

## ABSTRACT

Title of Document: THE INFLUENCE OF NATIVE PLANTS ON  
ARTHROPOD POPULATION DYNAMICS:  
CAN NATIVE PLANTS ENHANCE  
CONSERVATION BIOLOGICAL CONTROL?

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Conservation biological control aims to maintain sustainable natural enemy populations. Through increased urbanization, alien vegetation is being planted; these plants may be unacceptable hosts for herbivores. We tested the prediction that urban landscapes composed of native plants host a diverse herbivore population and attract and sustain a diverse community of natural enemies relative to landscapes composed of alien plants. Native and alien landscapes were created to test this prediction. I compared the colonizing arthropod communities, herbivore survival and the aesthetic injury of trees and shrubs in native and alien landscapes. In this two year project, I found only weak evidence to support my predictions. Native landscapes did not host an arthropod community significantly different than alien landscapes. There was a trend for several natural enemy families to have a greater abundance in native

landscapes. This did not have an impact on herbivore survival or aesthetic injury of the plants.

THE INFLUENCE OF NATIVE PLANTS ON ARTHROPOD POPULATION  
DYNAMICS: CAN NATIVE PLANTS ENHANCE CONSERVATION  
BIOLOGICAL CONTROL?

By

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## Dedication

I dedicate this work to my family, my fiancé and my friends. My parents, Anita Gilbert and Anthony Vodraska, have always encouraged me to continue my education and pursue my interests. Their unwavering love and support is deeply appreciated. My sister Adrienne Vodraska is my best friend and is always willing to listen and offer advice. My fiancé Erik Krause has been an incredible source of love, strength and reason for me over the past two years. My family and friends have made this possible and I am incredibly grateful.

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## Introduction

In managed agricultural and urban ecosystems, natural enemy - herbivore dynamics are often disrupted (Lewis et al. 1997, Altieri 1999). This leads to reductions in natural enemy abundance and diversity, and increases in herbivore abundance and, therefore, plant damage (Landis et al. 2000). Biological control is a pest management approach that aims to manipulate or restore natural enemy communities to keep phytophagous arthropod populations below economically damaging levels; thus reducing the need for insecticide applications (Barbosa and Castellanos 2005). An underlying principle of this management practice is that the efficacy of biological control will increase as natural enemy species diversity increases (Barbosa and Castellanos 2005). Conservation biological control is a form of biological control that tries to maintain a greater level of predator and parasitoid diversity and abundance through habitat manipulation and the avoidance of plant management practices that are detrimental to these arthropods. Implementing conservation biological control is, therefore, defined as taking “actions that preserve or protect natural enemies” (Gurr et al. 2000). Increasing and sustaining an abundance and diversity of natural enemies should result in greater predation and parasitism of herbivores in agricultural and urban settings (Landis et al. 2000). A reduction in pest populations should reduce plant damage, increase yield or aesthetics

of the desired crop and decrease the need for inputs of pesticides (Gurr et al. 2000, Barbosa and Castellanos 2005).

Habitat manipulation practices are implemented to make managed systems more habitable for natural enemies by providing key resources that may be lacking (Gurr et al. 2000, Landis et al. 2000). Several studies have shown that natural enemies are more abundant and, in some cases, effective at reducing herbivore populations and plant damage in managed habitats that are complex (Shrewsbury and Raupp 2000, 2006). Habitat complexity is explained by both the level of vegetation structure and plant species diversity (Shrewsbury and Raupp 2000, Raupp et. al. 2001b, Shrewsbury and Raupp 2006). Habitats with increased levels of structural complexity and plant species diversity support natural enemies by providing an array of desirable resources such as favorable microclimates, refuge from intraguild predation, and alternative food resources including nectar and pollen, and prey (Landis et al. 2000, van Emden 2002, Langellotto and Denno 2004, Shrewsbury and Raupp 2006, Fielder and Landis 2007). These alternative food resources may sustain the natural enemy populations when primary prey items are scarce (Gurr et al. 2000, Landis et al. 2000). In addition to habitat manipulations that attract and retain natural enemies, avoiding management practices, such as pesticide applications, can also conserve beneficial arthropods. The use of insecticide cover sprays and residual broad spectrum insecticides has been shown to reduce natural enemy populations and limit their effectiveness as biological control agents (Raupp et al. 2001a). In conservation biological control attempts are made to select and use pesticides with

low toxicities, which are selective, and have short periods of residual activity.

Ultimately, conservation biological control approaches should aid in pest management by restoring natural enemy – herbivore dynamics, as well as increasing biodiversity in managed ecosystems.

Urban landscapes provide a good system to evaluate conservation biological control approaches and the influence of these practices on herbivores and their natural enemies. Common landscape management practices in these perennial systems disrupt natural enemy – herbivore dynamics and may result in pest insect outbreaks (Landis et al. 2000, Raupp et al. 2001a). Moreover, insect outbreaks are sometimes related to landscape habitat complexity where landscapes with reduced vegetational structure and plant species diversity sustain more frequent outbreaks of pests (Raupp et al. 2001b, Shrewsbury and Raupp 2000, 2006). For example, azaleas in structurally simple landscapes supported significantly higher densities of azalea lace bug than complex landscapes (Shrewsbury and Raupp 2000). The mechanism underlying this pattern was related to low alternative prey abundance and lower natural enemy abundance in simple landscapes (Shrewsbury and Raupp 2006). It has been found that implementation of conservation biological control through habitat manipulations can reduce the likelihood of pest outbreaks. For example, incorporating herbaceous ornamental plants into managed landscape beds and along golf course fairways added structural complexity and alternative food resources. This resulted in increased alternative prey and natural enemy abundance, and reduced herbivore survival (Frank and Shrewsbury 2004, Shrewsbury et al. 2004). Tooker

and Hanks (2000) examined parasitism rates and abundance of pine needle scale and concluded that the management of this pest in urban landscapes was enhanced through increasing plant diversity and by providing floral resources to attract and sustain natural enemy populations. Floral resources were also used to increase parasitism of bagworms in urban systems (Ellis et al. 2005). These studies demonstrated the potential benefits of implementing conservation biological control practices in managed urban systems.

Including native vegetation may be another habitat manipulation approach that further enhances conservation biological control in urban landscape systems. The generally accepted definition of native plants is that natives are plants that occurred on the U.S. continent prior to European settlement (USDA 2000). Native plants are believed to have unique relationships with native herbivores. Many herbivores are thought to be restricted to feeding on plants with which they share an evolutionary history (Kennedy and Southward 1984, Bernays and Graham 1988). Native plants have been present in landscapes over evolutionary time. Alien plants, whose introduction into the United States is relatively recent, share no evolutionary history with native insects. A community of native plants should therefore be a suitable resource to a diverse community of native herbivores. These herbivores are likely to support a suite of natural enemies by providing primary prey and hosts as well as alternative prey and hosts (Price et al. 1980). A community of native plants, herbivores, and natural enemies, that have been associated over evolutionary time,

should sustain a balanced relationship where no particular herbivore species would reach population densities that cause significant damage to its host plant.

The amount of land used for urban development is growing rapidly in the United States and worldwide (Reichard and White 2001, McKinney 2002, Pimentel et al. 2005, Smith et al. 2006). Through increased urbanization, more alien vegetation is being planted (McKinney 2002). Many of the alien plants introduced into the United States were imported for ornamental purposes and the majority of plants used in the horticultural industry are not native to North America (Reichard and White 2001, McKinney 2002). A study of domestic gardens in Britain found that urban gardens contain a greater proportion and number of alien species than any natural area of equal size (Smith et al. 2006). Additionally, some alien plants escape cultivation and become invasive in natural ecosystems. For example, of the 25,000 alien plants species that are brought into Florida for ornamental purposes, 900 have established in natural ecosystems (Pimentel et al. 2005). A study of invasive woody plants found that 82% had been imported for use in landscapes as ornamentals (Reichard and White 2001).

The excessive abundance and use of alien plant species is a phenomenon that may negatively impact ecosystems in both natural and urban systems. A concern with the increased use of alien plants is that alien plants may not support native phytophagous invertebrate communities. Native plants have evolved with a complex community of native specialist and generalist herbivores; certain members of this community may not be able to use alien plant species as food resources (Tallamy

2004). The Enemy Release Hypothesis predicts that alien plant species, upon introduction to a novel region, should experience less herbivore pressure (Keane and Crawley 2002). The basis for this hypothesis is that alien plants have escaped their native specialist herbivores in their homeland, are not palatable to specialists native to the introduced region, and that generalists, native to the introduced region, will prefer to feed on native rather than alien plants (Keane and Crawley 2002). Native herbivores are predicted to find alien plants unsuitable hosts because herbivores are restricted to feeding on plants with which they share an evolutionary history (Ehrlich and Raven 1964, Bernays and Graham 1988). Alien plants, by definition, have evolved elsewhere and may not support the herbivores that have evolved in the introduced region. Several studies have found that alien plants experience less herbivory or were associated with less herbivore diversity in their introduced range compared to their native region (Samways et al. 1996, Wolfe 2002, Siemann and Rogers 2003, Agrawal et al. 2005, Carpenter and Cappuccino 2005).

Tallamy, 2004, predicted reduced diversity of native herbivores and their associated suite of natural enemies when alien plants are used in landscapes. This has consequences to pest management and conservation biological control in urban landscapes. Since natural enemies have been found to be more abundant in landscapes with a diversity of alternative hosts and prey (Shrewsbury and Raupp 2006), a reduction in herbivore diversity in alien dominated landscapes is predicted to reduce the density and diversity of natural enemies in those landscapes (Tallamy 2004). Increasing the abundance of native plants in urban landscapes should restore



native herbivore and natural enemy dynamics, enhancing conservation biological control and reducing the likelihood of pest outbreaks.

Alternatively to the enemy release hypothesis, some native generalist and specialist herbivores may be able to consume and take advantage of resources provided by alien plants (Samways et al. 1996, Keane and Crawley 2002, Parker and Hay 2005), and exotic herbivores may be able to use host plants that are alien or native (Parker et al. 2006). The ability of herbivores to feed on plants from different origins is predicted to be more common when the plants are closely related taxonomically (Agrawal et al. 2005). Congeners often share similar defense mechanisms; a native specialist herbivore may be able to take advantage of an alien congener of their host plant (Tallamy 2004). In either case, natural enemies may not be associated with these relatively new relationships and herbivores may establish resulting in greater levels of herbivory. Moreover, among the relatively few studies that have examined native dominated plant communities relative to alien, the relationships between native and alien herbivores and plants have not been consistent. Studies have found no difference in the species richness or diversity of herbivores on native and alien plants (Maron and Vila 2001, Agrawal 2005, Liu et al. 2006). Variability in the studies that both support and counter predictions on patterns of species richness and biodiversity of herbivores and natural enemies in native and alien plant communities demonstrate the need for further study.

