Biol Invasions (2008) 10:1159–1169
DOI 10.1007/s10530-007-9193-y

ORIGINAL PAPER

Effects of non-native plants on the native insect community of Delaware

Marion E. Zuefle · William P. Brown · Douglas W. Tallamy

Received: 8 June 2007 / Accepted: 15 November 2007 / Published online: 29 November 2007

Abstract Due to the lack of a co-evolutionary history, the novel defenses presented by introduced plants may be insurmountable to many native insects. Accordingly, non-native plants are expected to support less insect biomass than native plants. Further, native insect specialists may be more affected by introduced plants than native generalist herbivores, resulting in decreased insect diversity on non-native plants due to the loss of specialists. To test these hypotheses, we used a common garden experiment to compare native insect biomass, species richness, and the proportion of native specialist to native generalist insects supported by 45 species of woody plants. Plants were classified into three groupings, with 10 replicates of each species: 15 species native to Delaware (Natives), 15 non-native species that were congeneric with a member of the Native group (Non-native Congeners), and 15 non-native species that did not have a congener present in the United States (Aliens). Native herbivorous insects were sampled in May, June, and July of 2004 and 2005. Overall, insect biomass was greater on Natives than Non-native Congeners and Aliens, but insect biomass varied unpredictably between congeneric pair members. Counter to expectations, Aliens held more insect biomass than did Non-native Congeners. There was no difference in species richness or the number of specialist and generalist species collected among the three plant groupings in either year, although our protocol was biased against sampling specialists. If these results generalize to other studies, loss of native insect biomass due to introduced plants may negatively affect higher trophic levels of the ecosystem.

Keywords Insect communities · Invasive plants · Phytophagous insects

Abbreviation

USDA	United States Department of Agriculture

Introduction

Non-native plants have been intentionally and accidentally introduced to the United States since the arrival of the earliest European colonists. Intentional introductions include crops, wood and fiber plants, medicinal plants, and landscape plants. Landscape plants, defined by Reichard (1996) to include plants used as ornamentals, for soil protection, or wildlife habitat, make up 85% of all non-native plant introductions. The remaining non-native plants were introduced accidentally in contaminated soil, cotton,

M. E. Zuefle (✉) · D. W. Tallamy
Department of Entomology and Wildlife Ecology,
University of Delaware, Newark, DE 19716-2160, USA
e-mail: mzuefle@yahoo.com

W. P. Brown
Department of Biological Sciences, Kutztown University,
Kutztown, PA 19530, USA

wool, grain, machinery, or in ship ballast (Randall 1996). Many non-natives, whether introduced intentionally or not, have entered natural ecosystems and proliferated. Such plants are considered "invasive" (Randall 1996).

There are approximately 3,430 non-native plant species established in the United States (Qian and Ricklefs 2006), which may threaten natural ecosystems by out-competing native species and changing ecosystem functions such as the fire regime or hydrological cycling (Blossey 1999). Others increase soil erosion or alter nutrient availability, while still others such as white mulberry (*Morus alba*) and oriental bittersweet (*Celastrus orbiculatus*) hybridize with native congeners, potentially leading to the loss of native strains (Wilcove et al. 1998; Brooks et al. 2004).

Invasive plants possess general characteristics that allow them to out-compete native plants. They are highly adaptable and tolerate variable climatic conditions. Often, they are fast growing, easily dispersed, produce numerous seeds early in life, reproduce vegetatively, have a long reproductive life, and germinate without any special requirements (Rejmánek and Richardson 1996; Reichard and Hamilton 1997; Staples et al. 2000; Kolar and Lodge 2001). The general inability of native insects to eat non-native plants may release such plants from natural enemies and thus promote invasive behavior (Elton 1958; Lodge 1993; Yela and Lawton 1997). Similarly, non-native ornamental plants were historically selected because they lacked native insect herbivores (Dirr 1998). The effect of invasive, ornamental plants on the native insect community has received little empirical attention, however (Tallamy 2004).

The lack of native insect herbivores on non-native plants is predicted by the "enemy release" hypothesis (Williamson 1996; Keane and Crawley 2002). This hypothesis assumes that insects that specialize on non-native plants are not present in the introduced range, that host switching by native insect specialists onto non-native plants is rare, and that native generalist herbivores negatively affect native plants more than non-native plants. Several studies support the assumption that non-native plants have fewer insect herbivores in their introduced range (Goeden 1974; Strong et al. 1984; Andow and Imura 1994; Fenner and Lee 2001; Wolfe 2002), but few studies have looked at differences in insect herbivory between a non-native species and its native congener (Vila and Weiner 2004; Agrawal et al. 2005). Such a conservative comparison is necessary because insect herbivores are predicted to discriminate among non-native plants based on how closely related they are to the native food source (Ehrlich and Raven 1965).

