ABSTRACT

PARSONS, SARAH ERIN. Effects of Urbanization on Pest-Natural Enemy Systems in Ornamental Landscapes. (Under the direction of Dr. Steven Frank).

Plants in our urban landscapes provide many ecosystem services but are often stressed by pests and hot urban temperatures. High pest density and damage on urban plants are often thought to result from an escape of pests from their natural enemies, which may not be as abundant or diverse in urban habitats as in natural habitats. However, pest densities on plants can also be affected by other urban habitat features and conditions, such as impervious cover, hot urban temperatures, plant water stress, vegetation complexity or plant origin. My research highlights how several of these urban habitat elements affect a common street tree pest, crape myrtle aphid (*Tinocallis kahawaluokalani*), its natural enemies, and predation services on crape myrtle street trees in Raleigh, NC. I also explore how plant origin affects chewing herbivory, natural enemies, and predation services on ornamental landscapes in Washington, DC. This research addresses effects of urban habitats on pest-natural enemy systems and predation services, an area of study that has largely been unexplored.

I predicted that large-scale impervious cover drives *T. kahawaluokalani* abundance on crape myrtle trees and that local structural complexity around trees determines natural enemy abundance and predation services. I also predicted that hotter canopy temperatures caused by less local structural complexity around crape myrtles would mean more aphids on street trees. In a separate study with ornamental landscapes in D.C., I predicted that native ornamental landscapes would host a greater number and diversity of natural enemies and have higher rates of predation compared to exotic congener landscapes. I also predicted that native plants would have more chewing herbivory than exotic plants.

To test my hypotheses related to *T. kahawaluokalani*, its natural enemies, and predation
services, I collected data on crape myrtle trees on NC State campus and conducted lab experiments. I collected canopy temperature and arthropod data on study trees in the summer months and measured local structural complexity and impervious cover around trees, as well as plant water potential. Although aphid density increased with more impervious cover within 100-meters of trees, aphids decreased with hotter urban temperatures. Natural enemies and aphid and egg predation were not affected by temperature and were most correlated with local structural complexity and local impervious cover within 20 meters of trees. Local structural complexity within 10 meters of trees was not predictive of tree canopy temperature. Natural enemy abundance and aphid abundance were also not correlated in all the years sampled.

To test whether native ornamental landscapes would have more natural enemies and predation services than exotic landscapes, I collected arthropod data on USDA experimental plots at the U.S. Arboretum in Washington, D.C. Ornamental landscapes planted in native plants had higher natural enemy diversity, although the relationship with plant origin (native or exotic origin) was weak. However, plant origin had no effect on natural enemy abundance, spider biomass, or predation services. Leaf damage index values did not differ between native and exotic landscapes, and leaf area lost to chewing herbivory was highly variable among plant genera.

My findings suggest that increasing local structural complexity around trees may be a way to support robust natural enemy communities and predation services, particularly in highly urban areas where pests may be more abundant. Furthermore, plant origin may not be as important a consideration for supporting natural enemies and predation services on urban ornamental landscapes as other factors, such as plant traits that provide resources for natural enemies. My work highlights how landscape managers can design resilient landscapes in a
warmer, more urban world.
Effects of Urbanization on Pest-Natural Enemy Systems in Ornamental Landscapes

by
Sarah Erin Parsons

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Entomology

Raleigh, North Carolina
2019

APPROVED BY:

_______________________________  ______________________________
Steven Frank                     Thomas Wentworth
Committee Chair                  

_______________________________  ______________________________
George Hess                      Michael Reiskind
DEDICATION

I dedicate this dissertation to my family and friends (and James), who have helped me every step of this process. I really could not have done it without your love and support. I also dedicate this to my students, my nephew Michael, the children who have shared our home, and my friends’ children: Jada, Joe, Ali Jane, Lily Joy, Benjamin, Simone, Ellis, Sofia, Sergio, and Zoe. May this little piece of research contribute to a better, brighter world for your future.
BIOGRAPHY

Sarah Parsons was raised in Georgia, where her love for bugs was first born. Sarah grew up playing with her dogs (and bugs) on her family’s 3-acre property in Stockbridge. Her dad inspired and supported her love of nature, which defines both her person and her research even today. During her undergraduate career Sarah studied a cryptic caterpillar, *Stiria rugrifrons*, which lived on the granite rock outcrops of Georgia. She graduated from Emory University with a B.A. in Environmental Studies in 2008. She then attended Duke University and received her Masters in Environmental Management in 2012. Although her life took her away from bugs for a short while in her 20’s, Sarah came back to them. In 2015, she returned to NC State to pursue her PhD in Entomology. Sarah’s PhD research was inspired by her work as a sustainable landscape consultant during her professional career. Sarah wanted to explore ways to design landscapes that better served both the people and animals that used them. After graduation she hopes to continue informing landscape design through her research. However, two of her greatest passions are undergraduate teaching and research. Upon completion of her studies she hopes to teach Biology, Ecology, and Entomology at an undergraduate institution and inspire the next generation of ecologically-minded leaders.
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CHAPTER 1: Do habitat elements at different scales guide relations of pests with natural enemies in the city? Exploring drivers of Tinocallis kahawaluokalani (Hemiptera: Aphididae) and its natural enemies

Abstract

Trees provide many ecosystem services in our urban environments. However, city trees are often stressed by pests and urban temperatures that are typically higher than those in nearby natural areas. Our research highlights a potential mismatch in scale between the urban habitat elements that affect the densities of pests and their natural enemies on city trees. We tested a well-known ecological concept, the enemies hypothesis, in the city, where relationships of pests and their enemies have not been thoroughly studied. To test our hypothesis that natural enemies and aphid predation services on urban trees increase with more local structural complexity around trees, we collected data on crape myrtle trees on NC State University’s campus from 2016-2017. We measured local structural complexity of vegetation around study trees, quantified impervious cover among other urban habitat elements, collected crape myrtle aphids (Tinocallis kahawaluokalani) and their natural enemies on trees, and performed predation experiments. Consistent with results of previous urban ecology studies, we found that impervious cover at the landscape scale is a strong driver of T. kahawaluokalani abundance. Aphid abundance increased with an increase in impervious cover within 100 meters of crape myrtle trees. Greater local structural complexity within the 10x10 meter area around crape myrtles correlated with a higher abundance of natural enemies, especially the minute pirate bug, Orius insidiosus. Aphid predation was most predicted by local structural complexity and impervious cover within 20 meters of crape myrtle trees. Together, these findings suggest that
although the impervious nature of our cities correlates with the densities of some pests, local landscapes around trees may play an important role in maintaining certain species of natural enemies and predation services that can help regulate pest populations.

**Introduction**

Local habitat and vegetation structure can affect pests, their natural enemies, and biological control in urban, agricultural, and natural ecological systems (Root 1973, Andow 1991, Langellotto and Denno 2004, Raupp et al. 2010, Letourneau et al. 2011, Raupp et al. 2012, Dale and Frank 2018). Vegetation structure of a habitat includes plant species diversity and structural complexity, which describes how densely different layers of vegetation, such as turf, groundcover, shrubs, understory, and overstory, fill a habitat (Kareiva 1983, Shrewsbury and Raupp 2000, Price et al. 2011). Habitats with greater vegetation structure often benefit natural enemies by providing resources, such as alternative prey or hosts, nectar and pollen for omnivores, suitable microclimates, and habitat for multiple life stages. The enemies hypothesis holds that increasing vegetation structure will increase natural enemy abundance and diversity as well as pest regulation (Pimental 1961, Tahavanainen and Root 1972, Root 1973, Letourneau 1987, Andow 1990, 1991, Landis et al. 2000). The enemies hypothesis has been tested primarily in agricultural systems (Pimental 1961, Root 1973, Andow 1991, Langellotto and Denno 2004, Letourneau 1987, Letourneau et al. 2011) but some researchers have explored how vegetation structure affects biological control in urban ecosystems. For example, Shrewsbury and Raupp (2000, 2006) found that azaleas in residential landscapes with greater density and numbers of vegetation layers had fewer lacebugs, *Stephanitis pyrioides*, than azaleas in simpler landscapes. This complexity supported greater alternative prey for generalist predators, particularly
*Anyphaena celer* spiders, and greater top-down control (Shrewsbury & Raupp 2006). Likewise, pine needle scale insects, *Chionaspis pinifoliae*, were more abundant on pines in simple “impoverished” landscapes, such as roadsides and parking lots, compared to pines in more complex wooded habitats (Tooker and Hanks 2000). This was attributed to greater predation by generalist predators (Hanks and Denno 1993, Tooker and Hanks 2000).

In addition to its effect on natural enemies, the local habitat can affect pests directly by altering elements, such as light exposure and temperature, or indirectly by altering host plant quality. For example, in their study of residential landscapes, Shrewsbury and Raupp (2000) found that azaleas with more sun exposure, which was negatively correlated with local structural complexity, had more *Stephanitis pyrioides*. Similarly, decreasing local overstory and understory vegetation in the 10mx10m area around urban red maples increased canopy temperature, which had positive effects on *M. tenebricosa* fecundity and abundance (Dale and Frank 2014). Local impervious cover around trees can negatively affect tree health by reducing soil moisture and increasing plant water stress. These stressful conditions for trees can increase plant quality for some pests and correlate with higher pest densities (Speight et al. 1998, Huberty and Denno 2004, Dale et al. 2016, Dale and Frank 2017). For example, Sperry et al. (2001) assessed how impervious cover at both local and landscape scales affected different pests of honeylocust trees and found that more impervious cover at the local 10-meter scale was positively correlated with mimosa webworm (*Homaduala anisocentra*) and honeylocust spider mite (*Platytetranychus multidigituli*) densities. Plant water stress was implicated as the potential mechanism driving this positive relationship, with local impervious cover decreasing water accessibility to plants and increasing pest densities (Sperry et al. 2001). The plant stress hypothesis posits that drought stress can increase pest densities on plants via mechanisms of increased nutrient availability and
lower plant defenses (Huberty and Denno 2004) and may play a role in increasing pest densities on city trees with high local impervious cover.

Landscape-scale differences in habitat complexity and impervious cover within 100 meters or more of focal plants can also play an important role in pest management in agricultural and urban systems. Greater habitat complexity at the landscape-scale can bolster natural enemies and biological control in agricultural landscapes (Landis et al. 2000, Gardiner et al. 2009, Rusch et al. 2016). For example, in a quantitative synthesis of data from 15 studies, pest control by natural enemies was 46% lower in crop plots surrounded by homogeneous landscapes dominated by cultivated land when compared to crop plots surrounded by complex landscapes with a combination of land cover types, such as forest land (Rusch et al. 2016). Similarly, biological control of soybean aphids (*Aphis glycines*) was weaker in landscapes with high proportions of crop fields in the Midwest U.S. than in more diverse landscapes with forests and grasslands at the 1.5km-scale (Gardiner et al. 2009). Urban studies, however, suggest little to no effect of landscape-scale vegetation complexity on natural enemies and biological control services (Sattler et al. 2010, Bennett & Gratton 2012, Burkman and Gardiner 2014). For example, Sattler et al. (2012) found no relationship between landscape scale vegetation heterogeneity, measured at the 50 meter scale, and natural enemy species richness in three Swiss cities. Similarly, aphid predation was not correlated with impervious cover at the 300-meter scale along an urban gradient in south central Wisconsin (Bennett & Gratton 2012). Furthermore, in Southern England, local plant species richness in urban gardens was a strong predictor of hoverfly abundance while landscape-scale impervious cover was not (Rocha et al. 2018). The dissonance between agricultural and urban studies on the effects of landscape complexity on natural enemies
and pest management emphasizes the need for study in urban habitat to explore how best to optimize pest management on urban landscapes.

Increasing impervious cover at landscape scales increases temperature within cities, a phenomenon known as the urban heat island effect (Kim 1992). High temperature caused by impervious surfaces can benefit pests by increasing density, development rate, and fecundity (Meineke et al. 2013, Dale and Frank 2014, Dale et al. 2016). For example impervious cover at the landscape scale was more predictive of tree canopy temperature (at the 125 meter scale) and scale insect abundance (at the 60 meter scale) than local impervious cover measured at smaller scales between 10-50 meters (Dale et al. 2016). In addition to raising temperatures, impervious cover at large spatial scales can increase habitat fragmentation and reduce the ability of some natural enemies to travel among patches, which may help some pests escape natural enemies in highly urban areas (Niemela et al. 2002, Niemela and Kotze 2009, Burkman and Gardiner 2014).

Our hypothesis is that a mismatch exists between the factors regulating densities of pests and their natural enemies in urban areas. Because impervious cover restricts natural enemy dispersal and increases plant stress at landscape scales, pests may have a multifold advantage over their enemies on urban plants they colonize (Alarukka et al. 2002, Niemela and Kotze 2009, Magura et al. 2010). To test this hypothesis we studied crape myrtle (*Lagerstroemia* spp.) aphids (*Tinocallis kahawaiulokalani*), and a suite of aphidophagous generalist natural enemies on crape myrtle trees in Raleigh, NC, USA. We tested how local and landscape vegetation structure and impervious cover around trees affected *T. kahawaiulokalani* density, their natural enemies, and aphid predation compared to vegetation cover and impervious cover at the landscape scales. We predict that *T. kahawaiulokalani* increase in response to more impervious cover at the landscape scale surrounding host trees, while natural enemies increase in response to more
vegetation at the local scale, which would support our mismatch hypothesis. In our study, we explored the tension between the drivers of the abundances of pests and their natural enemies and shed light on how we can best design our city landscapes to support natural enemies, reduce pest load, and protect the beauty and health of our urban trees.

