Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities

Karin T. Burghardt,[1,†] Douglas W. Tallamy, Christopher Philips,[2] and Kimberley J. Shropshire

Entomology and Wildlife Ecology Department, University of Delaware, Newark, Delaware 19716 USA

Abstract. The impact of non-native plant invasions on ecosystems has been controversial because obvious local effects have not yet led to the global extinction of any native plant species on continents and large islands. We suggest that extinction is not the appropriate measure of impact on ecosystem function and present evidence that non-native plant invasions or the replacement of native plants with non-native ornamentals results in significant bottom-up reductions of energy available for local food webs. Using replicated common gardens we compared Lepidoptera species richness and abundance on native plants, non-native congeners of those natives, and non-native species with no close relatives in the study area. Non-native plants supported significantly fewer caterpillars of significantly fewer specialist and generalist species even when the non-natives were close relatives of native host plants. However, the effect size was smaller in the latter category indicating phylogenetic similarity to local natives may positively impact herbivory. Cluster analysis revealed that a non-native plant congener often supports a lepidopteran community that is a subset of the similar, but more diverse community found on its native congener. The proportion of the Lepidoptera community consisting of specialist species was about five times larger across native species within sites compared to non-native plant species. In addition, species accumulation trajectories suggested that in a fully sampled community the differences between the Lepidoptera supported by native and non-native plants may be even greater than presented here.

Key words: biodiversity; caterpillar; ecosystem services; food webs; invasive species; Lepidoptera; native plants; non-native plants; northeastern United States.

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[1] Present address: Ecology and Evolutionary Biology Department, Yale University, New Haven, Connecticut 06520 USA.

[2] Present address: Entomology Department, Virginia Tech, Blacksburg, Virginia 24061 USA.

[†] **E-mail:** karin.burghardt@yale.edu

Introduction

Non-native plant genotypes (those that evolved outside of local food webs) have replaced native plant communities to a greater or lesser extent in every North American biome, as well as in anthropogenic landscapes where they have been planted by the millions as ornamentals (Williamson 1996, Qian and Ricklefs 2006). Although it has been shown that the large-scale addition of non-native plants to ecosystems can alter soil moisture, pH, biota, and nutrients; and increase fire frequency and plant competition (Tyser and Worley 1992, Randall 1996, Duncan 1997, Wilcove et al. 1998, Gould and Gorchov 2000, Mack et al. 2000, Brooks et al. 2004, Butler and Cogan 2004 and many more), the ecological impacts of and our response to non-native plants has become increasingly controversial.

One of the sources of this controversy comes from defining "impact" in terms of native plant

extinctions (Slobodkin 2001, Sax and Gaines 2008, Davis 2009) rather than the disruption of ecological services delivered by native plant communities (Tallamy 2004). Davis (2009), for example, argues that the negative effects of non-native plant invasions have been overstated because non-native plant invasions on continents and large islands like New Zealand have not yet directly caused the extinction of any native plant species. Instead, their addition to local plant communities without the concomitant loss of native species has created more rather than less diversity. Such reasoning, however, ignores the most fundamental contribution of plants to ecosystem function, the generation of food. If species diversity is to be the currency by which we measure the impacts of non-native genotypes, then we suggest diversity should be compared across all trophic levels in invaded and uninvaded communities. This will determine whether non-native plants are the ecological equivalents of the native plants they displace in terms of trophic support of food webs.

Perhaps the best way to identify changes in food web complexity is to examine how the largest taxon of primary consumers, insect herbivores, respond to plants that evolved outside of their food webs. Plant-insect interaction theory predicts that insect herbivores should be the guild most sensitive to the replacement of native plants with non-native plant genotypes (Tallamy 2004). Most species are specialists that use only a few of the myriad plant lineages available to them for growth and reproduction (Bernays and Graham 1988, Novotny et al. 2006). A small percentage is more generalized in their use of host plants, and despite their low diversity can be far more common than specialists (Futuyma and Gould 1979). However, even the most generalized insect herbivores use only a small fraction of the plants in their environments (Tallamy and Shropshire 2009). Moreover, many generalists are far more specialized locally than their geographic host breadth indicates (Fox and Morrow 1981, Scriber 1983, Tallamy et al. 2010).

Specialists have followed an evolutionary path that has enabled them to circumvent particular plant defenses by developing highly specific behavioral and physiological adaptations that defuse such defenses. Thus, specialists are predicted (Ehrlich and Raven 1964) and have been repeatedly shown (e.g., Berenbaum 1990, Farrell and Mitter 1990, Weiblen et al. 2006) to be restricted to plant lineages that deploy the class of defensive compounds on which they have specialized. If non-native plants bearing novel defenses replace plant species to which specialists are adapted, specialists are predicted to be unable to adjust in ecological time and thus will be eliminated from the invaded community.

By this reasoning, however, if non-native plants use chemical defenses that are similar to those of a native plant, they may be acceptable food plants for adapted local specialists (Tallamy 2004). Because many members of a single plant lineage typically share chemical defenses based on a common compound (Berenbaum 1990), a non-native plant is most likely to share the chemical defense of a native species if it is closely related to that species. Thus, we predict that non-native introductions should be less detrimental to local food webs when the non-native is a member of one or more local native lineages. Conversely, when a non-native plant is not closely related to any local plant lineage, it is unlikely that local specialists will be able to use it for growth or reproduction.

Here we use common garden protocol to compare the species richness and abundance of specialist and generalist Lepidoptera on 1) common native woody plants, 2) non-native congeners of these plants (congeneric comparisons), and 3) non-native species that are unrelated to any local plants (non-congeneric comparisons). We predict that if insect abundance is not altered when non-natives replace natives, it will be due to the ability of generalists to use non-native plants for growth and reproduction.

METHODS

Both congeneric and non-congeneric comparisons were replicated using randomized complete block protocol in four common gardens that were established in 2006 and 2007 at the University of Delaware Agricultural Experiment Station farms in Newark and Middletown, DE, at Flint Woods preserve in Centerville, DE, and at Tyler Arboretum in Media, PA. Each garden was planted within 25 m of a mature woodlot that contained most or all of the native species within the

treatments. To ensure independence with respect to colonizing insect populations, each garden was geographically isolated from all other gardens in our study by at least 20 km. Our gardens were designed to control for the scale of the planting, fertilization and watering regimen, as well as the size, architecture, habit, exposure, and spacing of the plants examined. Such variables typically make comparisons within areas in which non-native plants have become naturalized difficult. To help compensate for the small size of each plant at the beginning of the experiment, we planted eight individuals of each species in two distinct groupings separated by one meter, each grouping consisting of four plants.

Lepidoptera were sampled only in their larval stages twice in 2008 (June and August) and three times in 2009 (June, July and August). We did not sample adults because many nocturnal species take cover during the day in any available foliage, regardless of its relationship to acceptable larval hosts. In 2008 we sampled larvae in two ways: first, we vacuumed insects from plant foliage using a reverse leaf-blower (Craftsman gasoline blow/vac, Item 7179469) fitted with a five-gallon paint strainer bag (Brook et al. 2008). We then meticulously searched targeted leaves and stems for any larvae that had not been removed by the leaf-blower (Wagner 2005). All leaves sampled were counted and the data were expressed per dry leaf gram sampled. Larvae were stored in 80% ethanol for later identification. In 2009 we employed only the total search method as it proved to be the most reliable approach for Lepidoptera larva. Using mean leaf mass for each plant species (dry weight average of 100 leaves per species) we estimated total leaf counts of sampled vegetation before sampling, enabling exact matching of sampled leaf mass between each congeneric and non-congeneric comparison. This allowed us to examine differences in species accumulation curves between treatments since sampling effort was equal.

Each larva was identified to species by chaetotaxy (Stehr 1987), images (Wagner 2005), specialist texts, rearing, and, when necessary, DNA bar-coding through the Biodiversity Institute of Ontario (Ratnasingham and Hebert 2007). Host plant specialization was determined for each species in two ways. First, we conducted an exhaustive literature search of host records for each Lepidoptera species collected (Tallamy and Shropshire 2009). Following Bernays and Graham (1988), species recorded in the literature on three or fewer plant families were considered specialists, while species recorded on more than three plant families were labeled generalists. In a second approach we used actual host use in our study to define local specialization (Futuyma and Gould 1979). One advantage of this approach is that individuals from lepidopteran groups with unresolved or nonexistent host-use records were able to be classified. We again defined specialists as species found on three or fewer plant families during the course of the study.

Congeneric comparisons

Lepidoptera specialist and generalist richness and abundance were quantified in 2008 and 2009 on one native and one non-native species representative of 13 woody plant genera representing 11 plant families (Table 1). The genera and species compared were selected because they were native and non-native congeners that were abundant in the study area. For example, the genus *Acer* was selected because native *Acer* species (maples) and non-native Norway maple are common and widespread at the study sites. *Acer rubrum* (red maple) was selected over other native species as the native representative of this genus because it is the most abundant and widespread native maple in the area. Both the native and non-native representatives of each genus were planted within two meters of each other. As the plants grew, the branches of the native and non-native species often intermingled. Thus, if a moth or butterfly was attracted to oviposit on one member of the congener, it had the opportunity to oviposit on the other member of the genus. All congeners on a site were sampled in a single day, alternating whether the native or non-native individual was sampled first. Both members of a pair were sampled by the same researcher to control for differences in search method. In 2008 leaves were counted after sampling so inter-sample matching was not possible, but Lepidoptera counts were standardized by dividing by leaf gram sampled. In 2009, a goal of 500 g of leaves per species per sampling date was set. If not enough leaves to reach that goal were present on one of the species sampled

Table 1. Plant species sampled in congeneric study; native and non-native pairs share a row.

Genus	Non-native species	Common name	Native species	Common name
Acer	*A. platanoides*	Norway maple	*A. rubrum*	red maple
Betula	*B. pendula*	European white birch	*B. nigra*	river birch
Carpinus	*C. betulus*	European hornbeam	*C. caroliniana*	American hornbeam
Cornus	*C. kousa*	kousa dogwood	*C. alternifolia*	alternateleaf dogwood
Ilex	*I. aquifolium*	English holly	*I. opaca*	American holly
Juglans	*J. regia*	English walnut	*J. nigra*	black walnut
Prunus	*P. serrulata*	Korean cherry	*P. serotina*	black cherry
Rhododendron	*R. mucronulatum*	Korean rhododendron	*R. periclymenoides*	pinxterbloom azalea
Rosa	*R. multiflora*	multiflora rose	*R. setigera*	prairie rose
Salix	*S. babylonica*	weeping willow	*S. nigra*	black willow
Tilia	*T. cordata*	little-leaf linden	*T. americana*	basswood
Ulmus	*U. parvifolia*	Chinese elm	*U. americana*	American elm
Viburnum	*V. dilatatum*	linden viburnum	*V. dentatum*	southern arrowwood

within a congeneric pair, an identical smaller mass of leaves was sampled from the other member of the pair. This method ensured that we were measuring each species pair at the same point on their species accumulation curves.