Non-native plants are predicted to have a greater percentage of their insect herbivore load comprised of generalists, while their native congeners are expected to have a higher percentage of specialized herbivores (Goeden 1974; Strong et al. 1984; Andow and Imura 1994; Fenner and Lee 2001); moreover, generalist insects may accept novel plant hosts more readily than specialists (Ehrlich and Raven 1965). It is estimated that 90% of phytophagous insects restrict their feeding to host plants in three or fewer families (Bernays and Graham 1988). For this reason, introduced plant species without a native congener are predicted to support even fewer insect herbivores than those that are congeneric with a native species in the introduced range (Rejmánek 1999).

Our objective was to determine if host use by native insect herbivores was influenced by plant origin (native or non-native). We determined differences in native insect biomass, native insect species richness, and the proportion of native specialist: generalist insects on native plant species, introduced congeners of native species, and introduced plants without a native congener present in the United States. We also determined if native insect biomass and native insect species richness differed between members of congeneric pairings. Congeneric comparisons constitute the most conservative measure of the ability of non-native plants to support native insect communities.

Methods

Study site

The study plot was located within White Clay Creek State Park (WCCSP), a 1,369 ha multiple use area located in New Castle County, Delaware. The plot measured 42 m × 31.5 m (0.13 ha) and was established in a level area of uniform soil composition (Chester Loam (ChB2); Matthews and Lavoie 1970) at the edge of a hayfield bordered by mature forest and a hedgerow. The hayfield had been in existence for 10 years and was hayed approximately three times annually. The plot, located in the hayfield, was separated from the forest by approximately 12 m to allow the perimeter of the hayfield to be mowed. A plastic mesh deer fence approximately 2 m high and five electrified strands of 12-gauge wire surrounded the plot.

Plant selection

Native plants (Natives) were defined as those plants native to Delaware (McAvoy and Bennett 2001). A native species was selected for study only if it could be found within the boundaries of WCCSP (MEZ, pers. obs.) and had a non-native congener present in Delaware. Non-native Congeners, defined as not having an evolutionary history in the Mid-Atlantic region of North America but having a native congener present in WCCSP, were identified from the USDA plants database (USDA 2003). Non-native Congeners were selected for study if they were commonly planted as ornamentals in the surrounding area or considered invasive in Delaware (McAvoy and Bennett 2001). Finally, Aliens, defined here as those plants not native to the United States (US) that had no native congener within the US, also were identified from the USDA plants database (USDA 2003). Aliens were selected for study if they were frequently planted in the surrounding landscape or considered invasive in Delaware (McAvoy and Bennett 2001).

Two additional criteria were used to determine which plants were selected for study. First, all plants had to be available through the nursery trade at a reasonable cost (<$100/plant). Second, all plants had to be woody, as life form is known to influence the herbivorous insect community (Ward et al. 1995). From these criteria, three groupings of 15 Natives, 15 Non-native Congeners, and 15 Aliens totaling 45 species in 30 genera were selected (Table 1).

Experimental design

The study plot was divided into 10 blocks of uniform area. All 45 species were randomly distributed within each block ($n = 10$ replicates of each species), but with each member of the congeneric pair (Native and Non-native Congener) always occurring next to each

Table 1 Family, scientific name, and plant code for the 15 Native, Non-native Congener, and Alien plant species used in this study

Family	Native	Code	Non-native Congener	Code	Family	Alien	Code
Aceraceae	*Acer rubrum*	ACRU	*A. platanoides*	ACPL	Lardizabalaceae	*Akebia quinata*	AKQU
Betulaceae	*Betula nigra*	BENI	*B. pendula*	BEPE	Fabaceae	*Albizia julibrissin*	ALJU
Betulaceae	*Carpinus caroliniana*	CACA	*C. betulus*	CABE	Rosaceae	*Cotoneaster lucidus*	COLU
Cornaceae	*Cornus florida*	COFL	*C. kousa*	COKO	Fabaceae	*Cytisus scoparius*	CYSC
Fagaceae	*Fagus grandifolia*	FAGR	*F. sylvatica*	FASY	Oleaceae	*Forsythia suspensa*	FOSU
Hamamelidaceae	*Hamamelis virginiana*	HAVI	*H. mollis*	HAMO	Ginkgoaceae	*Ginkgo biloba*	GIBI
Juglandaceae	*Juglans nigra*	JUNI	*J. regia*	JURE	Araliaceae	*Hedera helix*	HEHE
Moraceae	*Morus rubra*	MORU	*M. alba*	MOAL	Sapindaceae	*Koelreuteria paniculata*	KOPA
Rosaceae	*Prunus serotina*	PRSE	*P. serrulata*	PRSU	Lythraceae	*Lagerstroemia indica*	LAIN
Ericaceae	*Rhododendron periclymenoides*	RHPE	*R. mucronatum*	RHMU	Oleaceae	*Ligustrum vulgare*	LIVU
Rosaceae	*Rosa carolina*	ROCA	*R. multiflora*	ROMU	Scrophulariaceae	*Paulownia tomentosa*	PATO
Salicaceae	*Salix nigra*	SANI	*S. babylonica*	SABA	Rutaceae	*Phellodendron amurens*	PHAM
Tiliaceae	*Tilia americana*	TIAM	*T. cordata*	TICO	Rutaceae	*Poncirus trifoliata*	POTR
Ulmaceae	*Ulmus americana*	ULAM	*U. parvifolia*	ULPA	Rosaceae	*Pyrus pashia*	PYPA
Caprifoliaceae	*Viburnum dentatum*	VIDE	*V. dilatatum*	VIDI	Oleaceae	*Syringa vulgaris*	SYVU

See "Methods" for an explanation of the three plant groupings other. The plants were spaced 1.5 m apart and planted early April 2004. Plant heights were approximately 0.5–1 m at the time of planting and increased to as high as 3 m by August 2005.

