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Invasive Plant Ecology In Vermont: Insights From Spatial Analysis And Interactions Of Garlic Mustard (alliaria Petiolata) With Native Plants And Invertebrates

Chenin Kathleen Limback
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INVASIVE PLANT ECOLOGY IN VERMONT: INSIGHTS FROM SPATIAL ANALYSIS AND INTERACTIONS OF GARLIC MUSTARD (*ALLIARIA PETIOLATA*) WITH NATIVE PLANTS AND INVERTEBRATES

A Dissertation Presented

by

Chenin Kathleen Limback

to

The Faculty of the Graduate College

doing

The University of Vermont

In Partial Fulfillment of the Requirements For the Degree of Doctor of Philosophy Specializing in Natural Resources

May, 2016

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ABSTRACT

Causes and patterns of invasive plant species establishment and success depend broadly upon their ecology, including habitat suitability and interactions with other plants and animals. Here I examine the traits and distribution of invasive plants in Vermont, using spatial analysis, laboratory and field studies. I used GIS to investigate environmental factors correlated with presence of 19 invasive plant species in Vermont campgrounds. My results support the assumption that human dispersal of invasive plant seed and stock may be more important than natural dispersal of these plant species to new sites. I also investigate in-depth the relationships of invasive herbaceous garlic mustard (*Alliaria petiolata*) with native tree seedlings and co-occurring herbaceous plants in the greenhouse and Vermont forests, respectively. Shade from > 1 m tall *A. petiolata* plants may alter root:shoot ratios of neighboring tree seedlings and interact with nutrition quality of sites to affect their growth patterns. Invasive plants’ integration into novel environments is also mediated by their interactions with native invertebrate species. *A. petiolata* is associated with a unique assemblage of aboveground invertebrates compared with neighboring native plants. Observations indicate *A. petiolata* may also serve as an attractant for ants, bees, and wasps who feed from water and nectar at the base of the flower or siliqua during its flowering and seedling period. These results collectively inform our understanding of plant invasion patterns and management strategies of *A. petiolata* in Vermont. Community interactions are probably more important than allelopathy in determining the influence of *Alliaria petiolata* on native ecosystems.
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DEDICATION

Dedicated to my family, Glenn and Nancy Limback, Kristin and Dave Laughlin, and Ginger. I could not have come this far without all your love and support.
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CHAPTER ONE

Comprehensive Literature Review

Introduction

Non-native invasive species, those dispersed outside their original range by humans (Colautti and MacIsaac 2004, Heger et al. 2013), are a well-documented threat to Earth’s environmental resources (Pimentel et al. 2005) and forest biodiversity (Lodge 1993, Levine et al. 2003). Control of invasive plant species can cost up to $30 billion dollars each year in the United States alone (Pimentel et al. 2005). Knowing if introduction tends to give organisms specific ecological advantages or disadvantages in the novel habitat can help us to understand and control future invasions and protect the biodiversity of native ecosystems (Coutts et al. 2011). Invasive plants must compete with native plant species, as well as interact with associated invertebrate pollinators, antagonists, and predators (Byers et al. 2002, Higginson et al. 2010, Morales and Traveset 2009). The population dynamics, reproduction, and spread of invasive plant species thus depends upon their biology and biotic and abiotic interactions (Byers et al. 2002).

Ecological Hypotheses That May Affect Plant Invasiveness

Invasive plant species frequently result in negative effects on native plants (Alpert 2006). Understanding if and how these interactions are associated with successful plant invasions can help us understand current and predict future invasions (Coutts et al. 2011). It can also help managers to determine how to structure local natural communities to best
maintain diversity while discouraging native plant colonization (Hobbs and Huenneke 1992).

The Enemy Release Hypothesis (ERH) predicts that invasive species will escape from their co-evolved specialist natural enemies when colonizing new areas, thus contributing to their colonization success and improved performance of alien over native species (Elton 1958, Keane and Crawley 2002, Maron and Vilà 2001). Similarly, Darwin’s Naturalization Hypothesis as outlined in *On the Origin of Species* suggests that non-native plants which have close relatives in the novel range are less likely to establish due to factors such as competition and shared natural enemies (Darwin 1859), which are expected to be generalists (Müller-Schärer et al. 2004, Oduor et al. 2011). Also, generalist enemies may become more prolific on invasive plant species after the species has had time to become common in the novel ecosystem (Maron and Vilà 2001).

If herbivores are deterred by the presence of invasive plants this could lead to ‘associational susceptibility’ in neighboring native plants, a phenomenon which occurs when one plant causes another to receive greater herbivory than it would if not in the presence of the neighbor (Atsatt and O’Dowd 1976, reviewed in Barbosa et al. 2009). If herbivorous insects are repelled from a specific plant species, whether this is a long-distance or short-distance repulsion may affect which focal plants, if any, are colonized by the neighboring species (Potting et al. 2005). If one plant species is consistently targeted by herbivory, then neighboring plant species may be more successful due to reduced competition (Schowalter and Lowman 1999). In contrast, ‘associational resistance’, the opposite of associational susceptibility, may decrease damage on a focal
plant if adjacent neighboring plants confer protection on it through attraction of more herbivorous insects (Barbosa et al. 2009). If both plants are attacked by herbivores, the invasive may still increase in abundance if the native is more strongly impacted (Scherber et al. 2003). Susceptibility may also depend upon relative abundance, density, or biomass of focal and neighboring plant species, as well as competition for resources between the two species (Barbosa et al. 2009). Recent research has also suggested that specialist and generalist herbivores may respond differently to neighboring plants, affecting whether there is associational susceptibility in the focal plant (Guigo et al. 2012).

Interactions among multiple trophic levels may also influence invasive plant success in comparison to native relatives. The potential top-down effects of flower-dwelling invertebrate predators on pollinators and granivores of a host plant can have either positive or negative effects on plant fitness (Higginson et al. 2010). This model may be testable in the context of invasive species and closely related natives, which may share many of the same pollinators, granivores, and predators. Another effect that may be important in trophic relations is the concept of ‘ecosystem engineers’ (Jones et al. 1994, Pearson 2010). Ecosystem engineering occurs through indirect effects initiated by the plant. For example, the invasive plant Centaurea maculosa is larger and more structurally complex than its native relatives and provides more habitat for web-building Dictyna spiders, and the subsequent increase in predation decreases insect consumer populations and thus herbivory on the plant (Pearson 2009, 2010).

Many invertebrate and insect species use plants’ pollen, nectar, and seeds for food and can serve as indicators of the ecological health of complex forest ecosystems
Lawton 1994, Balvanera et al. 2001). Quantifying competitive and trophic interactions between invasive and native plants and associated pollinators and other invertebrates can increase understanding of naturalization of invasives, biodiversity, and complex ecosystems (Mitchell et al. 2009, Morales and Traveset 2009, Higginson et al. 2010) and the ecological services they provide (Grime 1997, Balvanera et al. 2001). Both data on abundance, richness, and diversity of invertebrates (alpha diversity), as well as species turnover defining specific assemblages and dissimilarity of invertebrate taxa (beta diversity), are useful to compare sites looking for differences to prioritize conservation measures (Oliver and Beattie 1996), and this could be useful for examining invasive plants’ effects on or integration into the novel ecosystem.

Many studies predict that invasive plant species will have a lower biodiversity of invertebrates in general than their neighboring native plant species, but this is often not the case (Maron and Vilà 2001). Interestingly, a meta-analysis by Levine et al. (2004) suggested that herbivory may be considered a type of biotic resistance (Maron and Vilà 2001) in which pressure by native herbivores may constrain the infiltration of invasive species into a new area, but not inhibit their entry entirely. If this is the case, herbivory may allow invasive species to become a functional, though not necessarily damaging, part of the ecosystem (Elton 1958, Levine et al. 2004), and the phrase ‘biotic containment’ in place of ‘biotic resistance’ has been coined to describe this phenomenon (Levine et al. 2004). The question was posed as to how native species continue to coexist with established invasives in these circumstances (Levine et al. 2004). It is possible that
comparisons of invertebrate colonization between co-occurring native and invasive plants may help to answer this question.

The Evolution of Increased Competitive Ability (EICA) hypothesis predicts that invasive plant species are more competitive in novel environments due to an increased allocation of resources to growth in the absence of a need to produce secondary defenses against specialist herbivores (Blossey and Notzold 1995), which they have presumably escaped (Keane and Crawley 2002). However, recent research suggests that instead of a trade-off, invasive plant species may rapidly evolve both increased growth as well as defense in novel communities (Oduor et al. 2011). Environmental factors may also interact to affect plant responses in disturbed ecosystems. For example, if disturbance decreases forest canopy cover the subsequent openings can result in increased light availability as well as precipitation and wind, and decreased interception of precipitation and evapotranspiration (Parker 1983, Schowalter and Lowman 1999).

Garlic Mustard – An Important Case Study

The invasive plant garlic mustard (Alliaria petiolata, Family Brassicaceae, Tribe Thlaspiideae) is native to Europe and was first recorded in the United States in 1868 (Nuzzo 1993, Al-Shehbaz et al. 2006). Its distribution currently extends to 37 American states and 5 Canadian provinces (USDA PLANTS Database). In Vermont, A. petiolata is classified as a “Class B Noxious Weed” (USDA PLANTS Database). It often grows in moist, shaded forest understory habitats (Al-Shehbaz et al. 2006), thus exploiting areas where many shade-intolerant plants cannot grow. It preferentially colonizes disturbed and edge habitats (Meekins and McCarthy 2001).
*Alliaria petiolata* is an obligate biennial in North America (Cavers et al. 1979). Seeds produced by second-year plants dehisce by late summer and require a period of winter stratification before germination early the following spring (Cavers et al. 1979, Baskin and Baskin 1992, Anderson et al. 1996). *Alliaria petiolata* spends its first year as a non-reproductive basal rosette, then stems elongate in early to mid-spring and produce flowers which remain through mid- to late-summer in the second year (Cavers et al. 1979, Anderson et al. 1996, Cruden et al. 1996). *Alliaria petiolata* is facultatively xenogamous, as flowers remain open during the day and are insect-pollinated, but self-pollinate in the evening when flowers close (Cavers et al. 1979, Anderson et al. 1996, Cruden et al. 1996). However, its cross-pollination levels are high enough to prevent inbreeding depression in the species (Cruden et al. 1996), although some research contests that self-pollination predominantes (Anderson et al. 1996, Durka et al. 2005). Insect pollinators include generalist syrphid flies and small bees, and perhaps some midges (Genders 1971, Cavers et al. 1979, Cruden et al. 1996). Studies suggest that phenology of *A. petiolata* differs in the various regions where its life cycle traits have been examined (Cavers et al. 1979, Cruden et al. 1996, Anderson et al. 1996, Byers and Quinn 1998), which could also be due in part to multiple introductions in different areas (Meekins et al. 2001, Durka et al. 2005). *Alliaria petiolata* has been shown to have allelopathic effects on both endo- and ecto-mycorrhizae of surrounding plants (Roberts and Anderson 2001, Wolfe et al. 2008, Barto et al. 2011). *Alliaria petiolata*’s allelopathic influences can also vary with the duration of the infestation, with older populations having reduced allelochemical impact (Lankau 2011a, 2011b, 2011c, 2012; Lankau et al.
2009), and potentially also contributing to its integration into the native community through time (Lankau et al. 2011c).

Compounds released by *A. petiolata* can be attractants for specialist predators as well as specialist ovipositing butterflies (Fahey et al. 2001, Chew 1988). However, Lepidopteran larvae feeding on the plant, including the West Virginia white butterfly (*Pieris virginiensis*) and the mustard white butterfly (*Pieris napi oleracea*), often exhibit reduced growth and increased mortality (Barto et al. 2010; Bowden 1971; Cipollini and Gruner 2007; Courant et al. 1994; Courant 1996; Huang et al. 1995; Porter 1994; Renwick et al. 2001; Rodgers et al. 2008a,b) due to chemical deterrents inhibiting feeding and growth (Haribal et al. 2001, Renwick et al. 2001). Other field studies have shown, in general, that herbivore activity on *A. petiolata* in its introduced range is small or negligible (Szentesi 1991, Nuzzo 2000, Blossey et al. 2001, Renwick et al. 2001, Evans and Landis 2007, Van Riper et al. 2010a). If this implies that herbivores are repelled by *A. petiolata*, associational susceptibility may cause enhanced herbivory on neighboring native plants enhancing the overall competition of *A. petiolata* (Atsatt and O’Dowd 1976, Barbosa et al. 2009). These effects may only be short term, however, as recent evidence suggests that *P. oleracea* may be adapting to *A. petiolata* as a host (Keeler and Chew 2008), and it is possible that other herbivore species may be doing the same. Some studies also suggest a relationship between high allelopathic potential and susceptibility to aboveground herbivory in *Brassica nigra*, an invasive relative of *A. petiolata* (Lankau and Strauss 2008, Lankau et al. 2011).
Little research has been done to date on the effects of pollination on the ability of *A. petiolata* to spread or outcompete native plants. Although cross-pollination is unnecessary in *A. petiolata*, it may provide an advantage by increasing genetic diversity of the population (Cruden et al. 1996), or by reducing pollinator visitation to other co-flowering plants, thus reducing their reproduction and having a greater available area to exploit. Research has also not addressed the role that predaceous invertebrates play on *A. petiolata*, the diversity that is found on the invasive in comparison to natives, and whether they are attracted to or preferentially colonize *A. petiolata* and feed on either herbivores or pollinators more or less than they would on native co-flowering species. Invasion of *A. petiolata* into disturbed habitats may also affect the amount of herbivores found on this plant as herbivores tend to respond distinctly to disturbances that alter or change the amount or types of plant species in an area (Schowalter and Lowman 1999).

**Conclusions**

Understanding the mechanisms by which invasive plants establish and outcompete natives can help managers formulate strategies to counteract the invasive spread and thus improve biodiversity in forest ecosystems. In the following studies, I attempted to determine 1) how invasive plants are distributed throughout Vermont, particularly in campgrounds, and what degree human disturbance and biotic and abiotic environmental factors appear to contribute to these distributions; 2) how invasive *A. petiolata* interacts with light availability and site nutrition to affect the growth and root:shoot ratios of neighboring tree seedlings; and 3) the relative influence of non-native invasive *A.*
*petiolata* on the biodiversity and activity of invertebrates on itself and neighboring native plants in invaded sites relative to uninvaded sites. Results from this research will inform our understanding of invasive plants and their function in ecosystems in Vermont and the northeastern US.
CHAPTER TWO

Site Susceptibility to Invasive Plant Colonization Identified Using GIS: Case Study Focused on Campgrounds in Northern Vermont

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Abstract

Causes and patterns of invasive plant species establishment depend broadly upon their ecology, including dispersal habits, habitat suitability, and niche availability. We used spatial analysis techniques including GIS, regression analysis, and ordination to investigate environmental factors correlated with invasive plant presence in campgrounds in northern Vermont. We identified thirty-eight campgrounds that had nineteen invasive plant species. We used campground descriptions and GIS to summarize biotic and abiotic attributes of each campground to develop predictive models of likelihood of invasive plant species presence. We also summarized co-occurrence among invasive plant species as well as phenological, growth, and reproductive traits of each species to test these relationships with invasion patterns. Invasive plant species presence was correlated positively with human development and infrastructure, density of roads, and annual temperature. Presence was related negatively to elevation and precipitation. Invasive woody shrubs were more likely to co-occur with other invasive woody shrubs than
herbaceous invasives. Human dispersal of invasive plant seed and stock may be more important than natural dispersal of these plant species to new sites. The relationships among invasive plant species and types of human disturbance can be used to help predict sites which may be more susceptible to particular invasive plant species than others and prioritize management efforts.

**Introduction**

Controlling invasive species on public lands often presents a management challenge. Management of these lands is often constrained by funding and time spent to identify and respond to plant invasions. State Parks and other recreational and public natural areas in the Northern Forest have many non-native species that have become invasive (Redstart, Inc. et al. 2012). An efficient way to prioritize sites for management may include determining particular traits of a site or disturbance types associated with increased invasion (Murray 2009). Some studies have proposed that invasive plant species may co-occur based on similar environmental or resource requirements (Murray 2009). For example, Common Buckthorn (*Rhamnus cathartica*) and Shrubby Honeysuckles (*Lonicera spp.*) are often co-located in invaded sites, and are similar biologically (Schulte et al. 2011). It is proposed that invasive plants may also facilitate each other’s colonization resulting in an “invasional meltdown” (Simberloff and Von Holle 1999). For example, an experiment by Leicht-Young et al. (2015) inferred possible growth facilitation between Oriental Bittersweet (*Celastrus orbiculatus*) and Japanese Barberry (*Berberis thunbergii*). Invasive plants such as Garlic Mustard (*Alliaria petiolata*) may open niches through allelopathic effects on neighboring native plants (Rodgers et al. 2008). Autumn Olive (*Elaeagnus*
*umbellata* may increase nutrient availability through nitrogen fixation (Goldstein et al. 2010).