The overall objective of this study was to compare the effects of using native or alien plants in urban landscapes, on arthropod community dynamics and

conservation biological control. I investigated whether landscapes dominated by native trees and shrubs support a more diverse herbivore and natural enemy community. Also, I predicted that herbivore injury reaches an unacceptable level less frequently in native landscapes than in landscapes dominated by alien trees and shrubs. Plants in urban landscapes are valued for their aesthetic qualities and therefore maintaining the appearance of these plants is central to any pest management plan (Sadof and Raupp 1996). Studies have found that homeowners consider a plant damaged when the amount of herbivore injury is less than 10% (Raupp et al. 1989, Sadof and Alexander 1993, Sadof and Raupp 1996). An aesthetic injury level (AIL) is the number of herbivores that cause an unacceptable amount of injury to a plant. For this study I used 10% injury as the point when the plant was considered damaged (Sadof and Raupp 1996). I predicted that urban landscapes with native plants will support a more diverse community of herbivores that will attract and sustain a diverse community of natural enemies. The actions of the natural enemies in native landscapes will keep populations of herbivore species below a level where they cause aesthetic injury that require control measures. Alternatively, landscapes dominated by alien trees and shrubs are predicted to host a less diverse community of herbivores and attract and sustain fewer natural enemies. The herbivore populations in these landscapes will be subject to less natural enemy pressure and are predicted to reach population levels that more frequently cause unacceptable levels of aesthetic injury.

Specific objectives of this study were to compare: 1) the colonizing herbivore and natural enemy communities associated with native and alien ornamental landscapes, 2) herbivore survival, as an indirect measure of natural enemy pressure, in native and alien landscapes, and 3) the aesthetic injury of trees and shrubs in native and alien landscapes. The results from this study will provide valuable insight into the role of native plants in urban ecosystems and pest management.

## Methods

### *Study system and experimental design.*

To compare the arthropod communities of native and alien landscapes and the influence of these landscapes on biological control I designed and planted replicated landscape plots composed of either: 1) native trees and shrubs, or 2) alien trees and shrubs. These two treatment landscapes were designed to fit a spatial scale and plant species richness and diversity comparable to a typical urban landscape.

Pairs of one native and one alien landscape were established at eight locations (replicates) in a randomized complete block design. Each location was a block (= eight blocks). There were four replicates in Maryland. One at the Central Maryland Research and Education Center (CMREC) Beltsville Facility in Laurel, MD, one at the CMREC Upper Marlboro Facility in Upper Marlboro, MD, and two at the CMREC Clarksville Facility in Ellicott City, MD. The two replicates at the Clarksville Facility were physically separated by a road and the woodlots adjacent to each replicate were not contiguous with each other. The other four replicates were

located in Delaware at St. Andrews School in Middletown, DE, the University of Delaware Agricultural Experiment Station at Middletown, DE, the University of Delaware Experiment Station at Newark, DE, and the Kranz Farm in the White Clay Creek Preserve, Newark, DE. Each treatment landscape was planted in an 18 m x 18 m plot, for a total area of 324 m<sup>2</sup>. Within each replicate, the native and alien landscapes were separated by a minimum of 50 m to minimize the likelihood of movement of arthropods between treatment plots. Each landscape was located 25 m from a wood edge which likely served as a source for colonizing arthropods. Landscapes were surrounded by a buffer at least 25 m wide of Kentucky 31 tall fescue on all sides (Fig. 1).

The landscapes were designed to maintain uniformity in the level of structural complexity and plant species richness and diversity between the native and alien treatments. Plants of comparable size and structure, and the same number of tree and shrub species were selected for each treatment landscape. The alien ornamentals were selected based on their availability and use in mid-Atlantic. The native plants were chosen for their recognition and use as ornamentals and their availability in the native ornamental industry. Each treatment landscape contained seven species of trees and six species of shrubs (subsamples). See Table 1 for a list of the native and alien trees and shrubs used. Of these, four pairs of congeneric plant species were used to compare related native and alien plants based on their origin and to reduce effects that might occur due to genetic differences (Table 2). The related alien and native plants, respectively, were from the genera *Prunus* (Japanese cherry, *P.*

*serrulata* and black cherry, *P. serotina*), *Tilia* (littleleaf linden, *T. cordata*, and basswood, *T. americana*), *Cornus* (Kousa dogwood, *C. kousa* and alternate leaf dogwood, *C. alternifolia*) and *Acer* (Norway maple, *A. platanoides*, and red maple, *A. rubrum*) (Table 2). Within each treatment landscape, each species of tree or shrub was represented by seven individual plants (sub-samples) that were planted together in 3 m x 2 m rectangular beds with hardwood mulch surrounding the plants. Multiple trees of the same species were planted for two reasons: 1) since the plants are young they did not have a great presence individually and using multiple plants increased the vegetative area and biomass represented by each species, and 2) using multiple plants allowed for sampling different individual plants throughout the growing season reducing potential bias caused by destructive (arthropod removal) sampling. Each tree species was randomly assigned to a bed in the outer ring of the landscape, while shrub species were planted in the inner ring of beds. Kentucky 31 tall fescue was planted between all the beds within the treatment plots (Figs. 1 and 2).

Additionally, in the center of each treatment landscape we prepared five 1m x 1m beds where I randomly planted six species of trees and shrubs that served as hosts for sentinel herbivore populations (Figs. 1 and 2). These plant species are common in landscapes and their associated herbivores often cause damage and require control measures in landscapes. The five beds were randomly assigned the following herbivore host plants: four eastern red cedars (*Juniperus virginiana*); four azaleas (*Rhododendron sp.*); four roses (*Rosa sp.*); four spireas (*Spirea tomentosa*); or two pin oaks (*Quercus palustris*) and 2 Washington hawthorns (*Crataegus phaenopyrum*).

Individual plants of each species were sub-samples. To limit the potential influence that these herbivore host plants had on the main native and alien treatments, both native and alien herbivore host plants were planted in each landscape (Table 3). Three of these central beds contain native herbivore host plants and the other two beds were dominated by aliens.

All treatment landscapes were established in the fall of 2005 with a few final plantings installed in the spring of 2006. Maintenance of the landscapes throughout the growing season was comparable to practices in typical urban landscapes to maintain healthy plants, excluding the use of insecticides. Plants were treated with a slow release fertilizer when they were planted to encourage root growth, and watered when necessary to avoid drought stress. The turf in the buffer zone and within the landscapes was mowed on a regular basis to prevent any weeds that might be present from flowering. Mulch in plant beds was replenished yearly. Weeds were removed by hand or spot treated with herbicide. Throughout the course of this study, plants that failed to establish were replaced with new plants of comparable size.

### *Composition of arthropod communities*

The objective of this component of the study was to identify and compare the structure of colonizing herbivore and natural enemy communities associated with the native and alien treatment landscapes. Sampling of arthropods was conducted on each plant species in the landscape treatment plots. Sampling was conducted in June and August of 2006 and repeated in June and August of 2007. Both the native and

alien landscapes at each location (replicate) were sampled on the same day and all 8 replicates were sampled within ten days of each other. For each tree and shrub species (subsamples) three individual plants of the seven plants (sub-subsamples) within a bed were randomly selected for the first sampling period, while three different plants of the 7 were sampled in the second sampling period to ensure that the samples were not biased from prior sampling within a year. The host plants for sentinel herbivore populations, located in the center of the landscapes, were not included in the arthropod community sampling. Arthropod sampling was conducted using two methods. First, each branch of the plant was sampled using a reverse leaf-blower with a mesh collecting bag. This collected the majority of arthropods. Second, the entire plant was visually sampled for any arthropods that were missed by the leaf blower. The arthropods collected in the leaf-blower bag and during the visual inspection were then placed in labeled vials in the field. The insects were taken to the lab where they were sorted, counted, and identified to family and trophic group. Due to difficulty in identification and the volume of samples to identify, some arthropods were not identified to the family level, but were grouped by order. Spiders (Araneae), miscellaneous Diptera, miscellaneous Lepidoptera, Ephemeroptera, mites (Acari), fungus beetles (Coleoptera), and Psocoptera were counted, identified and grouped. Arthropod samples were dried and weighed to determine biomass by trophic group.

All arthropod abundance and biomass data were standardized to number or amount of arthropods per gram of leaf dry weight to control for differences in plant size. This was done by counting the number of leaves on each plant sampled. The

number of leaves on a plant was then multiplied by the average dry weight of one leaf of that species. This gave us an estimate of the dry biomass of foliage on each plant sampled. Leaves on plants were counted for each year.

*Statistical analysis.* Results on arthropod community composition presented in this thesis represent data from 4 of the 8 replicates on two sampling dates, August 2006 and August 2007. This was due to the large number of samples, and the time required to process all the samples. The data included in this thesis are from the following four replicates: CMREC Upper Marlboro Facility in Upper Marlboro, MD, one replicate from CMREC Clarksville Facility in Ellicott City, MD, University of Delaware Agricultural Experiment station at Middletown, DE and the University of Delaware Experiment Station at Newark, DE on the August 2006 and August 2007 sampling dates. *P*-values less than 0.05 were considered significant throughout the study. All arthropod data were calculated as a mean of the subsamples. Analysis of variance (ANOVA) was used to compare the abundance and dry biomass of herbivores, predators and parasitoids on all plant species in the native and alien landscapes in 2006 and 2007 (SAS Institute 2002). Native and alien plants in each congener pair were also compared to look for differences in abundance and biomass of herbivores and natural enemies on related native and alien plants. These data sets were examined using Tukey adjusted pairwise comparison of least-square means (LS-means) (SAS Institute 2002). The number of families sampled (family richness) in each treatment landscape was also compared using ANOVA. The assumptions of normality and homogeneity of variance was examined for each analysis.



Comparisons of parasitoid abundance in 2007 were analyzed using the non-parametric Kruskal Wallace Test because the assumptions could not be met (SAS Institute 2002).

Changes in the family level structure of arthropod communities in native and alien treatment landscapes over time were examined using the principle response curve (PRC) method developed by Van den Brink and ter Braak (1999). This method provides a visual comparison of the arthropod communities in native compared to alien landscapes. The PRC is based on redundancy analysis (RDA). RDA is a constrained form of principle components analysis (PCA), that is, it explains variation in community structure based on a known explanatory variable, such as a treatment (native and alien landscapes) (Van den Brink and ter Braak 1999). Canonical coefficients of the treatment by time interactions of the first axis of RDA show the differences between the control and treatment over time; these are calculated by the weighted regression of taxa abundance on treatment and time variables (Van den Brink and ter Braak 1999, Dively 2005). The CANOCO program was used to run the RDA, and a Monte Carlo permutation test of the samples produced an F-statistic to test the significance of differences between the arthropod communities in native and alien landscapes (CANOCO version 4.5 1997). The counts of individuals in each family were log transformed. Data were blocked by replicate and analyzed as a split-plot in time; permutations were shuffled between treatments but not between replicate and year.

To create the PRC, the alien landscapes were designated as the control; the community of arthropods within these landscapes acted as a reference by which to compare the native landscape communities. The arthropod community in the alien landscapes was represented by a straight line at zero (Fig. 7). The canonical coefficients from the first axis in the RDA were back transformed and plotted on the graph to represent the community of arthropods in the native treatment in 2006 and 2007. The graph shows the relative abundance of taxa in the native landscapes relative to the alien landscapes in 2006 and 2007. Individual families were given a weight or score to indicate how that family responded to the treatments. Families with large positive weights are families whose abundance followed the trends depicted by the PRC. These families are contributing positively to the curve. Families with large negative weights are those who are showing a pattern opposite of the curve. Families with weights between 0.5 and -0.5 are not discussed and usually contribute little to the PRC or exhibit patterns unrelated to the model. The abundance of these heavily weighted arthropod groups was examined using repeated measures analysis of variance on the individual groups (SAS Institute 2002). Four covariance structures (autoregressive (1), heterogeneous CS, compound symmetry and unstructured) were examined in each analysis and the structure that provided the best fit for the data was used.