Non-congeneric comparisons

At the same common garden sites on a spatially distinct plot we compared Lepidoptera abundance, richness and community structure on 17 species of native woody plants common in northern Delaware and 17 species of non-native woody plants that are either invasive in the study area or are commonly used locally as landscape plants (Table 2). Native species represented 15 plant families while non-natives represented 14 families. The non-native species used in this comparison had no native congeners in the study area. The spatial design of each common garden was similar to that of the congener gardens with the exception that non-natives were not physically paired with a specific native. In 2008 the sampling method was identical to the congeneric sampling method described above. In 2009 an identical mass of native and non-native leaves was sampled (alternating which treatment was sampled first) by a matching method similar to that used for the congeneric comparisons. However, plant size rather than plant genus was used to match grams of leaves sampled between native and non-native individuals. This allowed the maximum grams of leaves to be sampled at each site while keeping sampling effort equal between treatments.

Statistical analyses

In both congeneric and non-congeneric com- parisons a factorial two-way ANOVA was used to test effects of plant origin, site (block), and plant origin x site on lepidopteran richness and abundance. These analyses were done using a general linear model (procedure GLM) with SAS software (version 9.2). A $\log_{10}$ transform was used to conform count data to assumptions of normality and homogeneity of variance. All results are reported as back-transformed means and back-transformed 95% confidence intervals and $\alpha = 0.05$ was used to test for significance. To further investigate the directional relationship between congeneric plant pairs we constructed a norm of reaction for both lepidopteran abun- dance and richness and performed a sign test. To test differences in the degree of host specializa- tion between native and non-native lepidopteran communities we performed a paired *t* test comparing the proportion of specialist species found within the native and non-native plant communities by sites (results reported as mean ± SE).

We also used the BiodiversityR package within the statistical software R 2.10.0 (R Development Core Team 2009) to construct species accumula- tion curves for the 2009 data by pooling by site and plant species. We were not able to do this with the 2008 data due to unequal sampling effort between treatments. Also using Biodiversi- tyR, we performed a divisive hierarchical cluster analysis with average linkage using Bray-Curtis ecological distance to explore caterpillar commu- nity composition across tree species (Kindt and Coe 2005). We selected this distance since it incorporates both species and abundance. How- ever, since Bray-Curtis similarity index gives abundant species more weight than rare ones

Table 2. Plant species sampled in non-congeneric study.

Non-native species	Common name	Native species	Common name
Ginkgo biloba	ginkgo	*Liriodendron tulipifera*	tulip tree
Cotoneaster lucidus	hedge cotoneaster	*Liquidambar styraciflua*	sweetgum
Albizia julibrissin	silktree mimosa	*Lindera benzoin*	spicebush
Koelreuteria paniculata	goldenrain tree	*Fraxinus pennsylvanica*	green ash
Lagerstroemia indica	crape myrtle	*Platanus occidentalis*	sycamore
Buddleja davidii	orange eye butterflybush	*Celtis occidentalis*	hackberry
Paulownia tomentosa	princesstree	*Quercus palustris*	pin oak
Forsythia x intermedia	forsythia	*Nyssa sylvatica*	black gum
Ligustrum obtusifolium	border privet	*Rhus copalina*	winged sumac
Pyrus calleryana	bradford pear	*Morus rubra*	red mulberry
Poncirus trifoliata	hardy orange	*Acer rubrum*	red maple
Rhamnus frangula	glossy buckthorn	*Cornus alternifolia*	alternateleaf dogwood
Berberis thunbergii	Japanese barberry	*Viburnum dentatum*	southern arrowwood
Syringa vulgaris	lilac	*Prunus serotina*	black cherry
Ailanthus altissima	tree of heaven	*Salix nigra*	black willow
Elaeagnus umbellata	autumn olive	*Juglans nigra*	black walnut
Euonymus alatus	burning bush	*Ulmus americana*	American elm

we performed the analysis on a square-root transformed matrix of caterpillar abundances in order to not have clusters entirely based on our most abundant generalists (Magurran 2004).

RESULTS

Congeneric comparisons

Both the abundance and species richness of Lepidoptera collected in our plots increased in 2009 over 2008 collections. In 2008, 37.00 kg of dried leaves were sampled from non-native plants and 51.02 kg were sampled from their native congeners. 303 Lepidoptera larvae were collected representing 72 species. Using lepidopteran host records, 21 species were classified as specialists and 51 as generalists. Classifying the same species by self-referencing resulted in 46 specialists and 26 generalists. In 2009 we collected 2212 larvae representing 106 species from 49.67 kg of non-native leaves and 49.77 kg of native leaves. 31 species were specialists while 62 were generalists in their host use. We were unable to categorize 13 species because of taxonomic uncertainties or poor larval host records in the literature. Self-referential host classification yielded 75 specialist species and 31 generalists (see Appendix A for species and classification information).

The two-way ANOVA revealed no significant effect of site and no significant interaction terms (See Appendix B for full ANOVA table and Fig. 1A for means and 95% C.I.). We found no difference between the total Lepidoptera larvae

supported by native plants and their non-native congeners in 2008 ($F_{1,96} = 1.4$, $P = 0.238$), but found over three fold more larvae on natives in 2009 ($F_{1,96} = 11.15$, $P = 0.0012$). In 2008 there was no difference in the abundance of generalists on native and non-native congeners ($F_{1,96} = 0.14$, $P = 0.7129$), but natives supported more than twice as many generalists as non-natives in 2009 ($F_{1,96} = 7.09$, $P = 0.0091$). In contrast to generalists, specialists were significantly more abundant on native plants in both 2008 ($F_{1,96} = 8.15$, $P = 0.0053$) and 2009 ($F_{1,96} = 11.5$, $P = 0.001$).

Species richness followed the same pattern as abundance (Fig. 1A). There was no difference in the total number of species collected on natives and their non-native congeners in 2008 ($F_{1,96} = 0.52$, $P = 0.407$) but more than twice as many species were found on native plants in 2009 ($F_{1,96} = 14.27$, $P = 0.0003$). Generalist richness did not differ between natives and non-natives in 2008 ($F_{1,96} = 0.09$, $P = 0.7686$) but there were twice as many generalists on natives in 2009 ($F_{1,96} = 7.1$, $P = 0.009$). Specialist richness was significantly greater on natives in both 2008 ($F_{1,96} = 9.09$, $P = 0.0033$) and 2009 ($F_{1,96} = 13.12$, $P = 0.0005$). This was also the case when specialists were defined by host use in our plots. The performance of generalists and specialists was unaffected by whether our definition of host specialization was defined by literature host records or by actual host use in our plots (Appendix B). Values reported here are from the former method.

Although the native plant representative of our congeneric comparisons on average supported
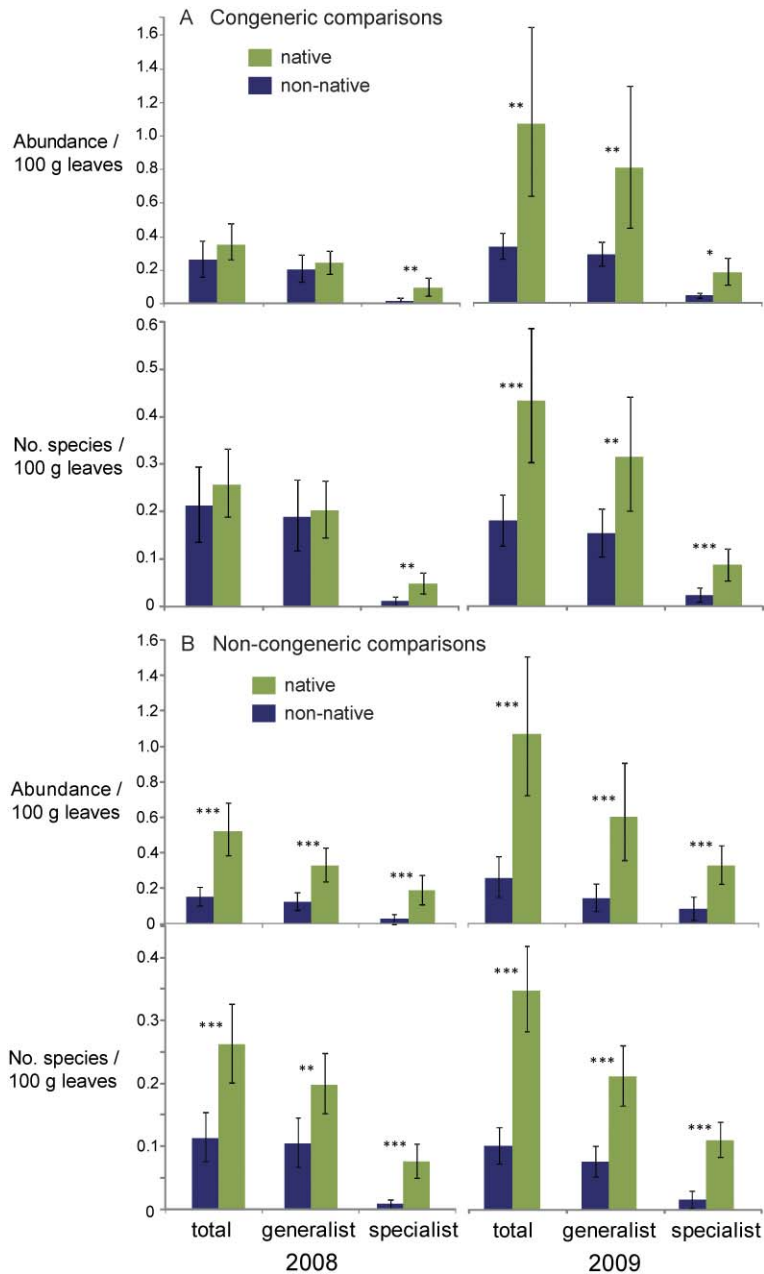
Fig. 1. The mean abundance and species richness with 95% confidence intervals of Lepidoptera found in 2008 and 2009 on (A) common native plants compared to non-native congeners (N = 52 per treatment) and (B) common woody native plants compared to non-native plants without close native relatives (N = 64 per treatment). Light green shading represents native plants while dark blue shading indicates non-native plant species. An * indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$.