Minton and Mack (2010) examined the effects of population size, population density, and human cultivation via irrigation on the success of four non-native Washington plants with the potential to become invasive. Much variation was seen between plant species, but there was a clear effect of irrigation on the reproductive success of the non-native plants, suggesting a link between human cultivation or ‘disturbance’ on successful invasive plant seed production and, thus, establishment (Minton and Mack 2010). Other studies have either suggested or demonstrated this link between human disturbance and invasibility, where human disturbance has been implicated in increasing the likelihood of invasive plant colonization (Burke and Grime 1996; Cavers and Harper 1967; Crawley 1986, 1987; Elton 1958; Ewel 1986; Hobbs and Atkins 1988; Hobbs and Huenneke 1992). It is proposed that disturbances decrease native plant abundance which, then, opens niches for invasive plants (Holzmueller and Jose 2009). The biotic resistance hypothesis suggests that invasive plants may have more difficulty establishing or experience constraints in spread into areas with a diverse native community that includes both competing plants as well as vertebrate or invertebrate natural enemies (Levine et al. 2004, Maron and Vilà 2001). Thus, undisturbed sites with increased native plant abundance may be naturally more resistant to invasive plant colonization. Research has demonstrated that there may be a more important role of abiotic factors of habitat in restricting invasion into communities, as well as interactions between biotic and abiotic factors (Levine et al. 2004).
The presence of suitable habitat for plants with specific growth types is hypothesized to be positively associated with these plants’ invasion (Murray 2009). Alternatively, there may be a negative association between similar plant species if they are competitors. Invasive plants such as Purple Loosestrife (*Lythrum salicaria*) and Japanese Knotweed (*Polygonum cuspidatum*), which are commonly dispersed through water, may flourish in sites with a higher density of streams or open water, as propagule pressure is an important component in invasive species spread to and persistence in new areas (D’Antonio et al. 2001, Levine et al. 2004). Similarly, wind-dispersed plants may experience higher levels of invasion in areas with greater recorded wind speeds. Non-native plants which are *r*-selected and have small seed sizes and high leaf area ratios have been suggested as more likely to become invasive (Rejmánek 1999), also supporting the supposition that enhanced dispersal promotes invasion into new sites. Temperature is expected to limit invasive plant establishment, especially minimum and maximum seasonal temperatures which could increase plant mortality.

This study explores the relationships between invasive plant presence and their characteristics with biotic and abiotic environmental factors of Northern Forest campgrounds in Vermont. We surveyed 38 campgrounds and determined how many different types of invasive plants were found at each campground and how densely those invasive plants colonized the campgrounds. Our objectives were to identify invasion patterns by determining if: 1) indicators of human disturbance are correlated positively with invasive plants and/or plant groups; 2) invasive plant species with similar growth habits and dispersal mechanisms co-occur, and 3) elevation, temperature, seasonal
patterns of precipitation, and wind and water dispersal mechanisms are associated with the presence of specific plant species or species complexes.

We predict that campgrounds located in areas with the highest levels of developed land for agriculture and infrastructure, and road density, will have the greatest degree of infestation of invasive plants, however the relationships may not be linear. Next, we predict that invasive plant species with similar structure (woody versus herbaceous), growth habits, and dispersal mechanisms will co-occur. Finally, we predict that environmental factors including elevation, temperature, precipitation, and seed and pollen dispersal mechanisms will effect which invasive plant species occupy sites in Vermont.

Results from this study can be used to prioritize invasive plant management to minimize time for complete surveys. The presence of human disturbance and environmental factors associated with high invasive plant colonization, especially those plants that are often found in high densities, are more threatening, or costlier to treat, may suggest which properties should receive the most management attention.

Methods

Site selection and initial characterization

From June–August 2010 non-native invasive plants were surveyed in 38 Vermont campgrounds (Table 1). We also recorded data on amenities offered by each of the parks (Table 1), in case number of amenities turned out to be a correlate of disturbance and/or predictor of enhanced human traffic in a site (www.vtstateparks.com).
We recorded the presence of 19 plant species listed as non-native and invasive or of concern to become invasive (Table 2). We recorded presence/absence and quantified level of invasion of each plant species in each park. To quantify invasion level, we used the descriptive summaries of the 19 plant species for each park and converted it into a quantitative measurement of 0 (plant not present in the park), 1 (plant minimally present in the park and deemed treatable), 2 (plant common in the park and treatment possible but difficult), and 3 (plant heavily infesting the park and treatment not likely viable) (Table 2). We summed these values across all non-native invasive plants present to serve as a plant invasion index for each site, then divided the total index by the number of possible invasive plants to obtain a mean infestation level for invasive plants in each park. We ranked the campgrounds by mean invasion index (Fig. 1) and compared them with GIS summarized data (Table 3).

**GIS data preparation**

We prepared site maps of the primary areas covered by the surveyors on each of the 38 parks and campgrounds using Google Maps (Map data ©2014 Google). We downloaded polygons of concern as a Keyhole Markup Language (KML) file (Google 2014) and imported into ArcGIS software (ESRI 2014) (ArcMap 10.2, Environmental Systems Research Institute [ESRI], Inc., Redlands, CA, USA). To account for any errors in the drawn maps, and to include data from areas immediately adjacent to the parks and campgrounds in analyses, a 1 km buffer was added around each campground polygon. The final resulting polygon layer was labeled “Vermont State Parks and Campgrounds”.

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Additional data layers used in the study were downloaded from the Vermont Center for Geographic Information’s (VCGI) website (vcgi.vermont.gov), and are listed in Table 3. Each data layer downloaded from VCGI was clipped (vector data) or extracted (raster data) to the extent of the Vermont State Parks and Campgrounds layer, using the “Clip (Analysis)” tool or the “Extract by Mask (Spatial Analyst)” Tool, respectively. For the PRISM Temperature data, we utilized only the data for mean annual temperatures in 2010, and the “Raster Analysis” Cell Size was changed to 10 m pixels to allow for better analysis. Both ArcGIS Attribute Tables and Microsoft Access software and queries were used to summarize the data for each clipped or extracted VCGI layer within each of the 38 sites.

**Statistical analysis**

We tested all dependent variables averaged within each campground, and residuals, for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots in SAS 9.1 software (SAS Institute Inc. 2011). To meet the assumptions of normality for independent variables and residuals in regression analyses, some data were natural log (x + 1) transformed, or analyzed nonparametrically via a generalized additive model (Hastie and Tishirani 1990) (SAS PROC GAM, SAS Institute 2011). These data are noted in the text and figures. Mean invasion index (degree of infestation) data across the sites was subjected to one-way ANOVA ($P \leq 0.05$), followed by Tukey’s HSD (Tukey 1953) to check for the presence of overall differences among campgrounds. We then performed linear regression analyses (SAS PROC REG) to test relationships between continuous
site variables and both total invasives present and mean invasion index. All univariate analyses were performed using SAS 9.1 and JMP Pro 11 software (SAS Institute Inc. 2011, 2013).

Data were summarized by campground to look for differences in the overall composition of invasive plants. We used Bray-Curtis dissimilarity (Bray and Curtis 1957) to analyze the invasive species presence data pre-treatment (pre-ordination) and followed with ordination via non-metric multidimensional scaling to assess dissimilarity between invasive plant compositions at each site. A 2D Stress value of less than 0.2 was considered a good representation of the distribution of sites (Clark and Gorley 2006). We used Euclidean distance to analyze mean annual temperature, mean annual precipitation, and percent development, to tease out the relative influences of these relevant data, and followed with Principal Components Analysis to determine which of these environmental variables were most characteristic of each site. All multivariate analyses were conducted using Primer-6 software (PRIMER-E, Clark and Gorley 2006).

**Results**

The mean invasion index values for each invasive species differed among sites (ANOVA, $F_{37,684} = 2.93; P < 0.0001$) (Fig. 1). The overall size of each campground did not contribute significantly to invasion index within the campgrounds (Regression Analysis, $F_{1,36} = 0.30; P = 0.59$). Additionally, the total number of amenities offered by each park was not correlated significantly with invasion index ($F_{1,36} = 0.26; P = 0.61$) or total numbers of invasive species present ($F_{1,36} = 0.03; P = 0.87$). Length of roads per site
area and percent development were correlated positively with the invasion index of non-native plant species (Fig. 2). However, length of trails per site area was not correlated significantly with the mean plant invasion index of non-native plant species (Fig. 2), nor with total number of invasive species present \((F_{1,36}=0.66; P = 0.42)\). Although road length (above) was correlated positively with the invasion index, it was not correlated with invasive richness alone \((F_{1,36} = 1.55; P = 0.22)\). Total numbers of ESITES (man-made buildings and other features) per area of each site (used as a measure of density of development) were also correlated positively with plant invasion index \((F_{1,36} = 4.72; P=0.04)\), but with a small contribution to the overall variation \((R^2 = 0.12)\). These structures, however, were not correlated significantly with numbers of invasive species alone without taking degree of infestation into account \((F_{1,36} = 1.14; P = 0.29; R^2 = 0.03)\).

Sites differed when plants were categorized into herbaceous, woody shrubs, and aquatic herbaceous functional groups (Fig. 3). All of the functional groups were correlated positively with the invasion index, especially herbaceous plants (Fig. 3). When these functional groups were regressed against land cover types, invasion by aquatic species was correlated negatively with total forested (deciduous, coniferous, and mixed) land cover \((t = -2.41; P = 0.02; \text{Nonparametric generalized additive model [GAM]})\); shrubs were correlated positively with agricultural (cultivated, hay/pasture) land \((t = 2.49; P = 0.02; \text{GAM})\) and commercially developed land \((F_{1,36} = 4.40; P = 0.04; R^2 = 0.11)\); and herbaceous plants positively correlated with only coniferous \((t = 2.09; P = 0.04; \text{GAM})\) and mixed forest \((t = -2.57; P = 0.01; \text{GAM})\), but not deciduous forest \((t = -1.28; P = 0.21; \text{GAM})\).
Elevation was correlated negatively with the degree of infestation of non-native plant species (Fig. 2). However, elevation results had stronger significance and $R^2$ values when looking only at invasive plant species richness without taking into account the degree of infestation ($F_{1,36} = 17.80; P < 0.001; R^2 = 0.33$). Annual precipitation was correlated negatively with the invasion index ($F_{1,36} = 9.26; P < 0.01; R^2 = 0.20$) as well as total number of invasive plant species ($F_{1,36} = 7.49; P < 0.01; R^2 = 0.17$). The strongest positive correlations with the plant invasion index were mean annual temperatures ($F_{1,36} = 39.39; P < 0.0001; R^2 = 0.52; \log(x+1)$ transformation of the index). A similar but weaker relationship was seen when looking only at total invasive species richness at the site ($F_{1,36} = 26.43; P < 0.0001; R^2 = 0.42$).

Invasion indices of plants with seeds commonly dispersed by water (see Table 2) were unaffected by the amounts of wetland and open water habitat ($t = 0.68; P = 0.50; \text{GAM}$) and did not differ in their distribution in these environments from non-water dispersed invasives ($F_{1,36} = 0.7017; P = 0.4077$). Annual precipitation was negatively correlated with invasion index levels for both water-dispersed ($t = -2.84; P = 0.0073; \text{GAM}$) and non-water-dispersed ($F_{1,36} = 6.2587; P = 0.0170$) invasive plants, and therefore did not differ from the overall effect of precipitation on all plants. Similarly, wind speed was not correlated with the mean invasion index of plants pollinated or dispersed by wind (see Table 2) ($t = -1.44; P = 0.16$). The remaining plants were also not correlated with wind speeds ($F_{1,36} = 1.5847; P = 0.2162$).

The turnover (assemblages and dissimilarity of invasive plants present) of sites estimated by Non-Metric Multidimensional Scaling (MDS) was a good fit based on an
overall 2D Stress value of 0.18 (Fig. 4) (Clark and Gorley 2006). Wild Chervil (ANSY) was found in less invaded sites. Glossy Buckthorn (FRAL4), Oriental Bittersweet (CEOR), and Japanese Barberry (BETH) co-occurred and were frequently found in the most highly invaded sites (Fig. 4). Also associated with these plants were Multiflora Rose (ROMU; Symbols defined in Table 2) and Common Buckthorn (RHCA3) (Fig. 4).

Principal Components Analysis (Fig. 5) supported the above correlations, confirming that mean annual precipitation was negatively associated with plant invasion levels. Precipitation also explained the largest variations in the data (Fig. 5). Percent total development and mean annual temperatures were higher in more invaded sites and explained the second largest portions of data variance, on the Principal Component 2 axis (Fig. 5).

**Discussion**

Results are consistent with literature suggesting that invasive plant colonization and spread into new sites is highly dependent upon biotic and abiotic factors and interactions therein (Levine et al. 2004). Our results also support the prediction that these factors may be used to forecast site susceptibility to plant invasion. Overall, our first hypothesis was supported as more developed sites with more roads were positively correlated with increased plant invasion index. It is likely that more developed campgrounds receive more human activity than those with less development. These sites may also be more highly disturbed. A higher density of roads in campgrounds, which are also likely associated with human activity, were also correlated with higher invasive species
presence. Contrary to expectations, the overall size of the campgrounds was not correlated with the invasion index. Larger campgrounds may not necessarily have more human traffic due to many of them having large areas of wilderness included. Additionally, campgrounds have different primary habitat types such as lake islands versus mountains, and thus it is likely that size is less relevant in comparison to land cover types, which was supported in our results as more forested campgrounds tended to have lower levels of plant invasion.

In contrast to roads, recreational trail density in campgrounds did not correlate significantly with plant invasion. Invasive plant dispersal by humans along trails may be less important than other forms of anthropogenic dispersal, perhaps because these trails are less frequented than roads, or possibly because humans using trails are more likely to follow the “Leave No Trace” practices espoused by many recreational areas encouraging visitors to not disturb the natural surroundings (www.lnt.org 2016). Man-made structures were correlated with degree of infestation but not with total number of species present, and thus likely have more of an effect on already-established communities than on actual invasive species entry into a site.

Our second prediction was partially supported as many, but not all, species with similar growth traits tended to be found together. Wild chervil was most common in sites with lower invasion index whereas honeysuckles and buckthorns appeared in more highly invaded sites. Woody invasives, whether shrubs or vines, seemed to associate most closely with each other, especially glossy buckthorn, multiflora rose, and oriental bittersweet, all of which are thick growing woody species which have been implicated as
a major invasion problem in the Northern Forest (www.vtinvasives.org 2016). Previous research has suggested that the presence of oriental bittersweet may increase soil nutrient availability and could facilitate the invasion of other plant species (Leicht-Young et al. 2015). If any of these woody invasive species are found at a site, it would be prudent for managers to enhance survey and eradication efforts to preclude the possibility of invasional meltdown (Simberloff and Von Holle 1999).

Plant life form had an important effect on which land cover types were most likely to be invaded, with aquatic herbaceous plants correlated strongly with man-made structures, terrestrial herbaceous plants associated with coniferous and mixed forest, and woody shrubs associated with high levels of agricultural and commercial development. Invasive herbaceous plants may be more sensitive to biotic resistance constraining their invasion than woody plants (Levine et al. 2004), which could explain why they showed fewer consistent patterns in our results, and why they were not associated with deciduous forests, which may have more plant life than coniferous and mixed forests which could resist the invasion of these plants. Competition between plant species is often more prominent at the local and microsite scales (D’Antonio et al. 2001, Levine et al. 2004, Pacala and Silander 1985), thus our study may have missed some of these effects as we examined larger areas as a whole.

Our third prediction received some support where elevation and precipitation were negatively associated with and temperature was positively associated with invasive plant colonization. Elevation was more negatively associated with the numbers of total invasive species in a site than with the degree of infestation of these species. This
suggests that higher elevation sites may resist invasion by more plant species but is not necessarily better at resisting the spread of plant species which do establish. Thus these sites should still be considered for management, at least initially, to determine whether any individual species may cause problems in the long run. There was a negative relationship between precipitation and overall degree of infestation of invasive species in campgrounds. This relationship was also negatively correlated with total numbers of species present. Native plants may thrive in wetter environments and constrain spread of invasive species (Levine et al. 2004) or these sites may have decreased human activity due to more adverse weather patterns discouraging recreation. Higher mean annual temperatures corresponded to greater degrees of invasion and invasive species numbers, suggesting that invasive plants may tolerate warmer weather better than natives due to phenotypic plasticity. Alternatively, these sites could be favored by campers, resulting in higher human traffic and a disturbance relationship. Testing for relationships with maximum and minimum seasonal temperatures may have been more informative in this study to identify their effects on the survival of specific plant species.