### *Survival of sentinel herbivores*

Quantifying the survival of sentinel herbivore populations allows for an estimate of natural enemy activity and a comparison of natural enemy impact between native and alien landscapes. Herbivore survival studies were conducted in all replicates (four in MD, four in DE). Each species of herbivore host plant, at the center of each treatment landscape, was paired with its known herbivore species (Table 3). The herbivores were chosen to represent three major insect groups that frequently damage ornamental plants; sternorrhynchans, heteropterans and lepidopterans. Four of the herbivore species used were native and two were exotic (Table 3). Several times during the 2006 and 2007 growing season host plants were infested with herbivores collected from landscapes in Maryland. Any flowers on the host plants were removed prior to the beginning of the trial. A branch on each host plant was labeled and a known number of herbivores were placed on the labeled branch. To limit the movement of herbivores off the plant either immature or wingless morphs were used. The number of trials, the dates on which they were conducted, and the number of herbivores used in the trials varied due to constraints in the number of herbivores that could be collected in the field (Table 4 A and B). To compare survival the number of live herbivores were counted daily following initial infestation. Postcounts continued until survival of all individuals from the initial infestation cohort reached or was less than 50%. At the end of each trial any remaining herbivores were removed. In each treatment landscape, daily counts of

herbivores were summed to remove branch and plant as subsamples. Pooled data were analyzed.

### **Herbivore / host plant systems.**

Two aphid species were used in the herbivore survival trials: rose aphid (*Macrosiphum rosae* (Linnaeus)) on commercial roses (*Rosa sp.*), and spirea aphid (*Aphis spiraeicola* (Patch)) on spireas (*Spiraea tomentosa*), (sub-order Sternorrhyncha). Aphids feed in the phloem tissue of plants causing discoloration and distortion. They can reproduce asexually and small populations can quickly reach damaging levels in a landscape. One survival trial was conducted on spirea aphid in both 2006 and 2007. Rose aphid survival was only examined once in 2007 (Table 4 A and B).

Hawthorn lace bug (*Corythucha cydoniae* (Fitch)) on Washington hawthorns (*Crataegus phaenopyrum*) and azalea lace bug (*Stephanitis pyrioides* (Scott)) on azalea bushes (*Rhododendron sp.*) were the herbivores representing the sub-order Heteroptera. These insects cause stippling of the leaf tissue. They also excrete tar-like fecal spots on the leaf surface. Lace bugs are common and often require control in landscapes. Third and fourth instar nymphs were used in these experiments to reduce the likelihood of dispersal. In 2006, two trials were conducted with azalea lace bugs and two with hawthorn lace bugs (Table 4A). In 2007, three hawthorn and two azalea lace bug trials were performed (Table 4B).

Two native caterpillars, bagworms (*Thyridopteryx ephemeraeformis* (Haworth)) on Eastern red cedars (*Juniperus virginiana*) and orangestriped oakworms (*Anisota senatoria* (J.E. Smith)) on pin oaks (*Quercus palustris*), were used to

represent the order Lepidoptera. As larvae these insects have chewing mouthparts and they defoliate landscape plants. Orangestriped oakworm caterpillars were collected from a nursery in Maryland. Caterpillars varied in age and size and care was taken to balance the size of caterpillars across treatments. Bagworms provided a unique opportunity to monitor an herbivore for more than a week since they survived longer than other herbivores in these studies. In 2006, two trials were conducted and populations were counted daily (Table 4 A). In 2007, two bagworm trials were conducted and bagworms were counted weekly for two weeks (Table 4 B).

*Statistical analysis.* The number of herbivores counted over time was analyzed using repeated measures analysis of variance (ANOVA); data was blocked by location (SAS Institute 2002). Survival trials where 50% of the herbivores were missing by the first day of post counts were analyzed using one-way analysis of variance. Normality and homogeneity of variances of the data were examined. If these assumptions were not met, data was  $\log_{10}$  transformed and the analysis was conducted on transformed data. A non-parametric Kruskal Wallace test was used if the data failed to meet the assumptions. All reported results are untransformed means  $\pm$  SEM.

### ***Aesthetic injury to landscape plants***

The aesthetic injury of native and alien plants was estimated in June and August of 2007. In each treatment landscape, one plant per species was randomly designated as the sampling unit for aesthetic injury ratings. This sampling plant was

not sampled in the arthropod community study. For most plants, with the exception of those described below, leaves at four cardinal points at two heights, either  $\frac{1}{4}$  or  $\frac{3}{4}$  of the distance from the ground (four locations / plant) were rated for injury. One or more branches were randomly selected at each point and height combination. A pre-determined number of fully expanded leaves were then rated on each branch. Ratings began on leaves at the tip of the branch and moved toward the center of the plant. For each leaf the percent of leaf area injured by insects was estimated. The estimations ranged from 0%, no injury, to 100%, when the leaf was completely damaged by herbivores. Percent injury was recorded in 5% increments. The type of injury (defoliation, discoloration or distortion) and the damaging pest was recorded when known. When more than one type of injury was found, the amount of each type of injury was recorded.

Individual plant species had to be rated differently to take into account differences in leaf size, plant size, and growth habit. A standardized sampling procedure was developed for each species that determined the number of leaves and branches to be rated (Table 5). The percent injury for most species was calculated from rating four branches, ten leaves per branch, for a total of 40 leaves (Table 5). Cotoneasters (*Cotoneaster lucida*) in the alien landscapes had many small leaves. For these plants 6 branches were sampled and 30 leaves were rated on each branch. On plants with compound leaves, green ash (*Fraxinus pennsylvanica*) and golden rain tree (*Koelreuteria paniculata*), ten leaflets on four compound leaves were rated (Table 5). The native and alien evergreens, white pine (*Pinus strobes*) and Norway

spruce (*Picea abies*), also had a unique sampling procedure. At each of the 4 cardinal points, eight two-inch sections of needles were examined where each two-inch section was given a score based on the percentage of needles with herbivore damage (Table 5). Congeneric pairs in the native and alien landscapes were always rated using the same procedure to allow for statistical comparison of their aesthetic injury.

*Statistical analysis.* An average percent injury was calculated for each plant in each replicate. Data was analyzed using three approaches. First, the average percent injury of all plants combined in the native and alien landscapes was compared in June and in August 2007 using ANOVA (SAS Institute 2002). Second, an injury level of 10% was used as a threshold and the frequency of plants that were ‘above’ or ‘below’ threshold were compared. Data were categorical, and a Pearson Chi-Square Test was used (SAS Institute 2002). Finally, the percent of area exhibiting each type of injury (defoliation, discoloration and distortion) was compared using ANOVA. Plants within each native / alien pair of congeners were compared to test for differences in injury of related to origin. These data were examined using Tukey adjusted pairwise comparison of least-square means (LS-means) (SAS Institute 2002). All analyses were blocked by location (SAS Institute 2002). Normality and homogeneity of variances of the data were examined; if these assumptions were not met, data was  $\log_{10}$  or square-root transformed and the analysis was conducted on transformed data. If the assumptions were still not met the data was analyzed with the non-parametric Kruskal-Wallis test (SAS Institute 2002). All reported results are untransformed means  $\pm$  SEM.

## Results

### *Composition of arthropod communities*

There was no difference in the total abundance of arthropods between the treatment landscapes in 2006 ( $F=0.70$ ;  $df=1, 3$ ;  $P=0.464$ ) or 2007 ( $F=0.08$ ;  $df=1, 3$ ;  $P=0.792$ ). In 2006, there was an average of  $0.33 \pm 0.06$  arthropods/ g leaf (dw) in the alien landscapes and  $0.41 \pm 0.13$  arthropods/g leaf (dw) in the native landscapes. In 2007, there were  $0.37 \pm 0.18$  and  $0.34 \pm 0.090$  arthropods/g leaves (dw) in the alien and native landscapes, respectively. The abundance of herbivores ( $F=0.85$ ;  $df=1,3$ ;  $P=0.425$ ), predators ( $F=0.05$ ;  $df=1,3$ ;  $P=0.830$ ) and parasitoids ( $F=1.71$ ;  $df=1,3$ ;  $P=0.282$ ) did not differ in 2006 (Fig. 3A). Similarly, in 2007 the abundance of herbivores ( $F=0.38$ ;  $df=1,3$ ;  $P=0.584$ ), predators ( $F=0.27$ ;  $df=1,3$ ;  $P=0.637$ ) and parasitoids ( $\chi^2=2.08$ ;  $df=1$ ;  $P=0.149$ ) did not differ between the native and alien landscapes (Fig. 3B). The biomass of herbivores ( $F=7.22$ ;  $df=1,3$ ;  $P=0.0746$ ), predators ( $F=1.17$ ;  $df=1,3$ ;  $P=0.359$ ) and parasitoids ( $F=7.40$ ;  $df=1,3$ ;  $P=0.0726$ ) did not differ in 2006 (Fig. 4A). The same was true in 2007 where the biomass of herbivores ( $F=0.29$ ;  $df=1,3$ ;  $P=0.630$ ), predators ( $F=0.68$ ;  $df=1,3$ ;  $P=0.471$ ) and parasitoids ( $\chi^2=0.33$ ;  $df=1$ ;  $P=0.564$ ) did not differ (Fig. 4B). The biomass of natural enemies (predators and parasitoids) in the alien and native treatment landscapes were compared and did not differ in 2006 ( $F=1.17$ ;  $df=1,3$ ;  $P=0.359$ ) (Fig. 4A), or in 2007 ( $F=1.26$ ;  $df=1,3$ ;  $P=0.343$ ) (Fig. 4B).



Comparison of the abundance of herbivores on the native and alien congener pairs was only significant for *Cornus*. In 2006, the native *Cornus* hosted more herbivores than the alien ( $t=2.93$ ;  $df=74$ ;  $P=0.005$ ) (Fig 5A). There were no differences in the abundance of herbivores, predators and natural enemies between the *Acer*, *Tilia* and *Prunus* congener pairs (Fig. 5A-C). The biomass of herbivores and natural enemies did not differ for any of the congeneric pairs ( $P>0.05$ ) (Fig. 6A,B).

There was no difference in arthropod family richness between native and alien treatment landscapes in 2006 ( $F=0.24$ ;  $df=1,3$ ;  $P=0.655$ ) or 2007 ( $F=4.20$ ;  $df=1,3$ ;  $P=0.133$ ). The mean numbers of families sampled in 2006 was  $42.50 \pm 5.24$  in the alien landscapes and  $43.75 \pm 3.54$  families in the native landscapes. In 2007, there were  $56.00 \pm 2.68$  families in the alien treatment and  $61.25 \pm 4.33$  in the native treatment.