Insect sampling

Insects were collected in mid-June, -July, and -August of 2004 and 2005. Approximately 3 days before collecting, the plot was mowed and all study plants were carefully weeded to ensure that insects were not sampled from the surrounding vegetation. Three replicates of the 15 congeneric pairings and three replicates of the 15 Alien plant species were randomly selected for insect sampling during each collection period, totaling 135 plants sampled per collection. Only three replicates were sampled per collection to prevent any effect sampling might have on reestablishment of insects prior to the next collection. No plant was sampled more than once a year.

During the 2004 season, Prentox® ExciteR™ containing 6% Pyrethrins and 60% Piperonyl Butoxide was sprayed on all surfaces of each plant targeted for insect sampling. Dead insects were collected from a sheet placed beneath the plant and stored in vials of 80% ethyl alcohol (ETOH). Sampling was completed between 5:30 and 7:30 a.m. on June 19–21, July 19–21, and August 19–21. As all 10 replicates of *Koelreuteria paniculata* died after the first planting, the first samples from *K. paniculata* were collected in July 2004 from replacement plants.

During the 2005 season, we used an inverted leaf blower to collect insects, rather than the spray used in 2004. We discovered that spraying left very small dead insects (i.e., aphids and cicadellids) stuck to leaf surfaces. Based on experimental trials conducted elsewhere, we determined that the leaf blower avoided this problem. A paint strainer bag was inverted into the end of the leaf blower and insects were "vacuumed" from each plant into the bag. The bags were labeled and placed into coffee tins containing ethyl acetate to kill the insects. Insects were then placed into labeled vials of 80% ETOH. Three individuals of each plant species were randomly sampled per collection, as in 2004. Samples were collected on June 16, July 14, and August 23, 2005; sampling lasted only 1 day per collection in 2005 as the inverted leaf blower technique was more efficient than spraying. As all plants were sampled using the same technique within a given year, and no comparisons between years were made, our results were not confounded by varying sampling protocols between years.

Leaf biomass

To determine leaf biomass, approximately 100 leaves were collected from each plant species throughout the 2004 growing season (10 leaves from each plant). These leaves were weighed on a Mettler AE100 scale to the nearest 0.01 g, providing an average biomass per leaf for each species. The total number of leaves for each plant was counted within a few days of sampling to provide an estimate of total leaf biomass for each plant at the time of sampling.

Insect identification and biomass

Each insect morpho-species collected was given a reference number, identified to family, dried, and weighed on a Mettler AE100 scale to the nearest 0.0001 g. A reference collection was created containing several representatives of each morpho-species, when available. This reference collection was then used to determine insect species or operational taxonomic units (OTU's; Futuyma and Gould 1979), if species identification was not possible. Species determinations were based on Delong (1948), Slater and Baranowski (1978), Hamilton (1982), White (1983), Stehr (1987), Arnett et al. (2002), Wagner (2005), and the University of Delaware's insect reference collection.

Only native herbivorous insects were considered in this study. As we were interested in the effect non-native plants had on native insect biomass, we assumed that each plant from which an herbivorous insect was collected was indeed a host plant. All identified insects were classified as either native to the US or non-native (see references for insect identification, above). Insects classified as OTU's were assumed native, providing a conservative estimate of the effect non-native plants had on the biomass and species richness of the native insect community.

Statistical analysis

Prior to analysis, insect biomass data were scaled to the leaf biomass of each host plant and log transformed using the following equation:

$$\mathrm{LOG}_{10}\left(((x+1)/y)*10^{6}\right)$$

where x is the total insect biomass collected from each plant and y is the total leaf biomass for each plant, determined at the time of insect collection. This transformed ratio is referred to hereafter as insect biomass. The log transformation was used to provide a normal distribution of data. As some plants had no insect biomass collected from them, we added 1.0 to insect biomass totals for each plant before transformation, thereby retaining plants without insects in analyses.

Species richness was determined as the total number of insect species and OTU's collected from each plant species (Krebs 1999) for 2004, 2005, and both years combined.