This study strongly supports the hypothesis that anthropogenic disturbance enhances invasive species colonization (Hobbs and Huenneke 1992). Environmental factors may also interact to affect plant responses in disturbed ecosystems. For example, if disturbance decreases forest canopy cover the subsequent openings can result in increased light availability as well as precipitation and wind, and decreased interception of precipitation and evapotranspiration (Parker 1983, Schowalter and Lowman 1999). Individual invasive plant species also respond differently to certain site variables such as land cover and types of
disturbance, thus managers should take into consideration which species may be more likely to invade certain campgrounds and survey more intensely for these species.

We found that larger scale patterns (e.g., elevation, temperature, precipitation, overall development) appear to affect invasion in campgrounds more so than smaller scale patterns (e.g., amenities offered by campgrounds, dispersal mechanisms relevant to specific plant species). However, the impacts of elevation in particular may be overgeneralized as many other environmental variables which we did not investigate may interact with elevation. Human dispersal of seed and vegetative stock may be more important than natural dispersal mechanisms for invasive plant colonization, since wind and water presence did not have any detectable effect on invasion levels of plants dispersed or pollinated via these mechanisms. Man-made structures and environmental factors including temperature and precipitation seem to affect degree of infestation more strongly than they affect the particular types of species that may invade a site. Elevation showed the opposite trend and may be more important in determining which invasive plants can grow well in a particular site. Since wild chervil causes skin irritation in the presence of ultraviolet light (www.vtinvasives.org), parks should be closely monitored and considered for management if this invasive is found, especially as our results showed that even in sites which are less invaded overall this plant might be present.

Results of this study suggest that sites which are highly developed, lower elevation and precipitation, and warmer should be considered for management and prioritized with regards to surveys. Therefore, other sites which may not fit the criteria for high invasive species content could be passed over and thus save time and money and increase efficiency and speed of management efforts. Studies incorporating other aspects of community
ecology investigating the relationships between plant species in various population, succession, or restoration scenarios may inform the ecology and interactions of invasive species with each other and with native species (Davis et al. 2001, Shea and Chesson 2002). It would benefit managers of invasive plant species to take into consideration the human disturbance and environmental factors described to prioritize management.

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Literature Cited


Tables

Table 1: Names, locations, months surveyed, and summary of amenities available for the 38 campgrounds surveyed for invasive species in this study. “LCC” = Lodges/Cottages/Cabins, “UA” = Universal Accessibility, “*” = Amenity available, “-” = Amenity not available.
<table>
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<th>Month</th>
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<td>July</td>
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<td>July</td>
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<td>June</td>
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Table 1 (Continued): Names, locations, months surveyed, and summary of amenities available for the 38 campgrounds surveyed for invasive species in this study. “LCC” = Lodges/Cottages/Cabins, “UA” = Universal Accessibility, “*” = Amenity available, “-” = Amenity not available.
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<td>North Hero State Park</td>
<td>44°54'50&quot;N, 73°14'33&quot;W</td>
<td>June</td>
<td>Amp</td>
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<tr>
<td>Quechee State Park</td>
<td>43°38'24&quot;N, 72°24'28&quot;W</td>
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<td>Amp</td>
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<td>Ricker Pond State Park</td>
<td>44°14'42&quot;N, 72°14'59&quot;W</td>
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<td>Silver Lake State Park</td>
<td>43°43'57&quot;N, 72°36'53&quot;W</td>
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Table 2: Summary of species, common name, symbol, and attributes for the 19 invasive plants identified in this study. “Vegetative” = Plant can reproduce vegetatively, “Aquatic” = Plant is associated with aquatic environments, “Vine” = Plant may grow as a vine, “Native” = Plant’s native range. (invasivespeciesinfo.gov 2015, USDA PLANTS Database 2015, vtnasives.org 2015).
<table>
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<tr>
<th>Species</th>
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<th>Vegetative</th>
<th>Aquatic</th>
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Table 2 (Continued): Summary of species, common name, symbol, and attributes for the 19 invasive plants identified in this study. “Vegetative” = Plant can reproduce vegetatively, “Aquatic” = Plant is associated with aquatic environments, “Vine” = Plant may grow as a vine, “Native” = Plant’s native range. (invasivespeciesinfo.gov 2015, USDA PLANTS Database 2015, vtinvasives.org 2015).
<table>
<thead>
<tr>
<th><strong>Species</strong></th>
<th><strong>Common name</strong></th>
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<th><strong>Seed dispersal</strong></th>
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<td>Direct</td>
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<td>Biennial</td>
<td>Insect</td>
<td>Animal/Wind/Water</td>
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Table 3: Summary of degree of infestation for each of the 19 invasive plant species (by symbol defined in Table 2) at each surveyed campground. “-” = Not present, “1” = Minimally present and treatable, “2” = Fairly common and less treatable, “3” = Widespread and treatment not feasible. (N=722).
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Table 3 (Continued): Summary of degree of infestation for each of the 19 invasive plant species (by symbol defined in Table 2) at each surveyed campground. “-” = Not present, “1” = Minimally present and treatable, “2” = Fairly common and less treatable, “3” = Widespread and treatment not feasible. (N=722).
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Table 4: Summary layer data used in GIS analyses. All are downloaded from vcgi.vermont.gov, are from datum D_North_American_1983, and were ultimately projected as NAD_1983_StatePlane_Vermont_FIPS_4400 using a Transverse Mercator Projection.
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Figure 1: Mean (± SE) invasion index for all invasive species combined per site. (N=722).
Figure 2: Side by Side graphical summary of sites and their overall area, mean elevation, length of roads per area, length of trails per area, and percent developed land. Ordered from most invaded (1 = Quechee) to least invaded (38 = Ricker Pond). Linear regression results below each graph describe its relationship with mean invasion index. (N=38).
Figure 3: Mean (± SE) invasion index for all invasive species by functional group per site. Data with "*" next to it means that regression was run using a nonparametric generalized additive model. (N=114).

- Herbaceous Plants
  - $y = 0.60x + 0.29$
  - $R^2 = 0.42$
  - $F_{1,36} = 13.19; P = 0.0009$

- Woody Shrubs
  - $y = 0.53x + 0.12$
  - $R^2 = N/A$
  - $t = 8.90; P < 0.0001$

- Aquatic Herbaceous Plants
Figure 4: Non-Metric Multidimensional Scaling of campgrounds ranked by invasion status with distribution of invasive plant species by code overlaid to show relationships. (N=38).
Figure 5: Principal Components Analysis of campgrounds ranked by invasion status with regards to mean annual precipitation ("Precipitation"), mean percent development (% Development), and mean annual temperature ("Annual"). (N=38).
CHAPTER THREE

Responses of Native Tree Seedlings to the Invasive Garlic Mustard in Varying Environmental Conditions

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Abstract

We examined the relationships between Garlic Mustard and Eastern Cottonwood, Silver Maple, Red Maple, and Sugar Maple seedlings under varying light and nutrient conditions in a greenhouse experiment. Seedlings were exposed to allelopathy from first year Garlic Mustard plants through shared soil, light was limited using shade from second year Garlic Mustard plants over 1 m tall, and nutrients were added using fertilizer. Tree seedling shoots grew tallest in the shaded environment without allelopathy. This trend varied within the growing season and among tree species. Seedlings growing in the shade treatment may have been taller and healthier due to lower water stress in the shaded environment. Fertilization increased seedling health as well as root:shoot ratio across all species but rarely interacted with shading and allelopathy. Tree seedlings growing with Garlic Mustard may respond to shade imposed by the invasive. We conclude that the overall growth response of tree seedlings growing with Garlic Mustard will vary with the water and nutrient conditions of specific sites.
Introduction

The invasive plant *Alliaria petiolata* (Bieb.) Cavara & Grande (Garlic Mustard) is native to Europe and was first recorded in the North America in 1868 (Al-Shehbaz et al. 2006, Nuzzo 1993). Its distribution currently includes 36 U.S. states and 5 Canadian provinces, from as far north and west as Alaska, as far east as Maine, and as far south as Georgia (USDA PLANTS Database 2015). In Vermont, Garlic Mustard is classified as a “Class B Noxious Weed” (USDA PLANTS Database 2015). As a shade-tolerant plant, it is capable of growing in moist forest understory habitats (Al-Shehbaz et al. 2006, Munger 2001) frequently outcompeting native vegetation (Munger 2001). Garlic Mustard is an obligate biennial in North America (Cavers et al. 1979). During its first year of growth it is a non-reproductive basal rosette; in its second year, stems elongate in early to mid-spring and produce flowers that remain through mid- to late summer and are both self and insect pollinated (Anderson et al. 1996, Cavers et al. 1979, Cruden et al. 1996).

Garlic Mustard has profound but somewhat varied effects on plant communities where it has invaded. Native plant diversity and evenness is reduced by Garlic Mustard invasion (Stinson et al. 2007) and rebounds when it is eradicated (Hochstedler et al. 2007, McCarthy 1997, Stinson et al. 2007). These negative effects on other plant species have been attributed Garlic Mustard’s allelopathic effects on both endo- and ecto-mycorrhizae of neighboring plants (Barto et al. 2010a, 2011; Cipollini et al. 2008a; Lankau 2011a, 2011b; Roberts and Anderson 2001; Wolfe et al. 2008), though in the former case this may only occur on endo-mycorrhizal innocula in the soil before they form a symbiosis with native plant roots (Barto et al. 2010b). Many tree seedlings have reduced growth in
the presence of Garlic Mustard (Meekins and McCarthy 1999, Stinson et al. 2006), though not all experience this effect (Meekins and McCarthy 1999). Garlic Mustard’s allelopathic influences are negatively related to the duration of the infestation (Lankau 2011a, 2011b, 2011c, 2012; Lankau et al. 2009). The degree of allelopathic influence may also vary by population and with microsite (Lankau 2010).

In addition to allelopathy, Garlic Mustard may compete with native plants for light resources and/or nutrients (McCarthy and Hanson 1998; Cipollini et al. 2008a,b), and invasive plant species have generally been shown to be better resource competitors than native plant species (Vilà and Weiner 2004). These effects may be non-additive, additive, synergistic, or interact resulting in no observed effects (McCarthy and Hanson 1998; Cipollini et al. 2008a,b). Because second-year Garlic Mustard plants can grow to dense stands of tall (over 1 m) plants, we expected that they may shade, and thus outcompete, native vegetation. Alternatively, thickly growing Garlic Mustard patches may induce a shade avoidance response in seedlings (Gilbert et al. 2001, Schmitt et al. 2003, Smith 1982), a phenotypically plastic response which could either benefit or hinder tree seedling health in the long term depending upon allocation of biomass to roots versus shoots and the ambient environmental conditions (Schmitt et al. 2003). Finally, it has been shown that the addition of soil nutrients can attenuate the effects of direct allelopathy on non-mycorrhizal plants from the invasive shrub Lonicera maackii (Cipollini et al. 2008a), although in this same study the authors found no allelopathic effects of Garlic Mustard at any fertilization level. It remains to be seen whether nutrient addition interacts with allopathic effects on native plants.
In field and laboratory settings Garlic Mustard negatively affects native trees Red Maple (Stinson et al. 2006, 2007) and Sugar Maple (Barto et al. 2011, Stinson et al. 2006, 2007), whereas native Eastern Cottonwood trees (Cooper 1990) and Garlic Mustard (Munger 2001) are often seen growing in similar riparian environments. All of the tree species form mycorrhizal associations which could potentially be affected by Garlic Mustard secondary metabolites (Bainard et al. 2011, Godman et al. 1990, Vozzo and Hacskaylo 1974, Walters and Yawney 1990). Our study examines the interactive effects of allelopathy, shade, and nutrient availability on the above tree seedlings as well as native Silver Maple. This will inform the literature on how allelopathy interacts with microsite factors to determine Garlic Mustard’s effects on tree seedlings.

The primary goal of this study was to determine whether shade and/or fertilization interact with allelopathic effects of Garlic Mustard to affect growth, health, and susceptibility to foliar herbivory of native tree seedlings. We hypothesized that 1) allelopathic effects of Garlic Mustard would decrease growth and health of tree seedlings, 2) shade would decrease tree seedling growth and health, 3) fertilization would increase tree seedling growth and health and mediate the negative impacts of allelopathy, and 4) seedlings exposed to these treatment combinations would be affected differentially by greenhouse insect herbivores. Some alternatives to our second hypothesis are that tree seedlings growing in the sun would experience increased temperature and evapotranspiration, which could result in reduced photosynthesis and reduced growth, or that seedlings would experience a decrease in overall root:shoot ratios due to a shade avoidance response. The results from this study provide insights into interactions between
Garlic Mustard and native tree seedlings, as well as inform management of Northeastern Forests to minimize the negative effects of Garlic Mustard via environmental impacts on native tree species.

**Materials and Methods**

**Experimental design and species selection**

We selected Garlic Mustard and four native tree species common to Vermont and northeastern forests: *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood), *Acer saccharinum* L. (Silver Maple), *Acer rubrum* L. (Red Maple), and *Acer saccharum* Marshall (Sugar Maple). The first three tree species were producing viable seed at the time of collection in early June, and Sugar Maple was added to the study later in the summer following germination of seed which had been collected in fall 2011 and were stratified following requirements outlined in Bonner and Karrfelt (2008) until mid-summer of 2012. We planted Garlic Mustard plants prior to the native trees to ensure that they would have the potential to act on endo-mycorrhizae prior to symbiosis formation with tree seedlings as discussed in Barto et al. (2010).

We transplanted first and second year Garlic Mustard plants from a wild-growing population at Grand Isle State Park, Grand Isle, VT (44°41’14”N, 73°17’41”W). We collected Eastern Cottonwood and Silver Maple seeds from the Intervale Center in Burlington, VT (44°29’36”N, 73°12’19”W), Red Maple seed from Airport Park in Colchester, VT (44°32’44”N, 73°16’15”W), and Sugar Maple seed from Hubbard Brook Long-Term Experimental Research Forest in NH (43°56’35”N, 71°42’36”W). We
germinated the seeds in the laboratory and then planted them in 48 plastic planters 122 x 61 x 20 cm (4 ft x 2 ft x 8 in) deep (GreenGrid, Weston Solutions, Inc., Glastonbury, Connecticut, USA) filled with raised bed mix soil from Green Mountain Compost in Vermont, containing compost, topsoil, peat moss, and organic nutrients (Green Mountain Compost 2015). We tested the soil before being used in the study, after growing with first year Garlic Mustard, and after growing with second year Garlic Mustard to have a baseline reference for the pH, organic matter, and nutrient content (Table 1). Soil samples were taken on 6 July 2012, prior to application of the fertilization treatment.

Planters were set up in six greenhouse replicates with eight planters per replicate. (Figure 1a). We assigned treatments to the planters in three separate 2 by 2 by 4 factorial experiments (Figure 1b,c,d). Within each planter, seedlings were planted in 537 cm$^3$ (32.77 in$^3$) containers with holes that allowed soil and root exchange with the larger planter (soil exchange). Seventy-one holes, made with a soldering iron, were evenly spaced around (10 rows of 6 holes each) and in the base (11 holes) of each container. To prevent root outgrowth, we lined containers with a 30 x 30 cm (11.81 x 11.81 in) piece of 100% cotton fabric. However, over the course of the experiments roots grew through the cotton fabric, and this outgrowth was qualitatively recorded and converted to an estimate of root length (cm) (see below). We transplanted first year Garlic Mustard plants in 15 to 20 cm (5.91 to 7.87 in) wide strips lengthwise through the center of each planter. We established an allelopathy treatment (Experiment #1, Figure 1b) by allowing seedling roots to interact with allelopathic chemicals released by first year Garlic Mustard plants. The containers for the two experiments with soil exchange (Experiment #1, Figure 1b;
Experiment #2, Figure 1c) were filled with soil from planters that had been exposed to Garlic Mustard. Seedlings planted in containers without holes (Experiment #3, Figure 1d) prevented this exchange (without soil exchange). Containers without holes were created by inserting a container with holes into a second container without holes. They were filled with fresh soil, unexposed to Garlic Mustard and placed in the planter with the lip of the outer container at soil level, thus preventing contact with soil exposed to Garlic Mustard. Half of the seedlings were fertilized and half were not to quantify interactive effects of fertilization and allelopathy. On 15 July we added Osmocote 18-6-12 granular controlled release fertilizer (8-9 months) to planters and containers at a rate of 4.2 g fertilizer per L soil. In addition, we applied granular Micromax micronutrients to all planters and containers at 0.6 g fertilizer per L soil to ensure that first year Garlic Mustard plants had adequate micronutrients to produce their suite of secondary root exudates.