There were a total of 15,149 insects from 141 families or groups sampled from the treatment landscapes. The arthropod communities between native and alien landscapes from 2006 to 2007 were not significantly different ( $F=1.561$ ;  $P=0.122$ ) (Fig. 7). In the redundancy analysis the first axis accounted for 7% of the total variance (raw data) and 63% of the variance (fitted data) explained by the treatments. Half (50%) of the total variance was explained by time. Families with high positive weights are families that have a greater presence in native landscapes relative to alien (Fig. 7). These arthropods include nine families of herbivores (Gelechiidae, Cecidomyiidae, Psyllidae, Acrididae, Papilionidae, Arctiidae, Tortricidae, Pyralidae

and Delphacidae), seven predator families (Anthocoridae, Chrysopidae, Empididae, Dolichopodidae, Coccinellidae, Lampyridae and Nabidae) and six families of parasitoids (Eulophidae, Cynipidae (Eucoilinae), Scelionidae, Ceraphronidae, Platygasteridae and Braconidae). The Gelechiids and Eulophids were the highest weighted groups. Arthropods with negative weights are responding to the treatment landscapes in the opposite way, they are expected to have a greater relative abundance in the alien landscapes (Fig. 7). These arthropods include eight herbivore families (Tingidae, Pentatomidae, Curculionidae, Psychidae, Tettigoniidae, Berytidae, Rhyparochromidae and psocopteran families), one group of predators (spiders, Araneae), two parasitoid families (Encyrtidae and Mymaridae) and two groups of non-plant feeders (miscellaneous Diptera, and gryllids). Of these families the two most negatively weighted families were the Tingidae and the Pentatomidae. The repeated measures ANOVA of individual groups of arthropods revealed that out of the 12 most heavily weighted groups, 6 positively weighted families and 6 negatively weighted families, two showed significant differences in abundance in the native and alien landscapes. These included the scelionids which followed the pattern seen in the PRC and had greater abundance in the native treatment landscapes ( $F=16.2$ ;  $df=1,3$ ;  $P=0.0276$ ), and the Curculionidae showed greater abundance in the alien landscapes ( $F=7.91$ ;  $df=1,3$ ;  $P=0.0329$ ).

### *Survival of sentinel herbivores*

In 2006, there were a total of eight herbivore survival trials conducted during the growing season (Table 4A). Differences in survival occurred in one trial, with bagworms which began on July 27, 2006 showed lower survival in native landscapes when counted daily for one week (Table 4A). The average number of bagworms in the alien plot was  $3.55 \pm 0.11$  and in the native landscapes it was  $2.85 \pm 0.12$ . Survival of spirea aphid, azalea lace bug, hawthorn lace bug and orangestriped oakworm did not differ in 2006 (Table 4A). In 2007, there were a total of 10 survival trials conducted (Table 4B). Only the azalea lace bug trial on June 18, 2007 experienced lower survival in the alien landscape compared to the native landscape (Table 4B).

### *Aesthetic injury to landscape plants*

In June 2007, the average combined injury to native plants was  $3.70\% \pm 1.10$  and the average of alien plants was  $4.08\% \pm 0.75$  (Fig. 8A). This difference was not significant ( $F=0.14$ ;  $df=1,7$ ;  $P=0.723$ ). As the season progressed there was more herbivore damage on the plants. In August, the natives had an average combined injury of  $11.18\%$  and the aliens had an average of  $10.70\%$ . This difference was not significant ( $F=0.09$ ;  $df=1,7$ ;  $P=0.776$ ) (Fig. 8B). The estimated AIL of individual plants was compared categorically as the frequency 'above' or 'below' the AIL threshold of  $10\%$ . In June, out of the 104 plants examined per treatment, only 8 natives and 7 aliens were above an AIL of  $10\%$  ( $\chi^2=0.0718$ ;  $df=1$ ;  $P=0.788$ ). In

August there was an equal number of natives and aliens exceeding 10% damage ( $\chi^2=0.00$ ;  $df=1$ ;  $P=1.0$ ).

The percent of each type of aesthetic herbivore injury was compared between the native and alien landscapes in June and August. In June there was no difference in the amount of defoliation ( $F=1.85$ ;  $df=1,7$ ;  $P=0.217$ ), discoloration ( $F=4.04$ ;  $df=1,7$ ;  $P=0.0842$ ) or distortion ( $F=0.01$ ;  $df=1,7$ ;  $P=0.939$ ) between natives and aliens (Fig. 8A). In August, the percent of defoliation injury ( $F=0.92$ ;  $df=1,7$ ;  $P=0.369$ ) and distortion injury ( $F=0.0$ ;  $df=1,7$ ;  $P=0.995$ ) did not differ (Fig. 8B). However, there was significantly more discoloration injury on alien plants compared to natives ( $\chi^2=4.12$ ;  $df=1$ ;  $P=0.042$ ) (Fig. 8B). Data on the amount of discoloration had to be log transformed in June and a non-parametric analysis was used for the August data.

Comparisons of aesthetic injury between native and alien congeners showed mixed results. In August there was significantly more injury on the native *Acer* species than the alien species ( $t=-3.29$ ;  $df=173$ ;  $P=0.001$ ) (Fig. 9A) whereas, the alien *Prunus* species incurred more injury than its native partner ( $t=-2.30$ ;  $df=173$ ;  $P=0.023$ ) (Fig. 9A). Further comparisons of the congeners showed more defoliation injury on the native *Cornus* ( $t=2.33$ ;  $df=173$ ;  $P=0.021$ ), alien *Prunus* ( $t=-2.99$ ;  $df=173$ ;  $P=0.003$ ) and alien *Tilia* ( $t=-2.10$ ;  $df=173$ ;  $P=0.037$ ) in August (Fig. 9B). In both June and August there was more discoloration on native *Acer* plants ( $t=-3.16$ ;  $df=181$ ;  $P=0.002$ ) ( $t=-10.10$ ;  $df=173$ ;  $P<0.001$ ) (Fig. 10A). Only the *Acer* species showed a difference in the amount of distortion in June ( $t=-3.37$ ;  $df=174$ ;  $P=0.001$ )

(Fig. 10B). The strongest pattern in injury was that *Acer* had greater injury on the native than alien congener.

## Discussion

There is a lack of clear evidence on how alien and native plants differ in terms of the herbivore and natural enemy communities they support (Vitousek 1986, Keane and Crawley 2002). Clarification of these differences are crucial because they have important implications to conservation of native biodiversity (Altieri 1999, Reichard and White 2001, McKinney 2002, Tallamy 2004 and Pimentel et al. 2005) as well as to management strategies aimed at enhancing biological control (Fiedler and Landis 2007 and Frank et al. 2008). Studies that compared arthropod communities on native and alien plants provide conflicting results. Some studies found that native herbivores can be successful on alien plants (Samways et al. 1996, Keane and Crawley 2002, Parker and Hay 2005, Parker et al. 2006). Other studies have found that herbivores prefer to feed on native plants with which they have evolved (Andow and Imura 1993, Wolfe 2002, Siemann and Rogers 2003, Carpenter and Cappuccino 2005). Understanding the mechanisms underlying these differences has implications to biological control; the relationship of herbivores with native plants may be utilized to attract natural enemies and enhance conservation biological control. Therefore, this study was designed to examine whether urban landscapes consisting of native woody trees and shrubs host an arthropod community that attracts and supports natural enemies relative to landscapes planted with alien woody trees and shrubs. In

this two year project, I found only weak evidence to support my predictions. Native landscapes did not host a significantly different assemblage of arthropods compared to aliens. There was a trend for several important natural enemy families to have a greater abundance in native landscapes compared to alien. In addition, the differences in natural enemy communities did not have a measurable impact on herbivore survival or aesthetic injury to the plants.

I predicted that native landscapes would host a more diverse herbivore community than alien landscapes, and that these insects would act as primary and alternative food resources for natural enemies. These predictions are based on the theory that native herbivores are restricted to feed on plants with which they have evolved and should be less capable of feeding on a novel or exotic host (Bernays and Graham 1988, Keane and Crawley 2002, Tallamy 2004). This theory is put forth by the enemy release hypothesis which states that plants, novel to an environment, should incur less herbivore injury than in their native environment since they are free of their native herbivores in their home range (Keane and Crawley 2002). This is based on the assumption that alien plants are less likely to be fed upon by native specialists than plants native to the region. Generalist herbivores are predicted to feed on both the alien and native hosts, but will have a greater affinity for the native plants with which they have evolved (Keane and Crawley 2002). If native plants are more preferred by native herbivores, then, as predicted by conservation biological control, this suite of potential prey should attract natural enemies (Landis et al. 2000). The native landscapes in this study, compared to alien landscapes, did not have a greater

abundance, biomass or family richness of herbivores and it is not surprising that I did not see a difference in the abundance, biomass or richness of natural enemy populations. These results from the first two years of the study do not support the enemy release hypothesis and do not provide evidence that planting native plants is an effective habitat manipulation technique to enhance conservation biological control. Similar to these results, other studies have found that herbivore communities were not lower in alien plantings relative to native. In a mini-review on the enemy release hypothesis, Maron and Vila (2001) found that alien plants are host to a large community of native herbivores and that these herbivores can limit the plant's growth and success (Maron and Vila 2001). This is supported by the findings of Parker and Hay (2005) who examined herbivory in aquatic systems and found that generalist native herbivores preferred to feed on exotic plants. If alien plants host larger herbivore populations than was originally predicted, this would explain the lack of differences between the abundance of herbivores and natural enemies in the present study.

A PRC analysis compares the number of families and their abundance in the native landscapes relative to the populations in the alien landscape. The results of the PRC indicated native landscapes did not host a significantly different assemblage of arthropods compared to alien landscapes. This agrees with the results found comparing the abundance, biomass and family richness of arthropod by trophic guild. However, the taxon weights associated with the PRC reveal that there are subtle differences between the arthropod communities. These differences, albeit mostly

statistically insignificant, may have important ecological consequences. Nine herbivore (5 families of Lepidoptera), seven predator and six parasitoid families had a greater abundance in the native landscapes. Compared to the eight herbivore families (none of which are of the order Lepidoptera), one group of predators and two parasitoid families that showed an affinity for the alien landscapes. The Lepidoptera families in the native landscapes may be an indication that herbivores are beginning to colonize the landscapes and show a preference for the native plants. Lepidoptera often have close relationships with their host plant (Ehrlich and Raven 1964, Andow and Imura 1994) and their association with native landscapes would fit the prediction that herbivores will prefer to feed on native plants. Also, the 13 families of natural enemies in the native landscape may indicate that natural enemies are beginning to respond to the native treatment, but whether they are responding to a greater diversity of primary and alternative food resources is still not clear. In time, these patterns may become more evident within the landscapes.

There is some evidence that arthropod communities associated with native plants may differ than those of alien plants. In studies aimed to conserve biodiversity it is commonly assumed that native arthropods are associated with native plants and as the diversity of plants increase, so will the diversity of native arthropods (Crisp et al. 1998, McKinney 2002). A study in New Zealand looked at diversity of native beetles (Coleoptera) found in areas with varying proportions of native and alien vegetation (Crisp et al. 1998). They found that as the amount of native vegetation increased, so did the diversity of native beetles. However, there was still high species



diversity in areas that contained larger proportions of alien plants; these beetle populations contained more introduced species (Crisp et al. 1998). Another study looked at ground dwelling invertebrate communities associated with native and exotic plant systems in South Africa (Samways et al. 1996). They found that the structure of the insect communities associated with native and alien ecosystems differed. There was a trend for lower arthropod species richness and diversity to be associated with exotic vegetation. These differences were most obvious in the arthropod communities at the species level (Samways et al. 1996). A few families (Tenebrionidae, Anthicidae and Meloidae) and several species of Reduviidae, Pompilidae, Scarabaeidae, Pyrrhocoidae and Formicidae were only found on native plants (Samways et al. 1996). These studies emphasize the need for the herbivores and natural enemies collected from the present study to be identified to the species level and their native origin determined to be able to fully explore the community differences between native and alien landscapes.

