



# Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods

Karin T. Burghardt<sup>1,2\*</sup> and Douglas W. Tallamy<sup>1</sup>

<sup>1</sup>Department of Entomology and Wildlife Ecology, University of Delaware, Newark, DE 19716-2103, USA, <sup>2</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA

## ABSTRACT

**Aim** Efforts to evaluate the impact of non-native plants on ecosystems rarely consider the role of such plants in sustaining local food webs of arthropods, or whether the effect is similar across arthropod feeding guilds and life stages. We assess this response by comparing arthropod herbivores on native plants (species with evolutionary histories within local food webs) and non-native plants (species without such histories). We further compare the impact of non-native plants that are congeners of local native species with those of non-natives with no close local relatives.

**Location** Suburban landscapes, Mid-Atlantic United States (Delaware, Pennsylvania).

**Methods** We manipulated the composition of the first trophic level by planting four large common gardens of 50 woody plant species replicated in time and space. After an establishment year, we sampled herbivorous arthropods supported by each plant species and classified them by herbivore species, feeding guild and life stage.

**Results** We found that (1) native plants support larger and more diverse herbivore communities, (2) arthropods with chewing mouthparts and immature herbivores were more sensitive to plant origin than arthropods with piercing-sucking mouthparts and adult herbivores, (3) arthropods laid more eggs on native plants, (4) internal feeders were rare on all non-native plants and (5) the reduction in herbivore populations on non-native plants was smaller, but still significant, if species had a close native relative.

**Main conclusions** Novel ecosystems comprised of plant species with no evolutionary history with local members of higher trophic levels may reduce the diversity and complexity of local food webs. Given the rate at which novel ecosystems are replacing coevolved plant communities worldwide, this result has global implications for the conservation of biodiversity. Using more native plants within human-dominated landscapes may help maintain the integrity of arthropod communities, as well as the populations of animals that consume arthropods.

## Keywords

Arthropods, diversity, feeding guilds, managed landscapes, native plants, non-native plants.

\*Correspondence: Karin T. Burghardt, Department of Ecology and Evolutionary Biology, Yale University, Osborn Memorial Laboratories, 165 Prospect Street, New Haven, CT 06511, USA.  
E-mail: karin.burghardt@yale.edu

## INTRODUCTION

In both natural and anthropogenic ecosystems, non-native plants (species that evolved outside of local food webs) are replacing native plant communities. Humans have planted

non-natives by the millions as ornaments and some of these species escape cultivation to become invasive (Williamson, 1996; Qian & Ricklefs, 2006). Although plant invasions can alter soil moisture, pH, biota and nutrients; increase fire frequency and plant competition; and significantly reduce local

biodiversity (Tyser & Worley, 1992; Randall, 1996; Duncan, 1997; Wilcove *et al.*, 1998; Gould & Gorchov, 2000; Mack *et al.*, 2000; Brooks *et al.*, 2004; Butler & Cogan, 2004 and many more), there is a growing literature describing how non-native species benefit the novel ecosystems that their introduction creates (Carroll, 2011; Gleditsch & Carlo, 2011; Marris, 2011; Schlaepfer *et al.*, 2011).

Ideally, species should be judged by the contributions they make to ecosystems rather than by their evolutionary origin (Davis *et al.*, 2011). In practice, ecologists know little about how the ecological benefits of non-natives compare with the ecological costs, making informed judgments difficult. Until detailed information is available for each individual species, using evolutionary information as a proxy for conservation value may be a useful approach. In this study, we compare the ecological value of introduced species in novel ecosystems with the contributions of the native organisms they replace. In the case of plants, we suggest that introduced species should be judged on their performance in one of their most important ecological roles: their effectiveness in supporting local food webs.

The production of arthropods is an important driver supporting most terrestrial food webs (Wilson, 1987), as arthropods are essential pollinators, seed dispersers and components of the diets of most terrestrial birds, rodents, lizards, amphibians, bats, as well as insect predators and parasitoids (Tallamy, 2004). Many recent studies have demonstrated the negative impact of invasive woody plant species on arthropod abundance, mortality and biomass (Gerber *et al.*, 2008; Proches *et al.*, 2008; Heleno *et al.*, 2009; Holmquist *et al.*, 2011; Vila *et al.*, 2011; Helden *et al.*, 2012). While valuable, most of these were observational studies of natural systems that focused on one plant invader (but see Heleno *et al.*, 2009). Often they do not account for the effect of noninvasive non-natives, the impact of invasion on nutritionally available plant biomass, or the impact of phylogenetic relationships (but see Proches *et al.*, 2008). In addition, no study to our knowledge has compared effects of plant invasion across differentially vulnerable stages of arthropod development or feeding guilds.

Most arthropod herbivores have highly specialized adaptations allowing them to avoid or tolerate the specific defences of their host plants (Bernays & Graham, 1988; Jaenike, 1990). Similar plant defences often reflect common evolutionary history (Novotny & Basset, 2005), suggesting that herbivores are more likely to feed on plant species that are closely related to their native hosts. As a result, we predict that phylogenetic relatedness to local flora may be a valuable proxy for the ability of herbivores to utilize a non-native plant species as a host.

There are also biological reasons to suspect that feeding strategy might influence the effect of host plant origin on arthropod herbivores. By interacting with host plant defences in fundamentally dissimilar ways, feeding guilds may differentially utilize non-native hosts (Meyer & Root, 1996). We predict that highly specialized internal feeders will be unable to utilize non-natives and that chewing herbivores will be

less able to use non-native plants than sucking herbivores that can feed selectively to avoid plant defences (Miles & Peng, 1989). Further, we predict that immature arthropods will be more sensitive to non-native plants than adults due to differing behavioural and physiological requirements.

Here, we use a replicated common garden experiment to compare the response of five feeding guilds of arthropod herbivores (chewing feeders, piercing mesophyll feeders, piercing phloem feeders, piercing xylem feeders and endophytic miners and gallers) on native and introduced woody plant congeners as well as on introduced plants that have no close relatives locally (non-congeners). Our study is unique in its combination of scope (approximately 2000 trees across 50 species), its focus on commonly used non-native landscaping plants rather than only invasive species, phylogenetic control of plant species, analysis of sensitive herbivore life stages and feeding guilds, and experimental control of plant age and biomass. Our focus on non-natives imported for use as ornamental plants is relevant to both managed landscapes and natural areas as 85% of the invasive woody plants in North America were introduced for landscaping purposes (Kaufman & Kaufman, 2007). We investigate (1) whether non-native plants support the same density and diversity of arthropods as native plants, (2) whether these relationships change if the non-native plant has a close native relative in the local flora and (3) whether herbivore feeding guilds or life stages respond differentially to non-native plants.

## METHODS

### Experimental design

#### *Common gardens*

Both congeneric and non-congeneric comparisons were replicated using randomized complete block protocol in four common gardens (at least 20 km apart) established in 2006 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. The gardens were designed to control for scale of 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 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 metre (see Fig. S1a in Supporting Information). In both 2007 and 2008, each group of four plants was treated as a sampling unit with one patch nondestructively sampled for arthropods in June and the other patch sampled in August. Plants were up to 2 m tall by the end of the experiment.