We used second year Garlic Mustard plants to shade the tree seedlings. Approximately 1-wk after transplantation, second year Garlic Mustard plants died. We assume that these plants experienced this stress because they had already finished flowering and producing seed and thus had expended most of their energy stores for their last year of growth. This is further evidenced by the fact that the first year Garlic Mustard plants did not die. Because of the death of the second year Garlic Mustard, all of the seedlings growing in planters containing these plants were assumed to be free from allelopathy. It is possible that chemicals secreted from these plants during their time alive may have resulted in some lingering allelopathic effects throughout the growing season,
however Garlic Mustard’s allelochemicals have short half-lives generally ranging from only 3 h to 2 d (Barto and Cipollini 2009; Gimsing et al. 2006, 2007) and this is unlikely. The dead plants remained intact and provided shade to the tree seedlings on their northern aspect. Containers with soil exchange on the south (no allelopathy or shade) side of these second year planters thus were able to provide a control for comparison of the effects of allelopathy on seedlings growing in containers with soil exchange in the first year Garlic Mustard planters (Experiment #1, Figure 1b). Containers with soil exchange on the north (shade) and south (full sun) sides of these second year Garlic Mustard planters allowed us to test effects of shade on the four tree species (Experiment #2, Figure 1c). Containers without soil exchange on the north (shade) and south (full sun) sides of these planters allowed us to test the effects of shade on the tree species once again (Experiment #3, Figure 1d). We placed iButton temperature loggers in the centers of both northern and southern aspects of each planter from late August through October to serve as a proxy to measure and confirm shade treatment. Results of a one-way ANOVA to test differences associated with the shade treatment revealed that temperatures were overall higher in the sun than in the shade (F1,190.462 = 188.65; P < 0.0001). Half of the seedlings were fertilized and half were not to quantify interactive effects of fertilization and shade. Tree seedlings growing in containers without soil exchange on the north and south sides of second year Garlic Mustard planters were also exposed to the shade and fertilization treatments (Experiment #3).

All containers were installed over a two-week period, ending 22 June 2012. The planters were placed on 6 greenhouse tables and their locations were randomized by
treatment for each replicate. The tables were treated as blocks with 8 planters per each of the 6 replicates. Planters were placed in 2 rows of 4 with east-west orientation (Fig. 1). Planters were watered daily or more depending on observed soil moisture throughout the study.

**Response variables measured**

Tree seedlings were measured on 2 July, 24 July, 22 August, and 28 September but not after they died. Sugar Maple seedlings were measured on 22 August and 28 September. Response variables included total height (nearest cm) degree of root outgrowth in the containers converted to an estimated length (as a proxy measure of biomass allocation to roots), seedling health estimated qualitatively on a scale of 1 (dead) to 5 (vigorous), and presence or absence of herbivory. Roots not penetrating the cotton cloth through the holes in the containers were given an estimated length of 6 cm, approximately half the depth of the container. Roots extending the length of the container and starting to penetrate the cloth were given an estimated length of 12 cm. Roots extending outside of the container were given an estimated length of 15 cm. Final estimated root length was divided by final measured shoot length to obtain an estimated root:shoot ratio. We assigned a health value of 1 to those seedlings that were dead; 2 to those that were wilting; 3 to those with drooping or discoloration on more than 50% of their leaves; 4 to those with discoloration on 10-50% of the leaves; and 5 to those with less than 10% discoloration of the leaves. We report the final health measurement, on 28
September, including mortality rates. On 28 September we also quantified herbivory on all living seedlings by noting presence or absence of signs of insect feeding on the leaves.

**Statistical analyses**

We compared response variables of seedlings exposed and not exposed to *A. petiolata* allelopathy in fertilized and unfertilized planters (Experiment #1), and with and without fertilizer in the shade and sun with soil exchange (Experiment #2) and without soil exchange (Experiment #3). They were analyzed by nonparametric rank-based two-way 2 by 3 factorial ANOVA in July (shade or allelopathy by species) and nonparametric rank-based three-way 2 by 2 by 4 factorial ANOVA in August and September following application of the fertilization treatment and introduction of Sugar Maple seedlings (shade or allelopathy by fertilization by species). Interactions between shade and allelopathy were not testable in this study. In addition, because Sugar Maple seed was planted gradually throughout August and September in place of other plants that had died, Repeated Measures Analysis was not appropriate for this study.

Soil samples were tested by one-way ANOVA to compare nutrients and characteristics across soils exposed to either first year Garlic Mustard, second year Garlic Mustard, or neither.

When ANOVA results were significant (*P* ≤ 0.05), pairwise comparisons were used to assess differences among treatments. In the case of the shade by fertilization interaction seen for herbivory, and in the soil sample tests, Tukey’s Honest Significant Difference test was used to assess differences among treatments (Tukey 1953, SAS
The Kenward and Roger (1997) method was used to approximate denominator degrees of freedom when data were unbalanced. Analyses were performed using SAS and JMP software (SAS Institute Inc. 2011).

**Results**

Direct effects of allelopathy (Experiment #1) on tree seeding height were seen on 24 July (Table 1a). Seedlings had an overall mean height (reported with standard error) of 6.12 ± 0.40 cm without allelopathy compared with 5.53 ± 0.27 cm with allelopathy (Table 1a). At the end of the season, there were no differences in health between seedlings exposed to allelopathy or not (F$_{1,5.67}$ = 0.34; $P = 0.5837$). Although there were no interactions between the allelopathy and fertilization treatments on seedling height or health (Table 1a), insect herbivory was most frequently observed on unfertilized Sugar Maple, Silver Maple, and Red Maple seedlings that were not exposed to allelopathy (F$_{3,436}$ = 2.86; $P = 0.0365$).

Root:shoot ratio estimates varied with exposure to allelopathy and by species (F$_{3,431}$ = 4.01; $P = 0.0078$). In descending order, root:shoot ratios of seedlings exposed to allelopathy were greatest in Red Maple, Sugar Maple, Eastern Cottonwood, and Silver Maple (Fig. 2a). This differs from root:shoot ratios of seedlings not exposed to allelopathy where Eastern Cottonwood and Red Maple were the greatest, followed by Sugar Maple, and then Silver Maple (Fig. 2a). Sugar Maple estimated root:shoot was greater when exposed to allelopathy than when not exposed. The allelopathy treatment did not affect estimated root:shoot for any of the other seedling species (Fig. 2a).
There were significant fertilization by species ($F_{3,431} = 11.26; P < 0.0001$) interactions. Fertilization decreased root:shoot ratios in Eastern Cottonwood, Silver Maple, and Sugar Maple, but not Red Maple seedlings (Fig. 2b). Overall root:shoot under fertilization was highest in Red Maple, followed by Sugar Maple, then Eastern Cottonwood, and lastly Silver Maple. Seedlings that were not fertilized had root:shoot ratios that were highest in Eastern Cottonwood, followed by Sugar Maple and Red Maple, and Silver Maple (Fig. 2b).

In the shade experiment with soil exchange (Experiment #2), shaded Silver Maple seedlings on 2 July were significantly taller ($7.87 \pm 0.44$ cm) than those grown in the sun ($6.50 \pm 0.54$ cm). Shade had no effect on the height of other species (Fig. 3; Table 1b). Shade had no effect on 24 July (Fig. 3; Table 1b). Tree seedlings were taller in the shade on both 22 August and 25 September (Fig. 3; Table 1b). In the shade experiment without soil exchange (Experiment #3), shading resulted in an average height of $2.92 \pm 0.19$ cm compared with $2.42 \pm 0.11$ cm in full sun on 2 July, but this condition was not detected for the remainder of the season (Table 1c).

Shade resulted in a higher mean health value ($3.58 \pm 0.11$) than unshaded trees ($3.20 \pm 0.11$) at the end of the growing season on 25 September ($F_{1,412} = 8.49; P = 0.0038$) in Experiment #2. An interaction among fertilization, shade, and seedling species was significant in Experiment #3 ($F_{3,835} = 2.62; P = 0.0497$). Overall, Eastern Cottonwood seedlings had the highest health value when fertilized and in full sun ($2.82 \pm 0.24$). In contrast, Silver Maple seedlings had the highest health value when fertilized in the shade ($3.14 \pm 0.22$).
Shade by species ($F_{3,302} = 5.24; P = 0.0015$) and fertilization by species ($F_{3,303} = 10.55; P < 0.0001$) interactions affected seedlings in Experiment #2. Root:shoot ratios were higher in the unshaded treatment for both Eastern Cottonwood and Red Maple, but in the shaded treatment for Sugar Maple, while Silver Maple showed no differences (Fig. 4a). Within the shaded treatment, ratios were highest in Red Maple and Sugar Maple, followed by Eastern Cottonwood and Silver Maple (Fig. 4a). Within the unshaded treatment, ratios were highest in Red Maple, then Sugar Maple with Eastern Cottonwood as an intermediate, and finally in Silver Maple (Fig. 4a). Fertilization decreased root:shoot ratios in Eastern Cottonwood and Silver Maple, but not Sugar Maple or Red Maple (Fig. 4b). Within the fertilization treatment, root:shoot ratios were highest in Red Maple, followed by Sugar Maple, and then Eastern Cottonwood and Silver Maple (Fig. 4b). When unfertilized, root:shoot was highest in Eastern Cottonwood along with Red Maple and Sugar Maple, while the lowest ratios were found in Silver Maple seedlings (Fig. 4b).

Results were similar in Experiment #3, except that root:shoot differences were only marginal for the shade by species ($F_{3,454} = 2.23; P = 0.0842$) and fertilization by species ($F_{3,456} = 2.12; P = 0.0974$) interactions. The effect of species alone, however, was significant ($F_{3,458} = 93.77; P < 0.0001$), with root:shoot highest in Red Maple seedlings, followed by Sugar Maple and Eastern Cottonwood, and lastly Silver Maple (Fig. 5a). Patterns in root:shoot ratios for the marginal shade by species interaction appeared similar to those in Experiment #2, except mean root:shoot in Eastern Cottonwood was higher in the shaded treatment rather than in the unshaded treatment (Fig. 5b). Similarly,
patterns generally matched Experiment #2 for the marginal fertilization by species interaction except that unfertilized Eastern Cottonwood and Silver Maple did not have greatly increased root:shoot ratios (Fig 5c).

In Experiment #2, seedlings which were neither fertilized nor shaded experienced the most herbivory ($F_{1,303} = 17.74; P < 0.0001$), while herbivory was lowest on fertilized unshaded trees. Herbivory in September was also greater on unfertilized Sugar Maple leaves than on any other fertilization by species combination ($F_{3,304} = 3.48; P = 0.0162$). Red Maple seedlings had the lowest incidence of foliar herbivory. In Experiment #3 herbivory was most prevalent on Sugar Maple seedlings ($32.61 \pm 4.91 \%$), followed by Silver Maple ($8.33 \pm 2.41 \%$), then Red Maple ($3.26 \pm 1.38 \%$). No herbivory was observed on Eastern Cottonwood leaves in the study ($F_{3,469} = 22.64; P < 0.0001$). Silver Maple seedlings that were fertilized experienced more herbivory ($12.99 \pm 3.86 \%$) than unfertilized conspecifics ($1.82 \pm 1.82 \%$) ($F_{3,467} = 2.55; P = 0.0550$).

Overall all of the seedlings grew throughout the duration of the study and the addition of the fertilization treatment generally increased shoot height (Table 2), though it decreased root:shoot ratios in Eastern Cottonwood and Silver Maple (Figs. 2 and 3). Silver Maple seedlings were the tallest for all treatment combinations early in the season but were surpassed in height by Eastern Cottonwood by September. These two species were also generally those with the lowest root:shoot ratios, except when cottonwood was shaded or fertilized. The approximate relative growth rate of shoots for all treatments was $0.11 \text{ cm per day for Cottonwood}$, $0.10 \text{ cm per day for Silver Maple}$, and $0.03 \text{ cm per day for both Red Maple and Sugar Maple}$. 

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Some soil nutrients and characteristics were different with Garlic Mustard than without Garlic Mustard (Table 2). There were no significant differences between soils exposed to the first and second year stages of Garlic Mustard. Soils with first or second year Garlic Mustard plants had a higher percentage of organic matter than control soil (Table 2). Percent of aluminum was greater in soils without Garlic Mustard than with Garlic Mustard (Table 2). Percent of potassium was higher in soils without Garlic Mustard than soil with second year Garlic Mustard (Table 2). In contrast, control soils had lower percent zinc than soils with first year Garlic Mustard plants, and a lower percentage of calcium than soils with second year Garlic Mustard plants (Table 2).

**Discussion**

Allelopathy may be temporal, as its negative effects on tree seedlings were stronger earlier than later in the growing season. The temporal effect may be synergistic with Garlic Mustard maximizing its photosynthetic rates in the spring (Myers and Anderson 2003), as light availability may affect the expression of its allelopathic defenses along with other environmental variables such as soil pH, soil moisture, or soil nutrient levels (Cipollini 2002). Alternatively, younger seedlings may be more sensitive to allelopathic exudates than older seedlings. It is also possible that watering diluted any allelochemicals in the containers (Leicht-Young et al. 2015). Only Sugar Maple seedlings had increased root:shoot ratios when exposed to allelopathy, suggesting that this species may be better at surviving in the company of Garlic Mustard than the other species.
The negative effect of allelopathy earlier in the season may have coincided with the additional planting of a first year Garlic Mustard “booster”. It is predicted that tissue decay is a significant source of the negative effects of Garlic Mustard on surrounding plant communities (Barto and Cipollini 2009, Smith and Reynolds 2014). Therefore, a release of allelochemicals from decaying Garlic Mustard tissue may also have contributed to a temporal pulsing of allelopathic effects. As plant species function as a primary link between aboveground and belowground subecosystems (Wardle et al. 2004), both first and second year Garlic Mustard plants may have resulted in altered soil chemistry simply because of their presence and ecological activity compared with control soils which did not have any plants. Effects of invasive plants on soils and neighboring native plant growth may be highly context-dependent, thus difficult to confirm in experiments testing for the presence of allelopathy (Hulme et al. 2013, Leicht-Young et al. 2015).

The shade treatment increased seedling height and health. It also decreased root:shoot ratios in Eastern Cottonwood and Red Maple Seedlings suggesting a shade avoidance response (Gilbert et al. 2001, Schmitt et al. 2003, Smith 1982). Shade treatment increased root growth of Sugar Maple, whereas Eastern Cottonwood seedlings appeared healthier in the sun when soil exchange was prohibited. This may be due to Eastern Cottonwood being the most shade intolerant (Cooper 1990) of our seedling species. Growth of individual tree species correlated positively with their shade tolerances. Eastern Cottonwood, the most shade intolerant species, and Silver Maple, an only moderately shade-tolerant species, experienced the most shoot growth overall, followed by shade
tolerant Red Maple, and very shade tolerant Sugar Maple (Cooper 1990, Gabriel 1990, Godman et al. 1990, Walters and Yawney 1990). In particular, Red and Sugar Maple seedlings experienced the lowest growth and fewest effects from treatments, and both of these species are known to be highly tolerant of shade and capable of surviving for long periods in the understory prior to release (Godman et al. 1990, Walters and Yawney 1990).

The overall positive effects of shade on shoot growth may be due to decreased direct sun and heat, and thus reduced transpiration and longer soil water retention (pers. obs.). Shaded environments retained water better than the non-shaded environment and therefore decreased root:shoot ratios may not be as costly, as predicted by Huber et al. (2004), which could explain why healthier seedlings were in the shade treatment in Experiment #2. This may be stronger in open areas colonized by Garlic Mustard, consistent with and simulated by our greenhouse environment, than in wooded areas beneath an intact forest canopy (Schmitt et al. 2003). Seedlings without soil exchange (Experiment #3) had limited volume for root growth, which is likely why root:shoot ratio results were less clear-cut in this experiment. This limited volume also reduced soil water retention (pers. obs.), and may explain why only in Experiment #3 did Eastern Cottonwood root:shoot ratios appear to respond positively to shade.