The purpose of the sentinel herbivore trials was to use the survivorship of herbivores as an indication of the effectiveness of the natural enemy community to lower herbivore populations and keep them below damaging levels. However, counter to predictions, these differences in the natural enemy community resulted in only a weak pattern for differential mortality in the herbivore survival trials. Out of eighteen trials, over two seasons, only 2 resulted in survival differences. In 2006, bagworm survival was lower in the native landscapes, and in 2007 azalea lace bug survival was lower in alien landscapes. Azalea lace bugs are an exotic herbivore on

an alien host plant. One explanation for this pattern is that in the alien treatment landscapes there were lace bug populations on the azaleas. It is probable that natural enemies were responding to these populations, which may have led to greater mortality of the sentinel lace bug populations. Spiders, for example, are often generalist predators and known to feed on azalea lace bugs (Shrewsbury and Raupp 2006). They showed a numerically greater, although insignificant, abundance in the alien landscapes. Bagworms, on the other hand are a native herbivore on a native host plant and natural enemies may be more effective at finding prey in native landscapes. However, these bagworm trials did not test for parasitism and reduction in bagworm populations may be due to other predators such as English sparrows and mice (Ellis et al. 2005).

The lack of difference in survival between native and alien landscapes for the other herbivore-host plant systems may be explained by other reasons. The PRC analysis found that half of the natural enemy families responding to the native and alien treatments were parasitoids. The herbivore survival trials in the present study were short lived and more likely to detect acts of predation rather than parasitism. Also, the herbivore species I used in the trials may not have been hosts for the parasitoids attracted to the landscapes. It is also possible the landscape treatment plants might be acting as a sink for the natural enemies rather than a source where they may not have migrated over to center of the landscape plots where the herbivore survival trials were conducted.

Since the value of ornamental plants is strongly based on the aesthetic appearance of the plant, an aesthetic injury level (AIL) and threshold is frequently used in the pest management of ornamental plant systems to determine when control measures should be applied (Sadof and Raupp 1996). Studies have determined that the public perceives a plant as damaged (= loss in value) when herbivore injury is visible on less than 10% of the foliage (Raupp et al. 1989, Sadof and Alexander 1993, Sadof and Raupp 1996). It is generally predicted that herbivory should be greater on native plants compared to alien plants (Keane and Crawley 2002, Tallamy 2004). There is evidence that alien plants may incur less herbivore damage than native plants (Andow and Imura 1993, Wolfe 2002, Siemann and Rogers 2003, Carpenter and Cappuccino 2005). For example, a survey of herbivore damage on the foliage of 30 native and 39 alien plants rated the number of holes, mines and galls and found more herbivore injury on native plants (Carpenter and Cappuccino 2005). I predicted, however, that the natural enemy community associated with herbivores in native landscapes would prevent herbivores populations from reaching the aesthetic injury level. Therefore herbivore injury to landscape plants should remain below 10% longer in native landscapes than in alien; and plants in native landscapes would less frequently reach an AIL of 10% than plants in alien landscapes. Interestingly, there was no difference in the AIL of plants in native compared to alien landscapes, and damage was relatively low overall. This study found no evidence in support of the enemy release hypothesis which predicts that alien plants are subject to less herbivory than native plant (Keane and Crawley 2002). There was more discoloration injury in

alien landscapes compared to native. This trend appears to be driven by lace bug species that occurred predominately on the azaleas, cotoneasters, andromeda and Japanese cherry. Lace bugs cause stippling and can be very damaging to landscape plants (Shrewsbury and Raupp 2000). If natural enemies do not respond to these growing populations of lace bugs, the alien landscapes could easily surpass the native landscapes in injury. As the community of herbivores becomes more established with time, changes in the amount of damage between the treatment landscapes may become more evident.

Another possible explanation for lack of differences in plant injury between native and alien plants is that 4 out of the 13 plant species used in the native landscape had a congener in the alien landscape. In line with the enemy release hypothesis, I predicted that the native congener, when compared individually to an alien congener, would be host to more herbivores and show more signs of herbivory. Our comparison of the four congeneric pairs of plants did not show any trend for the origin of the plant to predict the arthropod community (abundance and biomass of herbivores and natural enemies) or the level of herbivory. One of the predictions of enemy release hypothesis is that specialist herbivores that feed on a native plant should not be able to readily switch to feeding on an alien congener of that plant (Keane and Crawley 2002, Tallamy 2004). Several studies have looked at the ability of specialist herbivores to feed on an alien congener of their host plant (Maron and Vila 2001, Keane and Crawley 2002). Liu et al. (2006) compared the herbivore communities found on alien invasive, alien non-invasive and native congeners (genus

*Eugenia*) and found that herbivore richness did not differ between congeners. A meta-analysis that compared invasive plants in both their native and introduced environment as well as to a congener native in the environment found that the invasive plants did not receive less herbivore injury than the native congener (Hawkes 2007). A possible explanation for why specialists are sometimes able to switch from a native host to an alien congener is that often plants that are closely related share similar secondary metabolic compounds (Tallamy 2004). An herbivore that has evolved to metabolize these compounds may be able to overcome similar defenses of the alien congener of their host, and therefore the level of injury on the congeners may not differ. Others who have compared congeneric native and alien species have found variable results. For example, Agrawal and Kotanen (2003) found equal or greater herbivory on the alien plants. To further explore this question, Agrawal et al. (2005) looked at 30 species of congeneric pairs of native and exotic plants and they expanded their investigation to examine herbivores, fungi and viruses attacking the native and alien plants. They found that the native plants received greater herbivore injury, although there were no significant differences in the species richness and abundance of herbivores in the natives and exotics (Agrawal et al. 2005). Variation in the results from one year, to another, could possibly be explained by differences in the colonizing herbivore communities between years (Agrawal et al. 2005). In this study we found no evidence that the alien congeners escaped from their enemies, however, the identity of these herbivores will reveal the extent to which specialist herbivores are able to feed on both the native and alien congener. The herbivores

sampled from the native and alien congeners will be identified to the species level; this should reveal their degree of specialization.

Alternatively to the enemy release hypothesis, plant origin may not be as important in regulating arthropod community dynamics in urban systems. Habitat manipulation tactics have been successful in conserving natural enemies and enhancing biological control in urban landscapes where natural enemies have been attracted to landscapes that are more structurally complex, and have greater plant species diversity (Tooker and Hanks 2000, Raupp et al. 2001b, Frank and Shrewsbury 2004, Shrewsbury and Raupp 2006). In our efforts to design our experiment to look at the use of native plants as a form of habitat manipulation I controlled for plant species diversity and vegetative structure by using the same number of plant species of comparable size and structure in each treatment. A possible explanation for the lack of differences found in the present study may indicate vegetation structure and diversity of plants overall within the landscape is more important in attracting and sustaining natural enemies and providing them with alternative prey than whether the plants are native or alien in origin.

To date results from the present study do not provide strong support for the enemies hypothesis and the use of native plants to further enhance conservation biological control approaches. Future research should further identify arthropods to the species level and determine their level of polyphagy, trophic guild, and origin. This will allow for better interpretation of the interactions between native and alien plants and the arthropod community in urban systems. Methods used to estimate

natural enemy impact in the landscapes should test for the effectiveness of parasitoids as well as predators. Since many interactions of interest may be effected by temporal differences, studies in these native and alien landscapes should continue to further elucidate arthropod – plant community dynamics.

Table 1. Trees and shrubs planted in the native and alien treatment landscapes.

<b>Natives</b>		<b>Aliens</b>	
<b>Trees:</b>		<b>Trees:</b>	
Red Maple	<i>Acer rubrum</i>	Norway Maple	<i>Acer Platanoides</i>
Green Ash	<i>Fraxinus pennsylvanica</i>	Kousa Dogwood	<i>Cornus kousa</i>
Sweetgum	<i>Liquidambar styraciflua</i>	Autumn Olive	<i>Elaeagnus umbellata</i>
White Pine	<i>Pinus strobus</i>	Golden Rain Tree	<i>Koelreuteria paniculata</i>
Black Cherry	<i>Prunus serotina</i>	Japanese Cherry	<i>Prunus serrulata</i>
Willow Oak	<i>Quercus phellos</i>	Norway Spruce	<i>Picea abies</i>
Basswood	<i>Tilia americana</i>	Littleleaf Linden	<i>Tilia cordata</i>
<b>Shrubs:</b>		<b>Shrubs:</b>	
Chokeberry	<i>Aronia arbutifolia</i>	Cotoneaster	<i>Cotoneaster lucida</i>
Buttonbush	<i>Cephalanthus occidentalis</i>	Burning Bush	<i>Euonymus alatus</i>
Alternateleaf Dogwood	<i>Cornus alternifolia</i>	Forsythia	<i>Forsythia X intermedia</i>
Witchhazel	<i>Hamamelis virginiana</i>	Privet	<i>Ligustrum obtusifolium</i>
Winterberry	<i>Ilex verticillata</i>	Andromeda	<i>Pieris japonica</i>
Arrowwood	<i>Viburnum dentatum</i>	Azalea	<i>Rhododendron sp.</i>



Table 2. Pairs of congeneric plants located in the native and alien treatment landscapes.

<b>Genus</b>	<b>Native</b>	<b>Alien</b>
Acer	Red Maple <i>Acer rubrum</i>	Norway Maple <i>Acer platanoides</i>
Cornus	Alternate leaf dogwood <i>Cornus alternifolia</i>	Kousa Dogwood <i>Cornus kousa</i>
Prunus	Black Cherry <i>Prunus serotina</i>	Japanese Cherry <i>Prunus serrulata</i>
Tilia	Basswood <i>Tilia americana</i>	Littleleaf Linden <i>Tilia cordata</i>

Table 3. The herbivores, their host plants, and their origin that were used to compare herbivore survival in native and alien landscapes.

<b>Herbivore</b>	<b>Origin of Herbivore</b>	<b>Host Plant</b>	<b>Origin of Host Plant</b>
Bagworm <i>Thyridopteryx ephemeraeformis</i> (Haworth)	Native	Eastern Redcedar <i>Juniperus virginiana</i>	Native
Orangestriped oakworm <i>Anisota senatoria</i> (J.E. Smith)	Native	Pin Oak <i>Quercus palustris</i>	Native
Hawthorn lace bug <i>Corythucha cydoniae</i> (Fitch)	Native	Washington Hawthorn <i>Crataegus phaenopyrum</i>	Native
Azalea lace bug <i>Stephanitis pyrioides</i> (Scott)	Alien	Azalea <i>Rhododendron sp.</i>	Alien
Rose aphid <i>Macrosiphum rosae</i> (Linnaeus)	Alien	Commercial Roses <i>Rosa sp.</i>	Alien
Spirea aphid <i>Aphis spiraecola</i> (Patch)	Native	Spirea <i>Spirea tomentosa</i>	Native

Table 4 A. Survival (no. of herbivores) of sentinel herbivores in native and alien landscapes in 2006. Sentinel herbivores were placed on host plants in native and alien landscapes and counted daily until 50% of the initial cohort was gone. A *P*-value of 0.05 or less was considered significant (\*).