**Methods**

*Study System*

Crape myrtles (*Lagerstroemia indica x fauriei*) are common exotic trees planted in Southeastern U.S. landscapes, valued for their long bloom periods, attractive fall color, tolerance to drought stress, and their small number of insect and disease pests (Mizell and Knox 1993, Chappell et al. 2012, Riddle and Mizell 2016). Crape myrtle aphid (*T. kahawaluokalani*) is a specialist herbivore that lives on crape myrtles and eats phloem (Alverson and Allen 1991, Herbert et al. 2009, Frank 2019 in press). Unlike most other aphids, crape myrtle aphids do not have a known parasitoid either in the U.S. or in their native range in Southeast Asia (Mizell et al. 2002). Therefore, natural enemies of crape myrtle aphids are generalist predators, such as lady beetles (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), minute pirate bugs (Hemiptera: Anthochoridae), damsel bugs (Hemiptera: Nabidae) and syrphid flies (Diptera: Syrphidae), among others (Mizell 2007, Mizell and Schiffhauer 1987). Crape myrtle aphids have several generations each year and reproduce from April-September in Raleigh, NC (Alverson and Allen 1991). *T. kahawaluokalani* can negatively affect tree aesthetics when honeydew accumulates on leaves, which facilitates black sooty mold, *Capnodium* sp. (Dozier 1926, Alverson and Allen 1991). Dense populations can also cause leaves to yellow and drop (Dozier 1926, Alverson and Allen 1991).
Study Area and Study Sites

In 2016 we randomly selected 33 crape myrtles (Lagerstroemia indica x faureri ‘Natchez’) on the NC State University campus using a campus tree inventory that was provided by NC State’s Facilities Division. A map layer was created in ArcMap (ArcGIS Desktop 10; ESRI, Redlands, CA, USA) with all tree locations. Trees were at least 100 meters apart to reduce spatial autocorrelation. The habitat around trees ranged from 14.2% impervious cover within 100m to 75.2%. Furthermore elements of vegetation structure varied widely around trees (Supplementary Fig. S1). Some trees, for instance, were planted alone in mulched planting beds in parking lot islands while others were adjacent to forests with dense vegetation.

Environmental Data Collection

Measuring Local Vegetation Structure

We measured several local vegetation structural elements around study trees, including canopy volume, patch presence, and local structural complexity. We quantified canopy volume for each tree using UrbanCrowns software (UrbanCrowns, Forest Service, U.S. Department of Agriculture, USA) (Winn et al. 2011). We took pictures of each study tree in August when canopies were most full and uploaded data into UrbanCrowns to calculate crown volume. Crape myrtles were recorded as being in a “patch” with other crape myrtles if the study tree touched the canopy of one or more crape myrtle trees. Patch was recorded as a binary, presence or absence, variable.

Local structural complexity was quantified by adapting methods from Shrewsbury and Raupp (2000) (Supplementary Fig. S2). Temporary grids of 10mx10m were constructed on the ground around trees using two pieces of rope, which were marked every meter with a flag. Ropes were positioned on the ground perpendicular to one another, such that they created two
sides of a 10 meter square with the tree in the center. The first rope was always positioned on
the north side of the tree with the second rope laid perpendicular on either the east or west side of
the tree (Supplementary Fig. S2). To measure structural complexity in the 10mx10m grid space,
each vegetation stratum was identified and scored as present or absent in each 1mx1m square
within the grid. The five vegetation strata were turf, herbaceous vegetation, shrubs, understory
trees, and canopy trees. The maximum number of vegetation strata in any one 1mx1m square
therefore was 5. The maximum number of squares any one vegetation layer occupied was 100,
meaning the vegetation layer occupied all 1mx1m squares in the grid. The total structural
complexity index (SCI) could thus range from 0 to 500 (Shrewsbury and Raupp 2000). We also
calculated structural complexity using the Shannon Diversity Index (H’), a commonly used
measure for vegetation diversity, to account for how evenly all vegetation strata were distributed
around the tree. In an approach similar to that used by Dale and Frank (2014), we treated each
vegetation stratum as a “species” and 1mx1m grid counts within each strata (0-100) as
“abundance.” Shannon Diversity index values were calculated using the vegan package in R. H’
values ranged from 0-1.43, with 0 being assigned to those crape myrtles with no surrounding
vegetation and 1.43 being those trees with lots of layers of vegetation distributed evenly around
the tree.

Measuring groundcover at local and landscape scales

Impervious cover and coarse vegetation at the local 20 meter scale and the larger 100
meter scale around study trees were calculated using ArcMap (ArcGIS Desktop 10; ESRI,
Redlands, CA, USA). We used Bigsby et al.’s (2014) data, which delineated impervious cover
and coarse vegetation at a 1-meter resolution in Raleigh, NC. We chose to analyze impervious
cover and coarse vegetation cover because they are dominant elements of the urban landscape
around study trees. Impervious cover includes road, sidewalk, and building surfaces, and coarse vegetation includes both tree and shrub cover. Once the data were uploaded in ArcMap, current Google Earth™ images were used to compare how well the 2013 data matched current groundcover data. Building footprints of new construction on campus were added to the impervious cover layer. Impervious cover and coarse level vegetation cover around trees were calculated by creating a buffer of 20 meter and 100 meter around study trees in ArcMap. Surface area of impervious cover and coarse vegetation were converted to percentages for analyses. Percentages represented percent cover of impervious surface and coarse vegetation within the 20 meter and 100 meter buffer zones.

Arthropod Data Collection

Aphids

Aphid abundance was recorded 7 times in 2016 (25 and 31 May; 7, 14, and 21 June; 26 July; and 5 September) and 3 times in 2017 (16 May; 12 June; and 10 July). Adapting methods from Mizell (2007), we collected terminal twigs from the four cardinal directions of each tree and in high and low parts of the canopy using a pole pruner. All aphid instars were counted on the first 15 fully expanded leaves of each twig starting from the terminal end.

Natural enemies

Natural enemies were collected 6 times in 2016 (31 May; 7, 15, and 23 June; 26 July; and 5 September) and 3 times in 2017 (16 May; 12 June; and 10 July). On each sample date three areas of the lower canopy were beaten with a wooden dowel to dislodge arthropods into a tray. Trays were immediately rinsed with 75% ethanol into sample containers. Natural enemies were identified in the lab under a dissection scope. Most arthropods were identified to family, with the exception of spiders, parasitoid wasps, and earwigs (Dermaptera). We placed 7.6 x 12.7 cm
yellow sticky cards (Olson Products, Medina, Ohio, USA) in the lower canopies of trees above first lateral branches to survey flying natural enemies in 2016 (13 and 23 June; and 10 August). Sticky cards were taken down after two weeks and the arthropods identified under a dissecting scope.

*Predation Experiments*

Predation experiments were conducted 4 times in 2016 (9, 16, 23, and 31 August) and 3 times in 2017 (19 July; 4 August; and 8 September). Aphid colonies were reared on four ‘Natchez’ crape myrtles (Old Courthouse Nursery, Warsaw, NC, USA) in 3.8-liter pots in a climate-controlled greenhouse on the NC State University campus. Each time the experiment was conducted we took one colony tree into the field to inoculate study trees. One leaf from the colony tree with 30-50 aphids was secured with a twist tie to a leaf on a lower branch of each study tree, which was clean of aphids. A mesh bag was then secured over the branch with a binder clip to exclude predators. The bagged branch was left for two weeks to establish a colony of aphids on the branch. After two weeks, predator exclusion bags were removed. Apterous aphids were counted at the time of bag removal and again after 24 hours. Aphids missing after 24 hours were assumed to have been predated. Alate aphids were not counted because of high probability of emigration within 24 hours. In 2017, a similar protocol was followed but the number of apterous aphids was standardized to 200 at the start of each 24-hour trial. When exclusion bags were removed from infested branches, 200 apterous aphids were maintained on 1-3 arbitrarily selected leaves and all other aphids were removed with a small paintbrush. Separate analyses were performed for experiments in each year to account for the differences in methods.
Analysis

Local and landscape effects on aphid and natural enemy abundance

All analysis was performed in R Version 3.4.3 (The R Foundation for Statistical Computing, 2017). We first tested our hypotheses *a priori* by analyzing a selection of linear models. We analyzed the linear model which included impervious cover at 100 meters, local structural complexity at 10 meters, and their interaction as predictors for both aphid density and natural enemy density responses. For aphids we tested the model with impervious cover within 100 meters as a sole predictor. For natural enemies we tested the model with local structural complexity as a sole predictor. After we tested these models for each response we performed model selection. We used model selection to determine which factors, of all those measured, were best at predicting aphid and natural enemy densities on crape myrtles. Our candidate model set used for model selection included our models used to test our *a priori* hypotheses. Our responses for all analyses were aphid and natural enemy abundance, totaled for the season, and log10 transformed to improve the distribution of residuals and account for overdispersion (Zuur et al. 2009, 2010). We did separate analyses for 2016 and 2017.

Methods for model selection with Akaike information criterion (AIC) were adapted from Hamblin et al. (2018), and we used the MUMIn v.1.40.4 package in R (Barton 2016). Predictors of models used in model selection included impervious cover (within 20m and 100m of trees), coarse vegetation cover (within 20m and 100m of trees), canopy volume, patch presence, and local structural complexity (H’ or SCI). Because multicollinearity of predictor variables was weak, with variance inflation factors ranging from 1.25 to 2.44 (car v2.1-6 package) (Fox and Sanford 2011) and not exceeding 3 (Zuur et al. 2010), we included all predictors in the model selection process (Hamblin et al. 2018), with the exception of local structural complexity
measures of $H'$ and SCI. We ran two separate model selection processes with $H'$ and SCI, because they are different measures of the same predictor. The candidate set of linear models used for model selection included 12 models in total (Supplementary Table S1).

Models in model selection were ranked based on model weights and $\Delta$AICc (Akaike information criterion adjusted for small sample size) in relation to the topmost model in the model selection process using the model.sel function in R (MUMIn package). From the model selection process we also obtained importance values for each predictor. After performing the model selection process we used the best model set (models with $\Delta$AICc<2) to calculate model-averaged parameter estimates for all predictors using full model averaging to account for moderate model selection uncertainty (Burnham and Anderson 2002, Lukacs et al. 2009, Symonds and Mousalli 2011). We used model validation diagnostic plots and the gvlma v 1.0.0.2 package in R to detect and test for violations of linear regression assumptions for all top selected models ($\Delta$AICc<2). We also reported on the $R^2$ of all top models chosen in each selection. Lastly, Mantel tests were run on all top models using 9999 replicates to test independence of observations and to detect if there was any spatial autocorrelation.

A separate set of model selections were performed for the major groups of natural enemies found on crape myrtles. Responses in these model selections included lady beetle abundance, lacewing abundance, predatory thrips abundance, $O. \text{insidiosus}$ abundance, and spider abundance. Responses were $\log_{10}(x+1)$ transformed to help account for the overdispersion and heterogeneity in the data, as well as the high instances of 0’s in the data. When low spatial autocorrelation ($p<0.05$) was detected for three of the $O. \text{insidiosus}$ 2016 models, models and model selection were rerun with a 200m cutoff between trees. Four trees were excluded because they were less than 200m from other trees in the study area. With the
four trees excluded, no spatial autocorrelation was detected and model selection results were similar to the results found with the full data set (Supplementary Table S7).

Local and landscape effects on aphid predation

We used the same approach to analyses for aphid predation. The same *a priori* hypotheses tested for natural enemies were tested for aphid predation. We followed testing of the *a priori* hypotheses with model selection to explore which factors best predict aphid predation. However, we used generalized linear mixed effects models with a binomial distribution in our candidate model set. We used the binomial distribution because our response was analyzed as a proportion (proportion of aphids eaten, e.g. varies from 0-1). Generalized linear mixed effects models were used so that individual trees could be treated as “random” effects to account for repeated measures (Zuur et al. 2009). Separate analyses were conducted for 2016 and 2017. In 2016 the aphid populations at the start of each trial were not of the same size, and thus “initial aphid count” had to be included as a covariate, particularly given the often density-dependent response of natural enemies. In 2017 populations of aphids were maintained at 200 at the start of trials and thus “initial aphid count” was not included in models. Using the same protocol as that used for aphid and natural enemy abundance model selection, top models were selected based on ΔAICc<2 and importance values were reported. Marginal and conditional R² values were reported for top models using the `piecewiseSEM` v. 1.2.1 package in R (Lefcheck 2015).