significantly more Lepidoptera larvae and species than the non-native representative in 2009, reaction norms show that there was considerable variation in the response (Fig. 2). Responses

ranged from native *Prunus* and *Carpinus* that supported on average eight and five times more Lepidoptera individuals respectively than their non-native congener, to the native *Ulmus* that
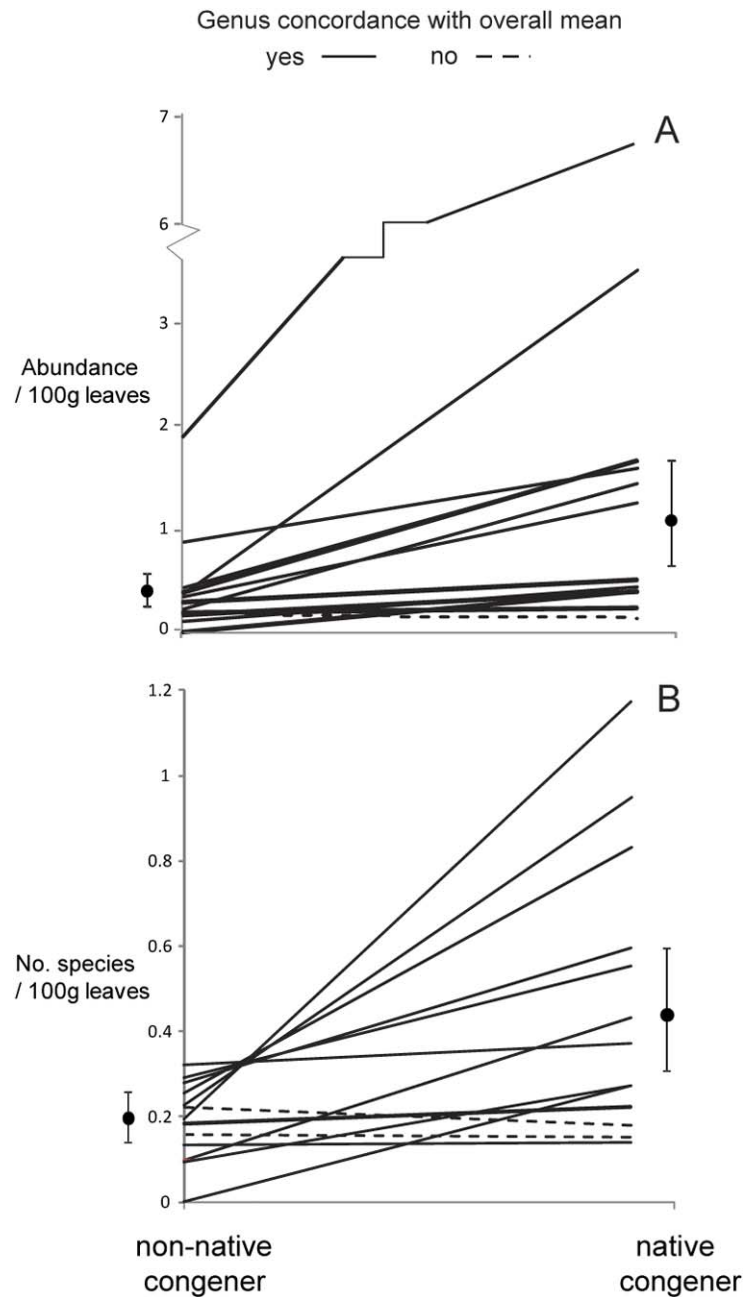
Fig. 2. Reaction norms illustrating the difference between lepidopteran (A) abundance and (B) richness on 13 native plants species and their non-native congeners in 2009. Lines connect either mean abundance (A) or number of Lepidoptera species (B) found on each non-native plant (N = 4) to its native congener (N = 4). The pattern of reaction norm slopes differed from what would be expected randomly for both abundance ($P = 0.003$) and richness ($P = 0.022$). Overall means with 95% C.I. (N = 52) are shown beside the reaction norm and differ significantly for abundance ($F_{1,96} = 11.15$, $P = 0.0012$) and richness ($F_{1,96} = 14.27$, $P = 0.0003$). Dotted lines indicate genera that do not follow the pattern of the overall means.

supported slightly fewer caterpillars than the non-native *Ulmus*. In terms of species richness, native *Carpinus*, *Acer*, and *Rhododendron* all supported at least three times as many species of Lepidoptera as their non-native congener, while native *Betula* and *Tilia* species supported slightly fewer species than their non-native congener. Sign tests showed significantly more slopes were positive between non-native and native congeners than would be expected randomly for both abundance ($P = 0.003$; Fig. 2A) and richness ($P = 0.022$; Fig. 2B). Within this pattern, however, there was variation in the ability of native plants of different genera to support species. For instance, there was eight-fold difference in the number of species of Lepidoptera per 100 grams leaves supported by the most species poor native (*Ulmus*) and the most species rich native (*Carpinus*).

Non-congeneric comparisons

As in the congeneric comparisons, our collections in 2009 were more abundant and more diverse than our collections in 2008. In 2008, 51.85 kg of non-native leaves and 68.06 kg of native leaves were sampled, resulting in 484 individuals of 90 species (33 specialist and 57 generalist species). The self-referenced classification of host specialization resulted in 60 specialist and 28 generalist species. In 2009, we collected 2762 individuals representing 136 species from 53.03kg of non-native leaves and 52.88kg of native leaves. 51 species were specialists while 63 were generalists in their host use. We were unable to identify the specialization status of 22 species because of taxonomic uncertainties or poor literature host records. However, the self-referenced approach classified 107 species as specialists and 29 species as generalists (see Appendix A for species and classification information).

As predicted, differences in the abundance and richness of Lepidoptera on common native woody plant species and non-native species with no close native relatives in the study area were consistently greater than the differences we observed in our congeneric comparisons (see Fig. 1B for means with 95% C.I.). We found significantly more caterpillars on the native species in both 2008 ($F_{1, 128} = 28.23$, $P < 0.0001$) and 2009 ($F_{1, 128} = 23.97$, $P < 0.0001$; Fig. 1B), both

in terms of generalists (2008: $F_{1, 128} = 16.02$, $P = 0.0001$; 2009: $F_{1, 128} = 14.54$, $P = 0.0002$) and specialists (2008: $F_{1, 128} = 17.33$, $P < 0.0001$; 2009: $F_{1, 128} = 15.32$, $P = 0.0001$). We also found significantly more species on native plants (2008: $F_{1, 128} = 17.20$, $P < 0.0001$; 2009: $F_{1, 128} = 55.17$, $P < 0.0001$), both as generalists (2008: $F_{1, 128} = 9.22$, $P = 0.0029$; 2009: $F_{1, 128} = 27.34$, $P < 0.0001$) and specialists (2008: $F_{1, 128} = 27.82$, $P < 0.0001$; 2009: $F_{1, 128} = 41.19$, $P < 0.0001$). As with our congeneric comparisons, these differences were similar regardless of whether we defined host specialization and generalization by literature host records or by host use on our plots (see Appendix B for full ANOVA tables). Interaction terms were not significant for any non-congeneric comparison, but there was one significant site effect for total Lepidoptera richness in 2009 ($F_{3, 128} = 3.18$, $P = 0.0264$).

Species accumulation curves

Species accumulation curves (Fig. 3A, B) demonstrate differences in the community structure of Lepidoptera on native plants and non-native species with no close native relatives. Lepidoptera species accumulated on native plants with the addition of each plant species to the analysis, but new species joined the community of Lepidoptera using non-native plants very slowly as new plants were examined (Fig. 3A). This same pattern was seen when the rate of species accumulation was examined over successive plots (Fig. 3B). New species accumulated on native sites quickly, but for the same sampling effort Lepidoptera added very slowly to the non-native plant community. A similar pattern was seen when comparing native plants to their non-native congeners (Fig. 3C, D). However, while native congeners still supported a larger and more specialized community than did non-natives, the slope of the accumulation curve for the non-native species with close relatives was much steeper than the curve for non-native plant species without close relatives in the area. Notably, only the lepidopteran communities that colonized the non-native, non-congeneric plant species (Fig. 3A) appear to be nearing an asymptote. This suggests we did not fully sample the community during the study (Magurran 2004). Thus, the magnitude of diversity differences recorded between native and non-native
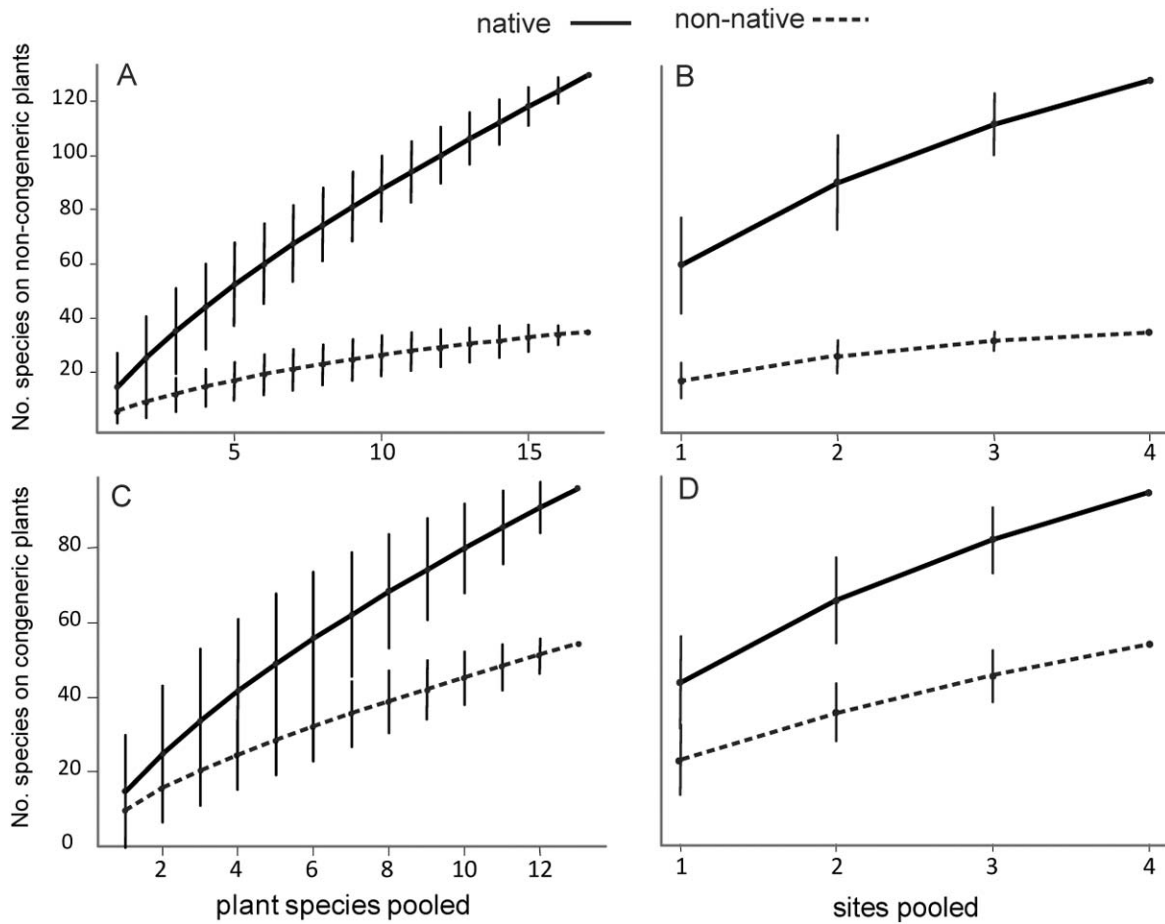
Fig. 3. Species accumulation curves for 2009 showing average pooled lepidopteran species richness ($\pm$ 2SD) for native plants compared to non-native plants without close native relatives (A, B) and for native plants compared to their non-native congeners (C, D). Figures on the left show lepidopteran richness as plant species are added to the community, while the figures on the right illustrate how lepidopteran species accumulate as sites are pooled. Dotted lines represent the non-native plant community and solid lines represent the native plant community.

communities is likely to widen as the community becomes sampled more completely.