Herbivore	Start Date (No. days of trial)	No. Replicates	n <sup>1</sup>	Initial No. Herbivores		Final No. Herbivores		<i>F</i> -statistic ( <i>P</i> -value)
				Alien	Native	Alien	Native	
Spirea Aphid	June 7 (1)	4	8	640	640	215	202	$\chi^2$ - 0.3415 (0.559)
Bagworm	June 6 (7)	8	112	320	320	155	151	Trt. - 0.00 (0.957) <b>Day - 13.55 (&lt;0.0001)*</b> Trt x Day - 0.83 (0.547)
Bagworm	July 27 (6)	7	84	140	140	44	39	<b>Trt. - 10.45 (0.0110)*</b> <b>Day - 5.88 (0.0002)*</b> Trt x Day - 0.77 (0.578)
Azalea Lace Bug	June 28 (1)	4	8	320	320	134	141	Trt. - 0.06 (0.829)
Azalea Lace Bug	August 7 (1)	4	8	320	320	124	99	Trt. - 4.56 (0.122)
Hawthorn Lace Bug	June 7 (3)	8	48	640	640	246	329	Trt. - 3.00 (0.124) <b>Day - 12.25 (0.0002)*</b> Trt x Day - 0.52 (0.599)
Hawthorn Lace Bug	July 25 (3)	8	48	640	640	253	239	Trt. - 1.99 (0.202) <b>Day - 21.08 (&lt;0.0001)*</b> Trt x Day - 1.25 (0.303)
Orange- Striped Oakworm	August 15 (2)	8	32	80	80	36	27	Trt. - 0.55 (0.482) Day - 4.16 (0.0607) Trt x Day - 0.26 (0.618)

<sup>1</sup>n is the number of samples (no. treatments x no. of replicates x no. days of trial)

Table 4 B. Survival (no. of herbivores) of sentinel herbivores in native and alien landscapes in 2007. Sentinel herbivores were placed on host plants in native and alien landscapes and counted daily (bagworms were counted weekly) from the start date. A *P*-value of 0.05 or less was considered significant (\*).

Herbivore	Start Date (No. days of trial)	No. Replicates	n	Initial No. Herbivores		Final No. Herbivores		<i>F</i> -statistic ( <i>P</i> -value)
				Alien	Native	Alien	Native	
Spirea Aphid	May 11 (2)	8	32	640	640	307	249	Trt. – 1.26 (0.304) <b>Day – 5.75 (0.0310)*</b> Trt x Day – 0.31 (0.587)
Rose Aphid	May 11 (2)	7	28	560	560	319	175	Trt. – 0.41 (0.533) † <b>Day – 14.07 (0.0028)*</b> Trt x Day – 0.00 (0.987)
Bagworm	June 25 (2 weeks)	7	28	420	420	219	190	Trt. – 2.48 (0.133) <b>Day – 127.55 (&lt;0.0001)*</b> Trt x Day – 0.02 (0.895)
Bagworm	July 18 (2 weeks)	8	32	320	320	147	142	Trt. – 0.02 (0.891) <b>Day – 23.70 (0.0002)*</b> Trt x Day – 0.62 (0.444)
Azalea Lace Bug	June 18 (3)	3	18	240	240	79	124	<b>Trt. – 24.26 (0.0101)*</b> <b>Day – 17.04 (0.0039)*</b> Trt x Day – 0.59 (0.587)
Azalea Lace Bug	July 9 (1)	5	10	400	400	196	164	Trt. – 2.07 (0.223)
Hawthorn Lace Bug	June 5 (3)	4	24	320	320	155	128	Trt. – 1.02 (0.380) <b>Day – 4.67 (0.0320)*</b> Trt x Day – 1.01 (0.392)
Hawthorn Lace Bug	June 11 (4)	8	64	640	640	253	277	Trt. – 0.51 (0.489) <b>Day – 35.03 (&lt;0.0001)*</b> Trt x Day – 0.75 (0.545)
Hawthorn Lace Bug	July 16 (2)	8	32	640	640	310	324	Trt. – 1.46 (0.248) Day – 6.85 (0.0972) Trt x Day – 2.38 (0.240)
Orange-Striped Oakworm	August 22 (5)	4	40	80	80	41	31	Trt. – 1.49 (0.281) <b>Day – 13.19 (&lt;0.0001)*</b> Trt x Day – 1.66 (0.195)

† n is the number of samples (no. treatments x no. of replicates x no. days of trial)

Table 5. The number of branches and leaves per branch examined for each plant species in the native and alien treatment plots during the aesthetic injury rating.

Treatment	Plant Species	# Branches examined	# Leaves rated per branch	Total # of leaves rated
Native-Tree	Basswood – <i>Tilia americana</i>	4	10	40
Native-Tree	Black Cherry – <i>Prunus serotina</i>	8	10	80
Native-Tree	Green Ash – <i>Fraxinus pennsylvanica</i>	4†	10†	40†
Native-Tree	Red Maple – <i>Acer rubrum</i>	4	10	40
Native-Tree	Sweetgum- <i>Liquidambar styraciflua</i>	4	10	40
Native-Tree	White Pine – <i>Pinus strobes</i>	4	8††	32††
Native-Tree	Willow Oak – <i>Quercus phellos</i>	8	10	80
Native- Shrub	Alternate leaf dogwood – <i>Cornus alternifolia</i>	4	10	40
Native- Shrub	Buttonbush – <i>Cephalanthus occidentalis</i>	4	10	40
Native- Shrub	Chokeberry – <i>Aronia arbutifolia</i>	4	10	40
Native- Shrub	Viburnum – <i>Viburnum dentatum</i>	4	10	40
Native- Shrub	Winterberry – <i>Ilex verticillata</i>	4	10	40
Native- Shrub	Witchhazel – <i>Hamamelis virginiana</i>	4	10	40
Alien - Tree	Autumn Olive- <i>Elaeagnus umbellate</i>	8	10	80
Alien - Tree	Golden Rain Tree – <i>Koelreuteria paniculata</i>	4†	10†	40†
Alien - Tree	Japanese Cherry – <i>Prunus serrulata</i>	8	10	80
Alien - Tree	Kousa Dogwood – <i>Cornus kousa</i>	4	10	40
Alien - Tree	Littleleaf Linden – <i>Tilia cordata</i>	4	10	40
Alien - Tree	Norway Maple – <i>Acer platanoides</i>	4	10	40
Alien - Tree	Norway Spruce – <i>Picea abies</i>	4	8††	32††
Alien - Shrub	Andromeda – <i>Pieris japonica</i>	4	10	40
Alien - Shrub	Azalea – <i>Rhododendron sp.</i>	4	10	40
Alien - Shrub	Burning Bush – <i>Euonymus alatus</i>	4	10	40
Alien - Shrub	Cotoneaster – <i>Cotoneaster lucida</i>	6	30	180
Alien - Shrub	Forsythia – <i>Forsythia x intermedia</i>	4	10	40
Alien - Shrub	Privet – <i>Ligustrum obtusifolium</i>	4	10	40

† = Compound leaves and leaflets, †† = Rated 2 inch sections of needles

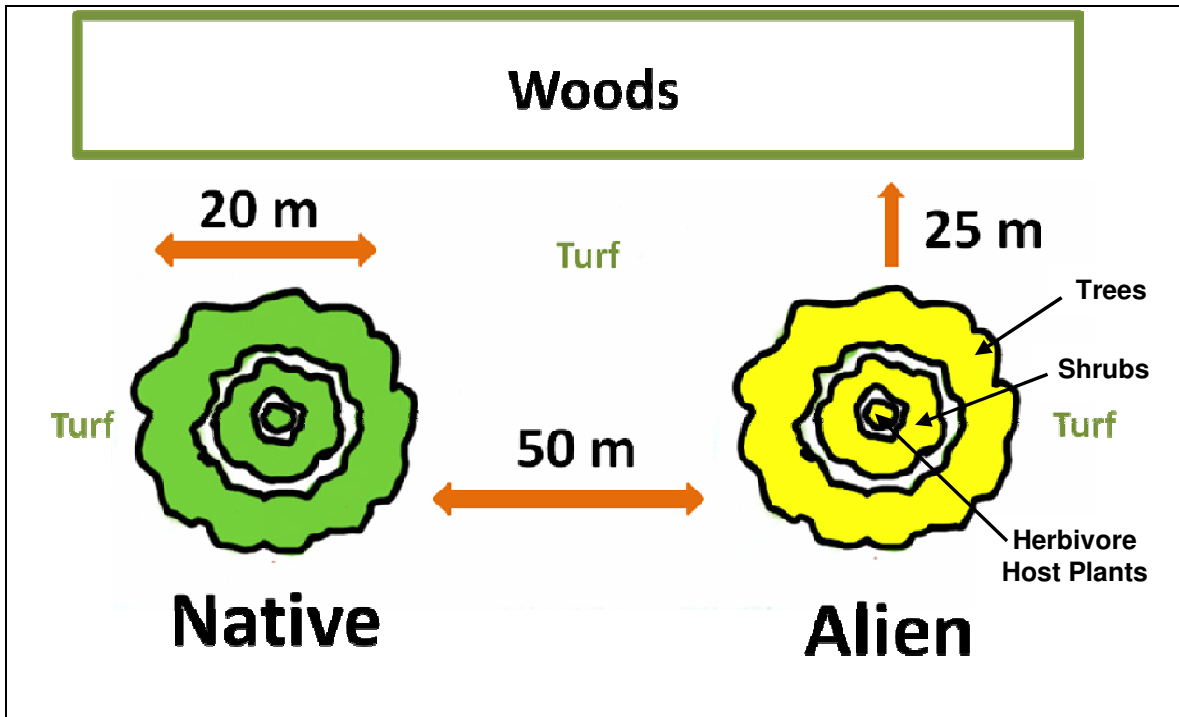


Fig. 1. Design of native and alien pairs of treatment landscapes. Each landscape plot was planted with native or alien trees (outer ring), shrubs (inner ring) and trees and shrubs that served as host plants for sentinel herbivores (center). The landscape plots are located 25 m from a woodlot edge and are surrounded by a turfgrass buffer.