Results

Habitat Analysis

More than half (63.6%) of crape myrtles were in patches with other crape myrtles. Crown volume ranged from 153.61 m³ – 3276.29 m³ ([mean +/- SD] 1213.26 +/- 837.26). Structural
complexity Shannon \( H' \) values ranged from 0-1.43 ([mean +/- SD] 0.77 +/- 0.38). Sites with a Shannon \( H' \) value of 0 only had one vegetation layer, the understory layer created by the individual study tree. Most often sites with a Shannon \( H' \) value of 0 included study trees in mulched parking lot islands with no surrounding local vegetation (Supplementary Fig. S1).

Total structural complexity index values ranged from 50-180 ([mean +/- SD] 123.39 +/- 37.88). All trees had understory vegetation, because study trees were included in understory strata measurements (Supplementary Table S2). Only 24\% of crape myrtles in this study had overstory trees within the 10mx10m grid space around trees. Crape myrtles grow best in full sun, which may explain the low percentage of study trees with local overstory. Local impervious cover within 20 meters of study trees ranged from 0-95\% cover ([mean +/- SD] 43.70 +/- 2.40), and landscape scale impervious cover within 100m of trees ranged from 14.2\%-75.2\% ([mean +/- SD] 49.00 +/- 15.10).

Local and landscape effects on aphid abundance

As predicted landscape scale impervious cover at 100 meters was significantly predictive of \( T. \) kahawaluokalani abundance \((R^2= 0.24, p<0.01 \text{ (2016); } R^2=0.17, p<0.05 \text{ (2017)})\). Model averaged parameter estimates showed that for every percentage gain in impervious cover at 100m we could expect to see an addition of 0.891 or 1.42 aphids on trees in 2016 and 2017, respectively (Table 1). However, the interaction between local structural complexity and landscape-scale impervious cover was not significant. Thus, our second tested a priori hypothesis was not supported. In other words, aphid abundance increased with landscape scale impervious cover, regardless of local structural complexity.

In model selection the simple linear regression with impervious cover at the landscape-scale as a predictor was selected as a top model in both years (\( \Delta AIC<2 \)) (Fig. 1) (Supplementary
Table S3). Importance values for impervious cover within 100m of crape myrtle trees were above 0.95 for 2016 and 2017 respectively (Table 1). Therefore, impervious cover within 100m of trees as a predictor had a more than 95% probability of being selected in the best models given the candidate set of models. Local structural complexity (H’ or Total SCI) was the second most important predictor for aphid abundance. Local structural complexity (H’) had importance values greater than 0.7 in 2016 and 2017 (Table 1). In 2017 the presence of a patch and crown volume also had importance values exceeding 0.5.

In 2016, the best model of the candidate set included impervious cover (100m) (parameter estimate +/- SE, 0.93 +/- 0.25) and local structural complexity (0.21 +/- 0.10) as predictors of aphid abundance (R²=0.34) (Supplementary Table S3). In 2017, the top model included impervious cover (100m) (1.46 +/- 0.51), local structural complexity (0.36 +/-0.24), patch presence (0.432 +/-0.17), and crown volume (0.00 +/-0.00) (Supplementary Table S3). Although, local structural complexity (H’) on aphid abundance had a positive effect on aphid abundance in both years (0.150 (2016); 0.255 (2017)), it had about one-fifth the effect on aphid abundance when compared to large-scale impervious cover (Supplementary Table S3). When total SCI was used as the measure of local structural complexity in models, the same top models were selected. We report on models using Shannon Index (H’) for local structural complexity, because the top selected models and models used in hypothesis testing overall had higher R² values with H’. No spatial autocorrelation was detected in aphid models. The model including natural enemy abundance as a predictor was not selected as a top model and had low importance values of 0.007 (2016) and 0.01 (2017).
Local and landscape effects on natural enemy abundance

As predicted local structural complexity (H’) was a significant predictor of natural enemy abundance (R²= 0.186, p<0.05 (2016); R²= 0.167, p<0.05 (2017)). Model averaged parameter estimates for local structural complexity (H’) were 0.407 (2016) and 0.149 (2017) (Table 1). However, the interaction between local structural complexity and landscape-scale impervious cover was not significant. Thus, our second tested a priori hypothesis was not supported. In other words, natural enemy abundance increased with local structural complexity, regardless of landscape scale impervious cover.

In model selection, the simple linear model with local structural complexity (H’) as a predictor was a top-selected model in both years (Supplementary Table S4, Supplementary Fig. S3). Importance values for local structural complexity (H’) were high, above 0.9 in 2016 and 2017 (Table 1). Importance values for local structural complexity using structural complexity index (SCI) measures were also high in both years, above 0.5, further validating that local structural complexity is a good predictor of natural enemy abundance. In 2016, local impervious cover within 20m was also an important predictor (importance value greater than 0.5).

The top model in 2016 included local structural complexity (H’) (parameter estimate +/- SE, 0.670 +/- 0.25), impervious cover (20m) (0.86 +/- 0.38), and the interaction between local structural complexity (H’) and impervious cover (20m) (-.79 +/- 0.43), (R²=0.34) (Supplementary Table S4). The interaction between impervious cover (20m) and local structural complexity was negative, such that when sites with high structural complexity were surrounded by high amounts of impervious cover natural enemies decreased. However, the overall effect of this interaction was small. In 2017, the top model included local structural complexity (0.24 +/- 0.08) and impervious cover (100m) (0.37 +/- 0.18) (R²=0.26) (Supplementary Table S4). In 2017
the same top models were chosen in model selection when SCI was used instead of H’ for local structural complexity. Although top models (AIC<2) did not match in 2016 when SCI was substituted for H’, local structural complexity with SCI was included in all top models. We report on models using Shannon Index (H’) for local structural complexity, because important models (i.e. top selected models and models used in hypothesis testing) overall had higher $R^2$ values with H’. The model including aphid abundance as a predictor was not selected as a top model. Aphid abundance as a predictor had low importance values of 0.026 (2016) and 0.005 (2017).

Local and landscape effects on natural enemy abundance by natural enemy group

*O. insidiosus* and spiders were the most abundant natural enemies in beat samples, constituting 35% (2016) and 47% (2017) and 43% (2016) and 37% (2017) of samples respectively (Supplementary Table S5). Predatory thrips 37.86% and *O. insidiosus* 25.48% were the most abundant natural enemies on sticky cards in 2016 (Supplementary Table S6). Local structural complexity (H’) was an important predictor of lady beetles, *O. insidiosus*, and spiders in 2016, and an important predictor of lacewings and *O. insidiosus* in 2017 (importance values >0.5) (Fig. 2, Table 2). *O. insidiosus* abundance was the only natural enemy group predicted by local structural complexity in both years. Local structural complexity was also predictive of *O. insidiosus* on sticky cards in 2016 (Table 2, Supplementary Table S7). Model selection also revealed a positive effect of large-scale impervious cover (100m) around trees on *O. insidiosus* in both years (Table 2, Supplementary Table S7).

Given the large proportion of *O. insidiosus* in beat samples and its close association with large-scale impervious cover, natural enemy models were also run, excluding *O. insidiosus*, to explore if large-scale impervious cover had a significant effect on other natural enemy groups.
Natural enemy models for 2016 without *O. insidiosus*, indicated that the only predictor values with importance values above 0.5 were local structural complexity (0.80 +/- 0.22), local impervious cover (1.12 +/- 0.34) and the interaction of local structural complexity and local impervious cover (-1.18 +/- 0.39). This interaction had a slight negative effect, such that natural enemies increased by slightly less when high amounts of impervious cover immediately surrounded a tree with high structural complexity. However, this interaction was weak, in that it did not change the overall trajectory of natural enemy abundance. Thus in the presence of both high local structural complexity and high local impervious cover, natural enemies still increased. Models for 2017 without *O. insidiosus* did not have any predictors with importance values above 0.5. A small amount of spatial autocorrelation was detected in 2016 for two of the top-selected natural enemy models including *O. insidiosus* (Monte-Carlo observed correlation, p<0.05). However, no spatial autocorrelation was detected in models when *O. insidiosus* was excluded. These results provide some support for our hypothesis that natural enemies are most predicted by local habitat elements, including local structural complexity, despite large-scale changes in impervious cover.

*Local and landscape effects on aphid predation*

We predicted that local structural complexity (H’ or SCI) would be most predictive of aphid predation. However, neither of our *a priori* hypotheses were good at explaining variation in aphid predation (Table 3). Both local structural complexity and the interaction between local structural complexity and landscape-scale impervious cover were not significant.

In model selection, importance values for local structural complexity were 0.615 (2016) and 0.201 (2017) (Supplementary Table S8), meaning that only in 2016 did local structural complexity have a greater than 50% probability of being selected in top models. Local
impervious cover (20m) also was an important predictor of aphid predation in 2017 (importance value >0.5).

The top selected model in 2016 was the simple linear model with local structural complexity (H’) as the predictor (1.04 +/- 0.55) (Table 3). The top selected model in 2017 was the simple linear model with local impervious cover within 20m of trees as a negative predictor – (3.87 +/- 1.44) (Table 3). In 2016 the model with local impervious cover, although not the top-most model was also highly ranked with AIC<2. Local impervious cover was a significant predictor of predation in 2017 (p<0.01), but not in 2016. When SCI was substituted for H’ as a structural complexity measure results were similar. However, with SCI the only model with AIC<2 was the model with local impervious cover (20m) as a predictor. We report on models with (H’) because top models with H’ had higher marginal and conditional R² values. Marginal and conditional R squares for all the top selected predation models (AIC<2) reported here were relatively low, ranging from 0.05-0.20, possibly signifying that overall the fixed and random effects were fairly poor at explaining aphid predation. No spatial autocorrelation was detected in predation models. The models including total aphid abundance and natural enemies as predictors were not selected among top models.

Discussion

Determining how pests and natural enemies are affected by urban environments will help inform how we design more resilient urban landscapes that protect tree health and functioning. Our study highlights a potential mismatch between landscape scale habitat drivers of pests and the local habitat drivers of natural enemies and predation services. In keeping with our hypothesis, T. kahawaluokalani abundance increased with impervious cover at the 100 meter
scale, and higher local structural complexity around crape myrtles was associated with more natural enemies and higher aphid predation. Aphid predation was also significantly and negatively correlated with local impervious cover. These results support previous findings in which trees surrounded by more impervious cover had greater pest densities (Speight et al. 1998, Sperry et al. 2001, Dale et al. 2016) and those surrounded by higher local structural complexity had more natural enemies and improved biocontrol services in city environments (Hanks and Denno 1993, Tooker and Hanks 2000, Shrewsbury and Raupp 2006, Raupp et al. 2010, Burkman and Gardiner 2012). By examining local and landscape habitat elements simultaneously we uncovered what may be a spatial mismatch between the factors driving pests and their natural enemies in urban areas. Together our results signify that the local environment matters when developing pest management on urban trees.

Our results concur with other studies that have found that herbivorous pests, particularly Tetranychid mites (Ehler and Frankie 1979, Kropczynska et al. 1988, Sperry et al. 2001) and piercing-sucking hemipterans, such as diaspidid scales (Stoetzal and Davidson 1971, Hall and Ehler 1980, Hanks and Denno 1993, Tooker and Hanks 2000, Raupp et al. 2010, Dale and Frank 2014), are more abundant on city plants surrounded by high amounts of impervious cover. Impervious cover can directly or indirectly affect pest abundance through alteration of canopy temperature, plant water relations, and habitat. Hotter temperatures associated with more impervious cover, for example, have been linked to higher pest fecundity, survival, and population growth in P. quercifex and M. tenebricosa scales in Raleigh, NC (Meineke et al. 2013, 2014, Dale and Frank 2014). Plant water availability and drought stress associated with impervious cover have also been implicated as drivers of M. tenebricosa and P. regalis scales in city settings (Speight et al. 1998, Dale and Frank 2017). However, the effects of drought on
piercing sucking insects has been varied, because some phytophagous insects respond negatively to drought stress (Hanks and Denno 1993) likely as a result of reduced turgor pressure and nutrient accessibility (Huberty and Denno 2004). Crape myrtles grow best in full sun (Chappell et al. 2012), maintain visual plant quality under drought stress (Davies and Castro-Jimenez 1989), and are valued as a blooming ornamental. Thus planners and designers may disproportionately plant more crape myrtles at higher densities in areas of high impervious cover with substantial sun exposure and higher temperatures compared to other urban trees. Manipulating the local habitat around crape myrtles to increase vegetation complexity may help compensate for the benefits of impervious cover on pests. Furthermore, this design strategy may be particularly important for trees in parking lots or along streets, where high amounts of local impervious cover may decrease pest control potential. Overall, we suspect that impervious cover may be indicative of a combination of factors, not excluding temperature, drought stress, and resource concentration, that aid in T. kahawaluokalani growth and abundance.