### Congeneric comparison

To address the question of whether non-native plants that have close native relatives support the same arthropod density, diversity and guild structure as natives, we planted one native and one non-native species from 12 woody plant genera representing 10 plant families (Table 1). The genera and species compared were selected because they were native and non-native congeners that were locally abundant. Both the native and non-native representatives of each genus were planted within two metres of each other (Fig. S1a in Supporting Information). Thus, if an insect was attracted to one congener, it could oviposit on the other member of the genus as well.

### Non-congeneric comparison

At the same common garden sites on a spatially distinct plot (Fig. S1b in Supporting Information), we compared arthropod density, diversity and guild structure on 15 species of native woody plants common in northern Delaware and 15 species of non-native woody landscaping plants that are now either invasive or commonly used locally as landscape plants (Table 2). The non-native species used in this comparison had no native congeners in the study area. The goal with species selection was to compare a group of non-native species to a group of native species that each could realistically represent the composition of a suburban yard in the Mid-Atlantic United States. This criterion limited the potential pool of species; however, it also ensures the direct application of results to management. Native species represented 15 plant families while non-natives represented 13 families. The spatial design was similar to the congener gardens except that species were arrayed randomly (Fig. S1b in Supporting Information). Statistics for phylogenetic signal were used to determine if native and non-native species selected were distributed randomly across a phylogenetic tree consisting of all study species. The phylogeny was constructed using the angiosperm megatree R20100701 with Phylomatic in Phylocom 4.2 (Webb *et al.*, 2008). In R, we used

two methods to test for phylogenetic signal (R Development Core Team, 2009). First, we used D within the package *caper* (Orme *et al.*, 2012), which is a measure explicitly designed for detecting phylogenetic signal in discrete traits (Fritz & Purvis, 2010). Because D is not as robust with small numbers of species, we also calculated K (Blomberg *et al.*, 2003) in the *picante* package (Kembel *et al.*, 2010). To test for significance, the observed variance of independent contrasts of the trait was compared against a null model where species were randomized repeatedly across branch tips ( $P < 0.05$  indicates phylogenetic clumping).

### Arthropod collection

Arthropod herbivores were sampled twice in 2007 and 2008 (June and August) to capture both spring flush and late summer feeders. A sampling unit of four trees was sampled nondestructively on each sample date. Any given patch was only sampled once a year to prevent early season sampling from impacting later season colonization. Arthropods were sampled 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 insects not removed by the leaf vacuum (Wagner, 2005). We also counted and collected voucher specimens of internal feeders (galls and leaf mines) and eggs. Internal feeders were treated separately during data analysis because we could not confirm that each individual gall or mine contained a living arthropod when counted, preventing direct comparison to live arthropod biomass. Root feeders were not considered in this study. After collection, insects were stored in 80% ethanol for later identification.

### Standardization by leaf weight

On each sample date, we counted the total number of leaves vacuumed and collected a subset of 100 leaves from each

**Table 1** Plant species community composition in congeneric study (12-paired genera).

Genus	Non-native species	Common name	Native species	Common name
<i>Acer</i>	<i>A. platanoides</i>	Norway maple	<i>A. rubrum</i>	Red maple
<i>Betula</i>	<i>B. pendula</i>	European white birch	<i>B. nigra</i>	River birch
<i>Carpinus</i>	<i>C. betulus</i>	European hornbeam	<i>C. caroliniana</i>	American hornbeam
<i>Cornus</i>	<i>C. kousa</i>	Kousa dogwood	<i>C. alternifolia</i>	Alternatleaf dogwood
<i>Ilex</i>	<i>I. aquifolium</i>	English holly	<i>I. opaca</i>	American holly
<i>Juglans</i>	<i>J. regia</i>	English walnut	<i>J. nigra</i>	Black walnut
<i>Prunus</i>	<i>P. serrulata</i>	Korean cherry	<i>P. serotina</i>	Black cherry
<i>Rhododendron</i>	<i>R. mucronulatum</i>	Korean rhododendron	<i>R. periclymenoides</i>	Pinxterbloom azalea
<i>Rosa</i>	<i>R. multiflora</i>	Multiflora rose	<i>R. setigera</i>	Prairie rose
<i>Salix</i>	<i>S. babylonica</i>	Weeping willow	<i>S. nigra</i>	Black willow
<i>Tilia</i>	<i>T. cordata</i>	Little-leaf linden	<i>T. americana</i>	Basswood
<i>Viburnum</i>	<i>V. dilatatum</i>	Linden viburnum	<i>V. dentatum</i>	Southern arrowwood

**Table 2** Plant species in non-congeneric study (paired by total leaf grams sampled, a proxy for size).

Non-native species	Common name	Native species	Common name
<i>Buddleja davidii</i>	Butterfly bush	<i>Acer rubrum</i>	Red maple
<i>Syringa vulgaris</i>	Lilac	<i>Morus rubra</i>	Red mulberry
<i>Ligustrum obtusifolium</i>	Border privet	<i>Lindera benzoin</i>	Spicebush
<i>Cotoneaster lucidus</i>	Hedge cotoneaster	<i>Platanus occidentalis</i>	Sycamore
<i>Berberis thunbergii</i>	Japanese barberry	<i>Nyssa sylvatica</i>	Black gum
<i>Rhamnus frangula</i>	Glossy buckthorn	<i>Liriodendron tulipifera</i>	Tulip tree
<i>Elaeagnus umbellata</i>	Autumn olive	<i>Celtis occidentalis</i>	Hackberry
<i>Ginkgo biloba</i>	Ginkgo	<i>Liquidambar styraciflua</i>	Sweetgum
<i>Ailanthus altissima</i>	Tree of heaven	<i>Viburnum dentatum</i>	Southern arrowwood
<i>Paulownia tomentosa</i>	Princess tree	<i>Salix nigra</i>	Black willow
<i>Forsythia x intermedia</i>	Forsythia	<i>Fraxinus pennsylvanica</i>	Green ash
<i>Koeleruteria paniculata</i>	Goldenrain tree	<i>Quercus palustris</i>	Pin oak
<i>Lagerstroemia indica</i>	Crape myrtle	<i>Rhus copalina</i>	Winged sumac
<i>Albizia julibrissin</i>	Silktree mimosa	<i>Prunus serotina</i>	Black cherry
<i>Pyrus calleryana</i>	Bradford pear	<i>Juglans nigra</i>	Black walnut

species, which were dried and weighed to yield an average leaf weight. To reduce potential bias due to unequal sample effort and represent the total trophic resource available to arthropods, all arthropod abundance data are expressed per dry leaf gram sampled as a density, and species accumulation measures are standardized by leaf biomass sampled.