There was a consistent pattern in the shade experiments of increased shoot growth in the shade on 2 July that then disappeared on 24 July. This was true in Silver Maple in Experiment #2 and for all tree species in Experiment #3. Garlic Mustard shading effects on tree seedling shoot growth thus appear to have a temporal component, where shaded
plants are taller and healthier early in the growing season. This could indicate an initial growth response to compensate for lower light conditions earlier in the season, often resulting in less growth allocation to roots. Silver Maple seedlings, in particular, have been characterized as tending to exhibit initial rapid growth. However, if they do not experience release, they may succumb to high mortality rates by the end of the first year (Gabriel 1990). Rapid growth early in their first season may confer an evolutionary advantage to Silver Maple seedlings by allowing them to access enough sunlight to be released, and it is possible that this response is stimulated by shaded environments. Interestingly, though shade strongly enhanced Silver Maple shoot growth, it did not result in any root:shoot ratio differences. These may have been undetected in our study or may become more apparent later in the growth of this species. Our results suggested that nutrition is the first limiting factor for Silver Maple, followed by shade.

Insect herbivory varied greatly across experiments, species, and treatments in this study. If fertilized trees utilize enhanced nutrition for shoot growth, they may not be able to mount as effective a defense against herbivores as their unfertilized counterparts, which appeared to be the case for Silver Maple in Experiment #3. It is also possible that stress from lower soil volumes decreased this species’ palatability to herbivores when unfertilized, in contrast to Experiment #2 where soil exchange was present. Conversely, in Experiments #1 and #2 herbivory tended to be highest when seedlings were unfertilized. Nutrient reserves of unfertilized trees may not suffice to mount the level of defense they would manage had they been fertilized. Herbivores also preferred to consume leaf material from tree seedlings which had not been exposed to allelopathy.
Thus it is possible that seedlings exposed to Garlic Mustard may incur decreased herbivory than those growing alone, whether due to direct effects of allelopathy or simply by proximity to a less palatable plant. Future research may be able to elucidate the reasons behind these relationships.

Overall, frequent interactions among variables caused mixed responses in the growth of the tree seedlings over the season. On average, shoot growth and health were maximized under conditions without allelopathy and with shade. Results suggest that the negative effects of allelopathy may have only a brief temporal component. Seedlings appear to grow faster and remain healthier under shaded conditions, but this may be related indirectly to factors such as heat stress or water availability, especially since we confirmed shade avoidance responses in Eastern Cottonwood and Red Maple. If, however, Garlic Mustard both stimulates a shade avoidance response in neighboring tree seedlings while also decreasing evapotranspiration of water resources, these seedlings may experience an overall growth benefit in the long term (Huber et al. 2004). Finally, fertilization did not seem to help plants counteract the allelopathic effects of Garlic Mustard. This, in addition to the fact that we saw little to no effects of allelopathy in our study, may be consistent with other studies which have failed to find allelopathic effects of Garlic Mustard (McCarthy and Hanson 1998), or have only found reduced allelopathic effects in the field as compared with experiments using Garlic Mustard extracts in the laboratory (Barto and Cipollini 2009, Cipollini et al. 2008a). Fertilization caused increases in seedling shoot growth and health responses overall, but decreased root:shoot ratios. Thus, it remains to be seen if fertilization is beneficial to these tree seedlings in the
long term and we reserve judgment on whether it should be recommended as a management technique. Shaded Silver Maple grew taller when fertilized, but also experienced greater herbivory when grown in a limited volume of soil, thus even application of fertilizers as a management strategy in these situations should be approached cautiously. Our results should also be extrapolated with caution over the long term as tree responses may change as they grow. However, the presence of Garlic Mustard may still have important implications in the initial recruitment of tree species in forests. This is especially true of shade intolerant species that may escape the negative effects of Garlic Mustard if they grow fast enough in the first year to access sunlight adequate for future growth and release. In conclusion, the effects of Garlic Mustard on the surrounding plant community varies strongly with resource availability, and contributes to complex ecological dynamics in Garlic Mustard invasions, which may not always result in negative effects.

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Tables

Table 1(a–c). Summary of analysis of variance of tree seedling height (cm) for a) Experiment #1, b) Experiment #2, and c) Experiment #3 (Non-parametric rank-based ANOVA, $\alpha = 0.05$) (Sample sizes vary and are indicated by degrees of freedom in the table). “Allelo” = Allelopathy, “Fert” = Fertilization, “--” = Not yet available to test due to absence of fertilization treatment, “N/S” = Not significant, “N/A” = Main effects not applicable due to presence of interactions.
<table>
<thead>
<tr>
<th>Time</th>
<th>Species</th>
<th>Allelo</th>
<th>Fert*species</th>
<th>Allelo*species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jun</td>
<td>$F_{2.341}=275.96; P&lt;0.0001$</td>
<td>N/S</td>
<td>--</td>
<td>N/S</td>
</tr>
<tr>
<td>Jul</td>
<td>$F_{2.453}=656.70; P&lt;0.0001$</td>
<td>$F_{1.451}=3.15; P=0.0767$</td>
<td>--</td>
<td>N/S</td>
</tr>
<tr>
<td>Aug</td>
<td>N/A</td>
<td>N/S</td>
<td>$F_{3.459}=4.53; P=0.0039$</td>
<td>N/S</td>
</tr>
<tr>
<td>Sep</td>
<td>N/A</td>
<td>N/S</td>
<td>$F_{3.439}=24.36; P&lt;0.0001$</td>
<td>N/S</td>
</tr>
</tbody>
</table>

TABLE 1a. Experiment #1 – Allelopathy – With soil exchange - Height (cm)

<table>
<thead>
<tr>
<th>Time</th>
<th>Species</th>
<th>Shade</th>
<th>Fert*species</th>
<th>Shade*species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jun</td>
<td>N/A</td>
<td>N/A</td>
<td>--</td>
<td>$F_{2.352}=3.48; P=0.0320$</td>
</tr>
<tr>
<td>Jul</td>
<td>$F_{2.307}=385.04; P&lt;0.0001$</td>
<td>N/S</td>
<td>--</td>
<td>N/S</td>
</tr>
<tr>
<td>Aug</td>
<td>N/A</td>
<td>$F_{1.311}=5.20; P=0.0233$</td>
<td>$F_{3.312}=5.48; P=0.0011$</td>
<td>N/S</td>
</tr>
<tr>
<td>Sep</td>
<td>N/A</td>
<td>$F_{1.303}=4.71; P=0.0308$</td>
<td>$F_{3.309}=17.57; P&lt;0.0001$</td>
<td>N/S</td>
</tr>
</tbody>
</table>

TABLE 1b. Experiment #2 - Shade - With soil exchange - Height (cm)

<table>
<thead>
<tr>
<th>Time</th>
<th>Species</th>
<th>Allelo</th>
<th>Fert*species</th>
<th>Allelo*species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jun</td>
<td>$F_{2.725}=331.85; P&lt;0.0001$</td>
<td>$F_{1.120}=4.08; P=0.0456$</td>
<td>--</td>
<td>$F_{2.726}=2.61; P=0.0743$</td>
</tr>
<tr>
<td>Jul</td>
<td>$F_{2.556}=649.27; P&lt;0.0001$</td>
<td>N/S</td>
<td>--</td>
<td>N/S</td>
</tr>
<tr>
<td>Aug</td>
<td>$F_{3.516}=175.87; P&lt;0.0001$</td>
<td>N/S</td>
<td>N/S</td>
<td>N/S</td>
</tr>
<tr>
<td>Sep</td>
<td>N/A</td>
<td>N/S</td>
<td>$F_{3.461}=6.67; P=0.0002$</td>
<td>N/S</td>
</tr>
</tbody>
</table>

TABLE 1c. Experiment #3 - Shade - Without soil exchange - Height (cm)
Table 2. Mean (± SE) measures of various soil characteristics and analysis of variance of their differences across soils exposed to either first year *A. petiolata* (“First”), second year *A. petiolata* (“Second”) or no *A. petiolata* (“Control”). Within each measurement column, means with different letters after them in superscript are significantly different from each other (ANOVA, \( \alpha = 0.05 \)) (N=18). “GM Year” = Garlic mustard year, “OM” = Organic matter, “Avail P” = Available phosphorous, “CEC” = Cation exchange capacity.
<table>
<thead>
<tr>
<th>GM Year</th>
<th>pH</th>
<th>% OM</th>
<th>Avail. P (mg/kg)</th>
<th>CEC (meq/100g)</th>
<th>Al (mg/kg)</th>
<th>Zn (mg/kg)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>8.28 ± 0.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.45 ± 0.45&lt;sup&gt;a&lt;/sup&gt;</td>
<td>190.00 ± 4.03&lt;sup&gt;a&lt;/sup&gt;</td>
<td>24.20 ± 0.31&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.00 ± 0.00&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.68 ± 0.07&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Second</td>
<td>8.23 ± 0.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>9.68 ± 0.210&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>183.50 ± 4.56&lt;sup&gt;a&lt;/sup&gt;</td>
<td>23.85 ± 0.24&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.17 ± 0.33&lt;sup&gt;b&lt;/sup&gt;</td>
<td>3.63 ± 0.07&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Control</td>
<td>8.30 ± 0.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.87 ± 0.38&lt;sup&gt;b&lt;/sup&gt;</td>
<td>182.67 ± 5.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>23.85 ± 0.59&lt;sup&gt;a&lt;/sup&gt;</td>
<td>8.50 ± 0.40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>3.40 ± 0.09&lt;sup&gt;b&lt;/sup&gt;</td>
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ANOVA F  
F<sub>2,15</sub>=1.07  
F<sub>2,15</sub>=7.47  
F<sub>2,15</sub>=0.72  
F<sub>2,15</sub>=0.23  
F<sub>2,15</sub>=7.30  
F<sub>2,15</sub>=4.27

ANOVA P  
P = 0.3692  
P = 0.0056  
P = 0.5028  
P = 0.7963  
P = 0.0061  
P = 0.0340

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<th>K (mg/kg)</th>
<th>Mg (mg/kg)</th>
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<th>% K</th>
<th>% Mg</th>
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<td>First</td>
<td>3,647.33 ± 47.72&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1,021.17 ± 45.24&lt;sup&gt;a&lt;/sup&gt;</td>
<td>399.83 ± 5.86&lt;sup&gt;a&lt;/sup&gt;</td>
<td>75.42 ± 0.44&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10.82 ± 0.40&lt;sup&gt;ab&lt;/sup&gt;</td>
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<td>Second</td>
<td>3,636.5 ± 38.36&lt;sup&gt;a&lt;/sup&gt;</td>
<td>936.67 ± 55.19&lt;sup&gt;a&lt;/sup&gt;</td>
<td>392.67 ± 3.52&lt;sup&gt;a&lt;/sup&gt;</td>
<td>76.22 ± 0.55&lt;sup&gt;a&lt;/sup&gt;</td>
<td>10.07 ± 0.55&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Control</td>
<td>3,535.17 ± 90.23&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1,104.17 ± 47.40&lt;sup&gt;a&lt;/sup&gt;</td>
<td>398.67 ± 6.67&lt;sup&gt;a&lt;/sup&gt;</td>
<td>74.20 ± 0.34&lt;sup&gt;b&lt;/sup&gt;</td>
<td>11.85 ± 0.34&lt;sup&gt;a&lt;/sup&gt;</td>
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ANOVA F  
F<sub>2,15</sub>=1.05  
F<sub>2,15</sub>=3.02  
F<sub>2,15</sub>=0.41  
F<sub>2,15</sub>=7.30  
F<sub>2,15</sub>=5.13  
F<sub>2,15</sub>=0.44

ANOVA P  
P = 0.3733  
P = 0.0792  
P = 0.6689  
P = 0.0061  
P = 0.0200  
P = 0.6544

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<th>Cu (mg/kg)</th>
<th>Fe (mg/kg)</th>
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<td>First</td>
<td>21.83 ± 1.99&lt;sup&gt;a&lt;/sup&gt;</td>
<td>35.05 ± 0.89&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.67 ± 0.03&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.28 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.68 ± 0.19&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Second</td>
<td>19.83 ± 3.43&lt;sup&gt;a&lt;/sup&gt;</td>
<td>32.17 ± 1.63&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.55 ± 0.03&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.26 ± 0.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>6.25 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>Control</td>
<td>25.00 ± 2.45&lt;sup&gt;a&lt;/sup&gt;</td>
<td>29.10 ± 1.70&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.61 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.29 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.00 ± 0.14&lt;sup&gt;a&lt;/sup&gt;</td>
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ANOVA F  
F<sub>2,15</sub>=0.71  
F<sub>2,15</sub>=3.36  
F<sub>2,15</sub>=1.85  
F<sub>2,15</sub>=1.09  
F<sub>2,15</sub>=3.46  
F<sub>2,15</sub>=2.43

ANOVA P  
P = 0.5072  
P = 0.0621  
P = 0.1912  
P = 0.3611  
P = 0.0580  
P = 0.1219
### Figures

#### A) Overall Design

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#### B) Experiment 1

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#### C) Experiment 2

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#### D) Experiment 3

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84
Figure 1. Diagram of A) a single replicate with planters randomly ordered by treatment combination, B) a representation of the subset of planters used for Experiment #1, C) a representation of the subset of planters used for Experiment #2, and D) a representation of the subset of planters used for Experiment #3. N = North, S = South, E = East, W = West. Rows of smaller squares represent containers for seedlings (randomly selected among *P. deltoides*, *A. saccharinum*, *A. rubrum*, or *A. saccharum*). Dotted lines surrounding containers represent shared soil while solid lines represent soil barriers. Seedlings in containers north of the second year central *A. petiolata* planting strips were exposed to light limitation through shading due to the height of the invasive plant. Each of the 8 planters are labeled either fertilized or unfertilized.
Figure 2(a–b). Mean (± SE) root:shoot ratios of all four tree species exposed to either a) allelopathy or not, and b) fertilization or not, in summer, 2012, in containers with soil exchange (Experiment #1). Bars with different capital letters are significantly different from each other within the a) allelopathy and b) fertilized treatments (Non-parametric rank-based ANOVA, $\alpha = 0.05$). Bars with different lowercase letters are significantly different from each other within the a) no allelopathy and b) unfertilized treatments (Non-parametric rank-based ANOVA, $\alpha = 0.05$). An asterisk (*) following the species on the x-axes means treatments differed from each other within that species (Non-parametric rank-based ANOVA, $\alpha = 0.05$). (N=451).
**Mean (± SE) Tree Seedling Height (cm) - Soil Exchange**

- **Eastern Cottonwood - Shaded**
- **Eastern Cottonwood - Unshaded**
- **Red Maple - Shaded**
- **Red Maple - Unshaded**
- **Silver Maple - Shaded**
- **Silver Maple - Unshaded**
- **Sugar Maple - Shaded**
- **Sugar Maple - Unshaded**

- **2 Jul***
- **24 Jul**
- **22 Aug**
- **26 Sep**
- **28 Sep**

*Significant differences
**Highly significant differences
Figure 3. Mean (± SE) height (cm) of all four tree species exposed to either shade or not, and fertilization or not, in summer, 2012, in containers with soil exchange (Experiment #2). An asterisk (*) following the date on the x-axis means that there was a significant shade by species interaction for that date overall. A double asterisk (**) following the date on the x-axis means that there was a significant overall shade effect for that date. A large asterisk (*) above a particular pairwise comparison means that a significant difference was seen for the pairwise comparison alone (Non-parametric rank-based ANOVA, α = 0.05) (N = 1,341).
Figure 4(a–b). Mean (± SE) root:shoot ratios of all four tree species exposed to either a) shade or not, and b) fertilization or not, in summer, 2012, in containers with soil exchange (Experiment #2). Bars with different capital letters are significantly different from each other within the a) shaded and b) fertilized treatments (Non-parametric rank-based ANOVA, $\alpha = 0.05$). Bars with different lowercase letters are significantly different from each other within the a) unshaded and b) unfertilized treatments (Non-parametric rank-based ANOVA, $\alpha = 0.05$). An asterisk (*) following the species on the x-axes means treatments differed from each other within that species (Non-parametric rank-based ANOVA, $\alpha = 0.05$). (N=319).
Figure 5(a–c). Mean (± SE) root:shoot ratios of all four tree species a) across all treatment combinations, b) exposed to shade or not, and c) exposed to fertilization or not, in summer, 2012, in containers without soil exchange (Experiment #3). Bars with different letters in graph “a” are significantly different from each other (Non-parametric rank-based ANOVA, \( \alpha = 0.05 \)) (N=479).
CHAPTER FOUR

Invertebrate biodiversity and activity on an invasive plant (*Alliaria petiolata*) and native plants in Vermont

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Abstract

Invasive plants species can alter the trophic interactions in their invaded communities. A novel plant can affect local community dynamics and relationships with invertebrate pollinators, herbivores, and predators. This could lead to host shifts and changes in behaviors. We examined invertebrate abundance, biodiversity and activity on the non-native invasive plant garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara & Grande [Brassicales: Brassicaceae]) in 2011, 2012, and 2013 in Vermont. We also examined invertebrate abundance, biodiversity and activity on the native orange jewelweed (*Impatiens capensis* Meerb. [Ericales: Balsaminaceae]), sweet cicely (*Osmorhiza* sp. Raf. [Apiales: Umbelliferae], and *Rubus* spp. L. [Rosales: Rosaceae]. We quantified abundance, richness, and diversity of the collected invertebrates in relation to plant species, plant density, patch size, and proximity to *A. petiolata*. Results revealed a unique
group of invertebrates associated with *A. petiolata*, which differed from those associated with native plants. Additionally, *A. petiolata* appears to be attractive to insects for nectar and water collection, potentially facilitating pollination and thus success of *A. petiolata*. One native aphid (*Lipaphis brassicae* [Hemiptera: Aphididae]) was consistently found infesting the plant later in the growing season, but did not cause extensive damage. Results of this study indicate that *A. petiolata* has few herbivores associated with it, but infested areas support diverse communities of invertebrates.