In addition to its effects on T. kahawaluokalani, more impervious cover at the landscape scale was also predictive of O. insidiosus in our study. Although urban studies have generally suggested little to no effect of landscape-scale habitat complexity on natural enemies and predation services (Sattler et al. 2010, Bennett and Gratton 2012, Burkman and Gardiner 2014, Rocha et al. 2018), more impervious cover within 100m of urban gardens was correlated with higher lady beetle abundance and diversity in the California central coast region (Egerer and Ong 2018). Water availability in urban gardens was thought to explain this positive relationship between lady beetles and large-scale impervious cover in California, where water is a limited resource across the larger landscape. However, given that Raleigh’s water regimen differs from that of the California central coast, we may ascertain that water availability at the landscape-
scale has less to do with *O. insidiosus* distribution and that other mechanisms, such as higher food availability, may be driving *O. insidiosus* abundance on crape myrtles. We suspect that *O. insidiosus* uses crape myrtles as a pollen resource in urban areas. Crape myrtles produce dimorphic pollen and may serve as valuable pollen reservoirs in urban areas during the summer months when pollen resources may not be as readily available (Riddle and Mizell 2016). *O. insidious*, an omnivore with a predilection for small Homopterans and flower resources, is known to aggregate in areas with high concentrations of pollen, such as corn fields during anthesis (Isenhour and Marston 1981, Corey et al. 1998). Therefore, we expect that more *O. insidiosus* are found in areas with higher impervious cover because crape myrtles, a pollen resource, are planted at a higher density in areas of high impervious cover, given growing conditions and landscape designer preference.

Local structural complexity had positive effects on natural enemy abundance and aphid predation. This supports the enemies hypothesis and related research in natural, agricultural, and urban systems. A meta-analysis on experimental agricultural studies, for example, found a significant effect of altered local habitat complexity on overall abundance of arthropod natural enemies (Langellotto and Denno 2004). Urban studies have also established a correlation between higher habitat complexity and more natural enemies, especially with regard to generalist natural enemies (Burkman and Gardiner 2012) on azaleas (Shrewsbury and Raupp 2006), on mulberry trees (Hanks and Denno 1993), in urban gardens (Philpott and Bichier 2017), and on golf courses (Frank and Shrewsbury 2004). Future work would need to assess if mechanisms, such as increased availability of alternative prey, carbohydrate resources, or refugia, are driving this phenomenon in crape myrtle systems (Landis et al. 2000). For example, in the case of omnivorous *O. insidiosus*, more alternative prey and carbohydrate sources may be most
responsible for high numbers of *O. insidiosus* on crape myrtles situated in structurally complex habitats (Pumarino et al. 2012). In agricultural settings, vegetation diversity can increase populations of *Orius* due to the availability of more pollen and nectar resources (Lundgren et al. 2009, Pumarino et al. 2012). Furthermore, to more accurately assess if a spatial mismatch exists between local and landscape scales of structural complexity on natural enemy abundance, future work would need to use the same measures of structural complexity at both scales. In this study, we calculated structural complexity with the aid of ArcGIS Desktop 10 software at the landscape scale using coarse vegetation cover. However, we used detailed field measurements to calculate local structural complexity. These measures are not the same, and, thus, future work would need to standardize measures to determine the extent to which a spatial mismatch in habitat complexity exists for natural enemies.

Local impervious cover surface around crape myrtles reduced aphid predation, a relationship that may best be explained by bottom-up effects of environmental conditions, such as temperature and drought stress. Hotter temperatures and drought stress associated with impervious cover at local scales can benefit pests (Speight et al. 1998, Dale et al. 2016, Dale and Frank 2017) but less is known about their effects on natural enemies. High temperatures can increase the metabolic rate of natural enemies, particularly spiders and predatory beetles, and increase risk of extinction via higher starvation rates (Rall et al. 2010). Low water availability in some urban areas can also alter the predator community on urban trees and may reduce biological control potential. For example, in an experimental field study, manipulations of water availability among trees in Raleigh parking lots showed that higher water availability resulted in higher densities of *Crematogaster* ants and lower densities of ghost ants, two common generalist predators (McCluney et al. 2018). However, local impervious cover did not have a negative
effect on natural enemy abundance in our study, with the exception of predatory thrips. Thus, we suspect that the negative effect of local impervious cover on aphid predation may have more to do with its effects on local structural complexity, which we know increases natural enemy abundance and predation. Notably, trees surrounded by more local impervious cover in our study, also often had lower structural complexity (Pearson’ product-moment correlation, p<0.01). Importantly, local structural complexity and local impervious cover, although correlated, were not collinear. Future work will need to disentangle the effects of temperature, drought stress, and local structural complexity to more clearly understand the drivers of aphid predation.

Impervious cover is and will be a ubiquitous feature of our current and future urban landscapes. Our work demonstrates that impervious cover, likely through increasing temperature and habitat fragmentation, can decouple pest population growth from that of their natural enemies. The resulting high densities of aphids or other pests can reduce tree aesthetics and services and may require insecticide applications or other costly maintenance (Dreistadt et al. 1990, Raupp et al. 1992, Raupp et al. 2012). However, our work shows how low-risk design strategies that increase local structural complexity and decrease impervious cover immediately around trees may help in regulating pests on our urban landscapes. Future work will need to explore the mechanisms driving these interactions, such as temperature and drought stress on trees, to best inform landscape design. A better understanding of the mechanisms that drive pests and their natural enemies in urban environments can inform landscape design and improve the biological and sustainability of future city landscapes.
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Table 1. Model averaged parameter estimates for models describing aphid and natural enemy abundance with importance values. Model averaged parameter estimates are calculated from the full model set. Estimates are averaged for models with a deltaAIC<2. Importance values in bold are above 0.5. Impervious cover at 100m was an important predictor (>0.9) of aphid abundance in both years, and local structural complexity was an important predictor for natural enemies in both years (>0.9).

<table>
<thead>
<tr>
<th>RESPONSE</th>
<th>PREDICTOR</th>
<th>ESTIMATE</th>
<th>SE</th>
<th>IMPORTANCE VALUE</th>
<th>PREDICTOR</th>
<th>ESTIMATE</th>
<th>SE</th>
<th>IMPORTANCE VALUE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>APHID ABUNDANCE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2016</td>
<td>Impervious (100m)</td>
<td>0.8913</td>
<td>0.2613</td>
<td>.985</td>
<td>Impervious (100m)</td>
<td>1.422</td>
<td>.527</td>
<td>.949</td>
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<tr>
<td></td>
<td>Local Veg.(H)</td>
<td>0.1491</td>
<td>0.1274</td>
<td>.719</td>
<td>Local Vegetation (H)</td>
<td>.255</td>
<td>.260</td>
<td>.740</td>
</tr>
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<td><strong>NAT. ENEMY ABUNDANCE</strong></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Impervious (20m)</td>
<td>.38031</td>
<td>.49453</td>
<td>.366</td>
<td>Impervious (100m)</td>
<td>.221</td>
<td>.237</td>
<td>.643</td>
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<tr>
<td></td>
<td>Local Veg. (H)</td>
<td>.40665</td>
<td>.29554</td>
<td>.939</td>
<td>Local Veg (H)</td>
<td>.234</td>
<td>.089</td>
<td>.518</td>
</tr>
<tr>
<td></td>
<td>Local Veg: Imperv.(20m)</td>
<td>-.35001</td>
<td>.48621</td>
<td>.348</td>
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<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Impervious (100m)</td>
<td>0.07309</td>
<td>.15053</td>
<td>.385</td>
<td></td>
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</tr>
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</table>
Table 2. Predictors explaining abundance of natural enemy groups in beat samples. Predictors are only reported with importance values above 0.5.

<table>
<thead>
<tr>
<th>Response</th>
<th>Predictor</th>
<th>Importance Value</th>
<th>Estimate</th>
<th>Rsquare</th>
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</thead>
<tbody>
<tr>
<td>Lady Beetle Abundance</td>
<td>Local Veg (H)</td>
<td>0.978</td>
<td>1.238</td>
<td>0.358</td>
</tr>
<tr>
<td></td>
<td>Impervious (20m)</td>
<td>0.852</td>
<td>1.710</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Local Veg: Impervious (20m)</td>
<td>0.838</td>
<td>-1.539</td>
<td></td>
</tr>
<tr>
<td>Lacewing Abundance</td>
<td>Impervious (20m)</td>
<td>0.810</td>
<td>-0.549</td>
<td>0.207</td>
</tr>
<tr>
<td>Predatory Thrips Abundance</td>
<td>Impervious (100m)</td>
<td>0.903</td>
<td>0.950</td>
<td>0.238</td>
</tr>
<tr>
<td></td>
<td>Local Veg (H)</td>
<td>0.727</td>
<td>0.379</td>
<td></td>
</tr>
<tr>
<td>Orius Abundance</td>
<td>Local Veg (H)</td>
<td>0.705</td>
<td>0.744</td>
<td>0.250</td>
</tr>
<tr>
<td></td>
<td>Impervious (20m)</td>
<td>0.564</td>
<td>1.092</td>
<td></td>
</tr>
<tr>
<td>Spider Abundance</td>
<td>Local Veg: Impervious (20m)</td>
<td>0.488</td>
<td>-1.093</td>
<td></td>
</tr>
</tbody>
</table>

NA- Response has no importance values above 0.5

Table 3. Top models (ΔAIC<2) with parameter estimates describing aphid predation in 2016 and 2017. Models are ranked by ΔAICc and model weights.

<table>
<thead>
<tr>
<th>Candidate Models</th>
<th>Intercept</th>
<th>Local Structural Complexity (H')</th>
<th>Impervious Cover (100m)</th>
<th>Impervious Cover (20m)</th>
<th>Initial Aphid Count</th>
<th>Local (H') : Impervious Cover (100m)</th>
<th>ΔAICc</th>
<th>ΔAICc</th>
<th>Weight</th>
<th>Marginal R²</th>
<th>Conditional R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Model O</td>
<td>-1.09</td>
<td>1.04</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>141.37</td>
<td>0.00</td>
<td>0.23</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Model Q</td>
<td>0.45</td>
<td>NA</td>
<td>NA</td>
<td>-1.66</td>
<td>NA</td>
<td>NA</td>
<td>141.44</td>
<td>0.08</td>
<td>0.22</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Model I</td>
<td>-7.49</td>
<td>6.59</td>
<td>11.12</td>
<td>NA</td>
<td>1.32</td>
<td>-9.92</td>
<td>141.88</td>
<td>0.51</td>
<td>0.18</td>
<td>0.14</td>
<td>0.14</td>
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<tr>
<td>Model A</td>
<td>-2.85</td>
<td>1.30</td>
<td>2.53</td>
<td>NA</td>
<td>1.64</td>
<td>NA</td>
<td>142.42</td>
<td>1.06</td>
<td>0.14</td>
<td>0.09</td>
<td>0.09</td>
</tr>
</tbody>
</table>

NA – Indicates that the predictor was not included in the candidate model.

Not shown here are the predictors crown volume, patch presence, aphid abundance, natural enemy abundance, coarse vegetation cover at 20m, coarse vegetation cover at 100m, and the interaction of local structural complexity with impervious cover at 20m. None of these predictors were included in top selected models.
Figure 1. Effects of impervious cover on aphid abundance on campus study trees. Relationships between percent impervious surface cover within 100 m of crape myrtles for (a) 2016 and (b) 2017. Impervious cover was a strong predictor of aphid abundance. Shaded areas represent 95% confidence intervals.
**Figure 2a.** Effects of local structural complexity (calculated as Shannon-Weaver Index, H’) on the abundance of different natural enemy groups in 2016.

**Figure 2b.** Effects of local structural complexity (calculated as Shannon-Weaver Index, H’) on the abundance of different natural enemy groups in 2017.
CHAPTER 2: Effects of temperature and habitat complexity on *Tinocallis kahawaluokalani* (Hemiptera: Aphididae), its natural enemies, and predation services in the city

Abstract

Trees provide many ecosystem services in our urban environments. However, city trees are often stressed by pests and hot urban temperatures. Our research highlights how temperature affects a common street tree pest, crape myrtle aphid (*Tinocallis kahawaluokalani*), its natural enemies, and egg predation services. This research addresses an area of study that has largely been unexplored, effects of temperature on urban natural enemies, and it sheds light on how hot urban temperatures may differentially affect piercing-sucking herbivores, a guild that is generally thought to be benefitted in hot city environments. To test our hypothesis that temperature increases *T. kahawaluokalani* density, fecundity and population growth, but does not similarly affect natural enemies or egg predation services, we collected data on crape myrtle trees on NC State campus and conducted lab experiments in 2018. We collected canopy temperature and arthropod data on study trees from May-August and measured local structural complexity around trees, as well as plant water potential. Contrary to our prediction, aphid density decreased with hotter urban temperatures. However, natural enemies and egg predation were not affected and were most correlated with local structural complexity. Local structural complexity was not predictive of tree canopy temperature. Together these findings suggest that increasing local structural complexity around trees may be a way to support robust natural enemy communities on both cool and hot urban trees to manage pests. Our findings also emphasize the need for similar studies that evaluate temperature effects on common tree pests to help landscape
managers prioritize pest targets and pest control in a warmer and more urban world.

