive plants may not universally support depauperate caterpillar communities. Nevertheless, invasive plants may be poor hosts to caterpillars. In this study, caterpillar performance trended lower on both invasive plants than on their native counterparts. Consequently, the replacement of native shrubs by invasive exotics could reduce ecosystem-wide abundances of Lepidoptera over the long term. The reason is two-fold: not only do non-natives replace high-quality hosts, but they may also serve as population sinks for caterpillars. This is because Lepidoptera may oviposit on these poor hosts, resulting in reduced fitness for their offspring and suppression of the overall caterpillar community.

Lo. maackii and *Li. obtusifolium* represent only a miniscule fraction of plants that have invaded North America. Current estimates suggest that nearly 6,000 have been introduced and naturalized on the continent (van Kleunen et al. 2015). Furthermore, the rate of invasion is likely to increase for the foreseeable future (Bradley et al. 2010; Seebens et al. 2015; Seebens et al. 2017). Caterpillars tend to be highly specialized, using a narrow range of hosts (Forister et al. 2015). Therefore, only a relatively small portion of native plant diversity would need to be lost to decimate the diversity of Lepidoptera.

Based on the results of this study, invasive plants may support poor growth and success in caterpillars. If invasive plants do not support populations of herbivorous caterpillars, this is concerning due to the essential roles they play in forest ecosystems and the ecosystem services they provide (Lill & Marquis 2003; Seress et al. 2018).

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Chapter 3 Differing Caterpillar Predation Rates on native and non-native shrubs

Abstract

Caterpillars are abundant herbivores in forest ecosystems. Unsurprisingly, they are a key food resource for a plethora of vertebrate and invertebrate predators. In Ohio woodland ecosystems, two recently invaded non-native shrubs often dominate the understory: Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum obtusifolium*). The herbivorous arthropod communities on these shrubs may be depauperate relative to those of native counterparts. Notably, both exotics appear to be poor hosts for caterpillars. Logically, due to non-native plants provide poor foraging habitat for insectivores. It follows that insectivores would allocate less hunting effort to these plants. Nevertheless, it is unclear whether insectivores preferentially forage on native rather than non-native plants when both are available. This is what I tested in the spring and fall of 2022. I compared rates of attack from birds and arthropods on model caterpillars fixed to native and non-native plants. We glued caterpillars to stems of four plant taxa: Amur honeysuckle (*Lo. maackii*), blackhaw (*Viburnum prunifolium*), border privet (*Li. obtusifolium*), and ash (*Fraxinus* spp.). We found no significant differences in attack rates during the spring; however, during the fall, attack rates were higher on native hosts overall. This was driven by greater bird predation on native plants. We infer two things from these results. First, birds, though not arthropods, forage more heavily on native than non-native plants. Second, caterpillars on non-native plants may

experience reduced predation pressure, thereby providing a selective advantage to caterpillars able to switch to these novel hosts. In the near term, this could limit the available food supply for birds in eastern North America—potentially reducing bird populations. In the long term, this may spur the colonization of exotic plants by native caterpillars.

Introduction

Arthropods form the largest portion of animal biomass on earth and constitute ~20 times the combined mass of all wild terrestrial vertebrates (Bar-On et al. 2018; Tuma et al. 2020). Consequently, they are a vital food source for many predators. Birds are among the most important insectivores, consuming 400-500 million tons of insects annually (Nyffeler et al. 2018). Though less conspicuous than birds, arthropods preying on other arthropods are at least as important as birds in terms of predation. Spiders alone kill 360-720 million tons of insects annually (Nyffeler & Birkhofer 2017). At least for caterpillars, there is a strong inverse relationship between arthropod predation and both latitude and elevation (Roslin et al. 2017). In contrast, bird predation does not correlate with either latitude or elevation (Roslin et al. 2017). So, birds may be the key predators of insects in the temperate zone.

