



Effects of native and exotic congeners on diversity of invertebrate natural enemies, available spider biomass, and pest control services in residential landscapes

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Abstract

Exotic plants are common in urban landscapes and are often planted by landscape managers in an effort to reduce herbivory damage and improve landscape aesthetics. However, exotic plants may be less palatable to many native insects and reduce herbivore biomass that may fuel higher trophic levels. Furthermore, a loss of herbivores in exotic ornamental landscapes may reduce top-down control by natural enemies. In this study, we compare herbivory in native and exotic congener ornamental landscapes. We also explore if caterpillar abundance, natural enemy abundance, diversity, community composition, spider biomass, and egg predation differ between the two landscape types. We predicted that herbivory, as well as natural enemy abundance and predation would be greater in native landscapes. Although we found that leaf area lost to herbivory was greater in native plots in one of the collection years, this relationship was weak. Natural enemy diversity differed between landscape types, but depended on plant genus. The relationship between plant origin and natural enemy diversity was also weak. Caterpillar abundance, natural enemy community composition, spider biomass, and predation services did not differ between treatments. Overall, our results suggest that ornamental landscapes planted in native plants may not differ from landscapes planted in exotic congeners in the pest management and conservation services they provide, particularly with regard to invertebrate natural enemies. However, our findings cannot be used to make more general claims about plant origin, especially with regard to native plants and non-congeners, as we only compared ornamental landscapes with native plants and their exotic congeners in this study. We conclude that for optimizing natural enemy diversity and biomass on city landscapes, plant choice and other plant traits may be as important as plant origin to consider. Our work demonstrates that both native and exotic congener ornamental landscapes provide valuable ecosystem services and will help guide landscape design that serves both the people and wildlife that use them.

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Introduction

As the world becomes more urban, humans play a greater role in determining the plant “palette” on which ecosystem processes function (Faeth et al. 2011). Urban landscapes often have more exotic plant species than surrounding natural areas due to high densities of exotic ornamental plants which may be exotic congeners of native plants or exotic plants with no native congeners (McKinney 2008; Faeth et al. 2011). However, more exotic plants on urban landscapes may mean fewer insect herbivores, which could have negative effects on biomass available to higher trophic levels and reduce urban biodiversity (Burghardt et al. 2009; Narango et al. 2017). The Enemies Release Hypothesis posits that plant species introduced into novel environments, where co-evolved herbivores are absent, will have fewer herbivores and less herbivory than in their native environment (Keane and Crawley 2002). Although the Enemies Release Hypothesis applies to exotic plant invasions, it has also been used to explain the low densities and diversity of herbivores on exotic ornamental plants in residential landscapes (Burghardt and Tallamy 2013; Narango et al. 2017). Landscape managers and homeowners may choose to install exotic plants to reduce herbivore damage and improve the overall aesthetic of ornamental landscapes (Raupp et al. 1992, 2010; Herms 2002). By reducing herbivores and herbivory, installing exotic plants may decrease the need for pesticides in residential and urban areas, an area of increasing concern based on risks to people, pollinators and other non-target animals, and the environment (Raupp et al. 1992, 2010). Overall, the perceived conservation benefits provided by native plants and the potential pest management benefits provided by exotic congeners and non-congeners of native plants can make plant selection difficult for many homeowners and designers trying to both conserve biodiversity and reduce pesticide use on city landscapes. Generally few studies have explored the extent to which plant origin affects biodiversity, especially with regard to invertebrate natural enemies, and herbivore damage on residential ornamental landscapes. Exploring this gap in the research will help designers and planners determine if plant origin, with regard to native plants and their exotic congeners, is an important factor to consider in the design of city landscapes that both promote animal diversity and reduce risk to human health.

Landscapes with native plants often have a greater number and diversity of insect herbivores, including chewing herbivores, leaf miners, and gall wasps (Owen 1983; Burghardt et al. 2009, 2010; Burghardt and Tallamy 2013) as well as more herbivory. For example, caterpillars were four times more abundant and three times more species-rich in suburban Pennsylvania landscapes with native plants when compared to landscapes planted in predominately exotic plants (Burghardt et al. 2009). Similarly, in ornamental landscapes in Washington, D.C., native plants hosted greater caterpillar biomass than exotic plants, including exotic congeners of native plants (Narango et al. 2017). More herbivores on native plants can also lead to more herbivory. For example, native plants had significantly more chewing, skeletonizing, mining, and galling damage than exotic plants, including exotic congeners of native plants, in both ornamental and natural landscapes in Cincinnati, Ohio (Matter et al. 2012). Likewise, in a survey of 39 exotic and 30 native plant species in natural areas of Ottawa, Canada, native plants had significantly higher chewing, mining, and galling leaf herbivory when compared to exotic confamilial plants (Carpenter and Cappuccino 2005). The association between native plants and herbivore diversity and biomass

has largely been attributed to the coevolution of herbivores with their hosts (Ehrlich and Raven 1964). Novel chemistries and unique metabolomic profiles of exotic plants can make them more defended or less palatable to native herbivores (Cappuccino and Arnason 2006; Forister and Wilson 2013; Macel et al. 2014). The majority of insect species are considered to be specialists and utilize a small number of plants with which they have a coevolutionary history (Rosenthal and Janzen 1979; Bernays and Graham 1988; Tallamy 2004; Burghardt et al. 2009; Tallamy et al. 2010). Even some generalist herbivores show preferences for native plant species with which they have co-evolved when exposed to alien plants. For example, generalist yellow-striped armyworms (*Spodoptera ornithogalli*), luna moths (*Actias luna*), bagworms (*Thyridopteryx ephemeraeformis*), and white-marked tussock moths (*Orgyia leucostigma*), starved when introduced to foliage of alien plants naturalized in the mid-Atlantic U.S. (Tallamy et al. 2010). Similarly, generalist cankerworms (*Paleacrita vernata*) consistently showed preferences for native foliage in choice experiments with foliage from native ornamental plants and their exotic congeners (Frank 2014).

A greater diversity and quantity of herbivores on native plants may also provide more food resources for birds and other animals at higher trophic levels, which can increase biodiversity of residential and city landscapes. Native landscape effects on bird predators of insect herbivores has been a focus of recent research (Burghardt et al. 2009; Pearse et al. 2013; Narango et al. 2017). For example, bird species abundance and richness increased in native urban landscapes when compared to landscapes of the same size planted largely in exotic plants, a phenomenon that was attributed to greater caterpillar abundance and richness (Burghardt et al. 2009). However, biomass of some invertebrate natural enemies, particularly spiders, can also contribute to the quantity of food resources available to birds and higher trophic levels (Gunnarsson 2008; Rogers et al. 2012), yet this area of research remains understudied in residential and urban landscape settings.