#### Arthropod classification

Each arthropod was identified to genus and species when possible, by chaetotaxy (Stehr, 1987; Triplehorn *et al.*, 2005), images (Wagner, 2005), specialist texts, specialist identification, the University of Delaware Insect Museum collection and rearing. When necessary, Lepidoptera larvae were identified using DNA barcoding through the Biodiversity Institute of Ontario (Ratnasingham & Hebert, 2007). For groups where specific identifications were not possible, a morpho-species approach was utilized. Foliar herbivore species were then separated into feeding guilds as primarily (1) chewers, (2) mesophyll feeders, (3) phloem feeders, (4) xylem feeders or (5) internal feeders such as gallers and miners (see Table S1 in Supporting Information). Herbivorous arthropods not known to feed on woody tree species were excluded. Non-native arthropods comprised a small portion of the total arthropod community (<1.5% on all sample dates) and were analysed separately. Individuals were partitioned by life stage as egg, immature (larva or nymph) or adult. Pupae were rarely collected. Only eggs that could be positively identified to a primarily herbivorous insect lineage were included in the analysis.

#### Statistical analysis

##### Density of external feeders and guild analysis

In the non-congeneric comparison, a linear mixed model (LMM) with plant origin as the fixed effect and site (block)

as a random effect was used to test the effect of plant origin on arthropod abundance per kg leaves sampled. An additional crossed random effect of genus was included in the model for the congeneric comparison to account for the paired experimental design (Bolker *et al.*, 2009). A plant species patch was the sampling unit, and a separate model was run for each sample date. A log<sub>10</sub> transformation was used to conform count data to assumptions of normality and homogeneity of variance. All results are reported as back-transformed means ( $\pm$  95% CI), and  $\alpha = 0.05$  was used to test for significance of the fixed effect. R 2.10.0 was used for all analyses unless otherwise noted (R Development Core Team, 2009). The models were run within the *lme4* package (Bates *et al.*, 2012), and *P*-values were generated using *pvals.fnc()* within the *languageR* package (Baayen, 2011).

##### Density of internal feeders

The same models were used to test whether internal feeders differed between native and non-native plants species. Because galls and mines may have been created at any time over the course of the season, we used a cumulative measure of arthropod density for each plant species across sample dates.

##### Density of eggs

Because eggs may have been laid at any time over the season, a cumulative measure across season was again used. In addition, eggs were pooled across plant species due to a large number of zeros. We used a *t*-test paired by site ( $n = 4$ ) to test for treatment differences. We report mean  $\pm$  SEM.

##### Rarefied richness

Because richness does not increase linearly with sampling effort (Magurran, 2004), we standardized statistical

comparisons using rarefied arthropod richness measures for each plant species across sites and sample dates using leaf grams sampled to standardize the accumulation curves. We report mean  $\pm$  SEM and performed paired t-tests on species pairs [paired by genus for the congeneric comparison ( $n = 12$ ) and by cumulative leaf grams sampled, a proxy for size, for the non-congeneric comparisons ( $n = 15$ )], to test whether rarefied richness differed by plant origin within each comparison. All diversity analyses were performed with the *BiodiversityR* package (Kindt & Coe, 2005).

#### Species accumulation

Species accumulation curves for the entire herbivore community were constructed for both the native and non-native plant communities using the exact method pooled across leaf grams sampled (Kindt & Coe, 2005).

#### Diversity ordering

We calculated Renyi diversity profiles (mean  $\pm$  SEM reported) for the pool of arthropod species found on native and non-native plant species with site as replicate ( $n = 4$ ) at  $\alpha$  values 0, 0.25, 0.5, 1, 2, 4, 8 and  $\infty$  (Kindt & Coe, 2005). The Renyi diversity index family consists of one equation with a scaling parameter ( $\alpha$ ) that encompasses all possible proportional weights of abundance and richness; at  $\alpha = 0$ ,  $H_\alpha$  is related to total species number, at  $\alpha = \infty$ ,  $H_\alpha$  is related to a dominance measure, and at intermediate values, it is related to common diversity metrics such as Shannon's diversity index (Eqn 1) (Hill, 1973).

$$H_\alpha = \frac{\ln(\sum_{i=1}^s p_i^\alpha)}{1 - \alpha} \quad (1)$$

$S$  is the species richness of the community, while  $p_i$  is the proportion of individuals found of the  $i$ th species. This family of diversity indices is parametric and replication invariant (Tothmeresz, 1995).

## RESULTS

We collected 37,670 herbivores in 10 orders, 74 families and 532 species. We sampled 53,004 dry grams of native leaves and 52,419 dry grams of non-native leaves in the congeneric comparison, as well as 62,236 dry grams of native leaves and 64,023 dry grams of non-native leaves in the non-congeneric comparison. Unfortunately, the June 2007 sample of insects was damaged, so the results presented here are from the three subsequent samples. The congeneric comparison was phylogenetically controlled by design. No phylogenetic signal or clumping by origin was detected within the study plants of the non-congeneric comparison by either a discrete ( $D = -1.9$ ,  $P = 0.07$ ) or continuous measure (Blomberg's  $K = 0.318$ ,  $P = 0.11$ ).

### Density of external feeders

Early season herbivore density (June 2008) was two times greater on native plants compared with non-native plants in both the non-congeneric ( $F_{1,115} = 7.45$ ,  $P = 0.007$ ) and congeneric ( $F_{1,79} = 8.91$ ,  $P = 0.003$ ) comparisons (see Fig. 1 for means  $\pm$  95% CI). There were no significant differences between the same groups during the late season assays in August 2007 for non-congeners ( $F_{1,115} = 0.02$ ,  $P = 0.881$ ) or congeners ( $F_{1,79} = 0.06$ ,  $P = 0.799$ ) or in August 2008, respectively ( $F_{1,115} = 2.61$ ,  $P = 0.108$ ;  $F_{1,79} = 0.28$ ,  $P = 0.596$ ).

### Density of internal feeders

Cumulative measures of endophytic leaf miners and galls were 25 times higher on native species (mean = 2.51 indivls kg<sup>-1</sup>, 1.13–4.78 95% C.I.) than non-native species (mean = 0.09 indivls kg<sup>-1</sup>, 0.0–0.20 95% C.I.) in the non-congeneric comparison ( $F_{1,115} = 12.98$ ,  $P = 0.0005$ ) and nearly 45 times higher on native species (mean = 9.61 indivls kg<sup>-1</sup>, 3.54–13.80 95% C.I.) than non-native species (mean = 0.21 indivls kg<sup>-1</sup>, 0.0–0.56 95% C.I.) in the congeneric comparison ( $F_{1,79} = 21.49$ ,  $P = <0.001$ ).