Specialists/generalists

To determine if there were differences in the number of specialist insects among Natives, Non-natives Congeners, and Aliens, we followed the methods of Futuyma and Gould (1979). All insects found on more than three plant families were classified as generalists. The remaining species were classified as specialists only if we collected at least 10 individuals of each species over the course of the study. All other species were removed from consideration because the number of individuals must be large enough to determine feeding preference (Futuyma and Gould 1979) and to verify that they were not spuriously collected. Chi-square tests were used to determine differences in the ratio of specialists: generalists among our three plant groupings.

Insect biomass

To determine if there were differences in mean insect biomass among Natives, Non-native Congeners, and Aliens in 2004 and 2005, we used a repeated-measures ANOVA (PROC MIXED; SAS Institute, Inc. 2004), due to the three sampling periods (June, July, and August) in each year (data for 2004 and 2005 were not combined). To control for any differences among the blocks of our study plot due to microhabitat or edge effects, block number was considered as a random effect in the model. The MIXED procedure uses maximum likelihood, an iterative process that may require several passes through the data to estimate stable coefficients. In some cases, no convergence on stable estimates was possible, even after a large number of iterations. While poor model specification may cause lack of convergence, misspecification is often associated with trying to estimate coefficients that are close to or equal to zero, which, in turn, leads to lack of convergence. For analyses presented here, specified models did not always converge for comparisons with no or few insects collected from one member of the congeneric pair or plant grouping (e.g., Aliens) in a given collection period, or even in a year; these results were indicated where appropriate. If there was a difference among plant groupings within a year (based on the F-distribution and Type III sums of squares), pair-wise comparisons were evaluated within the context of the MIXED model based on an approximated t-distribution for each pair member (SAS documentation, SAS Institute, Inc. 2004).

To examine insect biomass between congeneric pair members in 2004 and 2005, we compared the difference in insect biomass between Natives and Non-native Congeners to zero using a repeated measures design (PROC MIXED), with month specified as a repeated measure. Block number was included as a random term in the model.

Species richness

Least squares means regression (PROC GLM; SAS Institute, Inc. 2004) was used to determine differences in species richness among plant groupings (Natives, Non-native Congeners, and Aliens). Samples from all replicates were combined to give an overall insect species richness for each plant species in each year of the study, which removed the need for a repeated measures design. Least squares means also were used to test the difference in species richness between each congeneric pair in 2004, 2005, and the combined years.

As with insect biomass, differences in species richness between congeneric pair members in 2004, 2005, and both years combined also were compared to a value of zero using a repeated measures design, with month specified as the repeated measure. Block number was included as a random term in the model.

Results

We collected a total of 4,816 individual insects comprising 163 native herbivorous insect species or OTU's for 2004 and 2005 combined. The 163 insect species or OTU's belonged to 45 insect families and six insect orders (Orthoptera, Hemiptera, Homoptera, Coleoptera, Lepidoptera, and Hymenoptera; see Appendices D, E, and F in Zuefle (2006) for a list of insects found on each plant species).

Specialists/generalists

Of the 163 native insect species collected in this study, 106 species were not classified as specialists or generalists because we collected fewer than ten individuals on three or fewer plant families. Of the remaining 57 species, 51 were generalists (found on more than three plant families), and six were specialists ($\geq$10 individuals found on three or fewer families). Of the 51 generalists, 44 were found on Natives, 49 were found on Non-native Congeners, and 47 were found on Aliens. Of the six specialists, four were found on Natives, five were found on Non-native Congeners, and three were found on Aliens. Based on Chi-square tests, there was no difference in the ratio of specialist to generalist insects found on Native, Non-native Congener, and Alien plant species groupings ($P > 0.05$ in all pair-wise comparisons).

Insect biomass

Insect biomass among Natives, Non-natives Congeners, and Aliens differed in 2004 ($F = 26.6$, $P < 0.0001$). Natives supported more insect biomass than Non-native Congeners ($t = 4.2$, $P < 0.0001$). The difference between Natives and Aliens as well as Non-native Congeners and Aliens were non-estimable for 2004 (models did not converge). Insect biomass among Natives, Non-native Congeners, and Aliens also differed in 2005 ($F = 9.5$, $P = < 0.0001$) and for this year we were able to estimate pair-wise differences among all three groups. The insect biomass on Natives was greater than on Aliens ($t = -2.2$, $P = 0.03$) and greater than Non-native Congeners ($t = 4.4$, $P < 0.0001$). Aliens, however, held more insect biomass than Non-native Congeners ($t = 2.1$, $P = 0.03$). Although some species in each group held little to no insect biomass, biomass results were not skewed by disproportionate contributions from a small number of plant species in each group (see Appendices B and C in Zuefle 2006).

Of the 15 congeneric comparisons from 2004, seven Natives had greater insect biomass, four Non-native Congeners had greater insect biomass, and four showed no difference (Table 2). Similar results were obtained for 2005; six Native pair members had greater insect biomass, three Non-native Congeners had greater insect biomass, and there was no difference in insect biomass between members of the remaining six pairings (Table 2). The results differed between the two years because native *Fagus* and non-native *Hamamelis*, which had greater insect biomass in 2004, did not differ from their non-native congeneric pair member in 2005.