Degree of host specialization

In the 2009 congeneric comparison, the proportion of specialist species was greater on the native plant community (23.9% $\pm$ 3.22) than the non-native plant community (5.1% $\pm$ 3.38, $P = 0.003$). A similar reduction in the specialist proportion of the community was seen in the 2009 non-congeneric comparison. Within a site, 33.3% ($\pm$ 4.05) of the lepidopteran community consists of specialists on native plants compared to only 4.3% ($\pm$ 3.60, $P = 0.004$) on non-native species without a close native relatives.

Cluster analysis

The dendrogram that depicts similarity between lepidopteran communities on congeneric plant pairs (Fig. 4) reveals a strong grouping of communities based on genus (divisive coefficient $= 0.277$, mantel statistic $r = 0.8225$, $P = 0.01$). This pattern, while not universal, indicates that the less diverse communities found on non-native congeners tend to consist of a subset of the species found on each respective native congener. Patterns revealed by the cluster analysis of the lepidopteran communities found on plants in the non-congeneric comparison (Fig. 5) are less clear than in the congeneric comparison (divisive coefficient $= 0.273$, mantel statistic $r = 0.8713$, P
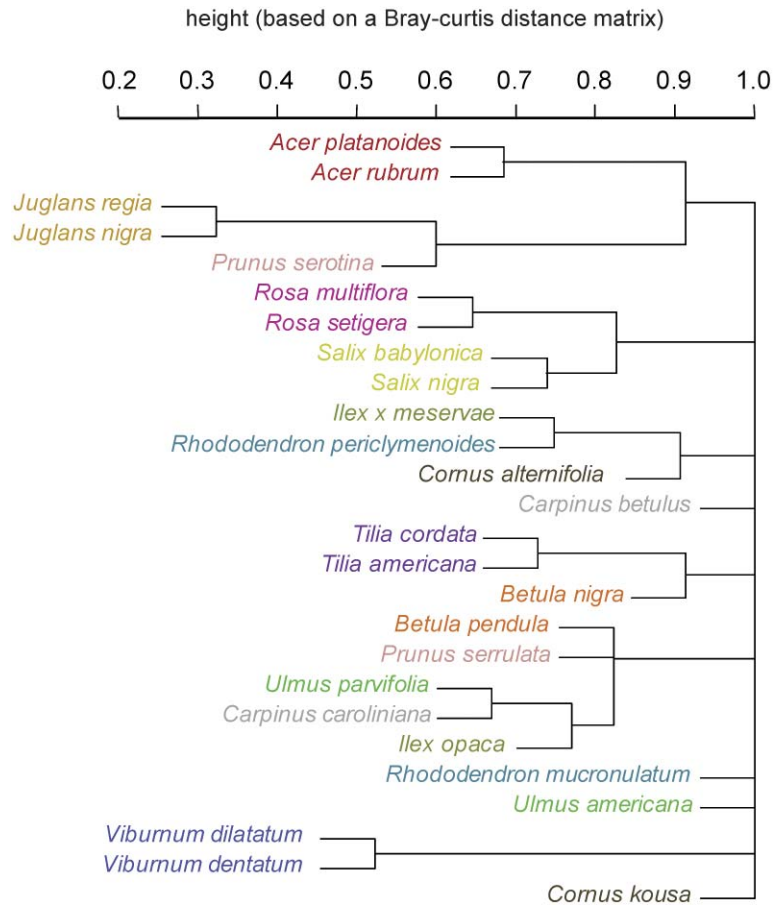
height (based on a Bray-curtis distance matrix)

Fig. 4. A cluster analysis using Bray-Curtis ecological distance to compare caterpillar communities across all congeneric tree comparisons. Note that close relatives (indicated by same color) tend to support similar lepidopteran communities. The dendrogram was created using divisive hierarchical analysis using average linkage on a square-root transformed dataset (divisive coefficient = 0.277, mantel statistic r = 0.8225, $P = 0.01$).

= 0.01); however, the formation of one large cluster (*Syringa, Juglans, Nyssa* etc.) was certainly influenced by the presence of the most abundant generalist in the study, *Hyphantria cunea*.

DISCUSSION

Host use by insect herbivores is mediated primarily by phytochemicals; secondary metabolic compounds that impart a species-specific odor, palatability, and level of toxicity that influences the success with which various insect species can survive and reproduce on particular plant tissues (Weis and Berenbaum 1989). The phytochemical profile of plant species that are closely related is typically more similar than the chemical profile of plants with no immediate common relatives (Harborne et al. 1999). This suggests that insect herbivores adapted to the chemical challenges of particular native hosts may be able to adopt a novel plant species as a host if its phytochemistry is sufficiently similar to the original hosts.

In a general sense we found this prediction to be true; Lepidoptera were able to oviposit and feed on geographically novel plant species that were congeners of native host species more often than they would use novel species that were unrelated to native hosts. Despite this trend, however, novel congeners depressed the abundance and species richness of both specialist and generalist caterpillars, particularly in 2009 when
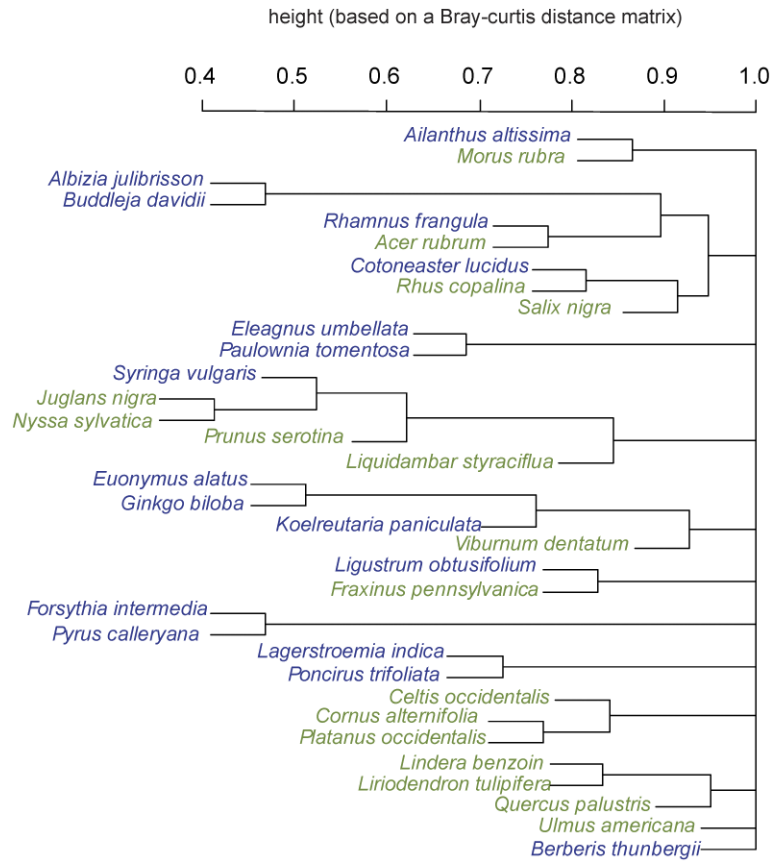
Fig. 5. A cluster analysis showing the similarity of caterpillar communities found on native (light green) and non-native (dark blue) species in the non-congeneric tree species comparison. The dendrogram was created using divisive hierarchical analysis using average linkage on a square-root transformed dataset (divisive coefficient = 0.273, mantel statistic r = 0.8713, $P = 0.01$).

our sampling techniques were improved and plantings were older. Geographically novel congeners were acceptable hosts to less than half of the generalists and only one fourth of the specialists that we found on native congeners in 2009.

The reduction of the Lepidoptera community at our study sites was even greater when novel hosts were not close relatives of local host plants; only 30% of generalist species and 7% of specialist species used novel hosts that were not congeners of any local species. In addition, only one third as many individuals were supported by these plants, indicating that generalist abundance does not compensate for the reduction in specialist abundance. Overall, 75% of total lepidopteran species and 93% of specialist species were found exclusively on native plant species,

while only 5% of lepidopteran species were found exclusively on non-native plants without close native relatives. Of the latter group, only two species were moth specialists, the barberry looper, *Coryphista meadii* (Packard 1874), and the Ailanthus webworm, *Atteva punctella* (Cramer 1781). Interestingly, both species were able to use the non-native plant in our study because they had earlier jumped from closely related native host plants to Japanese barberry (*Berberis thunbergii*)and tree of heaven (*Ailanthus altissima*), respectively, in other parts of their geographic range.

Even though our collecting techniques improved between 2008 and 2009, the large number of new species recorded in 2009 in both the congener and non-congener plantings suggests that colonization of both studies by local Lepi-

doptera was still in its early phase. It is notable that the majority of these new species were collected on native species. Of the 56 new species that were recorded in the congener study in 2009, 70% were found only on native congeners. Similarly, 80 new species were collected in the non-congener plantings in 2009, 86% of which were found only on native species.

Species accumulation curves constructed by site and species show that native plants gained new Lepidoptera species far faster than non-natives in both studies and fail to reach an asymptote. Therefore, we predict that the ultimate differences in the ability of natives and non-natives to support Lepidoptera are considerably greater than we were able to detect in the brief period of our study.

Cluster analysis of the lepidopteran community supported by the species within the congeneric comparison study (Fig. 4) revealed that plants within the same genus often share a similar lepidopteran fauna. In addition, reaction norms (Fig. 2B) show consistently higher lepidopteran species richness on the native plant within a congeneric plant species pair. In tandem, these two results suggest that the lepidopteran community found on the non-native plant in the congeneric pair supports a similar but depauperate community compared to its native congener.

Ultimately, the degree to which non-native plants reduce insect herbivores in ways that are detrimental to higher trophic levels will depend on 1) how much non-native plants reduce the availability of native host plants and 2) how well generalists compensate for the loss of specialists in the production of insect biomass. If non-native plants join the community without reducing the biomass or richness of native plants, the food web supported by that plant community should not be impaired. If, however, the addition of non-native plants to the community reduces the biomass of native plant species, as has been shown in invasions by Norway maple, bush honeysuckle, Phragmites, kudzu, cheatgrass and others (Wechsler 1977, Martin 1999, Gould and Gorchov 2000, Collier et al. 2002, Gratton and Denno 2006, Chambers et al. 2007), our results indicate that the production of insect biomass will be compromised. Therefore, adding non-native plants to native plant communities might increase net plant richness at a given locality, but

does not result in additive effects on lepidopteran diversity or abundance.

As predicted, the loss of abundance and richness in both the congeneric and non-congeneric comparisons was greatest in specialists, although generalists suffered as well. Thus, our results do not support the contention that generalists alone can support insectivores in higher trophic levels when native plant communities have been replaced by non-native plants. Generalists may be far less flexible in host selection than typically assumed. Considering that most insect herbivores are capable of developing on just a tiny fraction of the plant species available to them (Bernays and Graham 1988, Novotny and Basset 2005) and that many generalists exhibit geographically specialized diets (Fox and Morrow 1981, Tallamy et al. 2010), the potential for novel plants to decimate the abundance and diversity of insect herbivores is considerable. Any reduction in insect abundance should negatively impact insectivores such as birds that have been repeatedly shown to be food-limited (Marra et al. 1998, Duguay et al. 2000, Sillett et al. 2000, Strong and Sherry 2000).