**Introduction**

Trees in urban landscapes provide many services, such as atmospheric cooling, beautification of streetscapes, and carbon sequestration (Nowak and Dwyer 2000, Meineke et al. 2016). Unfortunately, urban trees often have more pests than trees in rural areas (Hanks and Denno 1993, Speight et al. 1998, Raupp et al. 2010). Pests reduce tree aesthetics and services and may require insecticide applications or other costly maintenance (Raupp et al. 1992, Dreistadt et al. 1990, Raupp et al. 2012). High pest density and damage on urban plants are often thought to result from an escape of pests from their natural enemies which may not be as abundant or diverse in urban habitats as in natural habitats (Niemela et al. 2002, Niemela and Kotze 2009, Burkman and Gardiner 2014). Pest densities can grow in response to the urban heat island effect, a phenomenon facilitated by the presence of more impervious cover, such as buildings and roads (Kim 1992). These hotter temperatures can increase pest development rate, fecundity, and survival (Zvereva and Kozlov 2006, Dale and Frank 2014, Meineke et al. 2013). Thus, a mismatch could result from the combined negative effects of urbanization on natural enemies and positive effects of hotter urban temperatures on pests. In addition, little work has explored if high temperatures alter natural enemies communities or diminish efficacy of biocontrol. Understanding effects of temperature on pests and natural enemies will shed light on how designers can create more sustainable and resilient landscapes in a hotter and more urban world.

Hot city temperatures can benefit insect performance by increasing survival, development rate, weight gain, and fecundity, for a number of different feeding guilds, including mining,
chewing and sucking guilds (Zvereva and Kozlov 2006). More impervious cover or less vegetation immediately around trees can increase temperature within tree canopies where pests feed and benefit pest fitness (Dale and Frank 2014, Meineke et al. 2013). For example, egg set increased by 14 eggs for every 1 degree increase in canopy temperature for the scale insect Melanaspsis tenebricosa on red maples in Raleigh, NC, USA, a finding correlated with more impervious cover around trees (Dale and Frank 2014). Benefits of high temperatures in urban trees have also been documented for other piercing-sucking pests (Sperry et al. 2001, Schneider et al. 2000, Kropczynska et al. 1988). For example, E. tiliarium spider mites increased on Tilia by fourfold on hotter, more sun-exposed street sides when compared to Tilia on shaded street sides (Schneider et al. 2000). Plant water stress is worsened by high temperatures and can affect pests, although the consequences for herbivores varies by feeding guild (Hanks and Denno 1993, Huberty and Denno 2004, Dale and Frank 2017, Meineke and Frank 2018).

Although hot urban environments may be favorable to some pests, they may not have the same effect on natural enemies. Natural enemies have been found to vary widely in their response to hot urban environments. For example, although spider abundance did not differ between hot and cool sites on willow oaks in Raleigh, spider communities differed, such that fewer Anyphaenids, an important spider group in biological control, were found in hotter sites (Meineke et al. 2017). In addition there is a direct negative correlation between impervious cover, the mechanism fueling hot temperatures in cities, and habitat complexity (Faeth et al 2011, McKinney 2008), which is in turn a major driver of natural enemy abundance and diversity (Root 1973, Pimental 1961, Shrewsbury and Raupp 2006, Raupp et al. 2010). Many studies have linked greater structural complexity, plant diversity, and plant species richness at the local scale in urban areas to more natural enemies and greater biological control of pests.
The negative relationship between vegetation complexity and impervious surface, which increases temperature, suggests a potential for interactions between these variables in their effects on natural enemies. Thus natural enemy communities could be more robust in structurally complex habitats because they provide resources, such as alternative prey, food and shelter, because they are cooler, or both (Landis et al. 2000). Furthermore, effects of temperature and vegetation likely vary among arthropods in different feeding guilds, of different sizes, and with different dispersal behaviors, among other factors. For example in lab trials, spiders and carabid beetles, two groups that are more limited in flight dispersal, were considered more at risk of starvation in warmer conditions (Rall et al. 2010). Risk of starvation was attributed to increases in the metabolic processes associated with warming among the groups (Rall et al. 2010). Other natural enemy groups, particularly larval coccinellids and neuropterans, which are also limited in dispersal abilities, may be similarly vulnerable to warming and could be more affected by hot canopy temperatures in urban areas than other natural enemy groups.

Crape myrtles (*Lagerstroemia spp.*) are one of the most prevalent ornamental trees planted on Southeastern, US, landscapes (Chappell et al. 2012). Crape myrtles are valued because they are heat tolerant (Chappell et al. 2012), drought tolerant (Davies and Castro-Jimenez 1989), and require low fertilizer inputs (Chappell et al. 2012). Although crape myrtles have relatively few insect and disease pests (Mizell and Knox 1993, Riddle and Mizell 2016), the most common pests on crape myrtles are crape myrtle aphid (*Tinocallis kahawaluokalani*) (Frank 2019 in press). This specialist herbivore, which was cointroduced with its host and eats plant phloem, has no known parasitoid here or in its native range (Mizell et al. 2002). Thus the natural enemies of crape aphids are generalist predators, such as lady beetles (Coleoptera:}
Coccinellidae), lacewings (Neuroptera: Chrysopidae and Hemerobiidae), minute pirate bugs (Hemiptera: Anthocoridae), damsel bugs (Hemiptera: Nabidae) and syrphid flies (Diptera: Syrphidae) (Mizell 2007, Mizell and Schiffhauer 1987). Crape myrtle aphids have several generations each year and reproduce from April to September in Raleigh, NC (Alverson and Allen 1991). *Tinocallis kahawaluokalani* can negatively affect tree aesthetics when honeydew accumulates on leaves, which facilitates black sooty mold *Capnodium* sp. (Dozier 1926, Alverson and Allen 1991). Dense populations can also cause leaves to yellow and drop (Dozier 1926, Alverson and Allen 1991). *Tinocallis kahawaluokalani* can become more abundant on crape myrtles on urban trees surrounded by large amounts of impervious cover. In addition large amounts of impervious cover at the local scale (20 meters) can decrease predation of *T. kahawaluokalani* (Parsons and Frank unpublished). Since impervious surface cover increases canopy temperature of urban trees, temperature may directly increase *T. kahawaluokalani* density by increasing development rate and fecundity or indirectly by reducing predation.

We predict that temperature plays a central role in the mismatch between *Tinocallis kahawaluokalani* and its natural enemies in urban areas, especially on hot urban trees that are surrounded by little vegetation. Our overall hypothesis is that aphid densities will increase as canopy temperature increases but that greater local structural complexity around trees may mean fewer aphids via means of lowering temperatures and increasing natural enemies and biocontrol. We tested three specific hypotheses by measuring temperature and aphid abundance and natural enemies in urban crape myrtles: 1) aphid abundance will increase as tree temperature increases but less so on trees in complex habitats; 2) natural enemy abundance will not be associated with temperature; 3) natural enemy abundance and predation of factious prey will be associated with local structural complexity *rather than* temperature. We also test the hypothesis that the highest
densities of aphids will be found on hotter trees that are less water stressed. To test our hypotheses, we measured temperature, plant water potential, and local structural complexity around trees affected *T. kahawaluokalani* density, their natural enemies, and predation of *Helicoverpa zea* eggs in the field. Then, we conducted lab experiments to further determine how temperature affects aphid fecundity and population growth. Our study explores the specific mechanisms that may drive pests, their natural enemies, and predation services, and provides insight into which design elements can be implemented to reduce pests and improve biocontrol services on street trees.

**Methods**

*Study Sites*

We conducted this study on North Carolina State Campus in Raleigh, NC, USA from May-August 2018. We randomly selected 33 crape myrtles (*Lagerstroemia indica* x *faureri* ‘Natchez’) on NC State campus using a campus tree inventory that was provided by NC State’s Facilities Division. A map layer was created in ArcMap (ArcGIS Desktop 10; ESRI, Redlands, CA, USA) with all tree locations. Trees were at least 100 meters apart to reduce spatial autocorrelation.

*Environmental Data Collection*

*Measuring canopy temperature*

Canopy temperature data were collected on trees in 2018 from 16 May to 23 August. Canopy temperature was measured using iButton thermocon data loggers (Dallas Semiconductor, Dallas, Texas, USA). iButtons were placed in shaded places of the canopy, near the trunk, so as to avoid direct sunlight. iButtons were placed in iButton fobs and secured to
trees with a cable tie. We did not use radiation shields on iButtons, given recent literature that instrumentation efforts to shield iButtons have to date been ad hoc (Terando et al. 2017). Instead we adapted methods from Meineke et al. (2016) and set iButtons to record temperature at 3-hour intervals and only used sunset temperatures between 1800 and 2100 hours for analyses. Using averaged sunset temperatures minimizes the risk of reporting inflated and biased temperature measurements that may be associated with direct sunlight effects in early and mid-day (Meineke et al. 2016). Mid-day averages were also calculated. When compared, sunset averages were also better at predicting aphid abundance than mid-day averages.

Measuring Plant Water Potential

To assess tree water stress we measured pre-dawn (2:00am-6:30am) xylem water potential using a pressure chamber (PMS Instrument Company, Albany, OR) (Long et al. 2018, Dale and Frank 2017). A growing number of urban studies are using pre-dawn measurements to assess plant water potential of street trees (Long et al. 2018, Levinsson et al. 2015, Savi et al. 2015). We chose to use pre-dawn measurements, rather than mid-day measurements, because stomata are closed and all the leaves and stems of the plant are in relative equilibrium in pre-dawn hours (Santesteban et al. 2010). We pruned 1 or 2 terminal twigs, 15-20cm in length, from the canopies of study trees approximately 4-6 meters above the ground on the morning of August 16, 2018. Leaves were kept intact with twigs. Twigs were immediately placed in the pressure chamber after they were pruned and we recorded the water potential values (MPa) when water was released from the xylem of the twig. In cases where two twigs were pruned from canopies, MPa values were averaged.

Measuring Local Vegetation Structure

Local structural complexity was quantified by adapting methods from Shrewsbury and Raupp
Temporary grids of 10mx10m were constructed on the ground around trees using two pieces of rope, which were marked every meter with a flag. Ropes were positioned on the ground perpendicular to one another, such that they created two sides of a 10m square with the tree in the center. The first rope was always positioned on the north side of the tree with the second rope laid perpendicular on either the east or west side of the tree. To measure structural complexity in the 10mx10m grid space, each vegetation strata was identified and scored as present or absent in each 1mx1m square within the grid. The five vegetation strata were turf, herbaceous vegetation, shrubs, understory trees, and canopy trees. The maximum number of vegetation layers in any one 1mx1m square therefore was 5. Similarly, the maximum number of squares any one vegetation layer occupied was 100, meaning the vegetation layer occupied all 1mx1m squares in the grid. The total structural complexity index (SCI) could range from 0 and 500. We also calculated structural complexity using the Shannon Diversity index (H’), a commonly used measure for vegetation diversity, to account for how evenly all vegetation strata were distributed around the tree. Similar to Dale and Frank (2014), we treated each vegetation strata as a “species” and 1mx1m grid counts within each strata (0-100) as “abundance.” Shannon Diversity index values were calculated using the vegan package in R. H’ values ranged from 0-1.43, with 0 being those crape myrtles with no surrounding vegetation. Shannon Diversity Index values were used in analyses, given our previous work in this system (Parsons and Frank unpublished) that concluded that H’ values were better at explaining variation in aphid and natural enemy abundance than total structural complexity index values.

Arthropod Data Collection

Aphids

Aphid abundance was recorded 5 times in 2018 (23 May; 6 and 28 June; 18 July; and 14
August). Terminal twigs were collected from each cardinal direction of each tree and in high and low parts of the canopy using a pole pruner; thus, a total of four twigs were collected on each sample date. All aphid instars were counted on the first 15 fully expanded leaves of each twig starting from the terminal end.

**Natural enemies**

Natural enemies were collected 4 times in 2018 (15 May; 14 June; 18 July; and 14 August). On each sample date three areas of the lower canopy were beaten with a wooden dowel to dislodge arthropods into a tray. Trays were immediately rinsed with 75% ethanol into sample containers. Natural enemies were identified in the lab under a dissection scope. Most arthropods were identified to family, with the exception of spiders, parasitoid wasps, and Dermaptera.