**Key Words:** plant-insect interactions, garlic mustard, abundance, richness, behavior

**Introduction**

The invasive plant garlic mustard (*Alliaria petiolata* (M.Bieb.) Cavara & Grande [Brassicales: Brassicaceae]) is native to Europe and was first recorded in the United States in 1868 (Nuzzo 1993, Al-Shehbaz et al. 2006). Its distribution currently extends to 37 American states and 5 Canadian provinces (USDA PLANTS Database). In Vermont, *A. petiolata* is classified as a “Class B Noxious Weed” (USDA PLANTS Database). It is an obligate biennial in North America (Cavers et al. 1979). Seeds produced by second-year plants dehisce by late summer and require a period of winter stratification before germination early the following spring (Cavers et al. 1979, Baskin and Baskin 1992, Anderson et al. 1996). *Alliaria petiolata* spends its first year as a non-reproductive basal rosette, and during the second year stems elongate in early to mid-spring and produce flowers which remain through mid- to late-summer (Cavers et al. 1979, Anderson et al. 1996, Cruden et al. 1996).
*Alliaria petiolata* is both self-pollinated at night and insect-pollinated during the day, and pollinators include generalist syrphid flies and small bees, and perhaps some midges (Genders 1971, Cavers et al. 1979, Anderson et al. 1996, Cruden et al. 1996). Compounds released by this plant can be attractants for specialist predators as well as specialist ovipositing butterflies (Fahey et al. 2001, Chew 1988). However, Lepidopteran larvae feeding on the plant, including the West Virginia white butterfly (*Pieris virginiensis*) and the mustard white butterfly (*Pieris napi oleracea*), often exhibit reduced growth and increased mortality (Bowden 1971; Courant et al. 1994; Porter 1994; Huang et al. 1995; Courant 1996; Renwick et al. 2001; Cipollini and Gruner 2007; Rodgers et al. 2008a, 2008b; Barto et al. 2010) due to chemical deterrents inhibiting feeding and growth (Haribal et al. 2001, Renwick et al. 2001). Other field studies have shown, in general, that herbivore activity on *A. petiolata* in its introduced range is very low or negligible (Szentesi 1991; Nuzzo 2000; Blossey et al. 2001; Renwick et al. 2001; Evans and Landis 2007; Van Riper et al. 2010a,b). Herbivores tend to respond strongly to disturbances that alter or change the amount or types of plant species in an area (Schowalter and Lowman 1999). Thus, areas experiencing high levels of garlic mustard invasion may show altered herbivore diversity on neighboring native plants compared with areas with low or no *A. petiolata* infestation.

In this study we examine the direct and indirect effects of *A. petiolata* on native insect communities. We accomplished this by surveying invertebrates at sites invaded and uninvaded by *A. petiolata* and comparing invertebrate colonization between the invasive and nearby native plants. We surveyed 7 sites for 3 years to determine overall
invertebrate abundance, species richness, and diversity patterns. We also recorded the behavior of invertebrates in *A. petiolata* patches. Our goal was to explore if presence of *A. petiolata* influences invertebrate abundance and biodiversity in the community. Specific research questions include: (1) What is the influence of non-native invasive *A. petiolata* on the biodiversity of invertebrates in invaded sites compared to uninvaded sites?; (2) Are there spatial or temporal differences with these relationships?; and (3) Are there observable behavioral patterns of insect orders associated with the invaded system? This research quantifies the effects of *A. petiolata* on arthropod communities and relations to those communities of native plants.

**Materials and Methods**

**Study Sites and Species.** We surveyed invertebrate populations at seven sites in Vermont in 2011, 2012, and 2013 (Fig. 1; Table 1). We selected sites with *A. petiolata* and native plants *Osmorhiza* sp. Raf. (sweet cicely, Apiales: Umbelliferae), *Impatiens capensis* Meerb. (orange jewelweed, Ericales: Balsaminaceae), and *Rubus* spp. L. (Rosales: Rosaceae). The herbaceous *Osmorhiza* sp. is a woodland perennial plant that produces small white flowers with similar phenology as *A. petiolata* (Baskin and Baskin 1984, Brandenburg 2010). Another native plant, *I. capensis* is an herbaceous perennial found frequently in wooded areas throughout the eastern United States and grows in the same areas as *A. petiolata*, but does not flower until late summer (Brandenburg 2010). Plants in the genus *Rubus* spp. include raspberries, blackberries and their relatives, and are woody perennials that flower in spring and early to mid summer and are frequently found in thickets and recreational areas where they often co-occur with *A. petiolata*
(Petrides 1972). We compared insect abundance and diversity on these native plants of different life history characteristics, which co-occur with *A. petiolata* invasion.

In 2011, we compared invertebrate assemblages between *A. petiolata* and native plant *Osmorhiza* sp. at Mt. Ascutney State Park, and between *A. petiolata* and native plant *I. capensis* at Lake Carmi State Park. Both parks are wooded and are open for recreation throughout the summer (www.vtstateparks.com). These sites were selected based on non-native invasive species survey data collected in 2010 (Redstart, Inc. et al. 2012, Limback and Wallin 2015). At Mt. Ascutney State Park, *A. petiolata* and *Osmorhiza* sp. were found in neighboring large patches (>30 m$^2$) in a shaded understory. At Lake Carmi State Park, *A. petiolata* and *I. capensis* occurred in large (>30 m$^2$) and small (<10 m$^2$) patches throughout the park. In 2012, we continued to sample these sites, and added a site at Grand Isle State Park, another wooded campground with large and small patches of *A. petiolata*, co-occurring with native *Rubus* spp. In 2012, we also identified two wooded reference sites in Waterbury and Milton, Vermont where the native plants *Osmorhiza* sp. and *I. capensis*, and *Rubus* spp., respectively, grew, but not *A. petiolata*. In 2013, we made behavioral observations of insects on *A. petiolata* at two urban woodland sites in the cities of Essex Junction and South Burlington, Vermont.

**Biodiversity Sampling.** In 2011 and 2012 arthropods were collected weekly at Lake Carmi State Park and bi-weekly at all other sites. In 2011 we collected on a total of four dates at Mt. Ascutney State Park and seven dates at Lake Carmi State Park. In 2012 we collected on five dates at Mt. Ascutney, seven dates at Lake Carmi, five dates at Grand Isle, five dates at Waterbury, and four dates at Milton. We randomly selected four 1-m$^2$
plots within large patches and one 1-m² plot within each of four small patches each sampling date (Fig. 1). Thus, different micro-sites within the same patches were sampled each time, and repeated measures analysis was not appropriate for this study.

Invertebrates were collected using ten sweeps with an insect sweep net (Triplehorn and Johnson 2004). Collected specimens were stored in labeled vials of 95% EtOH. Samples were stored at the University of Vermont George D. Aiken Forestry Sciences Laboratory in South Burlington, VT until they were sorted and identified. Insects were sorted by morphospecies, taxa separated by differences in external morphology, which has been shown to provide an accurate surrogate for species in estimating richness (alpha diversity) and turnover (beta diversity) (Oliver and Beattie 1996). A subset of 2,670 invertebrates from 2012 collections (6,407 total) were identified to level of family. Ants (Hymenoptera: Formicidae) and bees (Hymenoptera: Superfamily Apoidea) within this subset were identified to genus. Ants are useful indicators of biodiversity using morphospecies (Oliver and Beattie 1996), and bee genera can be compared with other bee genera captured on A. petiolata in previous studies (Cruden et al. 1996). Each morphospecies was given a unique identifier across all subsampled taxa. We used size measurements in addition to external morphology to separate our morphospecies (Oliver and Beattie 1996, Krell 2004, Grimbacher et al. 2008). Total invertebrate abundance, morphospecies richness and Shannon-Weaver index (Shannon and Weaver 1949) was calculated from each individual sampling attempt and averaged across four individual sweeping samples by plant species and patch size per each sampling date.
Behavior Observations. In 2013, we visited 8 numbered sub-sites within both the Essex Junction and South Burlington sites, on seven sunny days between 27-V-13 and 9-VI-13, during the primary flowering period of *A. petiolata*. Sub-sites consisted of patches of second-year *A. petiolata* plants ranging from approximately 10 m² to 30 m² in size. We chose randomly-selected sampling plots of 0.25-m² within each sub-site in order to observe insect visitors to a subset of individual second-year *A. petiolata* plants. No other plant species were sampled this year. We made 33 total observations.

We observed our 0.25 m² area for 30 minutes or until 5 insect visitors were recorded. Insect visitors were visually identified to lowest taxon possible, and their behavior and activity described. Particular attention was focused on insect feeding on the junction of the stem with siliques, where frequent collection of water was observed in 2011 and 2012 studies (Fig. 2).

Statistical Analysis – Univariate. All data was tested for normality using the Shapiro-Wilk test (Shapiro and Wilk 1965) and residual plots in SAS software (SAS Institute Inc. 2011). Those data which did not meet the assumptions of normality were normalized using log (x + 1) transformation or were analyzed by non-parametric rank-based ANOVA and are indicated with asterisks in Tables 2 and 3. We analyzed data initially across collection dates and patch sizes using ANOVA to determine temporal patterns. These results are covered briefly in the text. We then pooled all dates together within each site and year and used one-way ANOVA to identify overall differences in invertebrate capture and diversity between the invasive and native plant species in large and small patches at invaded and uninvaded sites (Tables 2 and 3). For insect behavior
observations, we used 5 by 3 two-way factorial ANOVA to analyze the number of visits and average time per visit of insects (ants, bees, beetles, flies, and wasps) by part of plant foraging on (flower, corolla base, silique). When ANOVA results were significant ($P \leq 0.05$), pairwise contrasts as well as Tukey’s HSD (Tukey 1953) multiple comparisons were used to assess differences among treatments within insect taxonomic grouping. The Kenward and Roger (1997) method was used to approximate denominator degrees of freedom when data were unbalanced. All analyses were performed using SAS software (SAS Institute Inc. 2011).

**Statistical Analysis – Multivariate.** Differences in the overall composition of invertebrates on plant species were analyzed by pooling site and plant species among the subset of 2,670 invertebrates from 2012 collections. All multivariate analyses were conducted using PRIMER-E software (Clarke and Gorley 2006). We used Bray-Curtis dissimilarity (Bray and Curtis 1957) to analyze the data pre-treatment, and followed with ordination via Non-Metric Multidimensional Scaling to assess invertebrate morphospecies turnover among sites and species.

**Results**

A total of 1,627 invertebrates in 2011 and 6,407 invertebrates in 2012 were collected in biodiversity samples, for a total of 8,034 invertebrates. All of these invertebrates were rapidly separated by morphospecies within samples (not matched between samples) to compare abundance, richness, and diversity values across site and date in Tables 2-6.
**Biodiversity.** In 2011, at Mt. Ascutney State Park, high capture of a native aphid species (*Lipaphis brassicae* [Hemiptera: Aphididae]) (Fig. 3) resulted in abundances peaking during the July 10-16 sampling week (*F*$_{6,19}$ = 2.88; *P* = 0.036), contributing to significant differences in overall abundance (higher), and evenness (lower), on *A. petiolata* relative to *Osmorhiza* sp. plants at this site during this year (Table 2). A similar peak occurred in 2012 at this site, during the July 8-14 and July 22-28 sampling weeks (*F*$_{4,15}$ = 8.29; *P* = 0.001), but pooling data only resulted in lower Simpson and Shannon diversity on *A. petiolata* versus *Osmorhiza* sp. at either the invaded or uninvaded sites this year (Table 3). There were no differences in mean abundance and diversity values between *Osmorhiza* sp. growing in the sites with or without *A. petiolata* in 2012 (Table 3).

In Lake Carmi State Park in 2011, abundance and richness was higher on *I. capensis* than on *A. petiolata* regardless of patch size, while Shannon Diversity was higher only in large patches of *I. capensis* than in *A. petiolata* patches of both sizes (Table 2). Evenness was highest in small *A. petiolata* patches and lowest in small *I. capensis* patches (Table 2). Both large (*F*$_{4,14}$ = 4.24; *P* = 0.019) and small (*F*$_{3,9}$ = 10.95; *P* = 0.002) patches of *I. capensis* decreased in evenness by mid- to late-July temporally. Invertebrate abundance in *A. petiolata* patches peaked at the end of June (*F*$_{6,19}$ = 2.88; *P* = 0.036).

In 2012, we compared invertebrate capture and diversity between *I. capensis* growing in invaded and uninvaded sites, and *A. petiolata*. Both abundance (*F*$_{5,18}$ = 17.13; *P*<0.0001) and richness (*F*$_{5,18}$ = 5.83; *P* = 0.002) peaked in large *A. petiolata* patches at the end of June. Overall abundance was highest in small *A. petiolata* patches and large *I.
capensis patches, and very low in large I. capensis patches at the uninvaded Waterbury site (Table 3). Richness patterns were similar (Table 3). Richness, and both measures of diversity were lowest in the large I. capensis patch at the uninvaded site, though evenness was higher (Table 3). Patterns in Lake Carmi in 2012 revealed some increased diversity on I. capensis over A. petiolata, but were less dramatic than those in 2011 (Tables 2 and 3). Patch size seemed to reveal a slightly stronger pattern, with abundance, richness, diversity, and evenness values generally higher in smaller patches over larger patches.

Few consistent differences were seen between A. petiolata and Rubus spp. at the Grand Isle and Milton sites in 2012 (Table 3). Invertebrate abundance in small Rubus spp. patches at both the invaded ($F_{3,12} = 7.31; P = 0.005$) and uninvaded ($F_{3,12} = 12.29; P<0.001$) sites peaked in mid-July, but overall diversity was higher at Grand Isle and lower at Milton, especially in large patches, due to an abundance of snails at the latter site (Table 3). Abundance and richness were often higher in the smaller than in the larger patches, regardless of plant or site (Table 3). Overall diversity was highest on small Rubus spp. patches at the invaded site (Table 3).

Of the 2012 insects, 2,670 from a selection of sampling dates at each site were identified to lowest taxon possible and mapped via Non-Metric Multidimensional Scaling (Fig. 4). There appear to be relationships between both sites and plant species in regards to number and morphospecies identity of insects collected. In particular, A. petiolata samples appear to cluster together regardless of site, especially those collected from Lake Carmi and Grand Isle State Parks (Fig. 1). Invertebrates collected on Rubus spp. differed mostly by site, while I. capensis and Osmorhiza sp. are less separated by site in
comparison (Fig. 4). In all site and species combinations except for *I. capensis* at Lake Carmi and Waterbury, the native plants growing in the same site as *A. petiolata* had more similar invertebrate communities to those on *A. petiolata* than those growing in sites not occupied by *A. petiolata*. Therefore, there is some insect exchange between *A. petiolata* and neighboring plants *Osmorhiza* sp. and *Rubus* spp.

Invertebrates which were frequently collected on *A. petiolata* and the native plants are listed in Table 4. Spiders were ubiquitous in collected samples from all plant species, but were collected nearly twice as often on *A. petiolata* and *Osmorhiza* sp. as on *I. capensis* and *Rubus* spp. (Table 4). Spiders in the family Thomisidae were captured more often on *A. petiolata* and *Rubus* spp., while spiders in the family Salticidae were captured most often on *A. petiolata* (Table 4). The four most commonly collected insect orders were true bugs (Order Hemiptera), beetles (Order Coleoptera), flies (Order Diptera), and wasps, bees, and ants (Order Hymenoptera).