Most species of birds feed on insects; over 7000 of the ~10,000 species of birds alive today are insectivorous (Sekercioglu 2006). The dependence of birds on insects is great enough that the global decline in insect populations appears to be dragging down bird populations as well (Tallamy & Shriver 2021). Even primarily granivorous birds often depend on insects and other arthropods to feed their young (Wilson et al. 1999). Unsurprisingly, this dramatically affects trophic interactions (Sekercioglu 2006). Bird insectivory is particularly beneficial for plants (Marquis & Whelan 1994). Birds substantially reduce herbivory and mortality in both young and mature plants (Mäntylä et al. 2011). Insect larvae, free-living members of Lepidoptera and Symphyta, hereafter referred to as caterpillars, are a crucial food source for birds.

Bird foraging preferences typically skew dramatically toward caterpillars during the breeding season (Newell et al. 2014). In some cases, caterpillars constitute over 80% of the diets of nestlings (García-Navas et al. 2013). This may in part be due to the thin, easily digestible cuticle and high nutritional content of these insects (Jacob et al. 2021; Razeng & Watson 2015). During the breeding season, red-eyed vireos, a migratory insectivorous bird that breeds in eastern North America, require larger territories where caterpillar densities are low (Marshall & Cooper 2004). In some bird species, reproduction timing is associated with seasonal insect abundance. The effect of insect availability on these birds is so strong that egg-laying appears to have shifted to match changing insect phenology under climate change (Dunn et al. 2011). Even during the non-breeding season, insectivorous bird abundance, richness, and feeding effort are strongly associated with the density of native plants—presumably due to the arthropods supported by native plants (Smallwood & Wood 2023).

Though less conspicuous than birds, arthropods preying on other arthropods are at least as important as birds in terms of predation. Spiders alone kill 360-720 million tons of insects annually (Nyffeler & Birkhofer 2017). Though the collective appetite of spiders is impressive, Hymenopterans are also of great importance. In trials, plants from which ants have been excluded have been shown to host ~50% more herbivores and produce 23.7 % less biomass (Rosumek et al. 2009). Predacious wasps are especially important predators of caterpillars in eastern North American woodlands—at times consuming more caterpillars than all other sources combined (Steward et al. 1988).

Predators must balance resource acquisition against their own risk of being preyed upon (Werner & Anholt 1993). They do this by pursuing prey of types and in locations that offer the greatest compromise between risk and reward. For example, a foraging site with many large, accessible prey is preferable to one with fewer or less easily captured prey, as this will minimize the vulnerable foraging time (Werner & Anholt 1993). Insectivorous birds often rely on gleaning insects off vegetation; however, vegetation varies in prey quality. There is a correlation between exotic plant invasions and declining insect populations (Tallamy et al. 2021). Habitats dominated by non-native plants often host depauperate communities of herbivorous insects (Litt et al. 2014). Furthermore, caterpillar host records strongly correlate with bird foraging patterns in eastern North America (Piel et al. 2021).

Predation likely regulates caterpillar populations (Hooks et al. 2003). Birds alone reduce herbivorous arthropod densities by ~48% on average (Nell & Mooney 2019). However, direct observation is rarely possible, due to the small size and cryptic nature of these insects. Consequently, the use of plasticine caterpillar models has grown popular among researchers (Howe et al. 2009; Low et al. 2014; Roslin et al. 2017). These non-hardening models serve as sentinels for predation, as attacks by would-be predators leave identifiable marks in the clay (Low et al. 2014).

On average, caterpillar diversity is lower on invasive than native plants (Tallamy & Shropshire 2009; Burghardt et al. 2010). Past research indicates birds may preferentially hunt caterpillars on native plants (Narango et al. 2017). Therefore, even if caterpillars are poorly adapted to the nutrients or defenses of non-native plants, any larvae that can develop on these novel hosts may face reduced predation pressure. If so, this could counterbalance the fitness disadvantage of feeding on a suboptimal, non-native host.

Study System

In many woodlands of eastern North America, two non-native shrubs often dominate the understory: Amur honeysuckle (*Lonicera maackii*) and border privet (*Ligustrum Obtusifolium*). These Eurasian plants were introduced during the late 19th century and are now broadly invasive (Luken & Thieret 1996; Maddox et al. 2010). Perhaps due to the novelty of these species, the herbivorous arthropod communities on both may be depauperate relative to those on native counterparts (Keane & Crawley 2002).