### Density of arthropod eggs

Density of eggs was 10 times higher across native species (mean = 56.17  $\pm$  18.0 indivls kg<sup>-1</sup>) than non-native species

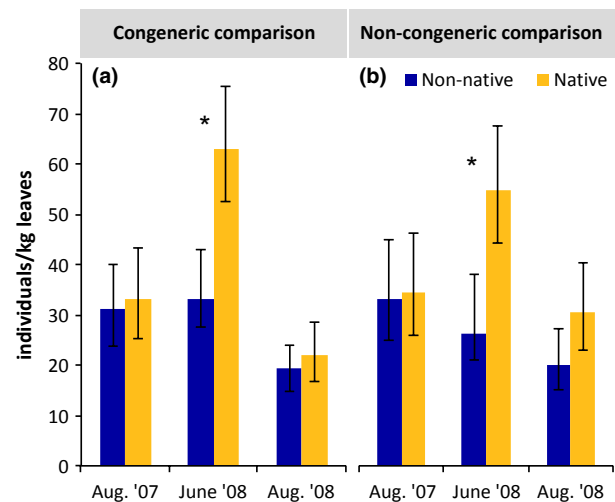


Figure 1 Total abundance of external arthropod feeders found across sample dates (means  $\pm$  95% C.I.). Early season abundance was significantly greater on native plants compared with non-native plants in both (a) a congeneric comparison where non-native plants are paired with a native plant within the same genus and (b) a non-congeneric comparison where non-native species that do not have a close native congener in the study area are compared to a pool of common native species. (\*) Indicates a significant difference at  $\alpha = 0.05$ .



in the non-congeneric comparison (mean =  $4.18 \pm 1.2$  indivls  $\text{kg}^{-1}$ ;  $F_{1,6} = 6.18$ ,  $P = 0.047$ ). In the congeneric comparison, density of eggs was marginally significantly higher across native species (mean =  $74.89 \pm 18.0$  indivls  $\text{kg}^{-1}$ ) than non-native species (mean =  $8.45 \pm 1.8$  indivls  $\text{kg}^{-1}$ ;  $F_{1,6} = 4.84$ ,  $P = 0.069$ ).

### Guild analysis

Differential responses of feeding guilds to non-native plants underlie the observed pattern of higher early season populations of herbivores on natives in both comparisons. Chewing insects and phloem feeders drove the differences between native and non-native insect communities.

In the non-congeneric comparison (Fig. 2a–d, Table 3), chewing herbivores were 2–4 times more abundant on natives compared with non-natives across all early and late season sample dates. Mesophyll feeders showed no significant differences. Phloem feeders were strongly suppressed on non-native plants in the early season sample, but not in the

late season samples. Xylem feeders showed no significant differences but were marginally more abundant on native plants in the early season, and marginally more abundant on non-natives for one of the late season samples.

In the congeneric comparison (Fig. 2e–h, Table 3), chewing herbivores were less numerous on non-native plants in the early season sample, but not in the late season samples. Mesophyll feeders showed no significant differences. Phloem feeders were three times more abundant on native plants in the early season sample, but not different in the late season samples. Xylem feeders showed no significant differences between native and non-native plants.

### Rarefied richness

On congeners, rarefied immature herbivore richness was higher on native ( $20.92 \pm 1.3$ ) than non-native plant species ( $14.46 \pm 1.1$ ;  $t = -2.63$ ,  $P = 0.02$ ). Rarefied adult herbivore richness was also higher on native ( $26.92 \pm 3.06$ ) than on non-native plant species ( $19.88 \pm 2.5$ ;  $t = -3.91$ ,  $P = 0.002$ ).

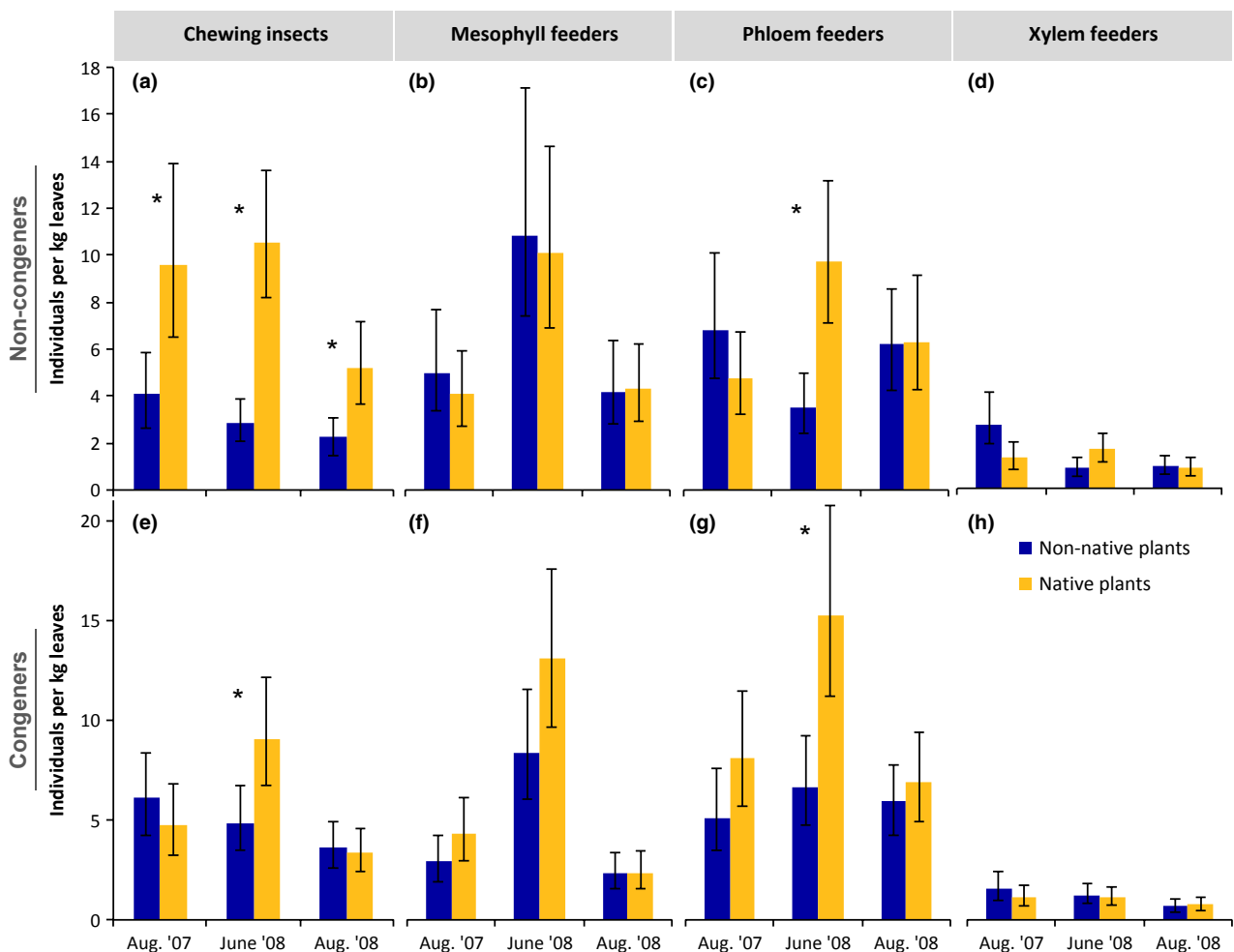
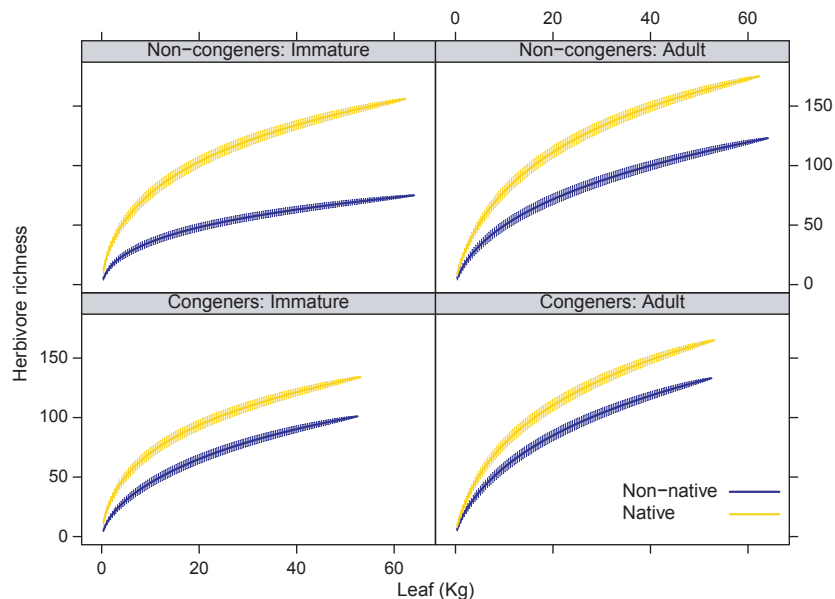