Total Hemiptera was abundant on *A. petiolata* but this was due to high capture of the aphid *Lipaphis brassicae* on this plant, a total of 1119 individuals (Table 4), 820 of which were captured at Mt. Ascutney State Park in July. When these numbers were excluded from the total Hemiptera catch, patterns were more even across plant species (Table 4). A commonly collected insect was *Nabis* spp. (Hemiptera: Nabidae), but these were most often collected on *Osmorhiza* sp. and *I. capensis*, less often on *A. petiolata* and *Rubus* spp. (Table 4). Coleopteran capture was highest on *A. petiolata*, although weevil (Coleoptera: Curculionidae) capture was also fairly evenly spread across plant species (Table 4).
When not considering the high aphid capture on *A. petiolata*, the majority of insect species captured on all plant species throughout the study were in the Diptera and Hymenoptera orders. Capture from both orders was highest on *A. petiolata* and *Rubus* spp. (Table 4). The majority of Hymenoptera capture on all species were of parasitic wasps. Bees were found only in collections from *A. petiolata* (*Augochloropsis* spp., *Lasioglossum* spp., *Agapostemon* spp.) and *Rubus* spp. (*Hylaeus mesillae*, *Ceratina* spp.) (Table 4). A total of 6 ant genera were found in *A. petiolata* samples (Table 4), while only 3 were found on *Rubus* spp. and 2 each on *Osmorhiza* sp. and *I. capensis*. Total ant abundance was also highest on *A. petiolata* (24), followed by *Rubus* spp. (13), *Osmorhiza* sp. (9), and *I. capensis* (2). Genera unique to *A. petiolata* were *Stenamma* spp., *Leptothorax* spp., and *Camponotus* spp. (Table 4).

**Behavior.** The most frequently recorded insect visitors to *A. petiolata* were ants, bees, beetles, flies, and wasps (Figs. 5 and 6). There was a significant interaction between insect visitors and the plant parts they visited for both the total number of times each part was visited ($F_{8,413} = 55.77; P < 0.0001$) (Fig. 5) and the average duration of time spent foraging on each plant part ($F_{8,414} = 37.08; P < 0.0001$) (Fig. 6). Bees and flies were most often recorded as landing on *A. petiolata* flowers, while in contrast ants and beetles spent most of their time collecting water from the junction between stems and silique (Fig. 5). Beetles spent significantly more time collecting water from seed pods than flies, with wasps and ants as intermediates, while flies and bees spent more time on flowers than wasps, collecting pollen (Fig. 6).
Discussion

**Biodiversity.** Overall, *A. petiolata* supported a unique collection of invertebrates compared with other plant species regardless of site. Compared with *Osmorhiza* sp., *A. petiolata* supported similar or greater numbers of insects, the latter usually due to high infestation of plants by aphid *L. brassicae*, which has been shown in other studies to feed on *A. petiolata* but not cause extensive harm to the plant (Van Riper et al. 2010b). However, diversity was generally lower on *A. petiolata*, especially in 2012. Abundance, richness, and diversity measures in 2012 were also similar on *Osmorhiza* sp. patches in both the *A. petiolata* invaded Mt. Ascutney State Park and the uninvaded Waterbury site, suggesting that the presence of *A. petiolata*, even in close proximity to *Osmorhiza* sp., does not strongly affect invertebrate abundance and diversity patterns on the native plant. However, it may affect the individual species associated, as ordinations revealed more similar composition between Ascutney *Osmorhiza* sp. and *A. petiolata* than Waterbury *Osmorhiza* sp. and *A. petiolata* or Ascutney *Osmorhiza* sp. Thus there is good evidence of associational relationships between neighboring *A. petiolata* and *Osmorhiza* sp. (Barbosa et al. 2009).

In general, and especially in 2011, *I. capensis* patches consistently hosted a greater abundance and diversity of insects than *A. petiolata* patches. This was less evident in the large *I. capensis* patch at Waterbury in 2012, but this comparison was also likely skewed by the decreased density of plants in this patch. Small patches also appeared to host more abundance and diversity than larger patches in most studies, which may be an effect of larger edge to area ratios in smaller patches, given enhanced diversity in edge
environments. *A. petiolata* invertebrate composition from Non-Metric Multidimensional Scaling (MDS) was more similar to *I. capensis* composition than either *Osmorhiza* sp. or *Rubus* spp. In contrast, there were few differences in abundance and diversity patterns between *A. petiolata* and *Rubus* spp., but overall, MDS results showed that *Rubus* spp. in the invaded site hosted a more similar composition of invertebrates to the invasive than *Rubus* spp. in the uninvaded site, suggesting that the presence of *A. petiolata* affected overall species composition of these sites. However, between *I. capensis* plants at each site there was more similarity than between *I. capensis* and *A. petiolata* at the Lake Carmi site. Therefore *A. petiolata* has a smaller effect on the invertebrate composition on *I. capensis* than on either of the other two species. Alternatively, since the State Parks are more frequented by tourists than the uninvaded sites, these results may be also influenced by disturbance levels in addition to plant composition, as both invasive plant abundance and different invertebrate groups may be influenced by site-level disturbances (Hobbs and Hueneke 1992, Schowalter and Lowman 1999).

Habitat-specific factors facilitating different levels of invertebrate colonization on invasive and native plants may also play a role here (Maron and Vilà 2001). Although generally *A. petiolata* had more similar invertebrate composition within its own species than compared to other plant species, invertebrates colonizing *A. petiolata* at Mt. Ascutney State Park differed from those colonizing *A. petiolata* at Lake Carmi and Grand Isle State Parks based on MDS ordinations. This appears to suggest that *A. petiolata* may host different species of invertebrates in different populations across a larger geographic
area, as Maron and Vilà (2001) suggested should be studied, though this was for the herbivore guild in particular.

**Behavior.** Frequently, *A. petiolata* was found to host more species of particular invertebrate groups than other plant species, and was only rarely the plant species on which was collected the least number of individuals from the most commonly collected groups. Spiders were found frequently associated with *A. petiolata* plants and *Osmorhiza* sp. plants, while found slightly less often on *I. capensis* and *Rubus* spp. Lie-in-wait crab spiders in the family Thomisidae and ambush jumping spiders in the family Salticidae were more common on *A. petiolata* than other plant species, save for *Rubus* spp. in the case of the Thomisids. In addition, personal observations by authors in the field revealed spiders often constructed webs in the silique clusters of post-flowering garlic mustard, which may function as a form of ecosystem engineering attracting predators which consume pollinators or pests of *A. petiolata* (Jones et al. 1994; Pearson 2009, 2010), and could thus contribute to it success. We also observed a Thomisid spider lying in wait on an *A. petiolata* flower and rearing back in an attempt to capture a passing fly in the family Syrphidae, which have been reported as pollinators of *A. petiolata* in the literature (Cruden 1979, Cavers et al. 1996). Spiders are important predators of pest insects in agricultural ecosystems (Kerzicnik et al. 2013). If predatory invertebrates such as spiders can live in *A. petiolata* patches and maintain numbers similar to or greater than those found on native species, we assume that they are able to access a similar prey resource as on the native plant species.
Because *A. petiolata* and *Rubus* spp. were most often flowering during collection times, these were the only plants on which bees were captured. The bees *Hylaeus mesillae* and *Ceratina* spp., were captured on *Rubus* spp. plants. Bees captured on *A. petiolata* were bees in the genera *Augochloropsis*, *Lasioglossum*, and *Agapostemon*. The former two were also identified as putative pollinators associated with *A. petiolata* in research sites in Iowa (Cruden 1996), while the latter is a new record and may be more associated with populations in Vermont and the northeast. Interestingly, Cruden (1996) found specimens of the small carpenter bee *Ceratina calcarata* associated with *A. petiolata* in Iowa, as well as bees in the genera *Apis*, *Bombus*, *Andrena*, and *Augochlorella*. We observed *Bombus* individuals flying in the vicinity of *A. petiolata* and collecting pollen from its flowers in our research sites, but none were captured in sweeping samples.

We observed abundant ant collection on *A. petiolata* in our sweeping samples, and also observed numerous ants collecting water at the stem-silique junction of post-flowering *A. petiolata* as well as occasionally collecting nectar from *A. petiolata* flowers. In fact, both abundance and species richness of ants were higher on *A. petiolata* than on any other plant species (Table 4). Ants in particular have been shown to be good candidates for the use of morphospecies as surrogates to represent true species richness (Oliver and Beattie 1996). Based on our results, ants appear to find patches of *A. petiolata* attractive sites to collect nectar and water as well as probably to tend populations of *L. brassicae*. Nectar and water collection on *A. petiolata* was also observed by beetles, bees, and wasps, and past research has confirmed nectar collection.
and pollination by Syrphid flies as well as various bees (Cruden 1979, Cavers et al. 1996).

Plants may attract insects in other ways not normally discussed by researchers. There has been little report of phenomena like the silique feeding we saw in this study reported in the literature, however Williams (2006) observed Chauliognathus pensylvanicus (Coleoptera: Cantharidae) beetles feeding at the corolla bases of Lobelia siphilitica flowers, suggesting that this may have been through holes in the bases of the flowers created by other insects to obtain nectar. Insects visiting A. petiolata were likely collecting both nectar and water as they were observed feeding both at the corolla bases of the flowers but also at the siliques bases long after the flowers had dropped. There is great value in personal observation of insect species in their natural environments as a way of examining natural history traits (Williams 2006).

A weakness of our observational study was that often there were only one or two observers, and thus time spent observing insect visitors and recording their behavior often precluded our ability to capture or more finely identify the species observed. Future studies should include a larger number of collectors so that observations, data recording, and collections may be made simultaneously and finer identifications of insect visitors to A. petiolata can be made and subsequently associated with specific behaviors. Data such as these are useful in determining how invasive plant species fit into the greater community and ecosystems in which they are found. Another limitation of our study was that we only collected aboveground invertebrates, whereas belowground invertebrates
and other soil fauna may contribute to important interactions with invasive plants and the aboveground fauna (Wardle et al. 2004).

Overall, our research shows that while *A. petiolata* may sometimes host reduced overall invertebrate abundance and diversity compared with native plant species, it still hosts a number of invertebrates, many of which are unique to this plant (Table 4, Fig. 4). This invasive species also appears to be highly attractive to certain bee and ant genera, for pollination as well as nectar and water collection. The aphid *L. brassicae* is also strongly associated with *A. petiolata* patches, although it does not appear to cause extensive damage to this invasive plant. As *A. petiolata* is a fast-growing biennial plant with a persistent seedbank (Munger 2001), it may be able to more easily compensate for herbivore damage as a population even if individual plants are negatively affected (Maron and Vilà 2001). Additionally, spiders which were frequently found on *A. petiolata* may function as strong selective agents decreasing herbivore abundance on the plant and thus perhaps contributing to its health and reproductive success. Overall, *A. petiolata* appears to be a generalist in its ability to attract pollinators and predators across varied invertebrate communities.

The abundance and diversity of invertebrates on *A. petiolata* compared with native plants often shows markedly different patterns than that of actual species composition on these plants, suggesting that the roles of the individual insects on the plants should be examined further to determine their effects on the natural history of invasive and native plants. Future research should also continue to examine the phenomenon of silique water collection on *A. petiolata* and attempt to determine the overall effect this has on the life
history of its associated insects. It may also help to attract pollinators to *A. petiolata* over native species and thus also contribute to the overall reproductive success of the invasive. Our results here demonstrate that community interactions of *A. petiolata* with invertebrates may contribute more to its success in novel environments than other proposed mechanisms, such as allelopathy, and these interactions should be considered more seriously. Although invasive species are an important biological and economic concern in the twenty-first century, attention should also be devoted to how they function in novel ecosystems as more often than not they are here to stay.

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Tables

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<th>Site Name</th>
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<tr>
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Table 2. Mean ± SEM a) Abundance, b) Morphospecies Richness, c) Simpson’s Diversity, d) Shannon-Weaver Diversity, and e) Shannon’s Evenness of all sampled invertebrates in 2011. A single asterisk (*) following the $P$-value indicates that data was log (x+1) transformed. A double asterisk (**) following the $P$-value indicates that data was nonparametric rank-transformed. Data followed by different letters are significantly different from one another based on Tukey’s HSD (ANOVA, $\alpha = 0.05$) (Sample sizes vary and are indicated by degrees of freedom in the table). “Large” = Over 30 m$^2$, “Small” = Under 10 m$^2$. 
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<th>Site</th>
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<td>$F_{3,74}=7.93;</td>
<td>$P=0.0001^{*}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$F_{3,74}=2.04;</td>
<td>$P=0.116^{**}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$F_{3,74}=4.85;</td>
<td>$P=0.004$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$F_{3,72}=4.91;</td>
<td>$P=0.004^{**}$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 3 (Takes up 2 Pages). Mean ± Standard Error a) Abundance, b) Morphospecies Richness, c) Simpson’s Diversity, d) Shannon-Weaver Diversity, and e) Shannon’s Evenness of all sampled invertebrates in 2012. A single asterisk (*) following the $P$-value indicates that data was log $(x+1)$ transformed. A double asterisk (**) following the $P$-value indicates that data was nonparametric rank-transformed. Data followed by different letters are significantly different from one another based on Tukey’s HSD (ANOVA, $\alpha = 0.05$) (Sample sizes vary and are indicated by degrees of freedom in the table). “Large” = Over 30 m$^2$, “Small” = Under 10 m$^2$. 

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<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Patch Size</th>
<th>Total Abundance</th>
<th>Morphospecies Richness</th>
<th>Simpson</th>
<th>Shannon</th>
<th>Evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ascutney</td>
<td>A. petiolata</td>
<td>Large</td>
<td>49.50 $\pm$ 17.8$^a$</td>
<td>6.55 $\pm$ 0.81$^a$</td>
<td>0.47 $\pm$ 0.07$^a$</td>
<td>1.13 $\pm$ 0.16$^b$</td>
<td>0.71 $\pm$ 0.09$^a$</td>
</tr>
<tr>
<td>Ascutney</td>
<td>Osmorhiza sp.</td>
<td>Large</td>
<td>9.53 $\pm$ 1.07$^a$</td>
<td>7.68 $\pm$ 0.75$^a$</td>
<td>0.17 $\pm$ 0.01$^b$</td>
<td>1.89 $\pm$ 0.09$^a$</td>
<td>0.97 $\pm$ 0.01$^a$</td>
</tr>
<tr>
<td>Waterbury</td>
<td>Osmorhiza sp.</td>
<td>Large</td>
<td>9.50 $\pm$ 1.71$^a$</td>
<td>7.67 $\pm$ 1.16$^a$</td>
<td>0.21 $\pm$ 0.04$^b$</td>
<td>1.81 $\pm$ 0.17$^a$</td>
<td>0.97 $\pm$ 0.01$^a$</td>
</tr>
<tr>
<td>Lake Carmi</td>
<td>A. petiolata</td>
<td>Large</td>
<td>13.17 $\pm$ 1.81$^b$</td>
<td>8.58 $\pm$ 0.77$^{bc}$</td>
<td>0.19 $\pm$ 0.02$^b$</td>
<td>1.91 $\pm$ 0.10$^{ab}$</td>
<td>0.93 $\pm$ 0.02$^a$</td>
</tr>
<tr>
<td>Lake Carmi</td>
<td>A. petiolata</td>
<td>Small</td>
<td>29.14 $\pm$ 5.51$^a$</td>
<td>12.71 $\pm$ 1.12$^{ab}$</td>
<td>0.21 $\pm$ 0.03$^b$</td>
<td>2.04 $\pm$ 0.12$^a$</td>
<td>0.86 $\pm$ 0.03$^b$</td>
</tr>
<tr>
<td>Lake Carmi</td>
<td>I. capensis</td>
<td>Large</td>
<td>28.22 $\pm$ 3.35$^a$</td>
<td>14.50 $\pm$ 1.53$^a$</td>
<td>0.17 $\pm$ 0.02$^b$</td>
<td>2.23 $\pm$ 0.11$^a$</td>
<td>0.87 $\pm$ 0.02$^b$</td>
</tr>
<tr>
<td>Lake Carmi</td>
<td>I. capensis</td>
<td>Small</td>
<td>23.71 $\pm$ 3.72$^{ab}$</td>
<td>13.13 $\pm$ 1.14$^a$</td>
<td>0.16 $\pm$ 0.02$^b$</td>
<td>2.22 $\pm$ 0.09$^a$</td>
<td>0.91 $\pm$ 0.02$^{ab}$</td>
</tr>
<tr>
<td>Waterbury</td>
<td>I. capensis</td>
<td>Large</td>
<td>6.13 $\pm$ 1.02$^c$</td>
<td>5.06 $\pm$ 0.81$^c$</td>
<td>0.36 $\pm$ 0.07$^a$</td>
<td>1.33 $\pm$ 0.19$^b$</td>
<td>0.96 $\pm$ 0.02$^a$</td>
</tr>
<tr>
<td>Waterbury</td>
<td>I. capensis</td>
<td>Small</td>
<td>14.79 $\pm$ 2.83$^b$</td>
<td>11.16 $\pm$ 1.92$^{ab}$</td>
<td>0.21 $\pm$ 0.05$^b$</td>
<td>2.01 $\pm$ 0.20$^a$</td>
<td>0.96 $\pm$ 0.01$^a$</td>
</tr>
</tbody>
</table>