Although native plants may support high densities of invertebrate herbivores in many cases, plant origin can have variable effects on invertebrate natural enemies. For example, exotic annual plants *Alyssum*, buckwheat (*Fagopyrum*), and faba bean (*Vicia faba*) were as effective as native perennial plants in attracting natural enemies in Michigan plot studies, especially in the first year of establishment (Fiedler and Landis 2007). In contrast, Greenstone et al. (2017) found more spiders attending egg masses of sentinel *Halyomorpha halys* eggs in native ornamental landscapes when compared to exotic congener ornamental landscapes. Exotic plants may provide habitat complexity, cooler microclimates, ideal oviposition sites, alternative foods, and other resources for natural enemies even if they have fewer herbivores. Many of the exotic plants used in agricultural conservation biocontrol programs, for example, are prolific bloomers, have special plant or flower traits attractive to natural enemies, such as extrafloral nectaries and large floral areas, and provide natural enemies with nectar and pollen resources throughout the growing season when native plants may not (Fiedler and Landis 2007; Pumarino et al. 2012). *Orius insidiosus*, had greater survival and oviposition on exotic *Phacelia*, which was attributed to higher floral sugar content and an ideal plant substrate for ovipositing (Pumarino et al. 2012). Similarly, exotic coriander has been correlated with high syrphid fly abundance in several studies, a correlation often attributed to the structure of coriander flowers, which have short corollas and provide easy access to nectar and pollen (Colley and Luna 2000; Ambrosino et al. 2006; Fiedler and Landis 2007).

Overall, more research needs to compare the effects of native and exotic plant origin on natural enemy communities and biomass, with regard to native plants and their exotic congeners at the residential scale. Much of the natural enemy research to date has focused on sampling individual plants within mixed, agricultural landscapes. When entire ornamental

landscapes are native or exotic the effect of plant origin may be greater on the local arthropod community, particularly for arthropods with limited mobility, which may be unable to relocate to more suitable plants. Furthermore, if natural enemy density and diversity are affected by plant origin, then predation services may also be affected, yet few studies have explored this association. Understanding how plant origin directly or indirectly affects natural enemy communities and pest control services can inform urban landscape design that supports robust natural enemy communities and minimizes the risk of pest outbreak.

Given the documented relationship between native plants and their co-evolved insect herbivores, we predict that native ornamental landscapes will have greater chewing herbivory and more chewing herbivores when compared to ornamental landscapes planted with exotic congeners. We also predict that more herbivores on native ornamental landscapes will result in more diverse natural enemy communities, more spider biomass, and greater predation services. With this prediction we assume that prey availability plays an important role in structuring natural enemy communities on residential landscapes and that native landscapes provide more palatable vegetation for native herbivores, thus supporting more herbivores and more prey resources for natural enemies. We compared landscapes planted with native plants to landscapes planted with their exotic congeners as a conservative evaluation of how exotic plants affect biodiversity at the residential yard scale. To test our hypotheses we compared chewing herbivory on plants, caterpillar density, natural enemy abundance, diversity, community composition, spider biomass, as well as egg predation in U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS) experimental native and exotic congener ornamental landscape plots at the U.S. Arboretum in Washington, D.C., USA. Our study explores the extent to which plant origin, native plants or their exotic congeners, plays a role in reducing chewing herbivore damage on landscapes and bolstering invertebrate natural enemy communities and predation services. Ultimately, our work will help inform plant selection on residential landscapes that optimizes pest control and supports greater invertebrate biodiversity.

Methods

Study area and study sites

This study was performed in six USDA-ARS experimental plots at the U.S. Arboretum in Washington, DC, USA (38° 54' 36.84" N, 76° 58' 3.14" W). The plots were 25×25 m, had the same plant layout (Fig. S1, Table 1), and contained woody shrub and tree species common in ornamental landscapes of the mid-Atlantic region. Three plots contained native plant species and three contained exotic congeners. The plots were arranged in a randomized complete block design. Each block was in a different location in the arboretum and contained one "native" and one "exotic" plot to account for differences in abiotic conditions and surrounding vegetation (Cornelius et al. 2016). A pergola with vining *Wisteria* sp. and *Campsis* sp. sat in the middle of each plot and shrubs and trees were arranged in planting beds around the pergola and along the edges of the plot. Study species included 16 matched congeners that have been geographically separated for at least 1 million years (Cornelius et al. 2016, Table 1). A 10m perimeter around each plot was regularly mowed, and plots within blocks were separated by 50–99 m with a lightly managed meadow in between (Cornelius et al. 2016). Distances between blocks ranged from 300 to 900 m (Cornelius et al. 2016). Plots were well established and were approximately 6 years old at the time of this study.

Table 1 Plants in native and exotic plots at the U.S. Arboretum

	Native	Exotic	No. plants per plot ^a
Trees	<i>Acer saccharum</i>	<i>Acer platanoides</i>	2
	<i>Quercus alba</i>	<i>Quercus robur</i>	3
	<i>Catalpa bignonioides</i>	<i>Catalpa ovata</i>	1
	<i>Prunus virginiana</i>	<i>Prunus padus</i>	3
	<i>Ilex opaca</i>	<i>Ilex aquifolium</i>	2
	<i>Liriodendron tulipifera</i>	<i>Liriodendron chinense</i>	3
	<i>Pinus strobus</i>	<i>Pinus wallichiana</i>	1
	<i>Picea glauca</i>	<i>Picea abies</i>	2
	<i>Cercis canadensis</i>	<i>Cercis chinensis</i>	5
	<i>Cornus florida</i>	<i>Cornus kousa</i>	1
Shrubs	<i>Rhododendron calendulaceum</i>	<i>Rhododendron mucronulatum</i>	1
	<i>Hydrangea arborescens</i>	<i>Hydrangea paniculata</i>	20
	<i>Callicarpa americana</i>	<i>Callicarpa japonica</i>	15
	<i>Juniperus virginiana</i>	<i>Juniperus chinensis</i>	10
	<i>Viburnum dentatum</i>	<i>Viburnum dilatatum</i>	15
Vines	<i>Campsis radicans</i>	<i>Campsis grandiflora</i>	1
	<i>Wisteria frutescens</i>	<i>Wisteria floribunda</i>	1
Turf grass	<i>Festuca arundinacea</i>	<i>Festuca arundinacea</i>	Ground cover

Plant list courtesy of USDA-ARS-BARC

^aNumbers above represent number of individuals of species in plots in the planting plan. However, not all plots had the same number of individuals of each species during sampling, as some plants died after establishment

Herbivory

Leaf herbivory was measured once in 2017 (6 August), and four times in 2018 (9 and 30 June, 28 July, and 25 August). We measured chewing herbivory on leaves of maples (*Acer spp.*), oaks (*Quercus spp.*), and redbuds (*Cercis spp.*) in each plot. Trees and shrubs were randomly selected for sampling when possible, with the exception of those tree species that had one individual per plot (Table 1). To collect leaves, we pruned two terminal twigs (15–20 cm in length) 4–6 m above the ground from the North and South sides of the tree canopy. We arbitrarily selected one high area and one low area of the canopy to sample with pole pruners. Twigs with leaves attached were immediately put in zip-top bags and kept at 4 °C until measurement. Ten leaves were randomly selected from each twig to measure herbivory. Thus, twenty leaves total were analyzed for each tree on each collection date. Selected leaves were scanned and uploaded into ImageJ (Schindelin et al. 2012). In ImageJ both leaf surface area and area of leaf missing due to chewing herbivory were recorded in cm². Due to later resolved technical issues, in 2017 only ten of the twenty randomly selected leaves from the two sampled twigs for each tree were analyzed for herbivory. Separate analyses were performed for 2017 and 2018 to account for the difference. Two measures of leaf herbivory, total leaf herbivory (cm²) and Leaf Damage Index (LDI) values (proportion of leaves per tree that had damage exceeding 5% of surface area) (Alliende 1989; Kozlov et al. 2014) were used as responses in analyses. Total

leaf herbivory per tree provides a measure of the amount of leaf matter lost to herbivore consumption, whereas LDI per tree provides a measure of herbivory distribution throughout the tree canopy.