Figure 2 Differential response (means  $\pm$  95% C.I.) of herbivore guild abundance to native and non-native plants in the non-congeneric comparison (a–d) and congeneric comparison (e–h.). Chewing insects and phloem feeders showed significant differences in abundance at  $\alpha = 0.05$  (\*).

**Table 3** Linear mixed model results for analysis of the density of arthropod herbivores on native versus non-native trees by herbivore guild (effect sizes in Fig. 2). In the non-congeneric comparison, the model was specified with herbivore density as dependent factor, plant origin as fixed effect and site as random effect. An additional crossed random effect of genus was included for the congeneric comparison to account for the paired design. Bold values indicate significant differences between treatments at  $\alpha = 0.05$ . Effect sizes and confidence intervals can be found in Fig. 2.

	d.f.	August-2007		June-2008		August-2008	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Non-congeneric comparison							
Chewing	1,115	<b>6.400</b>	<b>0.013</b>	<b>27.280</b>	<b>&lt;0.0001</b>	<b>8.120</b>	<b>0.001</b>
Mesophyll feeders	1,115	0.280	0.598	0.034	0.855	0.001	0.922
Phloem feeders	1,115	1.050	0.306	<b>12.470</b>	<b>0.001</b>	0.001	0.967
Xylem feeders	1,115	3.770	0.055	3.390	0.068	0.067	0.796
Congeneric comparison							
Chewing	1,79	0.570	0.452	<b>4.134</b>	<b>0.045</b>	0.050	0.824
Mesophyll feeders	1,79	1.557	0.215	2.312	0.132	0.000	0.937
Phloem feeders	1,79	1.691	0.196	<b>10.500</b>	<b>0.002</b>	0.230	0.633
Xylem feeders	1,79	0.464	0.498	0.050	0.814	0.099	0.753



**Figure 3** Species accumulation curves (species  $\pm$  SD) for the entire herbivorous arthropod community constructed using the exact method across all sites and sample dates and standardized by leaf grams sampled. The left panels represent the immature arthropod community, and the right panels the adult arthropod community for both the non-congeneric comparison (top panels) and congeneric comparison (bottom panels).

The non-congeneric comparison showed the same pattern with higher immature herbivore richness on native species ( $21.32 \pm 1.2$ ) compared with non-natives ( $13.81 \pm 0.9$ ;  $t = -2.55$ ,  $P = 0.02$ ) and higher adult herbivore richness on native species ( $27.80 \pm 1.4$ ) compared with non-natives ( $19.34 \pm 1.1$ ;  $t = -2.78$ ,  $P = 0.01$ ).

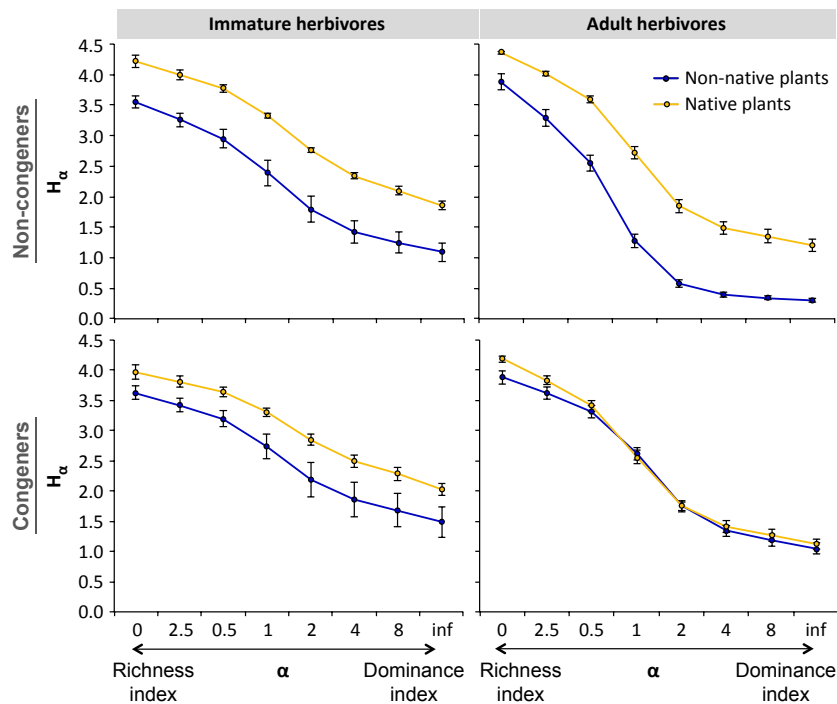
### Species accumulation

Pooled across all sites and sampling dates, native plants supported more adult and immature herbivore species in both congeneric and non-congeneric comparisons (Fig. 3). In

general, fewer immature herbivores could use non-native plants than could adult herbivores. Non-native plants with close native relatives supported more herbivores than those with no close relatives locally.