ANOVA

- $F_{2,48}=1.84;\ P=0.171^*$
- $F_{2,48}=0.84;\ P=0.437^*$
- $F_{2,48}=7.11;\ P=0.002^{**}$
- $F_{2,48}=9.51;\ P<0.001$
- $F_{2,47}=0.93;\ P=0.401^{**}$

- $F_{5,123}=11.14;\ P<0.0001^*$
- $F_{5,123}=8.28;\ P<0.0001^{**}$
- $F_{5,123}=2.37;\ P=0.043^{**}$
- $F_{5,123}=4.62;\ P<0.001^{**}$
- $F_{5,120}=6.36;\ P<0.0001^{**}$
<table>
<thead>
<tr>
<th>Site</th>
<th>Species</th>
<th>Patch Size</th>
<th>Total Abundance</th>
<th>Morphospecies Richness</th>
<th>Simpson</th>
<th>Shannon</th>
<th>Evenness</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grand Isle</td>
<td>A. petiolata</td>
<td>Large</td>
<td>23.08 ± 6.47&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>6.92 ± 0.94&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.39 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.31 ± 0.14&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.75 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grand Isle</td>
<td>A. petiolata</td>
<td>Small</td>
<td>34.61 ± 9.68&lt;sup&gt;a&lt;/sup&gt;</td>
<td>11.83 ± 1.50&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.27 ± 0.06&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.87 ± 0.17&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.81 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grand Isle</td>
<td>Rubus spp.</td>
<td>Large</td>
<td>10.73 ± 1.45&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>7.73 ± 0.91&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.24 ± 0.06&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.77 ± 0.15&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.93 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grand Isle</td>
<td>Rubus spp.</td>
<td>Small</td>
<td>31.06 ± 8.88&lt;sup&gt;a&lt;/sup&gt;</td>
<td>12.19 ± 1.49&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.19 ± 0.03&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.05 ± 0.15&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.87 ± 0.03&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Milton</td>
<td>Rubus spp.</td>
<td>Large</td>
<td>9.67 ± 2.20&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.00 ± 0.96&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.38 ± 0.09&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.37 ± 0.22&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.90 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Milton</td>
<td>Rubus spp.</td>
<td>Small</td>
<td>21.50 ± 3.54&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>10.81 ± 1.07&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.21 ± 0.04&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>1.93 ± 0.13&lt;sup&gt;ab&lt;/sup&gt;</td>
<td>0.84 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

ANOVA

\[ F_{5,84}=4.14; \quad F_{5,84}=4.53; \quad F_{5,84}=2.61; \quad F_{5,84}=3.03; \quad F_{5,84}=1.33; \]

\[ P=0.002^* \quad P=0.001 \quad P=0.030^{**} \quad P=0.015^{**} \quad P=0.260^{**} \]
Table 4. Total abundance of insects in different taxonomic groups on each of the four plant species sampled throughout the study, taken from a subset of 2,670 invertebrates from 2012 collections.
<table>
<thead>
<tr>
<th>Invertebrate ID</th>
<th>A. petiolata</th>
<th>Osmorhiza sp.</th>
<th>I. capensis</th>
<th>Rubus spp.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Class Arachnida, Order Araneae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Spiders</td>
<td>82</td>
<td>85</td>
<td>50</td>
<td>49</td>
</tr>
<tr>
<td>Crab Spiders (Thomisidae)</td>
<td>8</td>
<td>3</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Jumping Spiders (Salticidae)</td>
<td>12</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>Enoplognatha ovata</em> (Tengellidae)</td>
<td>14</td>
<td>31</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td><strong>Class Hexapoda</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Order Hemiptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Hemiptera</td>
<td>1152</td>
<td>51</td>
<td>36</td>
<td>77</td>
</tr>
<tr>
<td><em>Nabis</em> spp. (Nabidae)</td>
<td>2</td>
<td>12</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td><em>Lipaphis brassicae</em> (Aphididae)</td>
<td>1119</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Total Hemiptera (Excl. <em>L. brassicae</em>)</td>
<td>33</td>
<td>48</td>
<td>34</td>
<td>74</td>
</tr>
<tr>
<td><strong>Order Coleoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Coleoptera</td>
<td>32</td>
<td>8</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>Weevils (Curculionidae)</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>Order Diptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Diptera</td>
<td>210</td>
<td>67</td>
<td>41</td>
<td>241</td>
</tr>
<tr>
<td><em>Megaselia</em> spp. (Phoridae)</td>
<td>5</td>
<td>13</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Order Hymenoptera</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Hymenoptera</td>
<td>62</td>
<td>24</td>
<td>14</td>
<td>40</td>
</tr>
<tr>
<td>Bees (Superfamily Apoidea)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hylaeus mesillae</em></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Ceratina</em> spp.</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td><em>Augochloropsis</em> spp.</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Lasioglossum</em> spp.</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Agapostemon</em> spp.</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ants (Formicidae)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Leptothorax</em> spp.</td>
<td>2</td>
<td>8</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>Stenamma</em> spp.</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Lasius</em> spp.</td>
<td>5</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td><em>Dorymyrmex</em> spp.</td>
<td>7</td>
<td>0</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td><em>Tapinoma sessile</em></td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td><em>Camponotus</em> spp.</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 1. Map of Vermont showing the location of the seven collection study sites mentioned in Table 1 and in the text. Expansion shows the general pattern of patch and plot selection at sampling sites in 2011 and 2012. Sketched polygons represent selected large and small patches of *A. petiolata* and the native plants, while hollow black circles within patches represent randomly selected 1 m$^2$ sampling plots.
Figure 2. Small bee collecting water from the stem-silique junction on later-season *A. petiolata* seed pods at Grand Isle State Park.
Figure 3. *Lipaphis brassicae* feeding on late-season *A. petiolata* siliques.
**Figure 4.** Non-Metric Multidimensional Scaling of site and plant species combinations showing turnover of morphospecies taken from a subset of 2,670 invertebrates from 2012 collections. (N=9).
Figure 5. Mean (± SEM) number of insects on each part of *A. petiolata* plants across sampling plots and sites. Bars with different letters within taxonomic group are significantly different from one another (ANOVA, \( \alpha = 0.05 \)) (N=143).
Figure 6. Mean (± SEM) average duration (in seconds) spent by insects on each part of *A. petiolata* plants across sampling plots and sites. Bars with different letters within taxonomic group are significantly different from one another (ANOVA, $\alpha = 0.05$) (N=143).


APPENDIX I

The study presented in Chapter Three, comparing the effects of the invasive herbaceous biennial *Alliaria petiolata* (garlic mustard; Brassicaceae) allelopathy and shade on native tree species under varying nutrient conditions, contained certain miscalculations in the scientific research process which resulted in less robust final results than would have been preferable. That said, my work on the research leading to this paper, which is currently in submission for publication to the peer-reviewed journal *Northeastern Naturalist*, provided me with many valuable learning experiences as a scientist. Based on my experiences working on this research project, I feel that I have had the opportunity to identify flaws in my personal approaches to research and consider how better to approach this type of work in the future, including preparatory work, time management, efficient use of limited resources, responses to crisis, and both emotional and scientific maturity. Here I will outline the approaches which could have been improved and suggest particular improvements that could be made to better conduct this or a similar experiment in the future.

The research process for this particular project presented many challenges, some of which could have been responded to in a more rigorous scientific manner, which may have led to improved results. As a scientist, it is crucial that I learn to be able to respond to situations which do not turn out as expected. This is especially relevant in the natural sciences, as working with living material, whether plant or animal, often results in the research subjects responding in a way which may not be consistent with predictions (Karban et al. 2014).
In this study, the second-year *A. petiolata* plants which were transplanted from Grand Isle State Park were expected to survive, creating a scenario where both shade and allelopathy would have been inflicted upon native tree seedlings sharing soil with this species. This would have allowed me to test the effects of these factors both alone and combined and provided me with more interesting and informative data on interactions between allelopathy and shade. Unfortunately, these plants were at a later stage in their development, and as biennials they had used up the majority of their energy reserves in their second year by already having completed stem elongation and begun flowering. Thus, the energy stored in their roots which could have been used to survive the transplant, and indeed had allowed earlier-stage second year *A. petiolata* plants to survive (transplanted earlier that year for another planned study) was no longer available. These plants subsequently died, and were assumed to no longer be producing allelochemicals, therefore only providing shade to the neighboring tree seedlings. Were the study to be repeated, I propose to rectify this issue by introducing first-year garlic mustard plants in combination with second-year plants, thus providing both treatments while also mimicking natural conditions where both first and second year *A. petiolata* plants grow together, although oftentimes there is a dominance of one life stage over the other (Bauer et al. 2010).

Tree seedlings in this study which grew in containers without soil exchange had to be tested as an entirely separate experiment because the reduced volume of soil resulted in faster water evaporation, leading to a dry environment and overall reduced health in the tree seedlings due to the effects of the containers alone. In a repeat of the study these
containers would be supplemented with an extra watering regimen when needed. Additionally, larger containers would be used and planted with one tree seedling each rather than three, reducing competition for water and other resources, which is discussed in more detail below. A well-executed smaller-scale pilot study testing the performance of plants in these containers may provide the foresight to prepare for any other unexpected issues (Karban et al. 2014), thus this would be conducted on a subset of planters before setting up another full study. Plants in future pilot or full-scale studies will be monitored more vigorously to ensure that all environmental variation has been accounted for.

The original planned experimental design would have permitted study of a larger number of tree seedlings not exposed to the allelopathic effects of *A. petiolata*. As conducted, the study was only able to compare the shared soil containers growing with first year plants with those growing only on the south side of the second year plants, which were presumed to be free from allelopathy. However, as presented in the results of Chapter Three, it is possible that the decay of root tissue from these plants may have had some effect on the quality of soil (Barto and Cipollini 2009, Smith and Reynolds 2014), similar to that of the first year plants, especially considering that the first year plants seemed to have less allelopathic activity, and thus this may not have been a perfect comparison.

Repeating this study will necessitate planting the containers more thinly, with one seedling in each instead of three. This will reduce the time required to measure and record data on seedlings and thus make the study process more efficient, as fewer
seedlings will require only one person to record seedling data (height, root length, health, herbivory, biomass), thus eliminating any sampling bias which could arise from multiple recorders. In the initial study, another result of planting so many seedlings per container was that in many of them, one seedling ultimately outcompeted the others. Beginning with only one seedling per container will thus also save time and minimize potential differential effects of competition between seedlings in the same container.

Both because *A. petiolata* requires a period of winter stratification prior to emergence the following spring (Baskin and Baskin 1992) and because other researchers at the Forest Service building required greenhouse space, we chose to move the planters outside for the winter, and continue the study outside in 2013. However, there was not enough straw insulation utilized during the move to prevent cold shock. Thus, in spring of 2013, less than half of the tree seedlings had survived. This, in addition to other errors made in attempts to weed and shade the planters, resulted in data from 2013 which was so limited and weak we were unable to utilize it in the final paper. Additionally, the fact that seedlings exposed to first year *A. petioata* one year were now exposed to second year *A. petiolata* the next, any final biomass measures, had they been taken, may not have been informative.

Repeating this study, it would be much more informative to obtain data from two consecutive years of seedling growth. This necessitates utilizing the same *A. petiolata* treatments both years, and ensuring adequate time to transition the seedlings to the cold and provide proper insulation ensuring survival for a second year of study. During the second year of study, seedlings would be returned to the greenhouse prior to bud break,
thus ensuring growth in the same environment the second year as in the first year. In addition, to ensure the possibility of biomass measurement, a subset of seedlings from each replicate and treatment combination would be removed at the end of the first year to be oven-dried and weighed to obtain a measure of biomass. This will ensure that even if there are survival issues transitioning the seedlings from one year to the next, an informative measure of biomass will be available for interpretation of results. Then, seedlings surviving the second year of study would be oven-dried and weighed following the end of that growing season to obtain measures of biomass for all seedlings. The root:shoot estimates used as a proxy for biomass in Chapter Three, while valuable, are not as useful or robust as direct measurements of biomass on these tree seedlings would have been (Tackenberg 2007).

Other potential downfalls of the Chapter Three study include binomial and qualitative measures of herbivory and health, respectively. Quantitative measures on a ratio scale are more scientifically informative, and would have allowed for a more nuanced interpretation of results. In a repeat of the study, I propose to measure herbivory as leaf area removed, also accounting for differences in thickness in the leaves of the different seedling species. Herbivores would also be identified, rather than simply inferred from leaf damage, as it is possible different herbivore species respond differently to treatments which could not be revealed by a lump measurement of all herbivore damage.

Tree health at the end of the growing season each year in a repeated study would be quantified via foliage gas exchange rates $(A_{\text{max}})$ $(\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1})$ with a fluorescent leaf chamber using the Li-Cor LI-6400 portable photosynthesis system (Li-
Cor Biosciences, Lincoln, NE). Chlorophyll content would be measured using a Minolta SPAD 502 Chlorophyll Meter (Spectrum Technologies, Inc., Plainfield, IL), averaging two foliar readings per tree seedling. Chlorophyll meter readings (M) can be converted to μmol · m⁻² total chlorophyll content based on a standard curve developed for corn (Zea mays) plants (μmol · m⁻² chlorophyll = 10^(M^0.26)) (Chen and Poland 2009). Additional measures that could be considered in a repeated study include measures of available nitrogen in the soils, allelopathic chemicals, other secondary metabolites, and mycorrhizal colonization of tree roots, all of which would be highly informative in the quantification of mechanisms of allelopathy, if present.

For scientists, the pursuit of research endeavors is important for personal growth and development as well as insights into the workings of the field, and much of this can only be achieved through hands-on experience in the research process (Karban et al. 2014). Even as someone who is interested in a more teaching-focused career, it is crucial that I participate in research projects so that I am adequately prepared to communicate and collaborate with other scientists and to advise future students who are interested in research-based careers and who participate in undergraduate research. My experiences conducting this study as well as the studies presented in the other two chapters of my dissertation have helped me to learn my own strengths and limitations and use these experiences to further my grow as a scientist. I have come to much more deeply appreciate the need for adequate and thoughtful preparation as I approach a new study. For example, the study in Chapter Three had come to me as a sudden change from my initial plans to study insect pollinator visitation to A. petiolata. My difficulty adapting to
this abrupt transition was one contributor to some of the errors discussed in the previous paragraphs of this Appendix. I rushed ahead due to a certain amount of panic combined with an excessive perfectionism which I have come to recognize as a character flaw of mine which I shall need to more carefully manage as I approach future scientific endeavors. I should have taken a “step back” and utilized a more thoughtful, logical, and scientific approach to designing and understanding the study. Additionally, because I did not have as strong of a background in the plant physiology needed to address this study, I made some errors as it proceeded. Rather than allow the time stress to get to me, I should have spent more time reading the literature and focusing on design plans to create a study which I would have comprehended on a deeper level and been able to respond to more efficiently.

Ultimately, as a result of my experiences working on this project, I have learned to think more critically and logically, rather than worry about small details. My time and stress management capability has improved and I have had the opportunity to try something new, make mistakes, and learn from them to ensure improved, high quality work the next time I embark on a scientific research endeavor. Indeed, I believe that my experiences with the planter study in Chapter Three have helped me to better approach and write the other two papers in my dissertation. In addition, as a teacher, I have had experiences which will allow me to empathize with students who may be in similar positions and to offer them advice and strategies to counter and respond to any issues that they may encounter. This alone has made my experiences conducting this somewhat challenging study well worth it in my growth as both a scientist and a human being.
REFERENCES CITED IN APPENDIX I