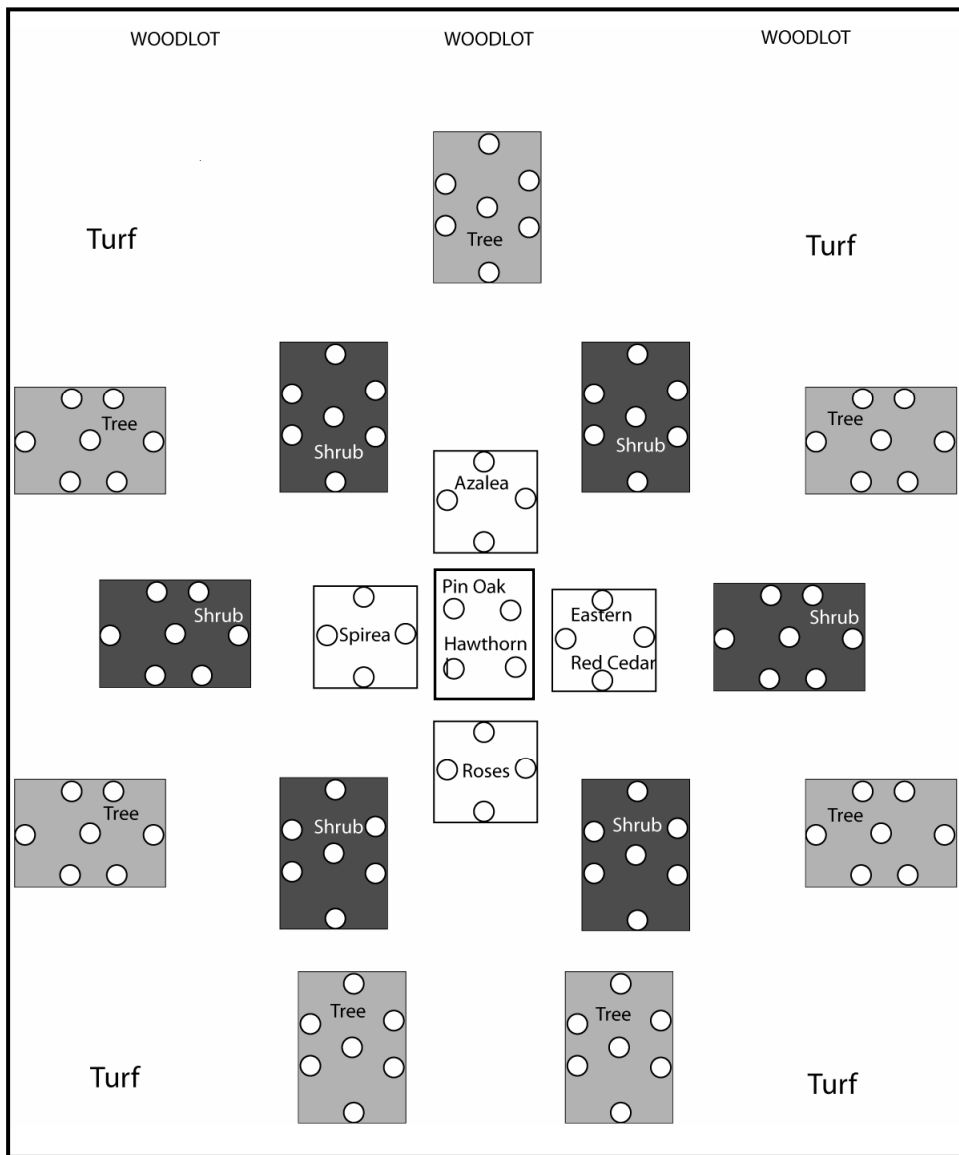
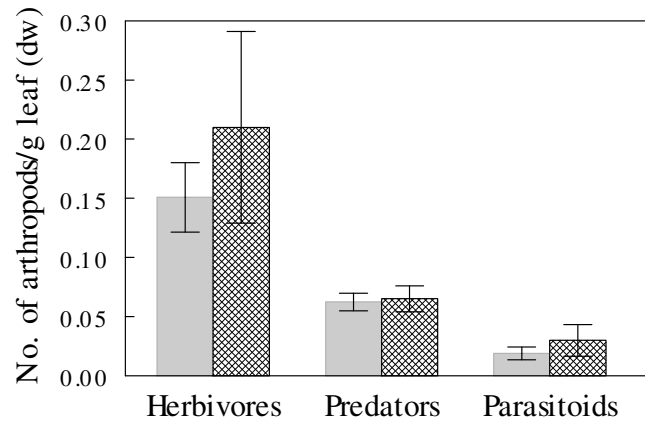


Fig. 2. Design of an individual treatment landscape. Each treatment landscape is composed of seven species of native or alien trees (light grey boxes, outer ring) and six species of native or alien shrubs (dark grey boxes, inner ring). Circles are individual plants (seven plants per species); hardwood mulch was placed between plants in each tree or shrub bed. Herbivore host plants were at the center of the treatment landscape and used to test the survival of sentinel herbivore populations. Each treatment landscape has five groups of herbivore host plants. These groups were: 1) four eastern red cedars, 2) four commercial roses, 3) four spireas, 4) four azaleas, and 5) two pin oaks and two Washington hawthorns. All treatment landscapes were located 25m from a woodlot and were surrounded by turf.

A. Abundance 2006



B. Abundance 2007

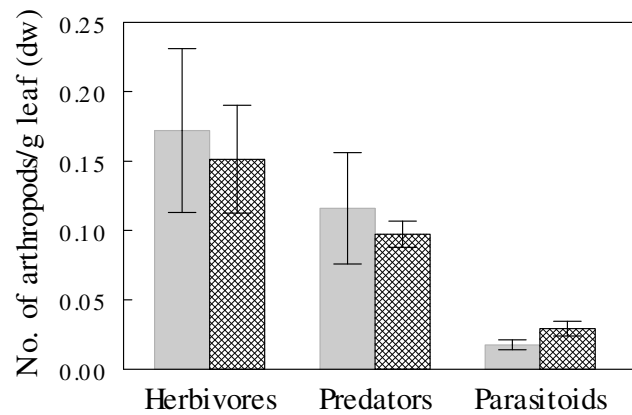
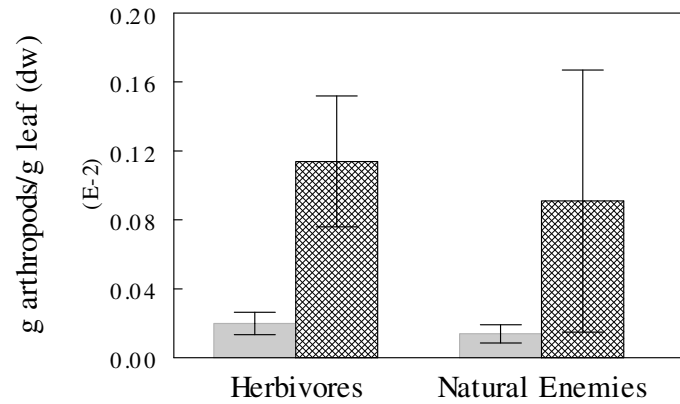


Fig 3. A,B. The mean arthropod abundance (number) / g leaf (dw) of arthropod trophic guilds (herbivores, predators, parasitoids) sampled in 2006 (A) and 2007 (B) in native (black hash bars) and alien (grey bars). Note: Y-axis differ between years. Bars without letters did not significantly differ within a trophic group ( $P < 0.05$ ).



A. Biomass 2006



B. Biomass 2007

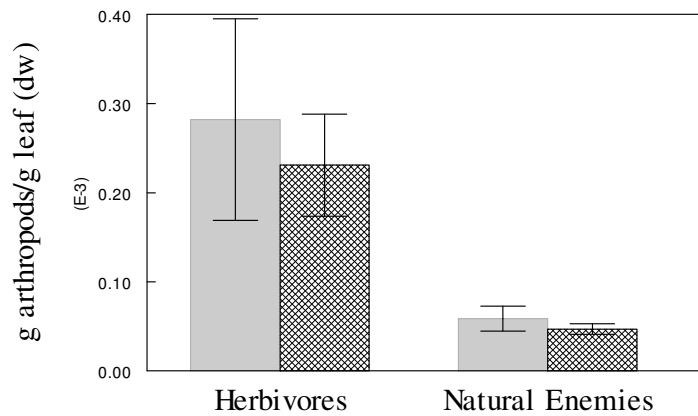
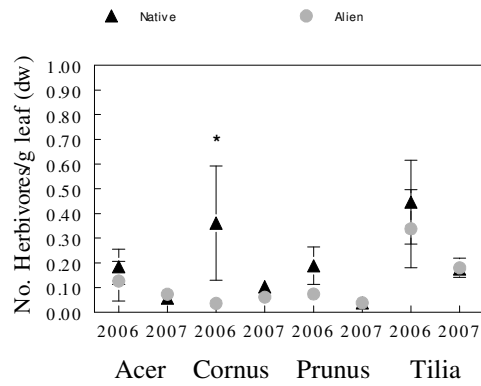
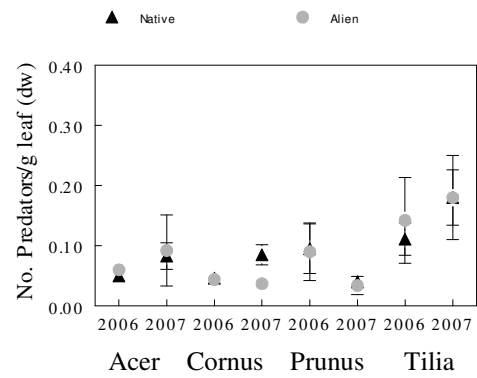


Fig 4. A,B. The mean biomass (g dw) / g leaf (dw) of arthropod trophic guilds (herbivores and natural enemies (predators and parasitoids pooled) sampled in 2006 (A) and 2007 (B) in native (black hash bars) and alien (grey bars). Note: Y-axis differ between years. Bars without letters did not significantly differ within a trophic group ( $P < 0.05$ ).

A. Herbivores



B. Predators



C. Parasitoids

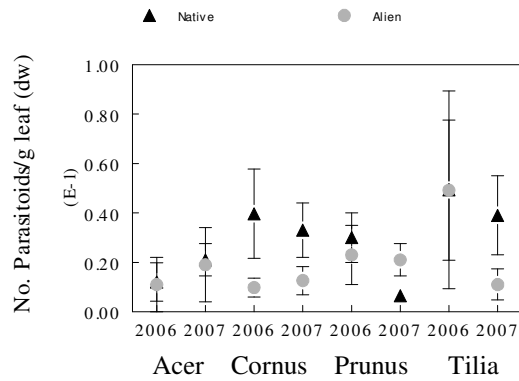
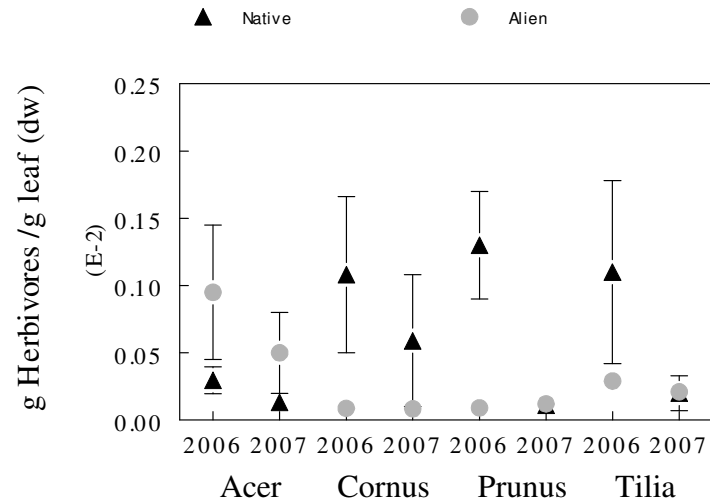


Fig. 5 A-C. The mean abundance (number) of herbivores (A), predators (B), and parasitoids (C) / g leaf (dw) sampled from alien and native pairs of congeneric plants in August 2006 and August 2007. A *P*-value less than 0.05 was considered a significant difference (\*) between native and alien congeners within a year.

## A. Herbivores



## B. Natural Enemies

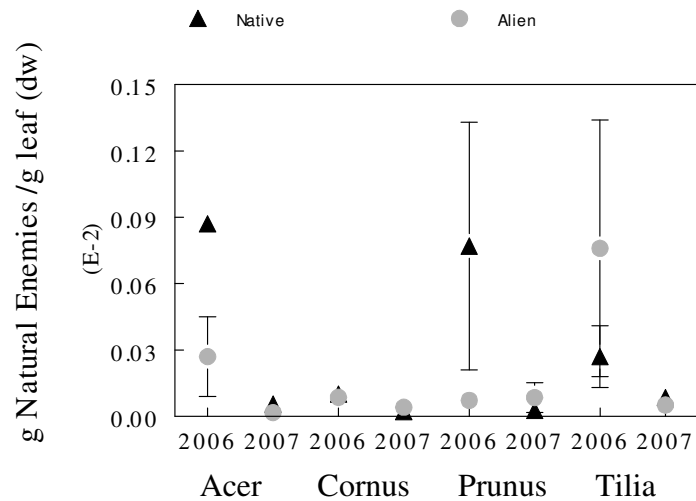


Fig. 6 A,B. The mean herbivore (A) and natural enemy (predators and parasitoids pooled) (B) biomass (g dw) / g leaf (dw) sampled from alien and native pairs of congeneric plants in August 2006 and August 2007. A *P*-value less than 0.05 was considered a significant difference (\*) between native and alien congeners within a year.