Although both species bear fall fruit that is palatable to birds (Maddox et al. 2010; Bartuszevige & Gorchov 2006), they may not support the arthropods adult birds need. Most concerning, they both appear to be poor hosts for caterpillars. Not only are caterpillars less abundant on *Lo. maackii* and *Ligustrum obtusifolium* than on native shrubs, caterpillars on these hosts may reach maturity less often (Stireman & Workman 2023; Horne et al. 2023). *Lo. maackii*, in particular, may contribute to low caterpillar abundance (Stireman et al. 2014). Logically, these non-native plants provide poor foraging habitat for birds. Therefore, it follows that birds would allocate less hunting effort to these plants. Nevertheless, it is unclear whether birds actually preferentially forage on native rather than non-native plants when both are available. That is what we tested in this study.

Lo. maackii is an interesting system to study predation for a couple of reasons. First, birds may be less inclined to forage on this exotic plant, as at least some species preferentially forage on native taxa (Narango et al. 2017). Second, spider abundance is 2-5-fold higher in plots with *Lo. maackii* than on comparable plots with exclusively native taxa (Loomis et al. 2014). Together, this could mean caterpillars on *Lo. maackii* escape bird predation but face heightened arthropod predation.

In this study, I tested whether predation rates on caterpillars differ between native and exotic plants. I anticipated that predators would attack caterpillars on native plants more frequently than exotic plants, as they would be more likely to forage on native plants. If correct, this would lend further support to the theory that relative to native plants, exotic plants do not equally contribute resources to higher trophic levels.

Methods

This predation study took place in the Glen Helen Nature Reserve during June and September of 2022. I attached two green plasticene clay caterpillars bent into an inchworm configuration to stems of my four focal taxa (Fig. 1) at breast height (~1.5 meters), with superglue I compared these to native counterparts—blackhaw (*Viburnum prunifolium*) and ash (*Fraxinus* spp.) respectively. For the sake of maximizing sample size, I did not separate *Fraxinus* according to species; however, I used individuals from three species: white ash (*F. americana*), green ash (*F. pennsylvanica*), and blue ash (*F. quadrangulata*). Model caterpillars remained on the plants for 7-14 days. Afterward, I collected them and scored them for attack damage. I ran this experiment twice, coinciding with the spring and fall bird migrations.

Figure 3-1 Model caterpillars used in this study. Caterpillar A exhibits typical arthropod damage whereas caterpillar B has suffered a bird attack.

Spring

Starting June 4, 2022, I placed 184 model caterpillars across my focal plants. I used super glue to fix the caterpillars to stems at approximately 1.5m off the ground. On each plant, I fixed two caterpillars, typically ~1m apart. I selected plants ~10m from one another, interspersing plant species where possible. After seven days, I collected the caterpillars and assessed them for damage in laboratory conditions with the aid of a stereoscope.

Fall

Between September 11, 2022, and September 25, 2022, I placed 158 model caterpillars across my focal plants. After seven to 14 days, I collected the caterpillars and assessed them for damage in laboratory conditions with the aid of a stereoscope.

Analysis

I used a binomial generalized linear model (GLM) to assess the effect of the host species on probability of attack while controlling for days in the field. I constructed separate models for each season and tested the effect of host on attack overall, by birds, and by arthropods. I conducted this analysis in RStudio with R 4.2.2 (R Core Team 2022).