### Diversity ordering

Renyi diversity profiles revealed striking structural differences in herbivore communities between native and non-native plants (Fig. 4). Natives supported a more diverse assemblage of immature herbivores at all scales of diversity (sensu Tothmeresz, 1995). The adult assemblage was also more diverse



**Figure 4** Renyi diversity plots (means  $\pm$  SE) of immature and adult arthropod communities on native plants compared with non-native plants with spatially separate common garden sites as replicate plant communities ( $n = 4$ ). Higher values of the richness index (left extreme,  $x$ -axis) indicate higher species richness, while higher values of the dominance index (right extreme,  $x$ -axis) indicate a more even community structure that is less dominated by a single species. Top panels (non-congeners) compare a group of common non-native species without close native relatives to a pool of common native species. Bottom panels (congeners) compare non-native species to a paired native plant species within the same genus. Arthropod communities on native plants are always more diverse than on non-native plants in the non-congeneric comparison. In the congeneric comparison, immature arthropod communities are more diverse on native trees, but adult communities are mostly equivalent between native and non-native trees. In general, adult arthropod communities have a less even structure than immature communities. Adult herbivores on non-congeneric non-native plants showed the least even community structure. To recover the common diversity metrics,  $y = \exp(H_\alpha)$  (Kindt & Coe, 2005). For instance, richness is  $\exp(H_0)$  so for immature arthropods on non-congeneric plants, mean richness of arthropods on native trees per site is about 71 species, while non-native trees support 35 species of arthropods.

on natives in the non-congeneric comparison. In the congeneric comparison, adults had higher species richness on natives, but there were no differences in dominance. The magnitude of differences between assemblages was larger for the non-congeneric comparison, indicating that non-native plants with close relatives in the area support an insect community more similar to a native community than do plants without a native relative. Adult herbivores on non-congeneric, non-native plants in particular had a very uneven community structure with the herbivore community on these trees dominated by only one or a few species.

## DISCUSSION

### Herbivore feeding guilds and life stages are differentially impacted by plant origin

Our study revealed that chewing insects, immature phloem feeders, internal feeders and eggs were all less abundant on non-native plants. The density of chewing insects was

significantly depressed on non-native plants, particularly when those plants were not close relatives of local host species. Numbers of piercing mesophyll and xylem feeders were not reduced on non-native plants, while piercing phloem feeders were significantly less abundant on non-native plants, but only early in the season, when immatures were most abundant. Arthropods that develop entirely within plant tissues (endophytic gallers and leaf miners) discriminated against non-native plants more than all other herbivores. Leaf miners and galling arthropods have developed some of the most specialized host plant relationships known (Gagné, 1989), and even slight differences in defensive chemistry and phenology typically render evolutionarily novel plants unacceptable. Finally, the eggs of insect herbivores were significantly less numerous on non-native plants, evidence that ovipositing females favoured natives when selecting plants for immature development.

For the most part, the results of our guild analyses followed decades old predictions about how insects should interact with plants (Rosenthal & Janzen, 1979). Most



insect herbivores are specialists with physiological, behavioural and life history adaptations that allow them to circumvent the defences of only a narrow range of plant lineages (Bernays & Graham, 1988; Jaenike, 1990; Novotny & Basset, 2005) (Fig. S4 in Supporting Information). Moreover, insects recognize potential host plants through chemical and visual cues; therefore, mismatches in host recognition systems or neural limitations may further limit diet breadth of an herbivore to native plants (Bernays, 2001).

Even though host plant specialization among insect herbivores is predicted to cause general discrimination against novel plants, the mechanism by which an insect feeds on its host may enable some feeding guilds to use novel plants more than others (Verhoeven *et al.*, 2009). Chewing herbivores such as caterpillars encounter and must mitigate toxin-based defences as they chew cell vacuoles in which constitutive chemical defences are stored. Specialization is therefore predicted to be strongest among chewing insects (Rosenthal & Janzen, 1979). Piercing-sucking herbivores, in comparison, may be able to minimize exposure to such defences through selective feeding around vacuoles or by feeding through inert tissue such as xylem (Miles & Peng, 1989). Thus, sucking insects may interact more with elicitor-receptor defences as opposed to constitutive defences where a mismatch could give an advantage to the herbivore rather than the plant (Verhoeven *et al.*, 2009).

Host-use patterns observed among the piercing-sucking insects in our study were equivocal regarding these predictions. As predicted, mesophyll and xylem feeders did not discriminate against introduced plants; however, phloem-feeding populations discriminated more than predicted. It is possible that attacker-specific induced defensive chemistry generated within phloem tubes is not present to the same degree in more inert tissue such as xylem tubes where we saw no reduction in herbivores. Alternatively, phloem feeders may have host selection behaviours or morphological traits that discriminate against the use of non-natives even if they might be palatable (Gripengberg *et al.*, 2010).

### Non-native species supported less diverse arthropod communities

Native plants also supported a more species-rich and diverse herbivore community, as measured through species accumulation curves across all sites, rarefied richness estimated for each plant species, and Renyi diversity profiles. These differences were most pronounced in immatures and in arthropods on phylogenetically novel non-natives. However, even non-native congeners of local native plants supported significantly fewer herbivore species. We consider this pattern to be a robust demonstration of general discrimination against novel plants by all major taxa of arthropod herbivores (e.g. Orthoptera, Coleoptera, Lepidoptera, Hemiptera, Thysanoptera and Acarina) and is the same pattern observed by Burghardt *et al.* (2010) in a more detailed study of generalist and

specialist Lepidoptera larvae on the same experimental plots (Fig. S4 in Supporting Information).

### Immature arthropods were more sensitive to plant origin

A clear result from this study was the immature arthropods populations are much smaller and less diverse on non-native plants. To support growth, immature arthropods need to eat large quantities of plant tissue soon after emerging from the egg. Being relatively immobile, they are thus intimately tied to the maternally selected host plant, creating strong selection for insect herbivores to restrict feeding to plants for which they are physiologically adapted (Richards & Davies, 1977). Highly mobile adults, in contrast, do not increase their body size; they are focused on reproduction rather than growth, require far less food than their immature stages and may use plants for mating, resting or protection. As a result, it is not surprising that we found immature insects to be more sensitive to plant origin than adults.

The depauperate immature arthropod community on non-natives has several non-mutually exclusive explanations. First, gravid females may avoid ovipositing on non-native plants if the visual or chemical signature of non-native leaves differs substantially from leaves of native hosts (Eigenbrode & Espelie, 1995). We found evidence for this mechanism; 10 times fewer eggs were laid on non-native plants, indicating that females discriminate against plants with which they have no prior evolutionary experience (this was particularly true for non-congeneric plants). Therefore, this study demonstrates a strong behavioural preference among arthropods for native plants. In addition, once they hatch, immatures may perform better on native plants. While this study did not directly measure performance of immatures, herbivore preference for host plants often correlates with performance (Gripengberg *et al.*, 2010). In addition, laboratory-based feeding trials have demonstrated that growth and survival of even the most generalized lepidopteran species is lower on non-native plants (Tallamy *et al.*, 2010).

### Results match other studies on woody, but not herbaceous, plants

While this study does not directly test the enemy release hypothesis (Keane & Crawley, 2002), our results clearly show a decrease in herbivore abundance and diversity on non-native plants, that is, a reduction in enemy pressure. Moreover, specialist herbivores were more likely to use non-native species that were closely related to the native flora (Burghardt *et al.*, 2010), providing support for the biotic resistance hypothesis (Elton, 1958). Our results run counter to the early results of a phylogenetically controlled experiment examining herbaceous species which found higher herbivore damage on exotic species (Agrawal & Kotanen, 2003), although a continuation of that study later found lower rather than higher herbivore damage on non-natives (Agrawal *et al.*, 2005). In

addition, a study of herbaceous con-familial pairs in strand-line communities found higher levels of herbivore damage on non-native plants (Heard & Sax, 2013), and higher cover estimates of the non-native species with insecticide treatments suggesting that herbivores suppress non-native plant growth more than native plant growth.