Arthropod data collection

Arthropod data were collected twice in 2017 (15 July and 6 August), and four times in 2018 (9 and 30 June, 28 July, and 25 August). Six tree and shrub congeners were selected in plots for sampling. Genera included *Cercis*, *Quercus*, *Hydrangea*, *Viburnum*, *Catalpa*, and *Liriodendron*. Trees and shrubs were randomly selected for sampling when possible, with the exception of those tree species that had one individual per plot. On each collection date five places on each selected shrub and the lower canopy of selected trees were beaten with a wooden dowel to dislodge arthropods into a tray. Samples for each shrub and tree were kept separate. Trays were immediately rinsed with 75% ethanol into sample containers. Caterpillars were counted and natural enemies were identified in the lab under a dissection scope. We chose to count caterpillars, because they have been a major focus in studies exploring the effects of plant origin on insect herbivores in ornamental landscapes in recent years (Burghardt et al. 2009, 2010; Burghardt and Tallamy 2013; Narango et al. 2017). They were also one of the largest groups of chewing herbivores in beat samples. Caterpillars were only counted for 2018 samples. Most natural enemies were identified to family, with the exception of spiders, parasitoid wasps, and earwigs (Dermaptera), which were identified to order. Total number of natural enemies and caterpillars collected by tree or shrub species was used as the response in analysis. Natural enemy diversity for each sample tree and shrub species was also calculated using the Shannon Diversity Index (H') in R with the *vegan* package (Oksanen et al. 2017) for analysis. H' values ranged from 0 to 1.75, with lower values being those communities that were less species rich and did not have an even distribution of natural enemies.

Spider dry weight biomass

Spiders were sorted from 2018 beat samples and grouped together in vials, such that all spiders collected on a particular tree and collection date were put in the same vial. We analyzed spider dry weight biomass because spiders made up the majority of natural enemies in both years (> 50%). Thus, we considered spiders a representative group of natural enemies. We were interested in secondary consumer biomass because we wanted to explore how biomass available to higher trophic levels may differ in native and exotic ornamental landscapes. Glass vials with spiders were left open under a fume hood for six days to allow ethanol to evaporate. Vials were then placed in a drying oven at 30 °C for 48 h, after which point the temperature was elevated to 45 °C for 24 h. Spiders were weighed on a Satorius Cubis MSA3.6P0TRDM (Goettingen, Germany) balance the nearest 0.01 milligrams. Total amount of spider dry weight collected by tree or shrub species was used as the response in analysis.

Predation experiments

Sentinel *Helicoverpa zea* eggs were set out in plots and counted before and after 24-hours to assess egg predation among plots. Predation experiments were conducted three times in 2018 (30 June, 28 July, and 25 August). Frozen *H. zea* eggs were purchased from Frontier Agricultural Sciences (Newark, DE). Eggs were received frozen on a circular mesh cloth with approximately 1000–2000 eggs. We cut 1 × 1 cm squares from the cloth, such that at least 30 eggs were on each square. Cloth squares with eggs were stored in a – 80 °C freezer before use in field trials and kept in a cooler when going into the field. On 30 June and 25 August predation experiments were conducted on *Wisteria*, *Liriodendron*, and *Viburnum* and on 28 July experiments were conducted on *Wisteria*, *Cercis*, and *Hydrangea*. Experiments were conducted on one plant per genus in each plot. A branch on each study tree or shrub was arbitrarily selected, and single caged and un-caged egg cloth squares were attached to a leaf on the branch with a staple. Branches were marked so that they were not used in future trials. Caged cloth squares on leaves were covered with a clip cage made of a hairclip, a foam base, a 4 cm plastic tube, and a mesh top. Total number of eggs before and after 24-hours were recorded. We used predation effect size as the response in analyses. Predation effect size was calculated as the $\ln(\text{proportion of prey removed on uncaged leaves}) - \ln(\text{proportion of prey removed on caged leaves})$.

Model analysis

All analysis was performed in R Version 3.4.3 (R Core Team 2017). We hypothesized that native ornamental landscapes, or native “treatments,” would have more chewing leaf herbivory, more caterpillars, greater natural enemy abundance, richness, diversity, spider biomass, and egg predation when compared to ornamental landscapes planted in exotic congeners, or exotic congener “treatments.” We tested this a priori hypothesis for each response using linear mixed effects models (LMM) with the *nlme* package in R (Pinheiro et al. 2017). The LMM model testing our hypothesis for each response included treatment as the fixed effect predictor and block, date, and sample tree as random group intercept terms to account for repeated measures on sample trees and variation in responses within blocks and across the multiple collection dates. Herbivory, caterpillar abundance, natural enemy abundance, and spider biomass responses were $\log_{10}(x + 1)$ transformed to improve the distribution of residuals and to account for overdispersion (Zuur et al. 2009, 2010). Marginal and conditional R^2 values, quantifying variation explained by fixed and random effects, were computed using the *piecewiseSEM* v. 1.2.1 package in R (Lefcheck 2015) and reported for models used in hypothesis testing. We checked residual plots and used model validation diagnostic plots in R to detect and test for violations of linear regression assumptions for all models. Lastly, if a significant effect of treatment was detected, then individual linear models for each sampled genus were analyzed. These latter models were used to determine which genera were significantly affected by treatment. Separate analyses were conducted for 2017 and 2018. Tree was the experimental unit for all responses.

We then used ANOVAs to test for interactions between treatment and genus to determine if the effect of treatment on responses depended on plant genus for all responses except egg predation. Lastly, to assess background variation among plant genera we also used ANOVAs to test differences among genera of sampled plants for each response. For all ANOVAs, responses were totaled for the season and an error term for block was

included. Post-hoc pairwise Dunn Tests were used (Dinno 2017) to further explore differences among genera. Separate analyses were conducted for 2017 and 2018. For predation response, we used linear mixed effects models, rather than ANOVAs, to test for interactions between treatment and genus and differences among genera, followed by post-hoc tests, if differences among genera were detected. We did not use ANOVAs, as we did for other responses, because we did not want to average effect sizes across dates for the whole season. Not all trees and shrubs were sampled with the same frequency and thus averaging would have introduced more error into our models.

For a few of the responses we did additional analyses. For herbivory, to determine if leaf area needed to be accounted for in herbivory models, we also assessed outputs from models with leaf area as the predictor. We also explored if there was a correlation between herbivory and caterpillar abundance with a LMM model using herbivory as the response and caterpillar abundance as the predictor. For egg predation, prior to predation analysis we compared number of missing eggs between caged and uncaged leaves to determine if cages effectively reduced egg removal. We conducted this analysis with a linear mixed effects model with proportion of eggs missing as the response and exclusion status, caged or uncaged, as a predictor. We calculated this model in R using the *glmer* function and assigned a binomial distribution to account for the proportion response (Bates et al. 2015).