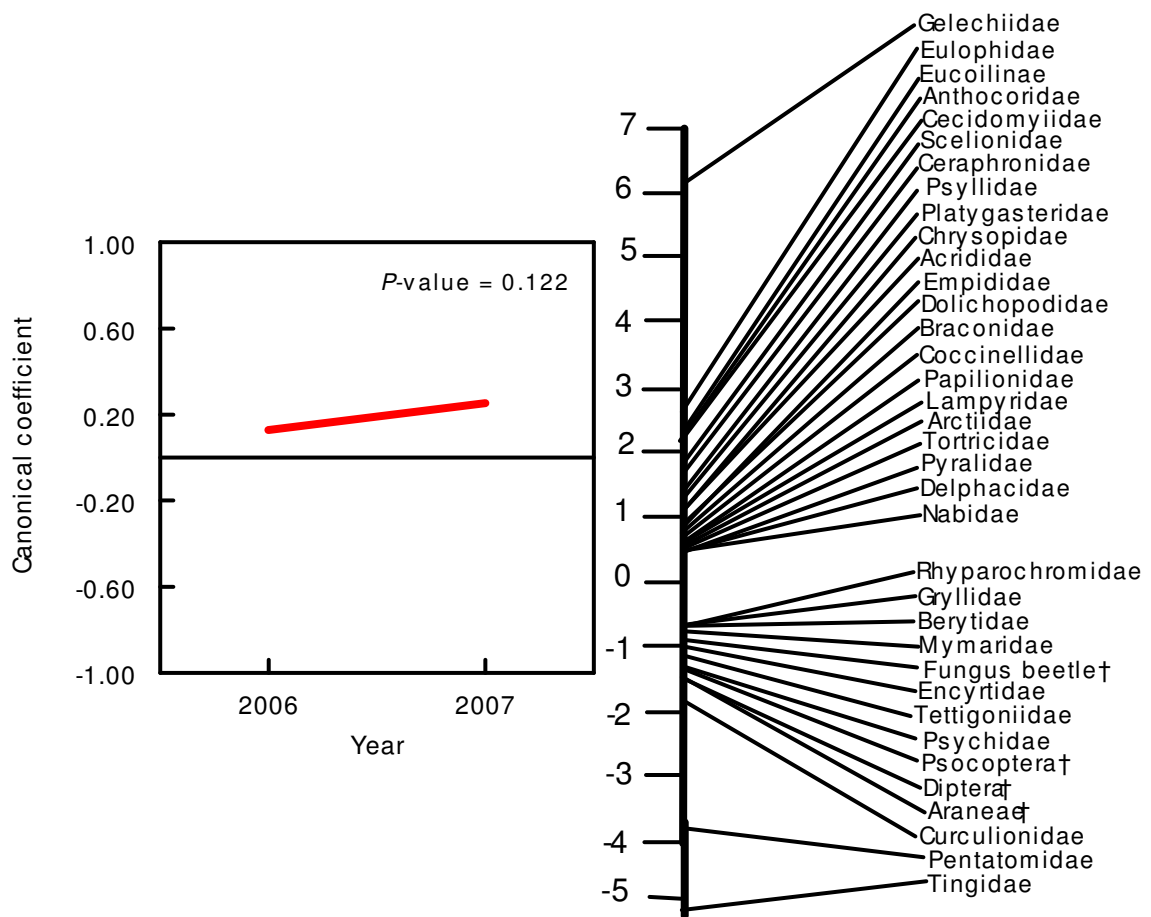
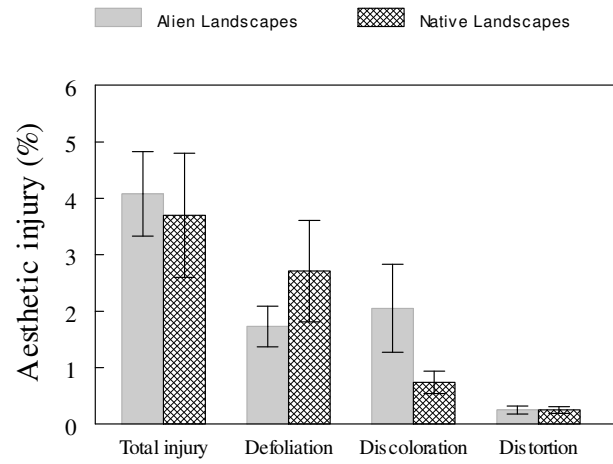


Fig. 7. PRC graph showing differences in the structure of arthropod communities at the family level in native and alien treatment landscapes. Alien landscapes were designated as the control and are represented by the straight line at 0. Native landscapes are represented by the red line. The structure of the arthropod communities in native and alien landscapes were not significantly different ( $F=1.56$ ;  $P=0.122$ ). The taxon weights show the association of certain arthropod families and groups to the PRC. Families with high positive weights are showing a pattern similar to that of the PRC; these families tend to be more abundant in native landscapes. Families with high negative weights are showing the opposite pattern and tend to be more abundant in the alien landscapes. Families with weights between 0.5 and -0.5 do not contribute to the pattern seen in the PRC. A ‘†’ indicates that the group of arthropods consists of several families.

A. June 2007



B. August 2007

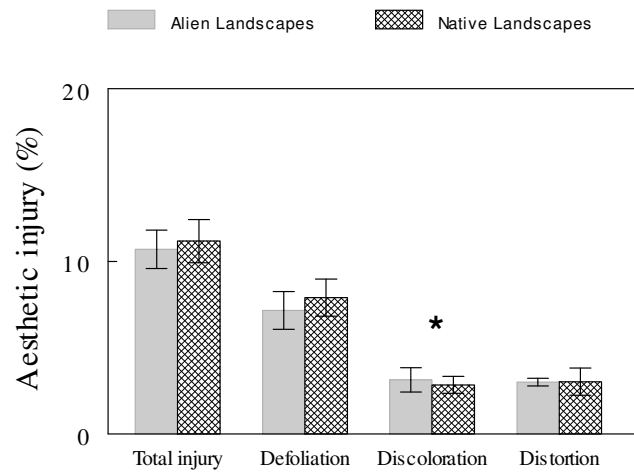
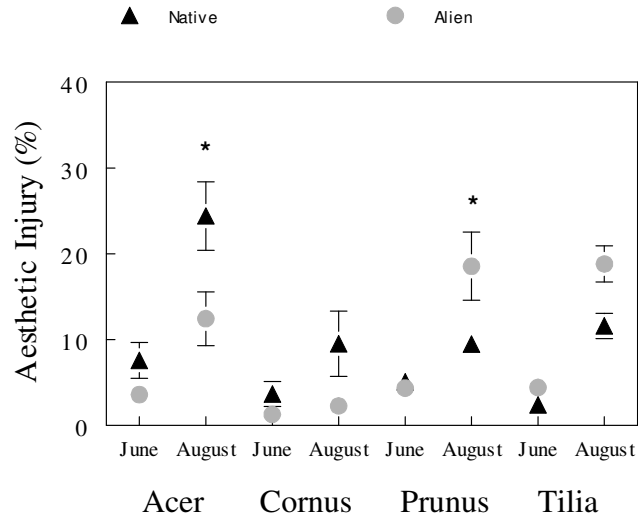


Fig. 8 A,B. Mean aesthetic injury (%) of alien and native landscapes in June (A) and August (B) 2007. The percent injury is presented as total damage and by injury type (defoliation, discoloration and distortion). A *P*-value less than 0.05 was considered a significant difference (\*) between native and alien landscapes within an injury category. Note: Y-axis are presented at different scales

### A. Total Injury



### B. Defoliation

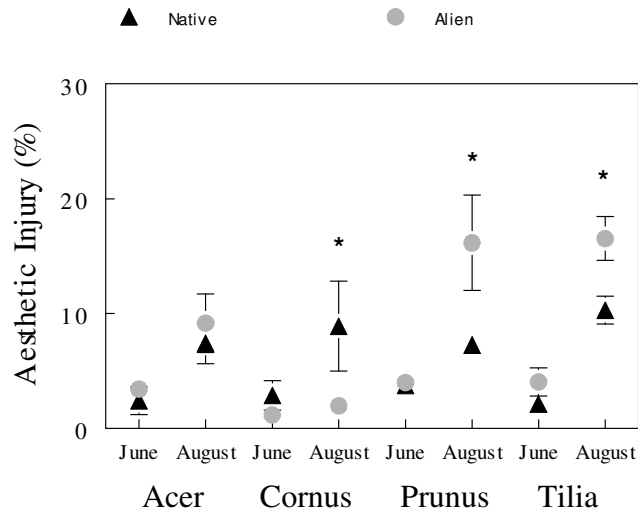
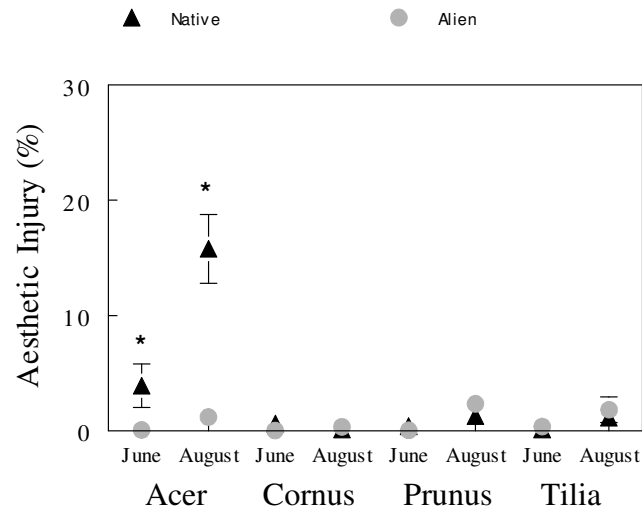


Fig. 9 A,B. Mean aesthetic injury (%) of congeneric pairs of alien and native plants in June and August 2007. For total injury (A) and defoliation injury (B) a  $P$ -value less than 0.05 was considered a significant difference (\*) between native and alien congeners within a date and injury type. Note: Y-axis are presented at different scales.

### A. Discoloration



### B. Distortion

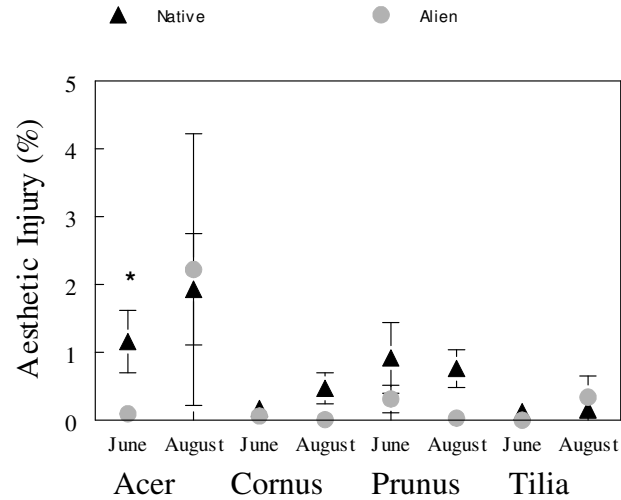


Fig. 10 A,B. Mean aesthetic injury (%) of congeneric pairs of alien and native plants in June and August 2007. For discoloration injury (A) and distortion injury (B) a *P*-value less than 0.05 was considered a significant difference (\*) between native and alien congeners within a date and injury type. Note: Y-axis are presented at different scales.

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