The reduction of caterpillar abundance and richness on non-native plants with no close relatives in the study area was predicted because of the likelihood that such plants would present novel defensive compounds to local insect herbivores. However, the sensitivity of both specialists and generalists to non-native congeners of native host plants was unexpected. Although there are many notable exceptions (Graves and Shapiro 2003), our results suggest that even minor differences in phytochemical profile can render a novel plant unavailable to many native insect herbivores.

The importance of insect herbivores in transferring energy captured by plants through photosynthesis to other trophic levels has been recognized since Elton first established the basic premises of food webs (1927). It is surprising, then, that the impact of non-native plants on insect herbivores has been woefully understudied. Although our study is not the first to demonstrate differences in the response of native insects to non-native plants, it is the first community wide study of a large phytophagous taxon in which the taxonomy was sufficiently accurate to distinguish unambiguously special-

ists from generalists. Several studies have documented reduced insect herbivory (Agrawal et al. 2005, Jogesh et al. 2008, Cincotta et al. 2009), abundance (Proches et al. 2008), and biomass (Heleno et al. 2009) on non-native plants. However, species-level identifications allowed us to tap into known host records and thus track changes in the community structure of Lepidoptera capable of developing on native and non-native plants. For instance, the lepidopteran community on native plants within each site consists of about five times the proportion of specialist species found on non-native plants. Therefore, we not only show that both specialists and generalists suffer when native plant communities are replaced by non-native plants, regardless of the taxonomic distance of such plants from the plants they are replacing, but also that host specialization is reduced within non-native communities.

If most phytophagous insect species are indeed specialists and if most specialists are unable to recognize or develop successfully on non-native plant species, the diversity of phytophagous insect communities should decline in habitats at a rate approximately proportional to the amount of native vegetation displaced by the invaders. Moreover, the species composition of such communities should shift dramatically from uncommon, species-rich specialists with strong trophic connections to more common, species-poor generalists with weaker trophic connections. How such a loss of diversity and shift in species composition might affect the stability and productivity of ecosystems in which native plant communities have been substantially replaced by non-native plants has yet to be investigated. However, evidence from both terrestrial and marine ecosystems suggests that, though complex and system specific, reductions in diversity tend to decrease both stability and productivity at all trophic levels (reviewed by Duffy 2009). More diverse communities are thought to be more productive because higher species redundancy and more diverse species composition increase the efficiency with which resources are used and retained within the system. Low diversity at higher trophic levels encourages trophic cascades that disrupt the entire system (Schmitz et al. 2000). Mulder et al. (1999) showed that the removal of insect herbivores has a greater effect on ecosystem productivity than a six-fold change in plant diversity. Because insect herbivores are near the hub of most terrestrial food webs, comprising essential food stuffs for an incredible diversity of insect predators and parasitoids, spiders, amphibians, lizards, rodents, bats, birds, and even higher predators such as foxes and bears, it is particularly important to understand changes wrought by non-native plants on this critical taxon (Wilson 1987, Tallamy 2004, Burghardt et al. 2009).

Our study suggests that measuring the health of invaded plant communities only in terms of the number of plant species present may be misleading. Instead, measuring the degree to which the production of ecosystem services has been compromised will tell us how well invaded systems (or systems planted with non-native ornamentals such as suburbs) are functioning. The reduction of the abundance and redundancy of both specialist and generalist Lepidoptera is the reduction of energy transfer from plants to higher trophic levels: a critically important ecosystem service. Past mass extinctions and ecological avalanches have been linked to a widespread collapse of the first trophic level (Vermeij 2004). Thus, the local and global effects of non-native plant invasions will be anticipated accurately only if we clearly understand the degree to which non-native invaders are the ecological equivalents of the plants they replace. With this in mind, the impact of non-native plants on native biota might better be measured in terms of food web impairment and/or loss of diversity in higher trophic levels than numbers of immediate plant extinctions.

ACKNOWLEDGMENTS

Literature Cited

Agrawal, A. A., P. M. Kotanen, C. E. Mitchell, A. G. Power, W. Godsoe, and J. Klironomos. 2005. Enemy release? An experiment with congeneric plant pairs and diverse above- and belowground enemies. Ecology 86:2979–2989.

Berenbaum, M. R. 1990. Coevolution between herbivorous insects and plants: tempo and orchestration. Pages 87–89 in F. Gilbert, editor. Insect life cycles. Springer Press, London.

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

Brook, A. J., B. A. Woodcock, M. Sinka, and A. J. Vanbergen. 2008. Experimental verification of suction sampler capture efficiency in grasslands of differing vegetation height and structure. Journal of Applied Ecology 45:1357–1363.

Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. DiTomaso, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. Bioscience 54:677–688.

Burghardt, K. T., D. W. Tallamy, and W. G. Shriver. 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conservation Biology 23:219–224.

Butler, J. L. and D. R. Cogan. 2004. Leafy spurge effects on patterns of plant species richness. Journal of Range Management 57:305–311.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by Bromus tectorum? Ecological Monographs 77:117–145.

Cincotta, C. L., J. M. Adams, and C. Holzapfel. 2009. Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (Acer platanoides L.) and the native sugar maple (A-saccharum L.). Biological Invasions 11:379–388.

Collier, M. H., J. L. Vankat, and M. R. Hughes. 2002. Diminished plant richness and abundance below Lonicera maackii, an invasive shrub. American Midland Naturalist 147:60–71.

Davis, M. 2009. Invasion Biology. Oxford University Press, Oxford.

Duffy, J. E. 2009. Why biodiversity is important to functioning of real-world ecosystems. Frontiers in Ecology and the Environment 7:437–444.

Duguay, J. P., P. B. Wood, and G. W. Miller. 2000. Effects of timber harvests on invertebrate biomass and avian nest success. Wildlife Society Bulletin 28:1123–1131.

Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. American Naturalist 149:903–915.

Ehrlich, P. R. and P. H. Raven. 1964. Butterflies and Plants- A study in coevolution. Evolution 18:586–608.

Elton, C. 1927. Animal Ecology. Sidgwick and Jackson, London.

Farrell, B. and C. Mitter. 1990. Phylogenesis of insect plant interaction: Have Phyllobrotica leaf beetle (Chrysomelidae) and the Lamiales diversified in parallel. Evolution 44:1389–1403.

Fox, L. R. and P. A. Morrow. 1981. Specialization: species property or local phenomenon? Science 211:887–893.

Futuyma, D. J. and F. Gould. 1979. Associations of plants and insects in a deciduous forest. Ecological Monographs 49:33–50.

Gould, A. M. A. and D. L. Gorchov. 2000. Effects of the exotic invasive shrub Lonicera maackii on the survival and fecundity of three species of native annuals. American Midland Naturalist 144:36–50.

Gratton, C. and R. F. Denno. 2006. Arthropod food web restoration following removal of an invasive wetland plant. Ecological Applications 16:622–631.

Graves, S. D. and A. M. Shapiro. 2003. Exotics as host plants of the California butterfly fauna. Biological Conservation 110:413–433.

Harborne, J. B., H. Baxter, and G. P. Moss. 1999. Phytochemical Dictionary: A handbook of bioactive compounds from plants. Taylor and Francis, London.

Heleno, R. H., R. S. Ceia, J. A. Ramos, and J. Memmott. 2009. Effects of alien plants on insect abundance and biomass: a food-web approach. Conservation Biology 23:410–419.

Jogesh, T., D. Carpenter, and N. Cappuccino. 2008. Herbivory on invasive exotic plants and their non-invasive relatives. Biological Invasions 10:797–804.

Kindt, R. and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. Nairobi. World Agroforestry Centre (ICRAF).

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. Ecological Applications 10:689–710.

Magurran, A. E. 2004. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts, USA.

Marra, P. P., K. A. Hobson, and R. T. Holmes. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Martin, P. H. 1999. Norway maple (Acer platanoides) invasion of a natural forest stand: understory consequence and regeneration pattern. Biological Invasions 1:215–222.

Mulder, C. P. H., J. Koricheva, K. Huss-Danell, P. Hogberg, and J. Joshi. 1999. Insects affect relation-

ships between plant species richness and ecosystem processes. Ecology Letters 2:237–246.

Novotny, V. and Y. Basset. 2005. Review - Host specificity of insect herbivores in tropical forests. Proceedings of the Royal Society B-Biological Sciences 272:1083–1090.

Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313:1115–1118.

Proches, S., J. R. U. Wilson, D. M. Richardson, and S. L. Chown. 2008. Herbivores, but not other insects, are scarce on alien plants. Austral Ecology 33:691–700.

Qian, H. and R. E. Ricklefs. 2006. The role of exotic species in homogenizing the North American flora. Ecology Letters 9:1293–1298.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Randall, J. M. 1996. Weed control for the preservation of biological diversity. Weed Technology 10:370–383.

Ratnasingham, S. and P. D. N. Hebert. 2007. BOLD: The Barcode of Life Data System ⟨www.barcodinglife.org⟩. Molecular Ecology Notes 7:355–364.

SAS Institute. 2009. SAS version 9.2. SAS Institute, Cary, North Carolina, USA.

Sax, D. F. and S. D. Gaines. 2008. Species invasions and extinction: The future of native biodiversity on islands. Proceedings of the National Academy of Sciences of the United States of America 105:11490–11497.

Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist 155:141–153.

Scriber, J. M. 1983. Evolution of feeding specialization, physiological efficiency and host races in selected Papilionidae and Saturniidae. Pages 373–412 in R. F. Denno and M. S. McClure, editors. Variable plants and herbivores in natural and managed systems. Academic Press, New York, USA.

Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. Science 288:2040–2042.

Slobodkin, L. B. 2001. The good, the bad and the reified. Evolutionary Ecology Research 3:1–13.

Stehr, F. W. 1987. Immature Insects. Kendall/Hunt Publishing, Dubuque, Iowa, USA.

Strong, A. M. and T. W. Sherry. 2000. Habitat-specific effects of food abundance on the condition of ovenbirds wintering in Jamaica. Journal of Animal Ecology 69:883–895.

Tallamy, D. W. 2004. Do alien plants reduce insect biomass? Conservation Biology 18:1689–1692.

Tallamy, D. W., M. Ballard, and V. D'Amico. 2010. Can alien plants support generalist insect herbivores? Biological Invasions 12:2285–2292.

Tallamy, D. W. and K. J. Shropshire. 2009. Ranking lepidopteran use of native versus introduced plants. Conservation Biology 23:941–947.

Tyser, R. W. and C. A. Worley. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). Conservation Biology 6:253–262.

Vermeij, G. J. 2004. Ecological avalanches and the two kinds of extinction. Evolutionary Ecology Research 6:315–337.

Wagner, D. L. 2005. Caterpillars of eastern North America: a guide to identification and natural history. Princeton University Press, Princeton, New Jersey, USA.