Community analysis

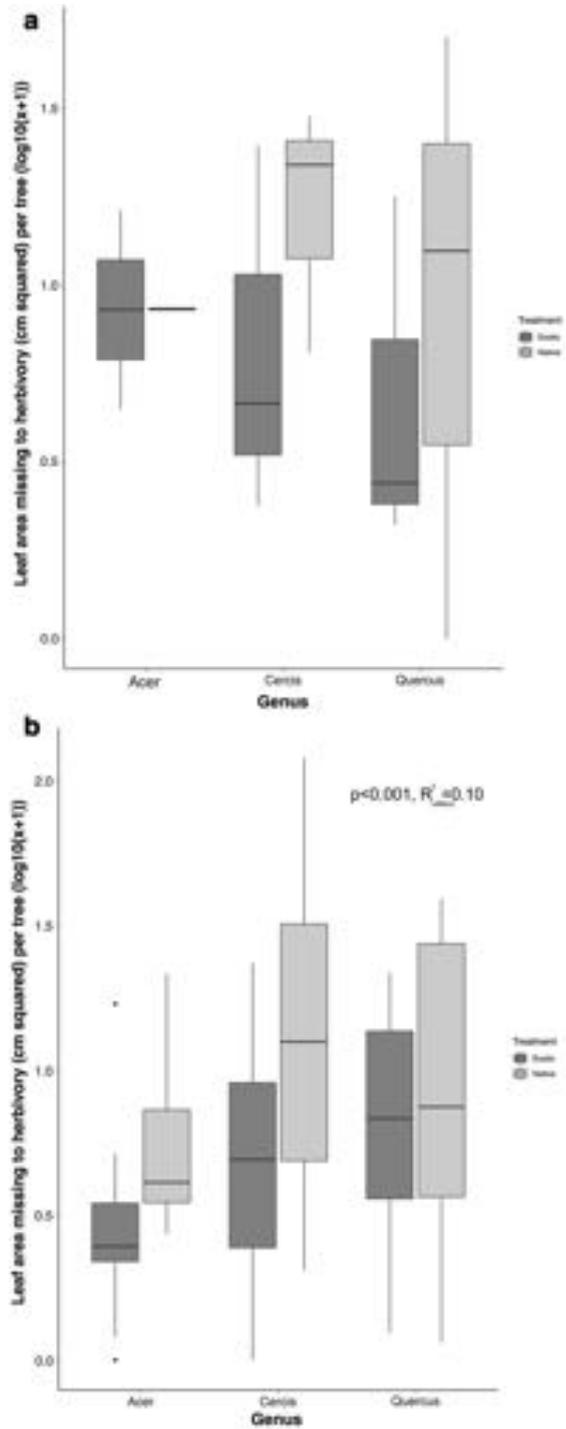
To test our prediction that natural enemy communities would differ between native and exotic ornamental landscapes, natural enemy communities were compared using NMDS (Non-metric Dimensional Scaling). NMDS is an ordination technique for analyzing ecological community data that does not make distributional assumptions about the data. It assumes the researcher does not have prior knowledge of how environmental gradients affect the communities in question, and we selected Sorensen distance measures to calculate dissimilarities between communities (Faith et al. 1987; Minchin 1987). We plotted ordinations and then tested if treatment (native or exotic) was a good predictor of community composition using the *envfit* function in the *vegan* package (Oksanen et al. 2017).

Results

Herbivory

Chewing herbivory was two times greater in native plots when compared to exotic plots in 2018 ($p < 0.001$) such that for every 1cm^2 of leaf missing due to chewing herbivory in exotic plots there was 2cm^2 of leaf missing in native plots [(Est \pm SE) 0.31 ± 0.86]. However, proportion of variance explained by plot treatment was low ($R^2_{\text{LMM(m)}} = 0.10$). In 2018, herbivory was significantly greater on native than exotic maple trees (*Acer* spp.) and redbud trees (*Cercis* spp), while oak trees (*Quercus* spp) had no difference in herbivory between treatments in 2018 (Fig. 1, Table S1). Herbivory was not different between native and exotic plots in 2017 (Fig. 1). Surface area was not a significant predictor of herbivory in either year. Genus was a predictor of chewing herbivory in 2018 ($p < 0.05$, $F_{2,12} = 4.49$) but not in 2017. Interactions between genus and treatment were also not significant in either year. Leaf area missing to herbivory per tree ranged from $1.1\text{--}23.86\text{ cm}^2$ [(mean \pm SD) 8.32 ± 8.31] to $0\text{--}22.44\text{ cm}^2$ [(mean \pm SD) 6.04 ± 6.52] in exotic plots and from $0\text{--}49.54$

Fig. 1 Herbivory in native and exotic treatments in **a** 2017 and **b** 2018. The boxplots here show the interquartile ranges of leaf area missing to herbivory per tree per sample date. The median of the data range is marked by the line that divides boxes. Native plot treatments overall had more herbivory than exotic plot treatments in 2018 but not in 2017



cm² [(mean ± SD) 16.45 ± 16.24] and 0.15–119.32 cm² [(mean ± SD) 19.15 ± 28.64] in native plots in 2017 and 2018 respectively.

Treatment was not a significant predictor of LDI in 2017 or 2018 (Fig. S2). However, genus was a significant predictor of LDI in 2018 ($p < 0.01$, $F_{2,12} = 10.98$). In 2018, *Quercus* overall had more leaves damaged by chewing herbivory, and had significantly more damaged leaves than *Acer* (Dunn Test, $p < 0.05$). Interactions of genus and treatment were not significant. LDI per tree ranged from 0–70% [(mean ± SD) 0.14 ± 0.24] and 0–68% [(mean ± SD) 0.09 ± 0.14] in exotic plots and from 0–80% [(mean ± SD) 0.275 ± 0.26] and 0–60% [(mean ± SD) 0.1 ± 0.13] in native plots in 2017 and 2018 respectively. Chewing herbivory and caterpillar density were not correlated ($p > 0.05$).

Caterpillar abundance

We predicted that caterpillar abundance would be greatest in native plots. Although, in some cases native plants had more caterpillars than their exotic congeners, in other cases exotic congeners had more caterpillars (Fig. S3). Thus, the effect of plant origin on caterpillar density depended on genus. Interactions between genus and treatment were detected ($p < 0.001$, $F_{5,22} = 7.92$). Genus was also a significant predictor of caterpillar abundance ($p < 0.001$, $F_{5,28} = 6.70$). A comparison across genera revealed that *Quercus* and *Cercis* had significantly more caterpillars than *Liriodendron*, which had the fewest caterpillars (Dunn Test, $p < 0.05$). Caterpillar density per tree ranged from 0–30 individuals [(mean ± SD) 1.53 ± 4.12] in exotic plots to 0–6 individuals [(mean ± SD) 0.84 ± 1.27] in native plots.