The differences in our results may stem from a mismatch in response variables (plant response or herbivore damage versus herbivore density and diversity). A lower-quality non-native resource may receive more damage from a smaller number of arthropods than a higher quality native due to compensatory feeding. Alternatively, herbaceous plants may exhibit different patterns of herbivore use than woody plants. Our results are similar to those found in a non-experimental studies of herbivores on tree species in the Western Cape of South Africa (Proches *et al.*, 2008), Tanzania (Dawson *et al.*, 2009) and Australia (Harvey *et al.*, 2012).

### Conservation implications

Our data do not suggest that *every* non-native plant species supports less biodiversity than *every* native plant species. In fact, there was significant variation among both native and non-natives species in our study (see Figs S2 & S3 in Supporting Information). However, if conservation goals include the maintenance of higher trophic levels, and time or money precludes the collection of rigorous, quantitative data about each plant species, our results indicate a general and useful rule. Plant origin is a good surrogate for immature herbivore abundance and diversity: native plants support the most biodiversity, followed by non-natives with a close native relative, while non-natives that are unrelated to the local flora produce a species-poor, uneven herbivore community.

The preferential use of native plants by native herbivores suggests that long periods of reproductive isolation between native and non-native members of the same plant genus have likely facilitated divergence in key chemical or physical defensive traits. These trait differences are then powerful enough to deter many native insects from using or recognizing non-natives as host plants. Whether the mechanism creating this preference is driven by phytochemistry, host selection behaviour, neural limitations or other constraints, the pattern suggests serious consequences for biodiversity in human-dominated ecosystems. Land management practises that favour non-native plants over native species (e.g. ornamental plantings, soil stabilization projects, reforestation efforts) are predicted to reduce the diversity and abundance of arthropod herbivores, thus potentially reducing prey availability for the many insectivores in higher trophic levels. Reducing prey redundancy destabilizes food webs, increasing the probability of their collapse (Price *et al.*, 1990; McCann, 2011); without sufficient prey, many insectivores simply drop out of local food webs (Marra *et al.*, 1998; Burghardt *et al.*, 2009).

### CONCLUSION

Our study demonstrates that non-native plant species support a less diverse community of fewer chewing and phloem-feeding arthropods, immature arthropods and arthropod eggs than do native plants. Plants that promote successful immature growth are often the limiting factor in the size or existence of an arthropod population. As a result, insect population dynamics and interactions may be fundamentally different in invaded areas or landscapes planted with non-native ornamentals (Tallamy, 2004). Therefore, replacing native plant communities with non-native species may impact valuable arthropod-derived ecosystem services in human-dominated landscapes (e.g. food for higher trophic levels, pollination, seed dispersal, etc.). These results suggest that non-native species are not the equivalent of native species when assessed by comparing their effectiveness at supporting terrestrial food webs. As a result, we argue that evolutionary origin (the native/non-native dichotomy) can be a useful proxy for the conservation value of plant species when more detailed data are lacking. Our results should provide a cautionary note to relaxing global vigilance against invasive plants (Davis *et al.*, 2011), the continued importation and use of non-native ornamental plants (Del Tredici, 2006; Marris, 2011), and the use of non-native plants in large-scale restorations (Aerts & Honnay, 2011). In addition, a conservation management strategy that focuses on landscaping with natives (or minimizes the replacement of natives with non-natives) may help maintain the ecological integrity of higher trophic levels.

### ACKNOWLEDGEMENTS

We thank R. Colbert and M. Karkowski of Tyler Arboretum and K. & P. Flint, B. Haldeman, and M. Weaver of Flint Woods preserve; the 12 undergraduate members of our field crew along with K. & B. Cutting, C. Phillips, M. Ballard, and K. J. Shropshire; C. Bartlett for invaluable help on insect identification; N. Moran, M. Donoghue, B. Forrestel, and the Schmitz laboratory for analytic comments; J. Shapiro and D. West for creative help; L. Burghardt for graphical and manuscript comments; and three anonymous reviewers. This research was supported by NSF Award # 0514247 and NRI Award # 35320-16182 to D.W.T. and a GRFP under NSF Grant # DGE-1122492 to K.T.B.

### REFERENCES

- Aerts, R. & Honnay, O. (2011) Seeds of change for restoration ecology. *Science*, **333**, 156–156.
- Agrawal, A.A. & Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters*, **6**, 712–715.
- Agrawal, A.A., Kotanen, P.M., Mitchell, C.E., Power, A.G., Godsoe, W. & Klironomos, J. (2005) Enemy release? An

- experiment with congeneric plant pairs and diverse above- and belowground enemies. *Ecology*, **86**, 2979–2989.
- Baayen, R.H. (2011) *languageR: Data sets and functions with “Analyzing Linguistic Data: A practical introduction to statistics”*. R package version 1.4., Available at: <http://cran.r-project.org/web/packages/languageR/index.html> (accessed 15 March 2013).
- Bates, D., Maechler, M. & Bolker, B. (2012) *lme4: Linear mixed-effects models using Eigen and Eigen++*. R package version 0.999999-2, Available at: <http://cran.r-project.org/web/packages/lme4/index.html> (accessed 22 February 2013).
- Bernays, E.A. (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *Annual Review of Entomology*, **46**, 703–727.
- Bernays, E. & Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology*, **69**, 886–892.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**, 127–135.
- Brook, A.J., Woodcock, B.A., Sinka, M. & Vanbergen, A.J. (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., D’Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677–688.
- Burghardt, K.T., Tallamy, D.W. & Shriver, W.G. (2009) Impact of native plants on bird and butterfly biodiversity in suburban landscapes. *Conservation Biology*, **23**, 219–224.
- Burghardt, K.T., Tallamy, D.W., Phillips, C. & Shropshire, K.J. (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere*, **1**, art 11.
- Butler, J.L. & Cogan, D.R. (2004) Leafy spurge effects on patterns of plant species richness. *Journal of Range Management*, **57**, 305–311.
- Carroll, S.P. (2011) Conciliation biology: the eco-evolutionary management of permanently invaded biotic systems. *Evolutionary Applications*, **4**, 184–199.
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Philip Grime, J., Mascaro, J. & Briggs, J.C. (2011) Don’t judge species on their origins. *Nature*, **474**, 153–154.
- Dawson, W., Burslem, D.F.R.P. & Hulme, P.E. (2009) Herbivory is related to taxonomic isolation, but not to invasiveness of tropical alien plants. *Diversity and Distributions*, **15**, 141–147.
- Del Tredici, P. (2006) Brave new ecology. *Landscape Architecture*, **96**, 46–52.
- 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.
- Eigenbrode, S.D. & Espelie, K.E. (1995) Effects of plant epicuticular lipids on insect herbivores. *Annual Review of Entomology*, **40**, 171–194.
- Elton, C. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Fritz, S.A. & Purvis, A. (2010) Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, **24**, 1042–1051.
- Gagné, R.J. (1989) *The plant-feeding gall midges of North America*. Comstock Pub. Associates, Cornell University Press, Ithaca, NY.
- Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R. & Schaffner, U. (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation*, **141**, 646–654.
- Gleditsch, J.M. & Carlo, T.A. (2011) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Diversity and Distributions*, **17**, 244–253.
- Gould, A.M.A. & Gorchov, D.L. (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.
- Gripenberg, S., Mayhew, P.J., Parnell, M. & Roslin, T. (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecology Letters*, **13**, 383–393.
- Harvey, K., Nipperess, D., Britton, D. & Hughes, L. (2012) Australian family ties: does a lack of relatives help invasive plants escape natural enemies? *Biological Invasions*, **14**, 2423–2434.
- Heard, M.J. & Sax, D.F. (2013) Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores. *Ecology Letters*, **16**, 206–213.
- Helden, A.J., Stamp, G.C. & Leather, S.R. (2012) Urban biodiversity: comparison of insect assemblages on native and non-native trees. *Urban Ecosystems*, **15**, 611–624.
- Heleno, R.H., Ceia, R.S., Ramos, J.A. & Memmott, J. (2009) Effects of Alien Plants on Insect Abundance and Biomass: a Food-Web Approach. *Conservation Biology*, **23**, 410–419.
- Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, **54**, 427–432.
- Holmquist, J.G., Schmidt-Gengenbach, J. & Slaton, M.R. (2011) Influence of invasive palms on terrestrial arthropod assemblages in desert spring habitat. *Biological Conservation*, **144**, 518–525.
- Jaenike, J. (1990) Host specialization in phytophagous insects. *Annual Review of Ecology and Systematics*, **21**, 243–273.