Wechsler, N. R. 1977. Growth and physiological characteristics of kudzu, *Pueraria lobata* (Willd), Ohwi, in relation to its competitive success. University of Georgia, Athens, Georgia, USA.

Weiblen, G. D., C. O. Webb, V. Novotny, Y. Basset, and S. E. Miller. 2006. Phylogenetic dispersion of host use in a tropical insect herbivore community. Ecology 87:S62–S75.

Weis, A. E. and M. R. Berenbaum. 1989. Herbivorous insects and green plants. Pages 122–162 in W. G. Abrahamson editor. Plant-animal interactions. McGraw-Hill, New York, USA.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.

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

Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). Conservation Biology 1:344–346.

APPENDIX A

Table A1. Lepidoptera species recorded.

Lepidoptera family	Species	Common name	No. reference list host families	No. plot host families
Arctiidae	*Estigmene acrea* (Drury 1773)	saltmarsh moth	27	4
Arctiidae	*Halysidota harrisii* Walsh 1864	sycamore tussock moth	3	1
Arctiidae	*Halysidota tessellaris* (J.E.Smith 1797)	banded tussock	22	15
Arctiidae	*Haploa confusa* (Lyman 1887)	confused haploa	8	1
Arctiidae	*Hyphantria cunea* (Drury 1773)	fall webworm	50	7
Arctiidae	*Lophocampa caryae* (Harris 1814)	hickory tussock moth	19	2
Arctiidae	*Spilosoma virginica* (Fabricus 1798)	yellowbear	44	7
Blastobasidae	Blastobasid sp. A (on *Acer, Ailanthus*)	—	†	2
Bombycidae	*Apatelodes torrefacta* (J.E.Smith 1797)	spotted apatelodes	17	1
Bucculatricidae	Bucculatricid sp. A (on *Nyssa*)	—	†	1
Bucculatricidae	Bucculatricid sp. B (on *Salix*)	—	†	1
Bucculatricidae	*Bucculatrix ainsliella* (Murtfeldt 1905)	oak skeletonizer moth	1	1
Bucculatricidae	*Bucculatrix canadensisella* (Chambers 1875)	birch skeletonizer moth	1	1
Bucculatricidae	*Bucculatrix eclecta* (Braun 1963)	—	1	1
Bucculatricidae	*Bucculatrix pomifoliella* (Clemens 1860)	—	2	1
Drepanidae	*Eudeilinia herminiata* (Guenée 1857)	northern eudeilinia	1	1
Gelechiidae	*Arogalea cristifasciella* (Chambers 1878)	—	1	1
Gelechiidae	*Chionodes* sp. A (on many plants)	—	†	11
Gelechiidae	*Coleotechnites* sp. A (on *Koelreutaria*)	—	†	1
Gelechiidae	*Dichomeris ligulella* (Hubner 1818)	palmerworm	9	6
Gelechiidae	Gelechiid sp. A (on *Nyssa*)	—	†	1
Geometridae	*Anavitrinelia pampinaria* (Guenée 1857)	common gray	29	15
Geometridae	*Antepione thisoaria* (Guenée 1857)	variable antepione	5	1
Geometridae	*Besma quercivoraria* (Guenée 1857)	oak besma	7	5
Geometridae	*Campaea perlata* (Guenée 1857)	fringed looper	23	6
Geometridae	*Cleora sublunaria* (Guenée 1857)	double-lined gray	6	2
Geometridae	*Coryphista meadii* (Packard 1874)	barberry looper	1	1
Geometridae	*Ectropis crepuscularia* (Denis & Schiffermüller 1775)	saddleback looper	21	4
Geometridae	*Ennomos subsignaria* (Hübner 1823)	elm spanworm	16	1
Geometridae	*Epimecis hortaria* (Fabricius 1794)	tulip tree beauty	3	2
Geometridae	*Eupithecia miserulata* Grote 1863	common pug	31	18
Geometridae	*Eutrapela clemataria* (Abbott & Smith 1797)	purplish-brown looper	21	4
Geometridae	*Glena cognataria* (Hübner 1824)	blueberry gray	5	1
Geometridae	*Glena cribrataria* (Guenée 1857)	dotted gray	4	4
Geometridae	*Hethemia pistasciaria* (Guenée 1857)	pistachio emerald	7	2
Geometridae	*Hypagyrtis unipunctata* (Haworth 1809)	one-spotted variant	18	17
Geometridae	*Iridopsis defectaria* (Guenée 1857)	brown-shaded gray	9	3
Geometridae	*Lomographa vestaliata* (Guenée 1857)	white spring moth	8	1
Geometridae	*Macaria aemulateria* (Walker 1861)	common angle	6	1
Geometridae	*Macaria* sp. A (on *Buddleja, Albizia*)	—	†	2
Geometridae	*Melanolophia canadaria* (Guenée 1857)	Canadian melanophia	21	9
Geometridae	*Nemoria rubrifrontaria* (Packard 1873)	red-fronted emerald	5	1
Geometridae	*Pero ancetaria* (Hübner 1806)	Hubner's pero	4	1
Geometridae	*Phaeoura quernaria* (J.E.Smith 1797)	oak beauty	8	2
Geometridae	*Pleuroprucha insulsaria* (Guenée 1857)	common tan wave	11	
Geometridae	*Prochoerodes lineola* (Drury 1770)	large maple spanworm	18	1
Geometridae	*Scopula limboundata* (Haworth 1809)	large lace border	9	2
Geometridae	*Synchlora frondaria* (Guenee 1858)		5	1
Geometridae	*Tetracis cachexiata* (Guenée 1857)	white slant-line	19	4
Gracillaridae	*Caloptilia azaleela* (Brants 1913)‡	azalea leafminer	1	1
Gracillaridae	*Caloptilia bimaculatella* (Ely 1915)	maple caloptilia	1	1
Gracillaridae	*Caloptilia blandella* (Clemens 1864)	—	1	1
Gracillaridae	*Caloptilia fraxinella* (Ely 1915)	ash leaf-roller	2	1
Gracillaridae	*Caloptilia rhoifoliella* (Chambers 1876)	—	1	1
Gracillaridae	*Caloptilia serotinella* (Ely 1910)	—	1	1
Gracillaridae	*Caloptilia stigmatella* (Fabricius 1781)	—	2	1
Gracillaridae	*Caloptilia syringella* (Fabricius 1794)	lilac leafminer	3	1
Gracillaridae	Gracillarid sp. A (on *Quercus*)	—	3§	1
Gracillaridae	*Parornix geminatella* (Packard 1869)	unspotted leafminer	1	1
Gracillaridae	*Parornix obliterella* or *vicinella* (Dietz 1907)	—	1	1
Gracillaridae	*Phyllocnistis liquidambarisella* (Chambers 1875)	—	1	1

Table A1. Continued.

Lepidoptera family	Species	Common name	No. reference list host families	No. plot host families
Gracillaridae	*Phyllocnistis liriodendronella* (Clemens 1863)	—	1	1
Gracillaridae	*Phyllonorycter propinquinella* (Braun 1908)	—	2	1
Gracillaridae	*Phyllonorycter* sp. A (on *Betula*)	—	1	1
Helionidae	Helionid sp. A (on *Paulownia*)	—	†	1
Hesperiidae	*Erynnis horatius* (Scudder & Burgess 1870)	Horace's duskywing	2	1
Hesperiidae	*Erynnis juvenalis* (Fabricius 1793)	Juvenal's duskywing	4	1
Limacodidae	*Acharia stimulea* (Clemens 1860)	saddleback caterpillar	27	11
Limacodidae	*Adoneta spinuloides* (Herrich-Schäffer 1854)	purple-crested slug	8	1
Limacodidae	*Apoda biguttata* (Packard 1864)	shagreened slug	2	1
Limacodidae	*Isa textula* (Herrich-Schäffer 1854)	crowned slug	7	1
Limacodidae	*Lithacodes fasciola* (Herrich-Schäffer 1854)	yellow-shouldered slug	13	2
Limacodidae	*Parasa chloris* (Herrich-Schäffer 1854)	smaller parasa	8	1
Lycaenidae	*Satyrium calanus* (Hubner 1809)	banded hairstreak	5	2
Lymantridae	*Lymantria dispar* (Linnaeus 1758)‡	gypsy moth	39	1
Lymantridae	*Orgyia antiqua* (Linnaeus 1758)	rusty tussock moth	16	1
Lymantridae	*Orgyia definita* (Packard 1864[1865])	definite tussock moth	9	3
Lymantridae	*Orgyia leucostigma* (J.E.Smith 1797)	white-marked tussock moth	54	13
Megalopygidae	*Megalopyge crispata* (Packard 1864)	black-waved flannel caterpillar	11	3
Nepticulidae	*Ectoedemia clemensella* (Chambers 1973) or *platanella* (Clemens 1861)	—	1	1
Nepticulidae	*Ectoedemia ulmella* (Braun 1912)	—	1	1
Nepticulidae	Nepticulid sp. A (on *Nyssa*)	—	†	1
Noctuidae	*Achatia distincta* (Hubner 1813)	distinct quaker	13	1
Noctuidae	*Acontia terminimaculata* (Grote 1873)	curve-lined acontia	2	1
Noctuidae	*Acronicta americana* (Harris 1841)	American dagger moth	17	3
Noctuidae	*Acronicta clarescens* Guenée 1852	clear dagger moth	3	1
Noctuidae	*Acronicta funeralis* (Grote & Robinson 1866)	paddle caterpillar	10	1
Noctuidae	*Acronicta grisea* (Walker 1856)	triton dagger moth	8	1
Noctuidae	*Acronicta hasta* (Guenée 1852)	cherry dagger moth	2	1
Noctuidae	*Acronicta impleta* (Walker 1856)	yellow-haired dagger moth	14	1
Noctuidae	*Acronicta radcliffei* (Harvey 1875)	Radcliffe's dagger moth	6	1
Noctuidae	*Acronicta rubricoma* (Guenée 1852)	ruddy dagger moth	3	1
Noctuidae	*Agriopodes fallax* (Herrich-Schaffer 1854)	the green marvel	2	1
Noctuidae	*Allotria elonympha* (Hübner 1818)	false underwing	3	1
Noctuidae	*Baileya australis* (Grote 1881)	small baileya	1	1
Noctuidae	*Baileya ophthalmica* (Guenée 1852)	eyed baileya	4	1
Noctuidae	*Catocala piatrix* (Grote 1864)	the penitent	4	1
Noctuidae	*Cerma cerintha* (Treitschke 1826)	tufted bird-dropping moth	4	2
Noctuidae	*Crocigrapha normani* (Grote 1874)	Norman's quaker	12	1
Noctuidae	*Hypena baltimoralis* (Guenée 1854)	baltimore bomolocha	3	1
Noctuidae	*Hypena madefactalis* (Guenée 1854)	gray-edged bomolocha	2	1
Noctuidae	*Hypena scabra* (Fabricius 1798)	green cloverworm	15	12
Noctuidae	*Isogona tenuis* (Grote 1872)	thin-lined owlet	1	1
Noctuidae	*Lacanobia subjuncta* (Grote & Robinson 1868)	speckled cutworm moth	13	1
Noctuidae	*Lacinipolia renigera* (Stephens 1829)	bristly cutworm	12	1
Noctuidae	*Lithophane innominata* (Smith 1893)	nameless pinion	10	1
Noctuidae	*Marathyssa inficita* (Walker 1865)	dark marathyssa	1	1
Noctuidae	*Morrisonia confusa* (Hubner 1831)	confused woodgrain	21	6
Noctuidae	*Morrisonia latex* (Guenée 1852)	fluid arches	17	4
Noctuidae	*Nycteola* sp. A (on *salix*)	—	2§	1
Noctuidae	*Paectes abrostoloides* (Guenée 1852)	large paectes	1	1
Noctuidae	*Palthis angulalis* (Hübner 1796)	dark-spotted palthis	16	7
Noctuidae	*Parallelia bistriaris* (Hübner 1818)	maple looper moth	4	1
Noctuidae	*Pseudaletia unipuncta* (Haworth 1809)	armyworm moth	16	1
Noctuidae	*Zale aeruginosa* (Guenée 1852)	green-dusted zale	2	1
Noctuidae	*Zale horrida* (Hübner 1818)	horrid zale	1	1
Noctuidae	*Zale lunata* (Drury [1773])	lunate zale	9	6
Noctuidae	*Zale lunifera* (Hübner 1818)	bold-based zale	2	1
Notodontidae	*Clostera inclusa* (Hübner 1829–31)	poplar tentmaker	7	1
Notodontidae	*Datana ministra* (Drury 1773)	yellow-necked caterpillar	14	3
Notodontidae	*Ellida caniplaga* (Walker 1856)	linden prominent	1	1
Notodontidae	*Furcula cinerea* (Walker 1865) or *occidentalis* (Lintner 1878)	gray or western furcula	2	1
Notodontidae	*Heterocampa guttivitta* (Walker 1855)	saddled prominent	18	3
Notodontidae	*Lochmaeus bilineata* (Packard 1864)	double-lined prominent	4	2