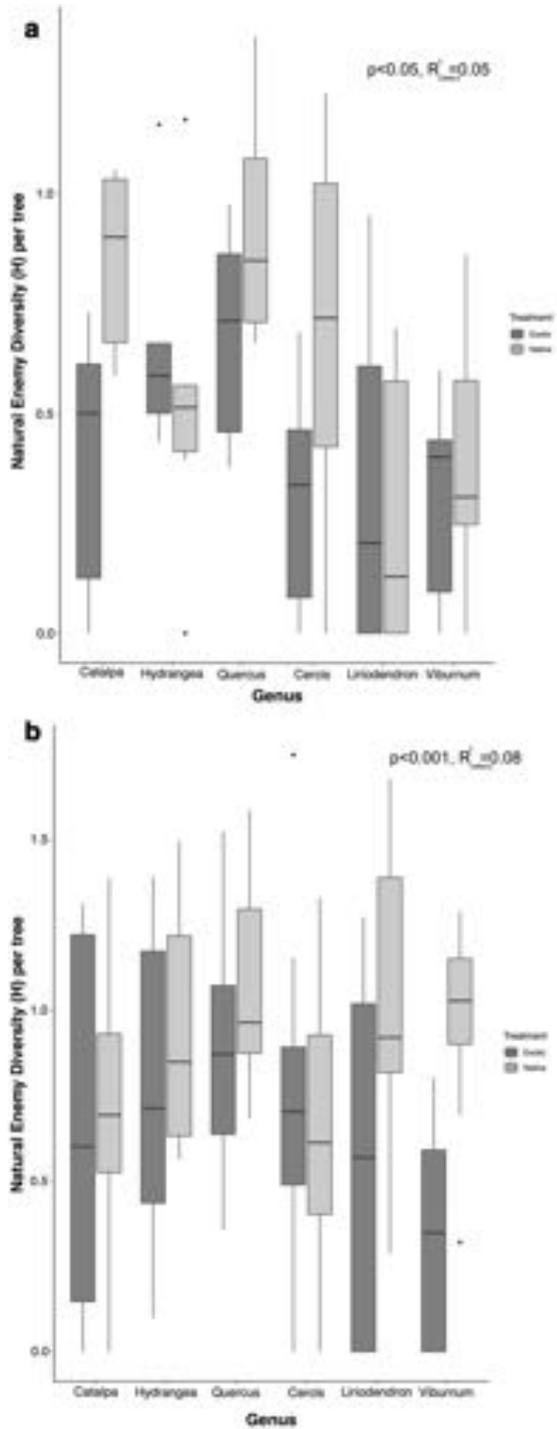
Natural enemy community analysis

We predicted that natural enemy abundance, richness, and diversity would be greatest in native plots. We also expected community composition to differ between native and exotic treatments. Contrary to our prediction, natural enemy abundance was not significantly predicted by plot treatment (Table S2, Table S3). Natural enemy diversity was greater in native plots in 2017 ($p < 0.05$, 0.16 ± 0.08) and in 2018 ($p < 0.001$, 0.24 ± 0.06) (Fig. 2) (Table S2, Table S3), although the proportion of variance explained by treatment was low (2017 $R^2_{\text{LMM(m)}} = 0.05$; 2018 $R^2_{\text{LMM(m)}} = 0.08$). Similarly, natural enemy species richness was greater in native plots compared to exotic plots in 2018 ($p < 0.01$, 0.61 ± 0.21); however variation explained by treatment was again low (2018 $R^2_{\text{LMM(m)}} = 0.05$) (Table S2, Table S3). Natural enemy species richness was not predicted by treatment in 2017.

Genus was a significant predictor of natural enemy abundance in 2017 ($p < 0.01$, $F_{5,28} = 4.41$) and 2018 ($p < 0.01$, $F_{5,28} = 5.04$) a significant predictor of richness in 2017 ($p < 0.05$, $F_{5,28} = 2.95$). A comparison across genera revealed that in both years *Hydrangea*, *Quercus*, and *Viburnum* had significantly more natural enemies than *Liriodendron*, which had the fewest natural enemies (Dunn Test, $p < 0.05$). In 2017 *Quercus* had the greatest richness of natural enemies and was significantly more species rich than *Viburnum* and *Liriodendron* (Dunn Test, $p < 0.05$). Natural enemy diversity was not predicted by genus.

Significant interactions between treatment and genera in 2018 revealed that the effect of treatment (i.e. plant origin) on natural enemy diversity ($p < 0.05$, $F_{5,22} = 2.64$) and richness ($p < 0.05$, $F_{5,22} = 5.64$) depended on plant genus. When compared to exotic congeners, native *Liriodendron* had significantly greater natural enemy diversity and richness (Table S4). Native *Viburnum* also had significantly greater natural enemy diversity and

Fig. 2 Natural enemy diversity in native and exotic plot treatments in **a** 2017 and **b** 2018. The box-plots here show the interquartile ranges of natural enemy diversity per tree per sample date. The median of the data range is marked by the line that divides boxes. Natural enemy diversity (Shannon H') was greater in native plot treatments in both years. However, plant origin overall was a weak predictor



richness (Table S4). None of the other native plants sampled significantly differed from their exotic congeners. Thus, native *Liriodendron* and native *Viburnum* congeners likely contributed to the positive effect of native treatment on both natural enemy diversity and richness on landscape plots in 2018.

In NMDS community analysis, natural enemy communities in native and exotic congener plots did not differ in either year ($p > 0.05$) (Fig. 3). Spiders were the largest group, comprising 74% and 59% of all arthropods collected in native samples and 82% and 62% of all arthropods collected in exotic samples in 2017 and 2018, respectively. Other arthropods found in beat samples included Opiliones, coccinellids (*Harmonia axyridis*, among others), lacewings (Chrysopidae, Hemerobiidae, and Coniopterygidae), predatory thrips (Aeolothripidae and Phlaeothripidae), *Orius insidiosus*, parasitoids, dolichopodids, mantids, nabids, Dermaptera, and reduviids (Table S5).

Spider biomass

Spider biomass did not differ between native and exotic plots or congeners in 2018. Interactions between genus and treatment were not significant. However, genus was a significant predictor of spider biomass. *Hydrangea* had the greatest biomass of spiders and had significantly more spider biomass than *Cercis* ($p < 0.01$), *Liriodendron* (Dunn Test, $p < 0.05$), and *Catalpa* (Dunn Test, $p < 0.05$) (Fig. 4). Spider biomass per tree ranged from 0–77.38 mg [(mean \pm SD) 5.38 ± 10.68] in exotic plots to 0–26 mg [(mean \pm SD) 3.31 ± 4.40] in native plots.