Species richness

There was no difference in species richness among Native, Non-native Congener, and Alien plant species in either year, nor in both years combined (Fig. 1).

Most of the 15 congeneric pair members did not differ in species richness in either year (we were unable to determine an estimate for several comparisons because the model did not converge; Table 3). In 2004, one Non-native Congener had greater species richness than its Native pair member. In 2005, one of the Natives had greater richness than its Non-native Congener.

Discussion

Our data did not support the hypothesis that phytophagous insects are predominantly specialists (Eastop 1973; Futuyma and Gould 1979; Chapman 1982; Price 1983; Bernays and Graham 1988).

Table 2 Insect biomass differences between congeneric pair members for 2004 and 2005 based on a repeated measures ANOVA

Year	Genus	Native	Non-native	*N*	Estimate	Standard error	*t*-value	*P*-value
2004	Acer	ACRU	ACPL	9	**0.58**	0.08	7.27	**0.002**
	Betula	BENI	BEPE	9	**−0.45**	0.07	−6.22	**0.002**
	Carpinus	CACA	CABE	9	−0.35	0.17	−2.11	0.111
	Cornus	COFL	COKU	9	0.08	0.12	0.63	0.564
	Fagus	FAGR	FASY	9	**0.33**	0.06	5.59	**0.007**
	Hamamelis	HAVI	HAMO	9	**−0.22**	0.07	−3.05	**0.036**
	Juglans	JUNI	JURE	9	**0.40**	0.10	4.22	**0.011**
	Morus	MORU	MOAL	9	**−0.76**	0.16	−4.89	**0.012**
	Prunus	PRSE	PRSU	9	**0.14**	0.03	4.08	**<0.0001**
	Rhodo.	RHPE	RHMU	9	**0.37**	0.03	10.84	**0.001**
	Rosa	ROCA	ROMU	9	0.19	0.12	1.52	0.180
	Salix	SANI	SABA	9	**0.90**	0.10	8.94	**0.001**
	Tilia	TIAM	TICO	9	0.23	0.14	1.62	0.171
	Ulmus	ULAM	ULPA	9	**0.42**	0.05	9.30	**0.002**
	Viburnum	VIDE	VIDI	9	**−0.34**	0.08	−4.25	**0.044**
2005	Acer	ACRU	ACPL	9	**0.44**	0.14	3.28	**0.031**
	Betula	BENI	BEPE	9	**−0.69**	0.12	−5.60	**0.021**
	Carpinus	CACA	CABE	9	0.07	0.13	0.54	0.612
	Cornus	COFL	COKU	9	0.10	0.15	0.68	0.537
	Fagus	FAGR	FASY	9	0.13	0.06	2.12	0.115
	Hamamelis	HAVI	HAMO	9	−0.16	0.11	−1.38	0.234
	Juglans	JUNI	JURE	9	**0.28**	0.07	4.01	**0.014**
	Morus	MORU	MOAL	9	**−0.46**	0.12	−3.85	**0.016**
	Prunus	PRSE	PRSU	9	**0.14**	0.03	4.03	**<0.0001**
	Rhodo.	RHPE	RHMU	9	**0.25**	0.04	6.29	**0.001**
	Rosa	ROCA	ROMU	9	0.25	0.16	1.53	0.210
	Salix	SANI	SABA	9	**0.92**	0.22	4.08	**0.014**
	Tilia	TIAM	TICO	9	0.04	0.09	0.48	0.659
	Ulmus	ULAM	ULPA	9	**0.32**	0.05	7.01	**0.002**
	Viburnum	VIDE	VIDI	9	**−0.38**	0.04	−8.23	**0.010**

If the estimate was positive then the Native pair member held more insect biomass, if the estimate was negative then the Non-native Congener held more insect biomass. Significant values are in bold. See Table 1 for plant codes

However, the rarity of two thirds of the herbivores we collected prevented their classification as generalists or specialists. Of the 57 insect species that we could categorize, 89% were generalists and 11% were specialists. This is inconsistent with other studies that have found that less than 10% of all phytophagous insects were generalists and 90% were specialists (see references in Bernays and Graham 1988). The young age of our study plants might explain this discrepancy. Specialist insects are predicted to be more numerous in habitats containing large numbers of their host plants than in areas with few hosts (Southwood 1961; Root 1973; Kareiva 1982; Strong et al. 1984; Auerbach and Simberloff 1988; Andow 1991). As we first sampled only two months after planting in 2004 and just over 1 year after planting in 2005, specialist insects may have been underrepresented in our study if they required more time than generalists to locate our study plot, or if they preferred larger or more numerous specimens than the plants we provided in our experiment. Also, our sampling methodology focused on folivores and