Results

Spring

Out of 183 model caterpillars, only 28 were attacked across all host plants. Of these, 12 were attacked by birds and 14 were attacked by arthropods. Overall predation trended higher on *V. prunifolium* (Figure 3-2), but differences were not significant (Table 3-1). However, this suggestive relationship vanished when limited to birds or arthropods (Table 3-1), possibly due to the low sample sizes involved. Although birds attacked almost half as many caterpillars on *Lo. maackii* as on *V. prunifolium*, 6.5% compared to 11.8 % (Figure 3-2), the difference was not significant (Table 3-1). The observed frequency of arthropod attacks on *Lo. maackii* was much lower than on *V. prunifolium*, at 2.2% compared to 9.8% (Figure 3-2); however, this difference was not statistically significant (Table 3-1). In the *Li. obtusifolium-Fraxinus* spp. comparison, overall predation was again non-significantly higher on the invasive (Table 3-1). Bird predation was higher on *Li. obtusifolium* than *Fraxinus* spp. (Figure 3-2); however, the difference fell far short of significance (Table 3-1). Arthropod predation also did not significantly differ between *Li. obtusifolium* and *Fraxinus* spp. (Table 3-1).

	Spring: Overall Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	0.6243	1.699	8.94E-02	0.604	-0.574	5.66E-01

	Spring: Bird Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	0.7386	0.877	3.81E-01	1.2443	0.46	6.45E-01

	Spring: Arthropod Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	1.115	1.423	1.55E-01	0.6855	-0.9	3.68E-01

Table 3-1 Summary of generalized linear models comparing rates of attack on model caterpillars in the fall of 2022. Host refers to the plant species on which model caterpillars were fixed.