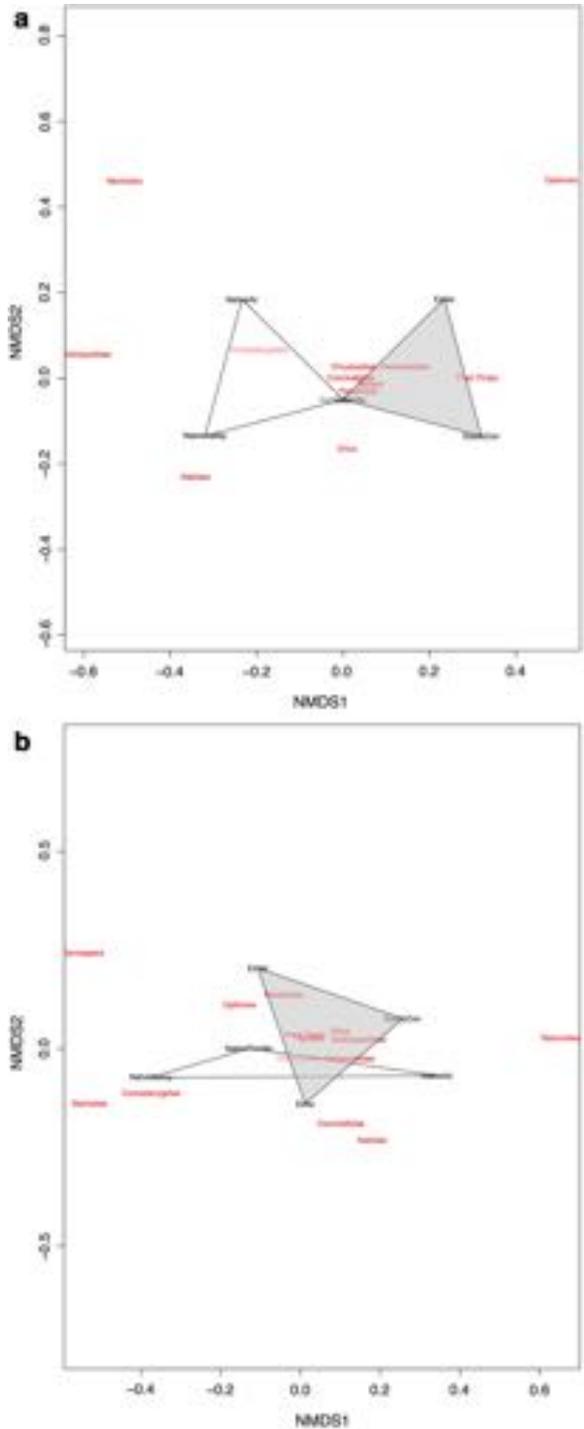
Predation

Uncaged leaves had three times as many missing eggs after 24-hours than caged leaves ($p < 0.001$, Est. \pm SE, 3.72 ± 0.787) (Fig. 5), signifying that cages excluded predators. Contrary to our predictions, native plots did not have more egg predation than exotic plots (Fig. 5). Egg predation also did not differ among tree genera. Egg predation effect size per tree ranged from -2.65 – 4.27 [(mean \pm SD) 1.18 ± 1.29] in exotic plots to -0.53 – 4.44 [(mean \pm SD) 1.78 ± 1.50] in native plots.

Discussion

Better understanding how the plants we install in residential landscapes affect arthropod communities can help us design landscapes that protect aesthetics and plant health while also supporting greater biodiversity in urban areas. Although many studies have quantified effects of plant origin on herbivores in residential landscapes, fewer have documented effects on trophic processes like herbivory and predation or assessed effects on higher trophic level communities, like invertebrate natural enemies. Additionally, few studies, if any, have assessed plant origin effects on invertebrate communities at the residential landscape scale using an experimental design with intentionally designed paired landscapes of native plants and their exotic congeners. In our study, although plant origin was significantly related to amount of leaf area lost to herbivory, the proportion of variation explained was low, indicating a weak relationship, likely a result of comparing congeners with similar phytochemical profiles. Furthermore, leaf damage index values and caterpillar abundance did not differ in native and exotic ornamental landscapes. Native and exotic congener

Fig. 3 Natural enemy communities in native and exotic plot treatments in **a** 2017 and **b** 2018. Natural enemy communities did not differ significantly between native and exotic plot treatments. Grey triangles outline exotic plot communities, while white triangles outline native plot communities. Overlapping triangles or touching triangles are good indicators that communities do not differ from one another. Points of the triangles signify plot communities. Points of the triangles closer together in the ordination space mean that they are more similar in their composition. Natural enemy groups are also included in the ordination plot



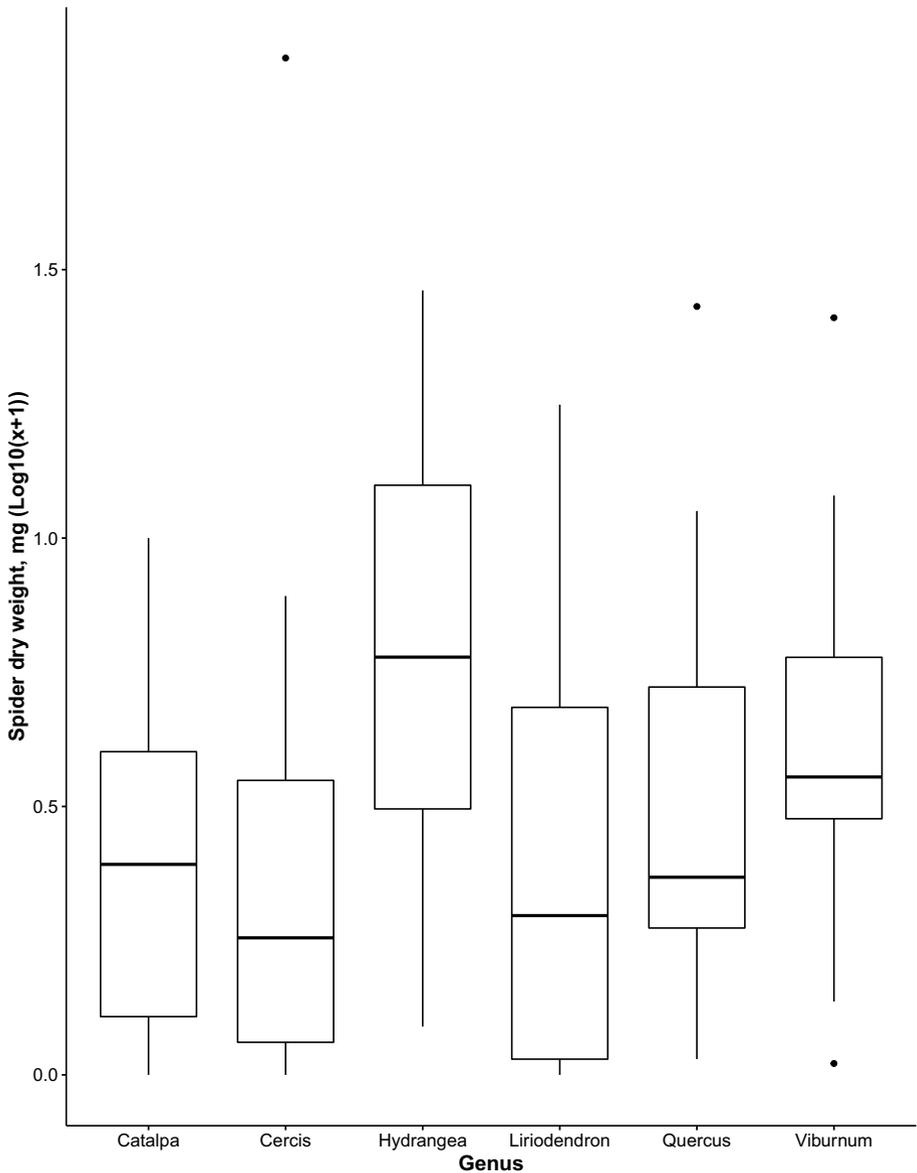


Fig. 4 Differences in spider biomass in 2018 among genera. The boxplots here show the interquartile ranges of spider biomass measured by dry weight in mg. The median of the data range is marked by the line that divides boxes. Boxes with different letters indicate significant differences among genera ($p < 0.05$). Hydrangea had significantly more spider biomass than Catalpa, Cercis, and Liriodendron

landscapes also did not differ in natural enemy abundance or spider biomass, and plant origin was only weakly correlated with natural enemy richness and diversity. Our study suggests that ornamental landscapes planted in exotic congeners of native plants may provide valuable predation services and support invertebrate natural enemy diversity and spider