- Kaufman, S.R. & Kaufman, W. (2007) *Invasive plants: a guide to identification, impacts, and control of common North American species*, 1st edn. Stackpole Books, Mechanicsburg, PA.
- Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kindt, R. & Coe, R. (2005) *Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Malden, MA.
- Marra, P.P., Hobson, K.A. & Holmes, R.T. (1998) Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*, **282**, 1884–1886.
- Marris, E. (2011) *The rambunctious garden: saving nature in a post-wild world*. Bloomsbury Press, New York, NY.
- McCann, K.S. (2011) *Food webs (MPB-50)*. Princeton University Press, Princeton, NJ.
- Meyer, G.A. & Root, R.B. (1996) Influence of feeding guild on insect response to host plant fertilization. *Ecological Entomology*, **21**, 270–278.
- Miles, P.W. & Peng, Z. (1989) Studies on the salivary physiology of plant bugs - detoxification of phytochemicals by the salivary peroxidase of aphids. *Journal of Insect Physiology*, **35**, 865–872.
- Novotny, V. & Basset, Y. (2005) Review - Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society B*, **272**, 1083–1090.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N. & Pearse, W. (2012) *caper: comparative analyses of phylogenetics and evolution in R*. R package version 0.5. Available at: <http://cran.r-project.org/web/packages/caper/index.html>. (accessed 28 January 2013).
- Price, P.W., Cobb, N., Craig, T.P., Fernandes, G.W., Itami, J.K., Mopper, S. & Preszler, R.W. (1990) Insect herbivore population dynamics on trees and shrubs: new approaches relevant to latent and eruptive species and life table development. *Insect-plant Interactions* (ed. by E.A. Bernays), pp. 1–38. CRC Press, Boca Raton, FL.
- Proches, S., Wilson, J.R.U., Richardson, D.M. & Chown, S.L. (2008) Herbivores, but not other insects, are scarce on alien plants. *Austral Ecology*, **33**, 691–700.
- Qian, H. & Ricklefs, R.E. (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. & Hebert, P.D.N. (2007) BOLD: the barcode of life data system. *Molecular Ecology Notes*, **7**, 355–364 Available at: (<http://www.barcodinglife.org>).
- Richards, O.W. & Davies, R.G. (1977) *Imm's general textbook of entomology: structure, physiology, and development*, 10th edn. John Wiley & Sons, New York, NY.
- Rosenthal, G.A. & Janzen, D.H. (ed.) (1979) *Herbivores: their interaction with secondary plant metabolites*. Academic Press, New York, NY.
- Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011) The potential conservation value of non-native species. *Conservation Biology*, **25**, 428–437.
- Stehr, F.W. (1987) *Immature insects*. Kendall/Hunt Publishing, Dubuque, IA.
- Tallamy, D.W. (2004) Do alien plants reduce insect biomass? *Conservation Biology*, **18**, 1689–1692.
- Tallamy, D.W., Ballard, M. & D'Amico, V. (2010) Can alien plants support generalist insect herbivores? *Biological Invasions*, **12**, 2285–2292.
- Tothmeresz, B. (1995) Comparison of different methods for diversity ordering. *Journal of Vegetation Science*, **6**, 283–290.
- Triplehorn, C.A., Johnson, N.F. & Borror, D.J. (2005) *Borror and DeLong's introduction to the study of insects*. Thompson Brooks/Cole, Belmont, CA.
- Tyser, R.W. & Worley, C.A. (1992) Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (USA). *Conservation Biology*, **6**, 253–262.
- Verhoeven, K.J., Biere, A., Harvey, J.A. & van der Putten, W.H. (2009) Plant invaders and their novel natural enemies: who is naive? *Ecology Letters*, **12**, 107–117.
- Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pysek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.
- Wagner, D.L. (2005) *Caterpillars of eastern North America: a guide to identification and natural history*. Princeton University Press, Princeton, NJ.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. (2008) Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics*, **24**, 2098–2100.
- Wilcove, D.S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (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.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Experimental plot design.

**Figure S2** Individual plant species accumulation curves for immature arthropod species on congeneric plant comparisons.

**Figure S3** Individual plant species accumulation curves for adult arthropod species on congeneric plant comparisons.

**Figure S4** Example of extreme specialization to native host (double-toothed prominent caterpillar).

**Table S1** Arthropod guild classification of collected families.

## BIOSKETCHES

**Karin T. Burghardt** is currently a PhD candidate at Yale University in the Department of Ecology and Evolutionary Biology and is broadly interested in how to conserve

biodiversity in human-dominated landscapes. Her undergraduate senior thesis examined the impact of native plants on butterfly and bird communities in suburban landscapes and led to a continuing interest in how plant–insect interactions shape ecosystems. As a result, her dissertation research (supported by a NSF pre-doctoral fellowship) investigates how plant/herbivore interactions structure nutrient cycling across landscapes. (website: <http://schmitz.environment.yale.edu/people-karin.html>).

**Douglas W. Tallamy** is Chair of the Department of Entomology and Wildlife Ecology at the University of Delaware. Early career work on plant defensive traits led to his current interest in the impact of novel plant assemblages on trophic integrity in both managed and unmanaged ecosystems.

Author contributions: D.W.T. conceived the idea; K.T.B. and D.W.T. collected the data; K.T.B. identified arthropods and analysed the data; and K.T.B. and D.W.T. wrote the paper.

---

Editor: Mark van Kleunen