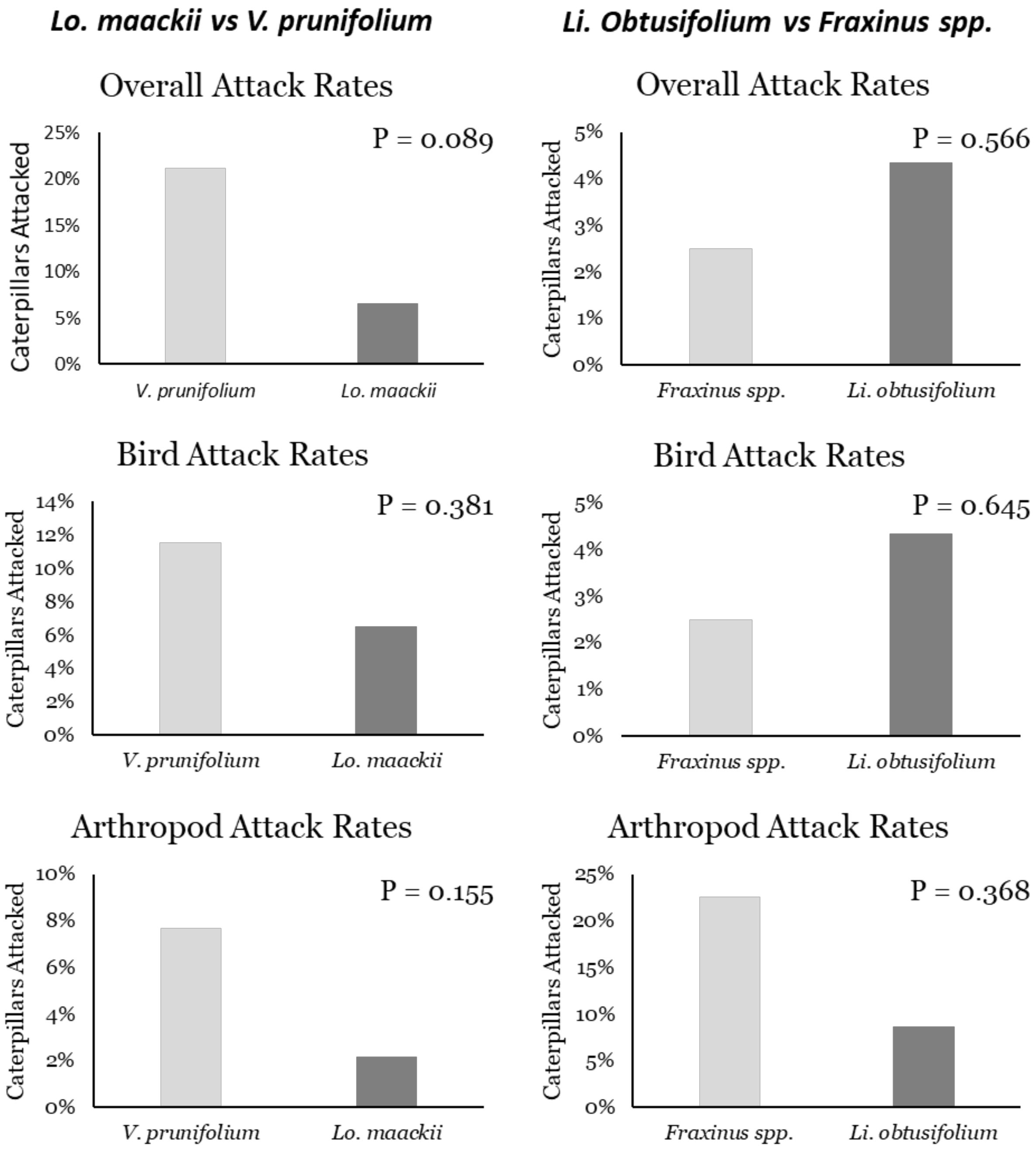

Figure 3-2 Spring attack rates overall, from birds, and from arthropods on focal plant taxa. *V. prunifolium* (n = 52), *Lo. maackii* (n = 46), *Li. obtusifolium* (n = 46), *Fraxinus* spp. (n = 40).

Fall

Overall attack rates trended lower for caterpillars on *Lo. maackii* than those on *V. prunifolium* (Figure 3-3). This was partially driven by bird attacks, which were far more frequent on the native *V. prunifolium* than on *Lo. maackii* (Table 3-2). However, arthropod attacks trended higher on *Lo. maackii* than on *V. prunifolium* (Fig. 3-3; Table 3-2).

Overall predation was lower on *Li. obtusifolium* than on *Fraxinus* spp. (Fig. 3-3; Table 3-2). There was also no significant diffence in bird predation on *Li. obtusifolium* and *Fraxinus* spp. (*Table 3-2*). similarly, arthropod predation was non-significantly lower on *Li. obtusifolium* (Table 3-2).

	Fall: Overall Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	0.4961	1.53	1.26E-01	0.552	-1.311	1.90E-01
Time	0.1537	1.607	1.08E-01	0.08909	0.863	3.88E-01

	Fall: Bird Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	0.68	2.893	3.81E-03	0.6381	-1.25	2.11E-01
Time	0.1594	0.947	3.44E-01	0.1054	0.918	3.59E-01

	Fall: Arthropod Attacks					
	Lo. maackii / V. prunifolium			*Li. obtusifolium / Fraxinus* spp.		
Predictor	*Std. Error*	*z value*	*P (>|z|)*	*Std. Error*	*z value*	*P (>|z|)*
Host	1.108	-1.916	5.54E-02	0.7368	-0.38	7.04E-01
Time	394.89	0.006	0.9949	0.1244	0.522	0.602

Table 3-2 Summary of generalized linear models comparing rates of attack on model caterpillars in the fall of 2022. Host refers to the plant species on which model caterpillars were fixed. Time refers to the number of days caterpillars were in the field (7 to 14 days).