Table A1. Continued.

Lepidoptera family	Species	Common name	No. reference list host families	No. plot host families
Notodontidae	*Lochmaeus manteo* (Doubleday 1841)	variable oakleaf caterpillar	9	3
Notodontidae	*Misogada unicolor* (Packard 1864)	drab prominent	2	1
Notodontidae	*Nadata gibbosa* (J.E.Smith 1797)	white-dotted prominent	8	1
Notodontidae	*Nerice bidentata* (Walker 1855)	double-toothed prominent	1	1
Notodontidae	*Oligocentria semirufescens* (Walker 1865)	red-washed prominent	6	2
Notodontidae	*Schizura badia* (Packard 1864)	chestnut schizura	1	1
Notodontidae	*Schizura ipomoeae* (Doubleday 1841)	checkered-fringe prominent	15	5
Notodontidae	*Schizura unicornis* (J.E.Smith 1797)	unicorn caterpillar moth	20	8
Nymphalidae	*Asterocampa celtis* (Boisduval & LeConte 1834)	hackberry emperor	1	1
Nymphalidae	*Asterocampa clyton* (Boisduval & LeConte 1833)	tawny emperor	2	1
Nymphalidae	*Limenitis archippus* (Cramer 1776)	viceroy	4	1
Nymphalidae	*Limenitis arthemis* (Drury 1773)	red-spotted purple	4	1
Nymphalidae	*Nymphalis antiopa* (Linnaeus 1758)	mourning cloak	9	1
Nymphalidae	*Polygonia comma* (Harris 1842)	eastern comma	3	1
Nymphalidae	*Polygonia interrogationis* (Fabricius 1798)	question mark	5	1
Oecophoridae	*Antaeotricha leucillana* (Zeller 1854)	well-marked leaf tier	11	5
Oecophoridae	*Machimia tentoriferrella* (Clemens 1860)	golden-striped leaf tier	14	3
Oecophoridae	*Psilocorsis reflexella* (Clemens 1860)	—	7	1
Oecophoridae	*Psilocorsis* sp. A (on *Quercus*)	—	†	1
Papilionidae	*Papilio glaucus* (Linnaeus 1758)	eastern tiger swallowtail	15	3
Papilionidae	*Papilio troilus* (Linnaeus 1758)	spicebush swallowtail	6	1
Psychidae	*Thyridopteryx ephemeraeformis* (Haworth 1803)	evergreen bagworm	48	15
Pterophoridae	*Emmelina monodactyla* (Linnaeus 1758)	—	8	2
Pyralidae	*Acrobasis indigenella* (Zeller 1848)	leaf crumpler moth	2	1
Pyralidae	*Framinghamia helvalis* (Walker 1859)	—	1	1
Pyralidae	*Glyptocera consobrinella* (Zeller 1872)	glyptocera moth	2	1
Pyralidae	*Nephopterix celtidella* (Hulst 1890)	—	1	1
Pyralidae	*Nephopterix sufuscella* (Ragonot 1887)	—	2	1
Pyralidae	*Nephopterix uvinella* (Ragonot 1887)	—	1	1
Pyralidae	*Palpita magniferalis* (Walker 1861)	ash leaf roller	1	1
Pyralidae	*Pantographa limata* (Grote and Robinson 1867)	basswood leaf roller moth	3	1
Pyralidae	*Phlyctaenia coronata* (Hufnagel 1767)	—	5	1
Pyralidae	*Pococera expandens* (Walker 1863)	striped oak webworm moth	1	1
Pyralidae	*Pococera militella* (Zeller 1848)	sycamore webworm moth	1	1
Pyralidae	Pyralid sp. A (on *Ulmus*)	—	†	1
Saturniidae	*Actias luna* (Linnaeus 1758)	luna moth	19	1
Saturniidae	*Antheraea polyphemus* (Cramer 1776)	polyphemus moth	26	2
Saturniidae	*Callosamia promethea* (Drury 1773)	promethea moth	20	1
Saturniidae	*Citheronia regalis* (Fabricius 1793)	hickory horned devil	19	1
Saturniidae	*Hyalophora cecropia* (Linnaeus 1758)	cecropia moth	43	1
Sphingidae	*Ceratomia undulosa* (Walker 1856)	waved sphinx	5	1
Sphingidae	*Darapsa choerilus* (Cramer 1780)	azalea sphinx	3	2
Sphingidae	*Hemaris thysbe* (Fabricius 1775)	hummingbird clearwing	2	1
Sphingidae	*Manduca rustica* (Fabricius 1775)	rustic sphinx	7	1
Sphingidae	*Paonias excaecatus* (J.E.Smith 1797)	blinded sphinx	11	3
Tisheriidae	*Tischeria* sp. A (on *Quercus*)	trumpet leaf miner	1§	1
Tortricidae	*Acleris flavivittana* (Clemens 1864)	masked leaf roller	1	1
Tortricidae	*Acleris schalleriana* (Linnaeus 1761)	—	4	1
Tortricidae	*Adoxophyes furcatana* (Walker 1863)	—	1	1
Tortricidae	*Amorbia humerosana* (Clemens 1860)	white-lined leaf roller	16	15
Tortricidae	*Ancylis comptana* (Frőlich 1828)‡	strawberry leaf roller	5	2
Tortricidae	*Ancylis platanana* (Clemens 1860)	—	3	1
Tortricidae	*Archips argyrospila* (Walker 1863)	fruit tree leaf roller	26	1
Tortricidae	*Argyrotaenia velutinana* (Walker 1863)	red-banded leaf roller moth	24	14
Tortricidae	*Choristoneura parallela* (Robinson 1869)	spotted fireworm moth	11	2
Tortricidae	*Choristoneura rosaceana* (Harris 1841)	oblique-banded leaf roller moth	26	12
Tortricidae	*Episimus argutana* (Clemens 1860)	—	9	1
Tortricidae	*Episimus tyrius* Heinrich 1923	maple tip borer	2	1
Tortricidae	*Grapholita prunivora* (Walsh 1868) or *packardi* (Zeller 1875)	—	3§	1
Tortricidae	*Gretchena bolliana* (Slingerland 1896) or *concitatricana* (Heinrich 1923)	—	1§	1
Tortricidae	*Lobesia aruncana* (Kearfott 1907) or *spiraeifoliana* (Heinrich 1923)	—	1§	1
Tortricidae	*Lobesia liriodendrana* (Kearfott 1904)	—	1	1
Tortricidae	*Olethreutes* sp. A (on *Prunus, Cornus*)	—	†	3

Table A1. Continued.

Lepidoptera family	Species	Common name	No. reference list host families	No. plot host families
Tortricidae	*Phaecasiophora confixana* (Walker 1863)	—	1	1
Tortricidae	*Platynota flavedana* (Clemens 1860)	—	11	5
Tortricidae	*Platynota idaeusalis* (Walker 1859)	tufted apple-bud moth	12	10
Tortricidae	Tortricid sp. A (on *Juglans*)	—	†	1
Tortricidae	Tortricid sp. A (on *Salix*)	—	†	1
Tortricidae	Tortricid sp. B (on *Juglans*)	—	†	1
Tortricidae	Tortricid sp. C (on *Rosa*)	—	†	1
Tortricidae	Tortricid sp. D (on *Frangula*)	—	†	1
Tortricidae	Tortricid sp. E (on *Ulmus*)	—	†	1
Tortricidae	Tortricid sp. F (on *Liriodendron*)	—	†	1
Tortricidae	Tortricid sp. G (on *Salix*)	—	†	1
Tortricidae	Tortricid sp. H (on *Prunus*)	—	†	1
Yponomeutidae	*Atteva punctella* (Cramer 1781)	Ailanthus webworm	1	1
Unknown	Unknown sp. A (on *Rhododendron*)	—	†	1
Unknown	Unknown sp. B (on *Viburnum*)	—	†	1
Unknown	Unknown sp. C (on *Viburnum*)	—	†	1
Unknown	Unknown sp. D (on *Lindera*)	—	†	1
Unknown	Unknown sp. E (on *Cotoneaster, Rhus*)	—	†	2
Unknown	Unknown sp. E (on *Fraxinus*)	—	†	2

Notes: † Indicates species host specialization could not be classified using host record lists. ‡ Species not native to North America (not included in analysis). § Indicates an individual whose identity was narrowed down to a few species with similar host plants. These individuals were considered specialists for the sake of the host record list comparison if their combined host range was 3 or fewer families.

APPENDIX B

Table B1. ANOVA for congeneric comparisons: Lepidoptera abundance.