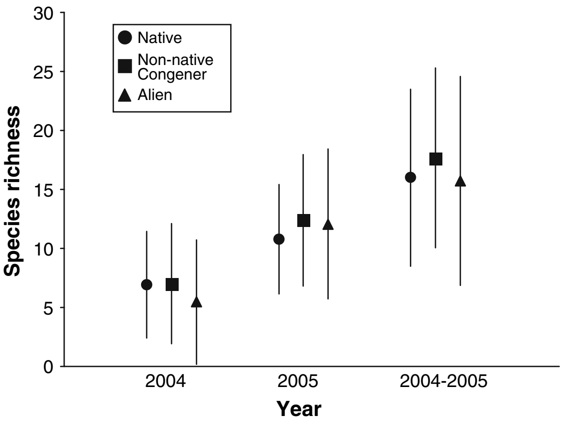

Fig. 1 Mean species richness for Natives, Non-native Congeners, and Aliens for 2004, 2005, and both years combined as determined by least squares means regression. Error bars represent one standard deviation. There were no differences among the groups in either year, nor in both years combined

ignored internal feeders such as gall-makers, root feeders, and stem borers, all of which tend to have specialized relationships (Fenner and Lee 2001).

All of these factors suggest that our sampling approach was biased toward generalists and against specialist herbivores and may explain why we did not find the predicted differences in insect species richness among Natives, Non-native Congeners, and Aliens. If 90% of the insect herbivores are specialists (Bernays and Graham 1988), and we failed to sample specialists accurately in our study, our comparisons in effect measured only how generalists react to plants that evolved elsewhere and thus our results were conservative. Moreover, the species richness of herbivores using a plant is directly related to the abundance and range of the plant, as well as the plant's architecture, including size and structural heterogeneity (Strong et al. 1984). When plant size increases, so does insect species richness. Although all of our plant species were locally common, our study specimens were generally small.

Nonetheless, the prediction that Non-native Congeners of native plant species should hold more insect biomass than Alien species with no North American relatives (Rejmánek 1999) was not supported in our study. In 2005, the only year data were sufficient to compare these two groups, insect biomass was greater on Aliens than Non-native Congeners. This unexpected result may be explained by the biotic resistance hypothesis, wherein novel hosts lack adequate defenses and are therefore more susceptible to native herbivores (Hokkanen and Pimentel 1989; Parker and Hay 2005). We expected to find greater insect biomass on Non-native Congeners than Aliens because non-native plants that are taxonomically isolated often possess chemical defenses that native herbivores have not previously encountered and cannot overcome in ecological time (Ehrlich and Raven 1965).

Our measures of insect biomass on Native plants supports Ehrlich and Raven's (1965) claim that most insect herbivores require an evolutionary history with a particular plant lineage to be able to exploit it as a host. Evidence suggests that most introduced plant species have not been in residence nearly long enough for local insect populations to adapt to their defenses. It is estimated that approximately 100 years are needed for a generalist insect to adopt a new host (Southwood 1984) and between 500 and 10,000 years for a specialist insect to switch hosts (Strong et al. 1984). This may explain why 89% of the insects we were able to identify were generalists and 11% were specialists. The relatively short amount of time elapsed between plant introduction and establishment may not have been long enough for specialist insects to have switched onto these new potential hosts.

Total insect biomass of several Alien species as well as four of our Non-native Congeners supports the prediction of the biotic resistance hypothesis, similar to the findings of Parker and Hay (2005) and Leger and Forister (2005). It is also possible that some non-native plants might support more insect herbivores because they have reallocated resources from defense to growth. Blossey and Nötzold (1995) suggest that such a shift in resources might be observed in non-native plants in the absence of herbivores. This shift would favor genotypes with increased growth rates and reduced defenses, yet could leave such plants vulnerable to herbivores when a host switch occurs. We did not attempt to determine which, if any, of our study species may have undergone a genetic shift in resource allocation since introduction to North America.

Conclusion

Native plants in our study supported more native insect biomass than non-native species (both Non-native

Table 3 Differences in species richness between congeneric pair members for 2004 and 2005 based on a repeated measures ANOVA