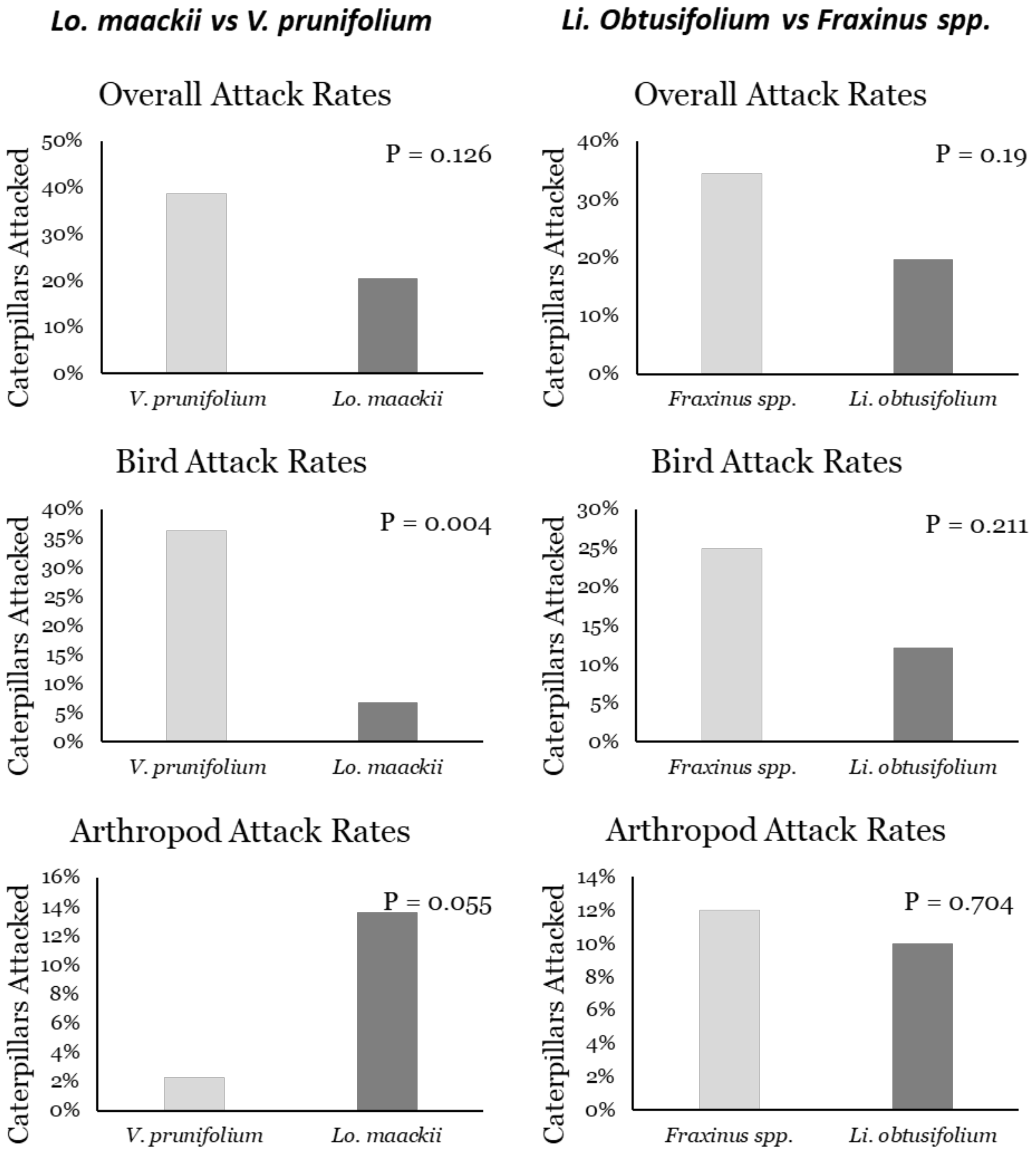

Figure 3-3 Fall attack rates overall, from birds, and from arthropods on focal plant taxa. *V. prunifolium* (n = 44), *Lo. maackii* (n = 44), *Li. obtusifolium* (n = 34), *Fraxinus* spp. (n = 34).

Discussion

Bird predation was significantly higher on *V. prunifolium* than on *Lo. maackii* during the fall. There are three related factors that may explain the observed difference in predation between this pair of native and invasive plant species: high herbivory damage on *V. prunifolium*, the poor host quality of *Lo. maackii*, and *Lo. maackii*'s dense growth structure. However, most of my other results were non-significant, possibly due to the small number of caterpillars attacked in each season (n = 28 and n = 47) across my four focal plant species.

In a concurrent experiment, I found far greater herbivory rates on *V. prunifolium* than on *Lo. maackii*, 12.8% compared to 4.2% ($P < 0.00001$, see chapter 2). Bird predation on herbivorous insects strongly increases with herbivory damage on plants (Sam et al. 2015; Gunnarsson et al. 2018). There are several likely reasons for this. First, herbivory is a clear visual indicator of caterpillars that birds appear to recognize (Heinrich & Collins 1983). Second, it may increase the visibility of caterpillars to insectivorous birds. Third, the volatiles emitted by plants under attack may attract insectivorous birds (Amo et al. 2013), which appears to be a learned behavior (Amo & Visser 2016).