**Predation Experiments**

Sentinel *Helicoverpa zea* eggs were used as factitious prey items to assess predation services (Gardiner et al. 2014, Nuessly and Sterling 1994, Pfanannenstiel and Yeargan 2002). Frozen *H. zea* eggs were purchased from Frontier Agricultural Sciences (Newark, DE). Eggs were received frozen on mesh cloth from which we cut 1cmx1cm squares with at least 30 eggs each. Cloth squares with eggs were stored in a -80 degree Celsius freezer before use in field trials and kept in a cooler when going into the field. Predation experiments were conducted 7 times in 2018 (23 and 30 May; 21 June; 10 July; 8, 10, and 22 August). On the day of each experiment a branch on the lower canopy of each study tree was arbitrarily selected, and we counted eggs on two 1cmx1cm squares, which were then adhered to the branch with a staple and stapler. One square was covered with a clip cage made of a hairclip, a foam base, a 4cm plastic tube, and a mesh top. The other square was uncaged. After 24 hours we collected the squares and recounted eggs.
**Fecundity Experiments**

Fecundity experiments were performed on 10 and 24 July, 2018. Aphid colonies were reared on three ‘Natchez’ crape myrtles in 3.785-liter pots in climate-controlled growth chambers on NC State campus. Crape myrtles were grown in three Percival Scientific environmental chambers and were covered with mesh cloth bags to contain aphids on trees. Chambers were set at 26°C +/- 1°C, 29°C +/- 1°C, and 32°C +/- 1°C during day time hours and 21°C, 24°C, and 27°C during night hours. Day hours extended from 6:00-20:00 (14-hours day/10-hours night). Daytime hours were based on July sunrise and sunset times for Raleigh, NC. Temperatures were chosen based on 30-year (1981-2010) daily minimum and maximum temperature normals for the month of July, the hottest month on record for Raleigh, NC (NOAA). Aphid colonies were reared for 2 weeks. 10-inch twigs were cut from one crape myrtle in the field. Twigs were cleaned of aphids and put in floral picks with tap water. Floral picks were refilled every two days. Twenty floral picks with twigs were randomly assigned to each environmental chamber. All twigs were kept in mesh exclusion cages within chambers to prevent movement of aphid alates among branches. One third instar aphid was transferred from the colony tree in each chamber onto each twig in the chamber. Clip cages were also put on twigs to contain aphids. Aphids were observed daily to note transition of third-instars into adults. Once adults, aphids were inspected every 24 to 48 hours for eight days to record the number of nymphs produced. Trials were terminated at eight days because all adults in the 32°C chamber died. The experiment was performed twice. Colony trees were rotated among chambers and acclimated to chambers for 48 hours before the start of the second trial.

**Population Growth**

The population growth experiment was performed on 4 September, 2018. Three ‘Miami’
crape myrtles in 3.785-liter pots were grown in climate-controlled growth chambers on NC State campus. Trees were reared in the same environment and had the same water and fertilizer regimes before being transferred to chambers. Trees were watered daily for the duration of the experiment. One experimental tree was assigned to each treatment chamber. Temperature settings and daylight hours for chambers were the same as for the fecundity experiment. The aphid colony tree in each chamber, same as those used for fecundity experiments, were covered with mesh cloth bags to prevent emigration of aphids from colony trees to experimental trees. Each experimental tree was cleaned of all aphids before putting in its chamber. One third instar nymph from the colony tree in each chamber was placed on five randomly selected branches of the experimental tree and covered with a clip cage. Additionally, a mesh bag was secured over the branch, to further prevent any immigration onto branches from colony trees. All aphids were counted after a week, after which the clip cage was removed. However, mesh bags on branches were maintained. Aphids were counted again on branches at two-weeks, at which point the experiment was terminated.

Analysis

Temperature effects on aphid, natural enemy abundance, and egg predation

All analysis was performed in R Version 3.4.3 (The R Foundation for Statistical Computing, 2017). Multiple linear regression analyses were performed first to test a priori hypotheses and interactions among variables (Table 1). Then model selection was performed to determine which variables were most important in determining aphid and natural enemy abundance, as well as H. zea egg predation.

Responses for model analyses included number of aphids and natural enemies collected on collection day and predation effect size. Response variables for aphid and natural enemy
models were \( \log_{10}(x+1) \) transformed to account for the large number of 0’s, improve the distribution of residuals and account for overdispersion, as the variance was larger than the mean in both responses (Zuur et al. 2009, 2010). Predation effect size was calculated using methods from Philpott and Birchier (2017) and is the \( \ln(\text{proportion of prey removed in uncaged treatments}) - \ln(\text{proportion of prey removed in caged treatments}) \). We used average sunset temperatures calculated for the week prior to collection dates for aphids and natural enemy models. These measures of temperature were best at explaining aphid and natural enemy response when compared to day-of and two-week averages. For predation models, average sunset temperatures for the day-of the 24-hour predation experiment were used. All models for analyses were set up to reflect a repeated measures split-plot design, such that date and temperature were treated at the split plot level, and study tree and static variables (structural complexity and tree water potential) were treated at the whole plot level. Linear mixed effects models incorporating random effect terms for tree and date were used to account for design, using the \textit{nlme} package in R (Pinheiro et al. 2017). Marginal and conditional \( R^2 \) values, quantifying variation explained by fixed and random effects, were computed using the \textit{piecewiseSEM} v. 1.2.1 package in R (Lefcheck 2015) and reported for all models in multiple linear regression analyses and model selection.

With multiple linear regression analyses we tested our \textit{a priori} hypotheses and interactions among variables (Table 1). For aphid abundance, we predicted that aphids would increase with temperature. We also predicted that low levels of local structural complexity would correlate with higher canopy temperatures and more aphids, and lastly we predicted that aphids would be most dense on hot trees that were less water stressed. The models used to test these hypotheses included: a model with temperature as a predictor; a model with temperature,
local structural complexity, and their interaction as predictor; and a model with temperature and water potential as predictors (Table 1). For both natural enemy abundance and egg predation effect size, we predicted that both responses would not be affected by temperature. We also predicted that both natural enemies and predation would increase with more local structural complexity. However, we did not anticipate that responses would be affected by lower canopy temperatures associated with higher structural complexity. The models used to test these hypotheses included: a model with temperature as a predictor; a model with local structural complexity as a predictor; and a model with temperature, local structural complexity, and their interaction as predictors. We also tested if local structural complexity correlated with canopy temperature, using a linear mixed effect model with temperature as the response. Lastly, we analyzed individual natural enemy groups separately against temperature to detect if any differences existed among groups.

After we tested hypotheses, we used model selection with Akaike information criterion (AIC) to explore the best possible models using our variables. The same candidate model set was evaluated for aphids, natural enemies, and egg predation (Supplementary Table). Models used to test predictions and interactions in multiple linear regression analyses were included in the candidate set. For model selection, we adapted methods from Hamblin et al. (2018) and used the \textit{MUMIn} v.1.40.4 package in R (Barton 2016). Because multicollinearity of predictor variables was weak, variance inflation factors not exceeding 3, (\textit{car} v2.1-6 package) (Fox and Sanford 2011), we included all predictors in the model selection process (Zuur et al. 2010, Hamblin et al. 2018). Models were ranked based on model weights and $\Delta$AICc (Akaike information criterion adjusted for small sample size) in relation to the top most model in the model selection process using the model.sel function in R (MUMIn package). From the model
selection process we also obtained importance values for each predictor. We report on models with a ΔAICc<2 (Burnham and Anderson 2002, Symonds and Mousalli 2011). We used model validation diagnostic plots in R to detect and test for violations of linear regression assumptions for all models. Lastly, mantel tests were run on all top models using 9999 replicates to test independence of observations and detect if there was any spatial autocorrelation.

*Temperature effects on aphid fecundity and population growth*

Response for fecundity analyses was total number of nymphs produced by a single female adult after 8 days. Response for population growth analyses was total number of aphids per branch after two weeks. Both responses were log10 transformed to improve distribution of residuals. Aphid fecundity and population growth was evaluated with a non-parametric Kruskal-Wallis test, to account for small sample size. A post hoc Dunn’s Multiple Comparison Test was used to further assess group differences for fecundity and population growth analyses.

**Results**

*Environmental Variables and Temperature*

Average mid-day and sunset temperatures from May-August, ranged from (20.25-37.75°C) and (20.75-35.5°C) respectively. Average sunset temperatures calculated for one-week prior to collection dates were most correlated with aphid abundance (marginal $R^2$=0.23, conditional $R^2$=0.37) when compared to 2-week mid-day (marginal $R^2$=0.12, conditional $R^2$=0.25) and sunset averages (marginal $R^2$=0.09, conditional $R^2$=0.20) and one-week mid-day averages (marginal $R^2$=0.21, conditional $R^2$=0.31). Therefore, average sunset temperatures for the week prior to collection date of aphids was used in all aphid models. Similarly, average sunset temperatures for the week prior to the collection date of natural enemies was used in
natural enemy models. The hottest collection date was July 18, on which the hottest site reached a mid-day temperature of 32.5 degrees. Local structural complexity Shannon H’ values ranged from 0-1.43 ([mean +/- SD] 0.77 +/- 0.38). Sites with a Shannon H’ value of 0 only had one vegetation layer. Sites with a Shannon H’ value of 0 included study trees in mulched parking lot islands with no surrounding local vegetation. Pre-dawn water potential for study trees ranged from -0.17MPa to -0.36 MPa ([mean +/- SD] -0.245 +/- 0.046). No significant correlations existed among the predictors: local structural complexity, drought, and temperature (Pearson Product Correlation p>0.05).

**Temperature Effects on Aphid Abundance**

As predicted, temperature was good at explaining variation in aphid abundance (p<0.001, marginal R²= 0.23, conditional R²= 0.92). However, contrary to prediction, aphid density decreased with hotter canopy temperatures ([Est. +/- SE] -0.122 +/-0.017) (Table 1); for every degree increase in temperature, aphid density decreased by 0.122 aphids. The interaction between local structural complexity and temperature was not significant, meaning that high levels of local vegetation around trees did not significantly correlate with lower canopy temperatures and less aphids. Separate analyses also showed that local structural complexity was not predictive of temperature. Therefore, our prediction that local structural complexity would decrease canopy temperature and aphid abundance was not supported. Temperature (p<0.001) and water potential (p<0.05) together were good at explaining aphid abundance (Table 1). Although, aphids responded negatively to water stress as predicted ([Est. +/- SE], 2.30 +/- 0.978), they also responded negatively to temperature ([Est. +/- SE], -0.123 +/- 0.016), which was unexpected. In other words aphids decreased by less on hot trees that were less water stressed. The model with temperature and water potential only explained 3% more of the
variation in aphid response when compared to the model with temperature as a single predictor. Although water potential had a significant relationship with aphid abundance, when assessed separately, the model with water potential as a single predictor was a fairly poor fit for the data (Table 2).

Model selection showed that temperature and plant water potential were the best predictors of aphid abundance, thus supporting one of our hypotheses, albeit temperature had the opposite effect on abundance than predicted. The highest ranked model of the candidate set included the model used to test our a priori hypothesis with temperature and plant water potential as predictors (Table 1). Importance values were 0.999 and 0.782 for temperature and water potential respectively (Table 3). Therefore, temperature as a predictor had 99.9% and water potential had 74.3% probability of being selected in the best models given the candidate set of models. Natural enemy abundance was not a good predictor of aphid density (p>0.05).

Temperature Effects on Natural Enemy Abundance

As expected, temperature did not explain much of the variation in natural enemy abundance (marginal $R^2=0.008$, conditional $R^2=0.91$) and was not a significant predictor of natural enemy abundance. Local structural complexity was a significant predictor of natural enemies ($p<0.01$) and explained 12% of variation in natural enemy response (Table 4); thus supporting our hypothesis. Also, in support of our hypothesis, the interaction of temperature with local structural complexity was not significant, suggesting that high levels of local vegetation around trees did not significantly correlate with lower canopy temperatures and more natural enemies. In further support of this latter finding, the linear mixed effects model with temperature as a response, revealed that local structural complexity was not predictive of temperature.
Model selection showed that local structural complexity was the most important predictor of natural enemies (p<0.01, importance value = 0.926) (Table 4). Local structural complexity had a positive effect on natural enemy abundance ([Est. +/- SE] 0.262 +/- 0.089) (Table 4) and the model with local structural complexity as a single predictor was ranked as one of the top models in model selection (ΔAIC<2). The other top model in model selection included local structural complexity, water potential, and their interaction as predictors (marginal R²=0.14, conditional R²=0.92). However this model only explained 2% more of the variation in natural enemy abundance and importantly, none of the predictors in this model were significant. Plant water potential and the interaction of water potential with local structural complexity were the only other predictors with importance values >0.5 in model selection (Table 3). Although these predictors had high importance values, neither water potential or its interaction with local structural complexity were significant predictors in any of the tested models. Model selection can overinflate the importance of a predictor if many of the predictors in the model set do not sufficiently explain variation in the response or if one predictor is prevalent in most of the models in the candidate set (Symonds and Mousalli 2011). Further it is biologically unlikely that plant water potential would have a direct effect on natural enemies. Thus, overall we conclude that water potential, and its interaction with structural complexity were not good predictors of natural enemy abundance. Aphid abundance was not a good predictor of natural enemy abundance (p>0.05).

An analysis of individual natural enemy groups against temperature revealed different responses among groups. Temperature had a significant and small positive effect on spiders (p<0.01, [0.071 +/-0.026]), while it had a significant and small negative effect on Orius insidiosus (p<0.001,[-0.12 +/-0.024]) and neuropterans (p<0.05, [-0.022+/-0.009]). All other
natural enemy relationships with temperature were nonsignificant.

Temperature Effects on Egg Predation

Caged and uncaged treatments differed in the percentage of \( H. \text{zea} \) eggs missing after 24-hours; thus indicating significant predation (\( p<0.001 \)) (Fig. 3).