	Lepidoptera specialization class based on literature host list						Specialization class based on study community			
	2008			2009			2008		2009	
	Total	Gen.	Spec.	Total	Gen.	Spec.	Gen.	Spec.	Gen.	Spec.
Non-native plants										
Mean indvls/100 g	0.258	0.203	0.015	0.335	0.285	0.045	0.237	0.018	0.110	0.099
95% C.I. upper	0.1137	0.0819	0.0146	0.1710	0.1596	0.0338	0.1105	0.0155	0.0547	0.0930
95% C.I. lower	0.0988	0.0733	0.0142	0.1419	0.1326	0.0319	0.0961	0.0151	0.0502	0.0805
Native plants										
Mean indvls/100 g	0.350	0.242	0.093	1.063	0.802	0.182	0.262	0.093	0.453	0.276
95% C.I. upper	0.1158	0.0744	0.0585	0.5836	0.4922	0.0845	0.0778	0.0585	0.2741	0.1354
95% C.I. lower	0.1019	0.0676	0.0533	0.4249	0.3572	0.0752	0.0706	0.0533	0.2129	0.1153
Origin										
DF	1	1	1	1	1	1	1	1	1	1
Type III SS	0.0639	0.0051	0.0986	1.9298	1.2536	0.2437	0.0051	0.0910	0.9761	0.3307
Mean square	0.0639	0.0051	0.0986	1.9298	1.2536	0.2437	0.0051	0.0910	0.9761	0.3307
F	1.4	0.14	8.15	11.15	7.09	11.5	0.14	7.45	10.94	5.52
P	0.2388	0.7129	**0.0053**	**0.0012**	**0.0091**	**0.001**	0.7129	**0.0076**	**0.0013**	**0.0209**
Site										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0980	0.0467	0.0338	0.3359	0.2003	0.0641	0.0467	0.0387	0.1159	0.0734
Mean square	0.0327	0.0156	0.0113	0.1120	0.0668	0.0214	0.0156	0.0129	0.0386	0.0245
F	0.72	0.42	0.93	0.65	0.38	1.01	0.42	1.06	0.43	0.41
P	0.5437	0.7404	0.4295	0.5869	0.7695	0.3927	0.7404	0.3717	0.7298	0.7474
Site × origin										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0332	0.0161	0.0128	0.0356	0.0148	0.0725	0.0161	0.0085	0.2610	0.0355
Mean square	0.0111	0.0054	0.0043	0.0119	0.0049	0.0242	0.0054	0.0028	0.0870	0.0118
F	0.24	0.14	0.35	0.07	0.03	1.14	0.14	0.23	0.98	0.2
P	0.8661	0.933	0.7873	0.9765	0.9937	0.3367	0.933	0.8737	0.4078	0.8981

Note: "Gen." column represents generalist caterpillar species; "Spec." column represents specialist caterpillar species.

Table B2. ANOVA for congeneric comparisons: Lepidoptera richness.

	Lepidoptera specialization class based on literature host list						Specialization class based on study community			
	2008			2009			2008		2009	
	Total	Gen.	Spec.	Total	Gen.	Spec.	Gen.	Spec.	Gen.	Spec.
Non-native plants										
Mean species/100 g	0.211	0.187	0.010	0.179	0.154	0.024	0.187	0.018	0.086	0.020
95% C.I. upper	0.0839	0.0779	0.0091	0.0556	0.0519	0.0148	0.0779	0.0142	0.0332	0.0179
95% C.I. lower	0.0750	0.0700	0.0089	0.0514	0.0480	0.0144	0.0700	0.0138	0.0314	0.0173
Native plants										
Mean species/100 g	0.256	0.201	0.047	0.432	0.313	0.086	0.201	0.047	0.184	0.089
95% C.I. upper	0.0752	0.0619	0.0230	0.1524	0.1286	0.0342	0.0619	0.0230	0.0596	0.0340
95% C.I. lower	0.0684	0.0569	0.0221	0.1310	0.1111	0.0323	0.0569	0.0221	0.0548	0.0321
Origin										
DF	1	1	1	1	1	1	1	1	1	1
Type III SS	0.0143	0.0021	0.0234	0.4912	0.2347	0.0628	0.0021	0.0144	0.1180	0.0756
Mean square	0.0143	0.0021	0.0234	0.4912	0.2347	0.0628	0.0021	0.0144	0.1180	0.0756
F	0.52	0.09	9.09	14.27	7.1	13.12	0.09	4.73	9.31	13.83
P	0.4721	0.7686	**0.0033**	**0.0003**	**0.0090**	**0.0005**	0.7686	**0.0320**	**0.0030**	**0.0003**
Site										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0263	0.0110	0.0045	0.1307	0.1273	0.0210	0.0110	0.0101	0.0290	0.0103
Mean square	0.0088	0.0037	0.0015	0.0436	0.0424	0.0070	0.0037	0.0034	0.0097	0.0034
F	0.32	0.15	0.58	1.27	1.28	1.46	0.15	1.1	0.76	0.63
P	0.812	0.9293	0.6265	0.2906	0.2844	0.2307	0.9293	0.3512	0.5176	0.597
Site × origin										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0029	0.0023	0.0007	0.2219	0.1392	0.0199	0.0023	0.0034	0.0290	0.0042
Mean square	0.0010	0.0008	0.0002	0.0740	0.0464	0.0066	0.0008	0.0011	0.0097	0.0014
F	0.04	0.03	0.09	2.15	1.4	1.38	0.03	0.38	0.76	0.26
P	0.991	0.9923	0.9645	0.0992	0.2464	0.2523	0.9923	0.7697	0.5176	0.8567

Note: "Gen." column represents generalist caterpillar species; "Spec." column represents specialist caterpillar species.

Table B3. ANOVA for non-congeneric comparisons: Lepidoptera abundance.

| | Lepidoptera specialization class based on literature host list | | | | | | Specialization class based on study community | | | |
| | 2008 | | | 2009 | | | 2008 | | 2009 | |
	Total	Gen.	Spec.	Total	Gen.	Spec.	Gen.	Spec.	Gen.	Spec.
Non-native plants										
Mean indvls/100 g	0.151	0.122	0.024	0.252	0.141	0.080	0.095	0.053	0.138	0.081
95% C.I. upper	0.0553	0.0518	0.0273	0.1265	0.0837	0.0710	0.0406	0.0387	0.0836	0.0711
95% C.I. lower	0.0553	0.0478	0.0259	0.1083	0.0740	0.0632	0.0380	0.0362	0.0739	0.0633
Native plants										
Mean indvls/100 g	0.521	0.323	0.183	1.064	0.597	0.322	0.198	0.293	0.597	0.322
95% C.I. upper	0.1604	0.1001	0.0867	0.4390	0.3104	0.1182	0.0571	0.1281	0.3104	0.1182
95% C.I. lower	0.1386	0.0893	0.0770	0.3428	0.2419	0.1033	0.0528	0.1103	0.2419	0.1033
Origin										
DF	1	1	1	1	1	1	1	1	1	1
Type III SS	1.2944	0.5025	0.4490	3.4338	1.8606	0.7826	0.1651	0.8299	1.8776	0.7716
Mean square	1.2944	0.5025	0.4490	3.4338	1.8606	0.7826	0.1651	0.8299	1.8776	0.7716
F	28.23	16.02	17.33	23.97	14.54	15.32	10.16	19.1	14.66	15.12
P	**<0.0001**	**0.0001**	**<0.0001**	**<0.0001**	**0.0002**	**0.0001**	**0.0018**	**<0.0001**	**0.0002**	**0.0002**
Site										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.3193	0.1166	0.1976	0.0455	0.2361	0.1252	0.1045	0.2039	0.2379	0.1290
Mean square	0.1064	0.0389	0.0659	0.0152	0.0787	0.0417	0.0348	0.0680	0.0793	0.0430
F	2.32	1.24	2.54	0.11	0.61	0.82	2.14	1.56	0.62	0.84
P	0.0783	0.2983	0.0592	0.9565	0.6065	0.4867	0.0979	0.2013	0.6037	0.4731
Site × origin										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.1064	0.0967	0.1245	0.0405	0.0372	0.1000	0.0921	0.0592	0.0333	0.0952
Mean square	0.0355	0.0322	0.0415	0.0135	0.0124	0.0333	0.0307	0.0197	0.0111	0.0317
F	0.77	1.03	1.6	0.09	0.1	0.65	1.89	0.45	0.09	0.62
P	0.5107	0.3826	0.1922	0.9631	0.9616	0.5826	0.1347	0.7148	0.9672	0.6022

Note: "Gen." column represents generalist caterpillar species; "Spec." column represents specialist caterpillar species.

Table B4. ANOVA for non-congeneric comparisons: Lepidoptera richness.

| | Lepidoptera specialization class based on literature host list | | | | | | Specialization class based on study community | | | |
| | 2008 | | | 2009 | | | 2008 | | 2009 | |
	Total	Gen.	Spec.	Total	Gen.	Spec.	Gen.	Spec.	Gen.	Spec.
Non-native plants										
Mean species/100 g	0.112	0.104	0.007	0.101	0.076	0.015	0.082	0.031	0.074	0.016
95% C.I. upper	0.0202	0.0200	0.0034	0.0301	0.0256	0.0136	0.0345	0.0175	0.0257	0.0138
95% C.I. lower	0.0195	0.0194	0.0033	0.0287	0.0246	0.0132	0.0326	0.0169	0.0246	0.0134
Native plants										
Mean species/100 g	0.260	0.197	0.075	0.346	0.210	0.110	0.132	0.127	0.210	0.110
95% C.I. upper	0.0316	0.0242	0.0135	0.0710	0.0496	0.0287	0.0378	0.0436	0.0496	0.0287
95% C.I. lower	0.0304	0.0234	0.0132	0.0655	0.0463	0.0274	0.0357	0.0407	0.0463	0.0274
Origin										
DF	1	1	1	1	1	1	1	1	1	1
Type III SS	0.2990	0.1312	0.0999	0.7619	0.2814	0.1822	0.0441	0.1778	0.2880	0.1770
Mean square	0.2990	0.1312	0.0999	0.7619	0.2814	0.1822	0.0441	0.1778	0.2880	0.1770
F	17.2	9.22	27.82	55.17	27.34	41.19	4.27	19.75	27.78	39.74
P	**<0.0001**	**0.0029**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0407**	**<0.0001**	**<0.0001**	**<0.0001**
Site										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0874	0.0582	0.0182	0.1316	0.0654	0.0200	0.0624	0.0259	0.0609	0.0214
Mean square	0.0291	0.0194	0.0061	0.0439	0.0218	0.0067	0.0208	0.0086	0.0203	0.0071
F	1.68	1.36	1.69	3.18	2.12	1.51	2.02	0.96	1.96	1.6
P	0.1756	0.2569	0.1719	**0.0264**	0.1013	0.2159	0.1148	0.4138	0.1237	0.1926
Site × origin										
DF	3	3	3	3	3	3	3	3	3	3
Type III SS	0.0190	0.0409	0.0214	0.0153	0.0111	0.0168	0.0604	0.0208	0.0092	0.0150
Mean square	0.0063	0.0136	0.0071	0.0051	0.0037	0.0056	0.0201	0.0069	0.0031	0.0050
F	0.36	0.96	1.99	0.37	0.36	1.27	1.95	0.77	0.3	1.12
P	0.7785	0.4142	0.1189	0.7746	0.7832	0.2881	0.1246	0.5122	0.8275	0.3419

Note: "Gen." column represents generalist caterpillar species; "Spec." column represents specialist caterpillar species