Alternatively, the relatively poor quality of *Lo. maackii* as a host for caterpillars (Tallamy et al. 2010) may explain the difference in predation rates. Poor hosts tend to support low densities of caterpillars that exhibit lower body masses than those on high quality hosts (Singer et al. 2012). Likely as a result of this, birds are far less likely to forage on plants that are poor hosts (Singer et al. 2012).

The growth structure of *V. prunifolium* and *Lo. maackii* may also influence predation on these plants. This is because insectivorous birds forage preferentially based on plant structure (Whelan 2001). *Lo. maackii* has an extremely dense branching structure, which may inhibit access to caterpillars by birds (Nell & Mooney 2019).

Lastly, the simple fact that *Lo. maackii* is non-native may explain the lower predation rates observed. A previous study of bird foraging habits found birds forage on non-native plants less frequently than on native plants (Narango et al. 2017). Birds may prefer to forage on native plants due to the low quality and abundance of prey items on exotic plants (Singer et al. 2012; Narango et al. 2017).

Regardless of the cause, the lower bird predation on *Lo. maackii* could be a boon to caterpillars able to switch to this novel host. However, the enemy-free space hypothesis suggests predators, not resources, shape communities (Jeffries & Lawton 1984). So, at least for caterpillars able to feed on both *Lo. maackii* and *V. prunifolium*, the reduced predation on *Lo. maackii* may be more valuable than the higher host quality of *V. prunifolium*.

Past studies suggest insectivorous birds and arthropods dramatically reduce the effect of herbivorous insects on plants. One exclosure study found that plants inaccessible to birds suffer nearly twice the herbivory of control plants—25% of leaf area removed compared to 13% (Marquis & Whelan 1994). Similarly, when ants are excluded, plants lose about half of their leaves to herbivory on average, though this effect is greatest in the tropics (Rosumek et al. 2009). Thus, it is curious that I observed dramatically higher herbivory on *V. prunifolium* than on *Lo. maackii*, despite the fact that bird attacks trended lower on *Lo. maackii* than *V. prunifolium*. It is clear that plants greatly benefit from insectivorous birds (Mäntylä et al. 2011); however, it seems exotic plants may not reap these benefits to the same degree as native plants.

Although model caterpillars similar to those in this study are widely used (Low et al. 2014), they do not perfectly replicate predation on live larvae. Zvereva and Kozlov (2022) found in trials that live prey are dramatically preferred by predators over models. The magnitude of preference for live prey in birds varied over the season: 8.4-fold in early summer down to 2-fold in late summer. The authors also reported 67-fold greater predation by invertebrates on live prey than on plasticine models. Together, this may explain the markedly lower spring vs summer bird predation rates I observed. Furthermore, this suggests my study may have dramatically underestimated the magnitude of arthropod predation.

Conclusions

Notwithstanding the limitations of clay caterpillar models, there were some significant trends in predation based on the host species. These were primarily present when comparing *Lo. maackii* and *V. prunifolium*. There are a few factors that might explain this: herbivory, caterpillar abundance, and plant structure. *V. prunifolium* exhibited far greater herbivory than *Lo. maackii* in the fall of 2022 (Chapter 2).

Results differed between the spring and fall experiments. This was primarily driven by bird predation, which was significantly higher on the native *V. prunifolium* than the non-native *Lo. maackii* during both experiments. This indicates birds may not forage on non-native invasive plants as intensively as they do on native plants. This points to two ways non-native plants may be affecting the ecosystem. First, caterpillars on non-native plants may experience lower predation, granting them a selective advantage. Second, non-native plants are not being utilized by birds for foraging as heavily as native plants. Consequently, the replacement of native plants by non-natives likely equates to an overall reduction in the available foraging territory. Ultimately, the continued spread of *Lo. maackii* and *Li. obtusifolium* through this region could contribute to declines in bird population in the woodlands of eastern North America.

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