Year	Genus	Native	Non-native	*N*	Estimate	Standard error	t-value	*P*-value
2004	Acer	ACRU	ACPL	9	−0.78	0.51	−1.53	0.22
	Betula	BENI	BEPE	9	0.22	0.29	0.76	0.48
	Carpinus	CACA	CABE	9	0.78	0.64	1.22	0.33
	Cornus	COFL	COKU	9	*	*	*	*
	Fagus	FAGR	FASY	9	−0.22	0.19	−1.15	0.29
	Hamamelis	HAVI	HAMO	9	0.56	0.47	1.18	0.31
	Juglans	JUNI	JURE	9	−0.22	0.31	−0.71	0.51
	Morus	MORU	MOAL	9	*	*	*	*
	Prunus	PRSE	PRSU	9	−0.14	0.10	−1.37	0.17
	Rhodo.	RHPE	RHMU	9	0.78	0.42	1.87	0.12
	Rosa	ROCA	ROMU	9	0.11	0.79	0.14	0.89
	Salix	SANI	SABA	9	0.44	0.72	0.62	0.57
	Tilia	TIAM	TICO	9	−0.44	0.51	−0.87	0.43
	Ulmus	ULAM	ULPA	9	−0.14	0.10	−1.37	0.17
	Viburnum	VIDE	VIDI	9	**−1.56**	0.52	−2.98	**0.04**
2005	Acer	ACRU	ACPL	9	*	*	*	*
	Betula	BENI	BEPE	9	0.11	0.66	0.17	0.87
	Carpinus	CACA	CABE	9	**1.56**	0.37	4.22	**0.01**
	Cornus	COFL	COKU	9	0.33	0.43	0.77	0.47
	Fagus	FAGR	FASY	9	−0.56	0.25	−2.24	0.08
	Hamamelis	HAVI	HAMO	9	−0.11	0.37	−0.30	0.78
	Juglans	JUNI	JURE	9	−0.44	0.53	−0.83	0.45
	Morus	MORU	MOAL	9	0.00	0.25	0.00	1.00
	Prunus	PRSE	PRSU	9	−0.14	0.10	−1.37	0.17
	Rhodo.	RHPE	RHMU	9	−1.22	1.02	−1.19	0.31
	Rosa	ROCA	ROMU	9	−0.22	0.78	−0.29	0.79
	Salix	SANI	SABA	9	0.67	0.46	1.46	0.20
	Tilia	TIAM	TICO	9	−1.11	0.52	−2.13	0.09
	Ulmus	ULAM	ULPA	9	−1.40	0.10	−1.37	0.17
	Viburnum	VIDE	VIDI	9	−0.33	0.66	−0.51	0.64

If the estimate was positive then the Native pair member had greater species richness, if the estimate was negative then the Non-native Congener had greater species richness. Not every comparison was statistically tractable. Significant values are in bold. See Table 1 for plant codes

*Model did not converge

Congeners and Alien species). Considering the degree to which invasive, non-native plants are replacing native vegetative biomass in natural areas throughout North America (Pimentel et al. 2005), and the traditional preference for using non-native ornamentals in urban/suburban landscapes, this result may have important implications for conservation biology. Insect herbivores are the primary means by which energy captured by plants is passed to higher trophic levels in most terrestrial ecosystems (Wilson 1987). If non-native species dominate natural areas, the resulting reduction of insect biomass is predicted to degrade ecosystem diversity, productivity, and function (Tallamy 2004). The level of insect biomass reduction that impairs these variables remains to be determined, however.

Further, common garden designs based on small, young, woody plants might be inappropriate venues for comparisons of herbivore species richness on native and non-native plants. Future comparisons of herbivore use among native plants, non-native congeners, and unrelated alien plants should employ long-term studies of large plants and be replicated across several insect source populations to provide better measures of generalists and specialist communities. Measures of energy availability and transfer from insects on native and non-native plants to higher trophic levels also are important to establish conservation priorities for native plant species.

Acknowledgments The Northern Research Station of the U.S. Forest Service (RWU NE-4502) funded this project. We thank the Kranz family and White Clay Creek State Park for housing the study site and John Pesek for continued statistical advice. The editor and an anonymous reviewer provided helpful criticism of the manuscript. We also thank the many volunteers who helped with the planting. Jennie Witmer assisted with plot maintenance and data collection.

References

Agrawal AA, Kotanen PM, Mitchell CE et al (2005) Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989

Andow DA (1991) Vegetational diversity and arthropod population response. Ann Rev Entomol 36:561–568

Andow DA, Imura O (1994) Specialization of phytophagous arthropod communities on introduced plants. Ecology 75:296–300

Arnett RH Jr, Thomas MC, Skelley PE et al (2002) American beetles Volume 2 Polyphaga: scarabaeoidea through Curculionoidea. CRC Press, Boca Raton

Auerbach M, Simberloff D (1988) Rapid leaf miner colonization of introduced trees and shifts in sources of herbivore mortality. Oikos 52:41–50

Bernays EM, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Blossey B (1999) Before, during and after: the need for long-term monitoring in invasive plant species management. Biol Inv 1:301–311

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. J Ecol 83:887–889

Brooks ML, D'Antonio CM, Richardson DM et al (2004) Effects of invasive alien plants on fire regimes. BioScience 54:677–688

Chapman RF (1982) Chemoreception: the significance of receptor numbers. Adv Insect Physiol 16:247–356

DeLong DM (1948) The leafhoppers, or cicadellidae of Illinois (eurymelinae-balcluthinae). Bull Ill Nat Hist Surv 24:97–376

Dirr M (1998) Manual of woody landscape plants. Stipes, Champaign

Eastop VF (1973) Deductions from the present day host plants of aphids and related species. Symp Roy Entomol Soc Lond 6:157–177

Elton CS (1958) The ecology of invasions by animals and plants. John Wiley, New York

Ehrlich PR, Raven PH (1965) Butterflies and plants: a study in coevolution. Evolution 19:586–608

Fenner M, Lee WG (2001) Lack of pre-dispersal seed predators in introduced Asteraceae in New Zealand. NZ J Ecol 25:95–99