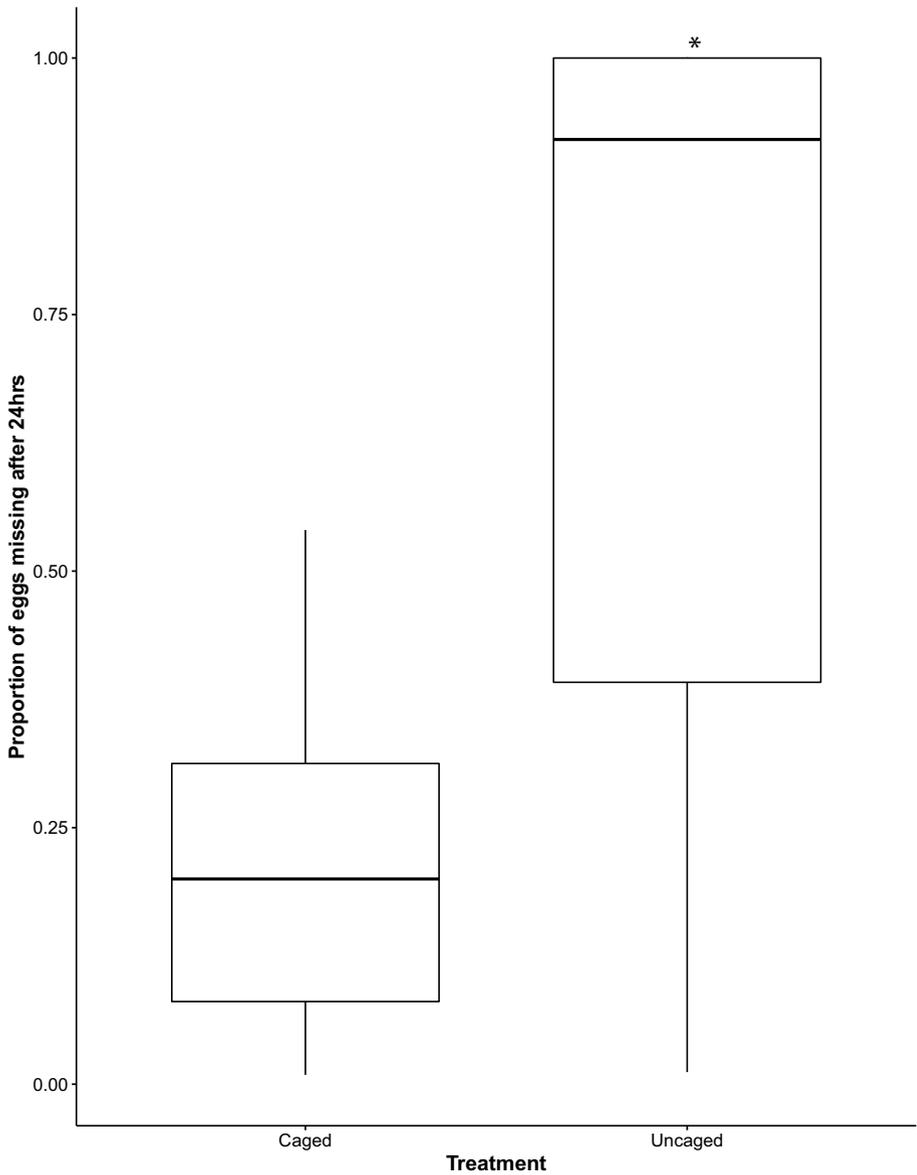


Fig. 5 Percentage of *H. zea* eggs missing in caged and uncaged treatments. The boxplots here show the interquartile ranges of percentages of eggs missing after 24 h. The median of the data range is marked by the line that divides boxes. Asterisks indicate significant differences. Uncaged treatments had significantly more eggs missing after 24 h than caged treatments, indicating predation

biomass comparable to native ornamental landscapes in urban areas, where generally there exist concerns for biodiversity loss and pest outbreaks.

Low rates of herbivory have been documented on introduced exotic plants in ornamental (Tallamy 2004; Tallamy et al. 2010; Matter et al. 2012; Frank 2014) and invaded

landscapes (Schierenbeck et al. 1994; Keane and Crawley 2002; Carpenter and Cappuccino 2005; Lieurance and Cipollini 2013; Williams and Sahli 2016). Although we found that plants in native ornamental landscapes had more leaf area lost due to chewing herbivory than plants in exotic congener landscapes in 2018, this was not the case in 2017. Furthermore, although significant, treatment was a weak predictor of chewing herbivory in 2018. We suspect that the relationship between plant origin and chewing herbivory was weak because we compared landscapes comprised of closely related native plants and their exotic congeners. Correlations between plant phylogeny and herbivory, herbivore performance, as well as herbivore communities have been highlighted in several studies (Ehrlich and Raven 1964; Dawson et al. 2009; Pearse and Hipp 2009; Burghardt and Tallamy 2015). For example, in a study of tropical alien plant species in East Africa, a smaller proportion of leaves were damaged via herbivory on plants without native congeners when compared to plants that had native congeners (Dawson et al. 2009). Even among congeners, a closer phylogenetic relationship may mean similar amounts of damage by herbivores. For example, Pearse and Hipp (2009) found that more closely related oak species had more similar amounts of herbivory when compared to distantly related oak species. Differences in herbivory among plants could be attributed to differences in phytochemical profiles, and other plant traits, which are more similar among more closely related species (Ehrlich and Raven 1964; Pearse and Hipp 2009). Similarly leaf damage index values in our study did not differ on native and exotic congeners in either year, meaning that a similar number of leaves had damage in native and exotic congener plots. In fact, exotic oak congeners had higher average LDI values than native congeners in 2018. This latter finding is particularly relevant for homeowners and landscape managers seeking to reduce herbivore damage on ornamental plants. We used LDI measures in an effort to quantify damage that may be perceivable to the homeowner. For many ornamental plant species, homeowners and landscape managers notice damage when 10% of a plant or canopy is compromised (Larew et al. 1984; Raupp et al. 1988, 1992; Coffelt and Schultz 1990). When damage exceeds this “aesthetic threshold,” homeowners or landscape professionals may turn to insecticide applications to reduce further damage (Raupp et al. 1988, 1992). In addition to exotic congener and native plots being more alike, than different, in their LDI values, overall values of LDI were low and did not exceed 10% in either landscape type in 2018 but were higher, 14% in exotic plots and 28% in native plots in 2017. Greater herbivory in native ornamental landscapes is often attributed to a greater abundance and diversity of chewing herbivores on native plants (Proches et al. 2008; Heleno et al. 2009; Burghardt et al. 2009; 2010; Perre et al. 2011; Richard et al. 2018). However, there was no difference in caterpillar abundance in native and exotic plots and we did not find a relationship between herbivory and caterpillar abundance, one of the largest chewing herbivore groups in our beat samples. Overall our findings, coupled with work that has found that chewing herbivory is lower in urban landscapes compared to natural areas (Nuckols and Connor 1995; Raupp et al. 2010; Moreira et al. 2019), suggests that planting the exotic congener tree and shrub species used in this study may not be particularly advantageous for homeowners seeking to reduce herbivore damage on landscape plants in residential settings.