None of the tested \( a \, \text{priori} \) models were good at explaining variation in predation effect size. In model selection water potential was the most important predictor (importance value = 0.93). However, the model with water potential as a predictor, all single predictor models (Table 5), and all top selected models were poor at explaining variation in predation effect size.

Temperature Effects on Aphid Fecundity

We predicted aphid fecundity to increase with temperature. Although adults in hotter treatments on average produced more nymphs after eight days, fecundity of adults did not differ significantly among treatments (Fig. 1). Trials were terminated at eight days, because adults in the 32\( ^\circ \)C chamber died after eight days in both trials.

Temperature Effects on Population Growth

We predicted that population growth would be highest at 32\( ^\circ \)C. Contrary to our prediction we found that the 29\( ^\circ \)C treatment had significantly more aphids than the 26\( ^\circ \)C treatment (Dunn Test, \( p<0.01 \)), and the 32\( ^\circ \)C treatment (Dunn Test, \( p<0.05 \)) (Kruskal-Wallis test, \( p<0.01 \)) (Fig. 2).

Discussion

As our world becomes warmer and more urban, understanding how temperature affects pests, their natural enemies, and biological control will be important in designing city landscapes
that are resilient against pest outbreaks and damage. We found that *T. kahawaluokalani* density was highest on the coolest trees and least stressed trees in our study. Furthermore, *T. kahawaluokalani* population growth was greatest in intermediate temperature treatments at 29°C. Our results are contrary to many studies that have found that pest survival, fecundity, and development increase with higher temperature on urban trees, particularly in the Raleigh area. Lower canopy temperatures that were associated with higher aphid densities were not correlated with higher local structural complexity. However, local structural complexity was a significant predictor of natural enemy abundance, while temperature was not. Together these results indicate that increasing structural complexity around street trees may be a design solution to bolster natural enemies on urban trees and help manage tree pests.

Hotter temperatures in urban areas may contribute to higher densities of some species of insect herbivores (Meineke et al. 2013, Meineke et al. 2014, Dale and Frank 2014, Schneider et al. 2000, Kropczynska et al. 1988), while other herbivore species may have the opposite response. For example, a study of arthropod communities at low, mid, and high latitudes along the eastern coast of the USA found that while overall aphid (Hemiptera: Aphididae) abundance increased in Boston in hotter areas of the city, it decreased in hotter areas of Baltimore, a lower latitude city, where aphids may exist closer to their thermal limit (Youngsteadt et al. 2016). Another study exploring urban bees showed that some species of bees were found at lower densities in hotter areas of the city, a trend they attributed to disparities in the critical thermal maxima of bees (Hamblin et al. 2017). Given that natural enemies in our study were not significantly affected by temperature, our findings may suggest that bottom-up mechanisms or insect traits, such as thermal limits, rather than top-down control, are responsible for low densities of *T. kahawaluokalani* on hot trees. Furthermore, the low density of *T.*
kahawaluokalani on the hottest trees in our study, coupled with greater population growth and fecundity in intermediate temperature treatments at 29°C in lab experiments, may suggest that T. kahawaluokalani exists above its thermal optima in Raleigh, NC. However, more work would need to assess the thermal optima of T. kahawaluokalani and its other traits, to determine what is driving low densities on hot trees.

Although aphids densities were higher on cooler trees, trees were not cooler because of high structural complexity. Thus, other habitat elements, such as canopy volume or impervious cover, may be driving canopy temperature and aphid density. The disconnect between canopy temperature and local structural complexity may be explained by the recommended growing conditions for crape myrtles. Crape myrtles grow best in full sun and do not grow well under shaded canopy (Chappell et al. 2012). More canopy can reduce light exposure and temperature in urban environments on focal plants (Shrewsbury and Raupp 2000, Dale and Frank 2014). Given that few of the trees in this study were planted under canopy (less than 30%), means that high structural complexity values were most attributed to understory, shrub, herbaceous, and turf vegetative layers, which may be less influential in altering microclimate on focal study trees.

Trees in our study that were more water stressed had significantly fewer aphids. However, the interaction between temperature and water stress was not significant, suggesting that water stress, independent of temperature, decreases aphid abundance. Herbivore responses to drought can vary (Huberty and Denno 2004, Koricheva et al. 1998). For example, Dale and Frank (2017) found evidence that M. tenebricosa increased in the presence of temperature and drought on urban maple trees. However, Pseudaulacaspis pentagona densities decreased on urban mulberry trees that were more water stressed (Hanks and Denno 1993). We suspect that T. kahawaluokalani density decreases on stressed plants, because it is a phloem-feeder and may be
more sensitive to reduced turgor pressure when plants become stressed (Wearing and van Emden 1967, Hanks and Denno 1993, Huberty and Denno 2004). Reduced turgor pressure may reduce piercing-sucking herbivore abundance by reducing accessibility of nutrients (Wearing and van Emden 1967, Huberty and Denno 2004). Soil compaction, high soil temperatures, and low soil water permeability due to impervious cover around trees, all common occurrences in urban areas, may also explain how water stress can affect trees and aphids in both hot and cool conditions (Speight et al. 1998, Graves 1994, Oke 1989). Although low water potential was a significant predictor of aphid density in our study, the relationship was overall weak. Future work will need to do more robust sampling of water potential, such as repeated measures of pre-dawn water potential throughout the season and mid-day water potential sampling, to more formatively assess the relationship of plant water potential with aphid abundance.

In keeping with our prediction, local structural complexity was the most important predictor of natural enemy abundance whereas temperature had no relationship with natural enemies. These findings may suggest that structurally complex sites harbor more natural enemies because they provide other resources, such as alternative prey, carbohydrate sources, or refugia not because of cooler microclimates they may provide. (Landis et al. 2000, Langellotto and Denno 2004, Letourneau 1987, Letourneau et al. 2011, Shrewsbury and Raupp 2006). Our work concurs with the Enemies Hypothesis (Root 1973, Pimental 1961) and other urban studies that have found that increases to local structural complexity and plant species richness and diversity increase natural enemy abundance and top-down control of pests (Rocha et al. 2018, Philpott and Bichier 2017, Shrewsbury and Raupp 2006). However, more work would need to be done to determine which mechanisms are driving natural enemy abundance in this system. Furthermore, natural enemy groups may be affected differently by temperature. For example, when we
analyzed groups separately temperature had a significant and small positive effect on spiders, yet a significant and small negative effect on Orius insidiosus. These antagonistic responses may explain why we overall did not find an effect of temperature when natural enemies were collapsed into a univariate response. These findings also emphasize the importance of separately assessing temperature and habitat on target natural enemy groups for pest control.

Research in urban gardens and ornamental landscapes have found that increasing structural complexity or plant species richness can increase both natural enemy abundance and predation biocontrol services. For example increasing local plant species richness in urban gardens correlated with higher lady beetle and hoverfly abundance in Southern England (Rocha et al. 2018) and more local structural complexity in urban gardens resulted in greater biocontrol of aphids in the California central coast region (Philpott and Bichier 2017). However, landscape-scale structural complexity and plant diversity on natural enemies and predation services in urban environments can be variable (Sattler et al. 2010, Bennett and Gratton 2012, Burkman and Gardiner 2014, Rocha et al. 2018, Egerer and Ong 2018). For example, Lowenstein et al. (2018) found that natural enemy abundance was similar across food gardens in residential and urban areas in Chicago and that flower resources within gardens were most predictive of natural enemy abundance. Local structural complexity did not affect egg predation services in our research. Previous work with our system (Parsons and Frank unpublished), showed that more structural complexity increased biocontrol of T. kahawaluokalani. However, the predator complexes of eggs and aphids can differ. For example, opportunistic and omnivorous feeders, such as Orius spp. and ants have been known to eat H. zea eggs (Nuessly and Sterling 1994, Pfanannenstiel and Yeargan 2002). In our study we observed both Orius insidiosus and ants on eggs during predation experiments, sometimes actively removing eggs. Although ants were not identified to
species at the time of predation trials, we suspect that Argentine ants (*Linepithema humile*), a known egg predator (Way et al. 1992) also known to be found on crape myrtles (Brightwell and Silverman 2011), were responsible for much of the predation by ants on several study trees. Trees that had ants actively feeding on eggs during predation trials were trees that had consistently had high densities of ants in beat samples. Some egg predators that may be more ubiquitous on crape myrtles in urban areas, such as *Orius insidiosus* (Parsons and Frank unpublished) and Argentine ants (Brightwell and Silverman 2011), may explain why egg predation was similar across trees in our study and did not correlate with local structural complexity. Furthermore, crape myrtles were blooming throughout much of the time that predation experiments were being conducted, and flowers may have attracted high densities of some natural enemies, particularly *Orius insidiosus* (Parsons and Frank unpublished), which may have contributed to similar predation rates on trees across the study area.

Our findings suggest that increasing local structural complexity around street trees may be an important design strategy to increase natural enemy abundance in hot urban areas. Our study fills a gap in the research by decoupling the effects of urban temperature on a pest and its natural enemies, an area of research that has been largely unexplored. As the climate gets warmer and cities get bigger, better understanding how pests, their natural enemies, and biological control respond to warming will be key in implementing effective urban pest management programs. Studies like ours can help identify design solutions that may mitigate the effects of pests on urban trees in a warming world.
REFERENCES


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Mizell RF, Schifauer DE. 1987. Seasonal abundance of the crapemyrtle aphid Saracallis kahawaluokalani (Kirkaldy) in relation to the pecan aphids Monellia caryella (Fitch) and Monellioopsis pecanis (Bissell) and their common predators. Entomophaga 32: 511–520.


Raleigh Parks, Recreation and Cultural Resources Department. https://www.raleighnc.gov/parks/content/Departments/Articles/ParksandRecreation.html


Table 1. Aphid models with temperature as a predictor. Linear mixed effect model outputs for all models analyzed with temperature as a predictor. Bold indicates predictors with significance (p<0.05). *Indicates top models selected in the model selection process.

<table>
<thead>
<tr>
<th>APHID MODELS</th>
<th>Marginal R²</th>
<th>Conditional R²</th>
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<th>SE</th>
<th>t-value</th>
<th>p</th>
</tr>
</thead>
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<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td></td>
<td></td>
<td>120</td>
<td>4.086</td>
<td>0.472</td>
<td>8.661</td>
<td>&lt;0.001</td>
</tr>
<tr>
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<td>-7.34</td>
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<tr>
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<td>0.365</td>
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</tr>
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<td></td>
<td></td>
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</tbody>
</table>

*See Coefficients for other interactions in this model in Supplementary Table

*Models with interactions of predictors excluding temperature were also run in the model selection process. None of the other models, excluding temperature, were ranked among top models. For full model candidate set, see Supplementary materials.

Table 2. Aphid models with single predictors. Linear mixed effect model outputs for single predictor models. Bold indicates predictors with significance (p<0.05).

<table>
<thead>
<tr>
<th>Aphid Models</th>
<th>Marginal R²</th>
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<th>SE</th>
<th>t-value</th>
<th>p</th>
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</table>
**Table 3.** Importance values for aphid and natural enemy models. Only importance values >0.5 are shown. Importance values were calculated in the model selection process and indicate the probability that a predictor will be chosen in the top model.

<table>
<thead>
<tr>
<th>APHIDS</th>
<th>NATURAL ENEMIES</th>
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<td>WATER POTENTIAL</td>
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<td>0.782</td>
<td>WATER POTENTIAL:</td>
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<td></td>
<td>LOCAL VEG. (H)</td>
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<td>0.654</td>
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</table>

**Table 4.** Natural Enemy models with single predictors. Linear mixed effect model outputs for single predictor models. Bold indicates predictors with significance (p<0.05).

<table>
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<th>Natural Enemy Models</th>
<th>Marginal R²</th>
<th>Conditional R²</th>
<th>df</th>
<th>Est.</th>
<th>SE</th>
<th>t-value</th>
<th>p</th>
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</thead>
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<tr>
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</tr>
<tr>
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<tr>
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</table>

**Table 5.** Predation models with single predictors. Linear mixed effect model outputs for single predictor models. Bold indicates predictors with significance (p<0.05).

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<th>Est.</th>
<th>SE</th>
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<td>0.009</td>
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</tr>
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<tr>
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<td>0.009</td>
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<td>-0.572</td>
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</table>
Figure 1. Total nymphal production of adults after eight-days at 26° C, 29° C, and 32° C. The boxplots here show the interquartile ranges of aphid nymphs produced after 8 days. The median of the data range is marked by the line that divides boxes. Although more nymphs were produced in hotter temperature treatments, Kruskal Wallis tests showed no significant difference among treatments. Trials were terminated after 8 days, because adults in 32° C chambers died at 8 days in both trials.
Figure 2. Aphid density after two weeks by temperature treatment. The boxplots here show the interquartile ranges of aphid densities. The median of the data range is marked by the line that divides boxes. Asterisks indicate significant differences from post-hoc Dunn tests. More aphids were found on branches in the 29°C treatment after two weeks when compared to 26°C and 32°C treatments.