Futuyma DJ, Gould F (1979) Associations of plants and insects in a deciduous forest. Ecol Monogr 49:33–50

Goeden RD (1974) Comparative survey of the phytophagous insect faunas of Indian thistle, *Cardus pycnocephalus*, in southern California and southern Europe relative to biological weed control. Environ Entomol 3:464–474

Hamilton KGA (1982) The insects and arachnids of Canada Part 10. The spittlebugs of Canada (Homoptera: Cercopidae). Canadian Government Publishing Centre, Ottawa

Hokkanen HMT, Pimentel D (1989) New associations in biological control theory and practice. Can Entomol 121:829–840

Kareiva P (1982) Influence of vegetation texture on herbivore populations: resource concentration and rival movement. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press, New York, pp 259–289

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. TREE 17:164–170

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trend Ecol Evol 16:199–204

Krebs CJ (1999) Ecological methodology. Benjamin/Cummings, Menlo Park

Leger EA, Forister ML (2005) Increased resistance to generalist herbivores in invasive populations of the California poppy (*Eschscholzia californica*). Divers Distrib 11: 311–317

Lodge DM (1993) Species invasions and deletions. In: Kareiva P, Kingsolver JG, Huey RB (eds) Biotic interactions and global change. Sinauer, Sunderland, pp 326–387

Matthews ED, Lavoie OL (1970) Soil survey of New Castle County, Delaware. United States Department of Agriculture, Soil Conservation Service, Washington

McAvoy WA, Bennett KA (2001) The flora of Delaware: an annotated checklist. Delaware Department of Natural Resources and Environmental Control, Dover

Parker JD, Hay ME (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. Ecol Lett 8:959–967

Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecol Econ 52: 273–288

Price PW (1983) Hypotheses on organization and evolution in herbivorous insect communities. In: Denno RF, McClure MS (eds) Variable plants and herbivores in natural and managed systems. Academic Press. New York, pp 559–598

Qian H, Ricklefs RE (2006) The role of exotic species in homogenizing the North American flora. Ecol Lett 9:1293–1298

Randall J (1996) Weed control for the preservation of biological diversity. Weed Technol 10:370–383

Reichard SE (1996) Prevention of invasive plant introductions on national and local levels. In: Luken JO, Thieret JW (eds) Assessment and management of plant invasions. Springer-Verlag, New York, pp 215–227

Reichard SH, Hamilton CW (1997) Predicting invasions of woody plants introduced into North America. Conserv Biol 11:193–203

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661

Rejmánek M (1999) Invasive plant species and invasible ecosystems. In: Sandlund OT, Schei PJ, Vilken A (eds) Invasive species and biodiversity management. Kluwer, Dordrecht, pp 79–102

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Monogr 43:95–124

Slater JA, Baranowski RM (1978) How to know the true bugs (Hemiptera-Heteroptera). Wm. C. Brown Company Publishers, Dubuque

Southwood TRE (1961) The number of species of insects associated with various trees. J Anim Ecol 30:1–8

Southwood TRE (1984) Insect-plant adaptations. In: Ciba foundation symposium 102, origins and development of adaptation. Pitman, London, pp 138–151

Staples GW, Herbst DR, Imada CT (2000) Survey of invasive or potentially invasive plants in Hawaii. Bishop Museum Occas Pap 65:1–35

Stehr FW (1987) Immature insects, vols. I and II. Kendall/Hunt Publishing Company, Dubuque

Strong DR, Lawton JH, Southwood R (1984) Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge

Tallamy DW (2004) Do alien plants reduce insect biomass? Conserv Biol 18:1689–1692

USDA, NRCS (2003) The PLANTS Database, Version 3.0 (http://www.plants.usda.gov) Data compiled from various sources by Mark W. Skinner. National Plant Data Center, Baton Rouge, Louisiana

Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? — evidence from pair-wise experiments. Oikos 105:229–238

Wagner DL (2005) Caterpillars of Eastern North America. Princeton University Press, Princeton

Ward LK, Hackshaw A, Clarke RT (1995) Food-plant families of British insects and mites: the influence of life form and plant family. Biol J Linn Soc 55:109–127

White RE (1983) A field guide to the beetles. Houghton Mifflin Company, New York

Wilcove DS, Rothstein D, Dubow J et al (1998) Quantifying threats to imperiled species in the United States. BioScience 48:607–615

Williamson M (1996) Biological Invasions. Chapman & Hall, London

Wilson EO (1987) The little things that run the world (The importance and conservation of invertebrates). Conserv Biol 1:344–346

Wolfe LM (2002) Why alien invaders succeed: support for the escape-from-enemy hypothesis. Am Nat 160:705–711

Yela JL, Lawton JH (1997) Insect herbivore loads on native and introduced plants: a preliminary study. Entomol Exp Appl 85:275–279

Zuefle ME (2006) The impact of non-native woody plants on the native herbivorous insect community of northern Delaware. Thesis, University of Delaware