Although native plants can support greater herbivore abundance and biomass in ornamental landscapes in some cases (Burghardt et al. 2009; Narango et al. 2017), little is known about plant origin effects on invertebrate natural enemy abundance and biomass. Contrary to our hypothesis, natural enemy abundance and spider biomass did not differ between native and exotic ornamental landscapes. Studies on the effect of plant origin on natural enemy abundance and biomass have had mixed results. For example, plant origin had no effect on natural enemy abundance on exotic congeners and non-congeners of native

plant species in South Africa (Proches et al. 2008). In contrast, native plants attracted and harbored greater numbers of natural enemies in comparison to exotic plants in other studies (Southwood et al. 2005; Fiedler and Landis 2007; Greenstone et al. 2017). Biomass of predators was almost double on native oaks when compared to exotic congeners (Southwood et al. 2005). Although plant origin did not have an effect on spider biomass in our study, genus was predictive of biomass. *Hydrangeas* had the most spider biomass of all genera and significantly more biomass than *Cercis*, *Liriodendron*, and *Catalpa*. This difference could be attributed to blooming, as *Hydrangea* bloomed in both exotic and native plots for much of the collection period. Flowering plants, both native and exotic species, which provide nectar and pollen in the spring and summer months, are generally known to increase abundance and diversity of natural enemies, including spiders, in agricultural and ornamental landscapes (Landis et al. 2000; Braman et al. 2002; Frank and Shrewsbury 2004; Lee and Heimpel 2005; Fiedler and Landis 2007). However, the well documented effect of vegetation structural complexity on spider communities may also explain why spiders were more abundant on some plants in our study (Finke and Denno 2002; Schmitz 2003, 2007; Malumbres-Olarte et al. 2013). For example, *Hydrangeas* may have had more spider biomass in our study because architecturally the plants were more complex and supported more spiders or because the architecture of *Hydrangeas* supported spider species that were larger in body size. Overall our results suggest that, when considering how to increase spider biomass to support birds and other wildlife, other habitat or plant properties, such as flower period or plant architecture, rather than plant origin, may be important to prioritize, especially if the choice is between native or exotic congeners.

Although native ornamental landscapes had more diverse natural enemy communities in our study, overall plant origin was a weak predictor of natural enemy species diversity and richness and had no detectable effect on natural enemy community composition. A less diverse community of natural enemies on exotic ornamental landscapes in our study could be attributed to a lower diversity of herbivores on exotic plants, as well as fewer specialist herbivores (Carvalho et al. 2010; Burghardt and Tallamy 2013; 2015; Peralta et al. 2018). For example, lower parasitoid richness and abundance have been found in forested and disturbed landscapes that have been invaded by exotic plants, a phenomenon attributed to the decrease in native plant species and specialist herbivore hosts (Carvalho et al. 2010; Peralta et al. 2018). However, in our system, temporal differences in bloom time of native and exotic vegetation may also have contributed to greater natural enemy diversity in native plots. For example, in native ornamental landscapes *Viburnum* bloomed for an extended time during the collection period, whereas *Viburnum* in exotic ornamental landscapes had passed peak bloom when we sampled. *Viburnum* was one of the greatest contributors to observed differences in natural enemy diversity between native and exotic plots in our study. Structural complexity (Root 1973; Andow 1990, 1991; Langellotto and Denno 2004; Raupp et al. 2010; Letoureau et al. 2011; Raupp et al. 2012; Dale and Frank 2018) and disturbance via maintenance (Morris 2000; Bell et al. 2001; Cattin et al. 2003; Buri et al. 2016), factors that may otherwise affect natural enemy communities, were controlled for in experimental plots. Thus, factors, such as habitat complexity or connectivity at the landscape scale, which can alter natural enemy community structure (Landis et al. 2000; Gardiner et al. 2009; Rusch et al. 2016), or other unique plant traits attractive to natural enemies not measured in our study, may have contributed to the variation in natural enemy diversity response. Similarly to our study, Frank et al (2018) found that exotic congeners conserved similar arthropod natural enemy abundance and community structure as their native congeners in urban areas, and suggested that urban habitat variables, such as habitat fragmentation and impervious cover, may have had as much an effect on natural

enemy diversity as plant origin. Although controlled for in our study, plant choice could also explain differences in the biodiversity supported by landscapes. For example, studies have highlighted that some native tree species are better than others at supporting biodiversity (Tallamy and Shropshire 2009; Southwood et al. 2005). Trees in the genus *Quercus* often support more invertebrates, especially Lepidopterans, than other tree genera, such as *Acer* (Tallamy and Shropshire 2009). Therefore, our study highlights the need to explore how other factors, such as plant choice, plant bloom time and duration, and landscape scale habitat complexity, may affect natural enemy communities on landscapes at the residential scale and structure higher level trophic processes in urban areas.

Predation of *H. zea* eggs did not differ in native and exotic plots. Similarly, Cornelius et al. (2016) found that predation and parasitism of *H. halys* eggs did not differ on the basis of plant origin. Common predators of *H. zea* eggs are primarily generalist natural enemies including Nabids, Coccinellids, *Orius insidiosus*, and Opiliones, among others found in our beat samples (Nuessly and Sterling 1994; Pfanannenstiel and Yeargan 2002; Gardiner et al. 2014). Predation of *H. zea* eggs can be affected by plant type, season, time of day, and pollen and alternative food availability, among other factors (Pfanannenstiel and Yeargan 2000). Similarities in natural enemy abundance and spider biomass among plots may explain similar predation responses, and indicate that predatory function may be maintained on both native landscapes and landscapes planted in exotic congeners.

Because we compared landscapes planted in native plants with those planted in exotic congeners, we cannot extrapolate our findings to all native and exotic landscapes. In particular, we cannot make predictions about the differences between native landscapes and exotic non-congener landscapes. Further we can only draw limited conclusions about the effects of plant origin on invertebrate natural enemy communities, given our conservative comparisons between landscapes with related species. Overall, however, our work is valuable in informing landscape designers on the extent to which plant origin matters for biodiversity when given the choice between native plants and exotic congeners, which are common and readily available in the region for landscaping.

Exotic plants are commonplace in cities (McKinney 2008; Faeth et al. 2011) and are frequently planted to reduce herbivore damage and improve landscape aesthetics (Raupp et al. 1992, 2010; Herms 2002). However, the extent to which plant origin affects herbivory has been largely unexplored. Furthermore, little is known about how exotic ornamental plants affect invertebrate natural enemy diversity and biocontrol services. Our study sheds light on how both native and exotic congener landscapes may support valuable pest control services, and suggests that ornamental landscapes planted in exotic congeners of native plants may support similar natural enemy communities and comparable levels of natural enemy biomass to ornamental landscapes planted with all native plants. As more of the world population moves to urban areas, balancing the health of humans and ecosystems will be a great challenge. Our study provides guidance to landscape designers and planners trying to weigh the benefits of native plants and their exotic congeners and demonstrates that plant origin may not be the only factor to prioritize when designing landscapes for both the people and animals that use them.

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Author contributions SEP and SDF conceived of experimental design. SEP and LMK collected and analyzed the data. All authors contributed to drafts and gave approval for publication.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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