Figure 3. 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 hours. The median of the data range is marked by the line that divides boxes. Asterisks indicate significant differences. Open treatments had significantly more eggs missing after 24 hours than caged treatments, indicating predation.
CHAPTER 3: Exotic ornamental landscapes support natural enemies, spider biomass, and biocontrol services comparable to native ornamental landscapes

Abstract

Exotic plants characterize many of today’s 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 result in a reduction in top-down control by natural enemies. In this study we compare leaf area lost to chewing herbivory in native and exotic ornamental landscapes. We also explore if natural enemy abundance, diversity, community composition, dry weight spider biomass, and egg predation services differ between the two landscape types. We predicted that herbivory, as well as natural enemy abundance and predation services would be greater in native landscape plots. We found that herbivory was greater in native plots in one of the collection years, but not the other. Other measures of leaf herbivory, particularly leaf damage index values, also revealed no difference between treatments. Natural enemy diversity differed between plots, but depended on plant genus, meaning that native congeners of some plant species, but not others, supported a greater diversity of natural enemies. Natural enemy community composition, spider biomass, and predation services did not differ between plot treatments. Overall our results suggest that native and exotic congener landscapes may not differ in their provisioning of pest management services. In general, both native and exotic Quercus supported the greatest richness of natural enemies in both years, and Hydrangeas supported the greatest amount of spider biomass. Overall, our work highlights that some plant congeners may be more similar than others in the natural enemy communities they support and the biomass they may provide to higher trophic
levels. Our work highlights the trade-offs between native and exotic ornamental landscapes and plant congeners and will help guide landscape design that serves both the people and wildlife that use them.

**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 (McKinney 2008, Faeth et al. 2011). The Enemies Release Hypothesis, also known as the Herbivore Escape Hypothesis, posits that plant species introduced into novel environments, where co-evolved herbivores are absent, will have 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). In fact, landscape managers and homeowners often choose to install exotic plants to reduce herbivore damage and improve the overall aesthetic of ornamental landscapes (Raupp et al. 1992, Herms 2002, Raupp et al. 2010). By reducing herbivores and herbivory, installing exotic plants can also decrease the need for pesticides on ornamental landscapes, an area of increasing concern based on risks to people, pollinators and other non-target animals, and the environment (Raupp et al. 1992, Raupp et al. 2010).

Herbivores, including chewing herbivores, leaf miners, and gall wasps (Burghardt and Tallamy 2013) are often more abundant and diverse in native landscapes (Owen 1983, Burghardt et al. 2009, 2010). For example, caterpillars were four times more abundant and three times
more species-rich in native suburban Pennsylvania landscapes when compared to landscapes planted in predominately exotic plants (Burghardt et al. 2009). Similarly, in ornamental landscapes in Washington, D.C., native plants hosted a greater biomass of caterpillars than exotic plants (Narango et al. 2017). The mechanism guiding these processes have largely been attributed to the coevolution of herbivores with their hosts and the novel chemistries and unique metabolic profiles of exotic plants that make them more defended or less palatable to native herbivores (Ehrlich & Raven 1964, Macel et al. 2014, Forister and Wilson 2013, Cappuccino and Arnason 2006). 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 herbivore generalists 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 and exotic ornamental plants (Frank 2014). A greater diversity and quantity of herbivores on native plants may also support more birds and other animals at higher trophic levels. Native landscape effects on bird predators of insect herbivores has been a large focus in recent research (Burghardt and Tallamy 2009, Narango et al. 2017, Pearse et al. 2013). For example, bird species abundance and richness increased in urban areas in native landscapes when compared to exotic landscapes of the same
size, a phenomenon that was attributed to greater caterpillar abundance and richness (Burghardt et al. 2009).

Although exotic ornamental landscapes may have less herbivore damage and require fewer pesticide inputs and although native landscapes may support a greater diversity of insect herbivores and birds, little is known about how either type of ornamental landscape affects invertebrate natural enemy communities or biocontrol services. Greenstone et al. (2017) found more spiders attending egg masses of sentinel *Halyomorpha halys* eggs in native ornamental landscapes when compared to exotic ornamental landscapes. Beneficial insects, including syrphid flies, were more abundant in fields with conservation strips planted in native plants (Walton and Isaacs 2011). High densities of natural enemies were attracted to several tested native plant species in Maryland (Frank and Shrewsbury 2008). In other experiments, however, natural enemy abundance and diversity were similar on native and exotic plants. For example, exotic annual plants alyssum, buckwheat, and faba bean were as attractive as native plants in attracting natural enemies in plot studies in Michigan (Fiedler and Landis 2007). Exotic plants can provide habitat complexity, microclimates, ideal oviposition sites, alternative foods, and other resources for natural enemies even if they have fewer herbivores. For example, exotic plants, such as alyssum, borage, coriander, dill, buckwheat, and phacelia, have been frequently used in agricultural conservation biocontrol programs to attract natural enemies that may help reduce pest populations on crop plants (Fielder and Landis 2007, Ambrosino et al. 2006, Pumarino et al. 2012). Many of the exotic plants used in agricultural conservation biocontrol programs are prolific bloomers, have special plant 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 (Pumarino et al. 2012, Fiedler and Landis 2007). For
example, *Orius insidiosus*, had greater survival and oviposition on phacelia, which was attributed to higher floral sugar content and an ideal plant substrate for ovipositing (Pumarino et al. 2012). Similarly, coriander has been correlated with high syrphid fly abundance in several studies (Amrosino et al. 2006, Colley and Luna 2000, Fiedler and Landis 2007).

Thus the overall effect of plant origin on natural enemies is mixed. Furthermore, much of the research has focused on sampling individual plants within mixed landscapes and it has usually been conducted in agricultural landscapes. When entire ornamental landscapes are native or exotic the effect of plant origin may be greater on the local arthropod community, because arthropods, particularly those with limited mobility, may be unable to relocate to plants that may be more suitable and provide needed resources. Furthermore, if natural enemy density and diversity are affected by plant origin, then predation services may also be affected. However, to our knowledge there is only one study to date that has explored differences in predation in native and exotic ornamental landscapes (Cornelius et al. 2016). Overall, more research is needed to explore how plant origin directly or indirectly affects natural enemy communities and pest control services to best inform urban landscape design that supports robust natural enemy communities and minimizes the risk of pest outbreak.

We predicted that native ornamental landscapes support more diverse natural enemy communities, more natural enemy biomass, and greater predation services when compared to exotic ornamental landscapes. To test this hypothesis we compared natural enemy abundance, diversity, community composition, dry weight spider biomass, as well as egg predation in U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS) experimental native and exotic ornamental landscape plots at the U.S. Arboretum in Washington, D.C. In keeping with the Enemies Release Hypothesis, we also predicted that herbivory will be less on exotic
ornamental landscapes. We tested this latter prediction with a comparison of leaf area lost to chewing herbivory between native and exotic plots. Our study addresses how invertebrate natural enemy communities and predation are affected by plant origin and will help inform landscape design that optimizes pest control on city landscapes.

Methods

Study Area and Study Sites

This study was performed in six USDA-ARS experimental plots at the U.S. Arboretum in Washington, DC. The plots were 25mx25m, designed to mimic residential landscapes, had the same plant layout (Fig. 1), and contained woody shrub and tree species common in residential landscapes of the mid-Atlantic region. Three plots contained only native plant species and three contained only exotic species which were congeners of native species. The plots were arranged in a complete block design. Each block was in a different location in the arboretum and contained one native and one exotic plot to control 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. Plant species in plots included 16 matched congeners that have been geographically separated for at least 1 million years (Cornelius et al. 2016). The 10-meter perimeter around each plot was regularly mowed, and plots within blocks were separated by 50-99 meters with a lightly managed meadow in between (Cornelius et al. 2016). Distances between blocks ranged from 300-900 meters (Cornelius et al. 2016). Plots were well established and were approximately 6 years old at the time of this study.
**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, we pruned 2 terminal twigs (15-20 cm in length) 4-6 meters above the ground from opposite sides of the tree canopy. Twigs with leaves attached were immediately put in zip-top bags and kept in a refrigerator at 4°Celsius until they could be measured. Ten leaves were randomly selected from each twig to assess 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. Because many of the selected leaves were incorrectly scanned in 2017, only ten of the twenty randomly selected leaves from the two sampled twigs for each tree were analyzed for herbivory in 2017. The ten selected leaves used for analysis had been properly scanned. Incorrectly scanned leaves, not included in analysis, were those that were not properly placed on the scanner, and thus images were not representative of actual leaves. Separate analyses were performed for 2017 and 2018 to account for the difference.

**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. Congeners 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. Natural enemies were identified in the lab under a dissection scope. Most arthropods were identified to family, with the exception of spiders, parasitoid wasps, and earwigs (Dermaptera).

*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. 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 hours, after which point the temperature was elevated to 45°C for 24 hours. Spiders were weighed on a Satorius Cubis MSA3.6P0TRDM balance that measured to the nearest microgram. Spiders were weighed to the nearest 0.01 milligrams.

*Predation Experiments*

Sentinel *Helicoverpa zea* eggs were set out in plots and counted before and after 24-hours to assess predation services among plots. Predation experiments were conducted three times in 2018 (30 June, 28 July, and 25 August). Frozen *Helicoverpa zea* eggs were purchased from Frontier Agricultural Sciences (Newark, DE). Eggs were received frozen on a circular mesh cloth with approximately 1,000-2,000 eggs. We cut 1cmx1cm squares from the cloth, such that at least 30 eggs were on each square. Cloth squares with eggs were stored in a -80°C Celsius freezer before use in field trials and kept in a cooler when going into the field. Two shrub genera and a tree genus were chosen in each plot on which to conduct experiments. 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 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 4cm plastic
tube, and a mesh top. Egg numbers before and after 24-hours were recorded.

Analysis

Treatment effects on herbivory

All analysis was performed in R Version 3.4.3 (The R Foundation for Statistical
Computing, 2017). To test our hypothesis that native ornamental landscapes would have more
chewing leaf herbivory, we used linear mixed effects models with the nlme package in R
(Pinheiro et al. 2017). Our a priori hypothesis model included herbivory at the plot level,
measured in cm$^2$, as the response and treatment (native or exotic) as the predictor. Herbivory
response was log10(x+1) transformed to improve the distribution of residuals and to account for
overdispersion, because the variance was larger than the mean (Zuur et al. 2009, 2010). Models
were also analyzed with leaf area as a predictor to determine if leaf area needed to be accounted
for in herbivory models. In mixed effects models a random effect term for block was included in
both 2017 and 2018 models; date and sample tree were also included as a random effects in 2018
models to account for variation in herbivory and leaf surface area across the multiple collection
dates and repeated measures on sampled trees. 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 a priori models. We used model validation
diagnostic plots in R to detect and test for violations of linear regression assumptions for all
models. 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.

We calculated Leaf Damage Index (LDI) values (proportion of leaves per tree that had damage exceeding 5% of surface area) (Alliende 1989, Kozlov et al. 2014) in native and exotic ornamental landscapes at the plot level. Our a priori hypothesis was that there would be higher LDI values in native plots. We calculated LDI values because they provide a measure of herbivory distribution throughout the tree canopy. Using the same approach for total herbivory, our a priori linear mixed effects model included LDI values (number of leaves in the sample damaged above 5%) as the response and treatment as the predictor. We used number of leaves damaged, rather than proportion, because number of leaves sampled per tree was standardized in both years. LDI response was slightly skewed toward zero, given the high number of zeros in the data. However, overall residuals were normally distributed in linear models.

We used ANOVAs to test for interactions between treatment and genus and differences among genera. Total herbivory for the collection season in cm² and total LDI values were used as the responses for ANOVAs, and an error term for block was added to models. Responses were log10(x+1) transformed to meet linear regression assumptions. Post-hoc pairwise Dunn Tests were analyzed (Dinno 2017) to further explore differences among genera.

Treatment effects on natural enemy communities

To test our prediction that natural enemy abundance, richness, diversity, and spider biomass would be greatest in native plot treatments, we performed a series of linear mixed effects models using similar methods to those used in our herbivory analysis. Our a priori hypotheses models included natural enemy abundance, species richness, species diversity, and spider dry weight biomass by collection date as responses and treatment (native or exotic) as the
predictor. Natural enemy species diversity was evaluated using the Shannon Diversity Index (H’). Shannon Diversity index values were calculated using the vegan package in R. H’ values ranged from 0-1.75, with lower values being those communities that were less species rich and did not have an even distribution of natural enemy species. 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. We log10(x+1) transformed abundance, richness, diversity and dry weight responses to account for overdispersion. Random effect terms for block, date, and tree were included in both 2017 and 2018 models to account for variation in abundance, richness, and diversity across the multiple collection dates and repeated measures on sampled trees. We 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.

We used ANOVAs to test for interactions between treatment and genus and differences among genera. All responses were totaled for the season and log10(x+1) transformed to meet linear regression assumptions. An error term for block was added to all models. Post-hoc pairwise Dunn Tests were analyzed (Dinno 2017) to further explore differences among genera.

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 (Jari et al. 2017).

Treatment effects on 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). Once a cage effect was determined then predation effect size was calculated as the ln(proportion of prey removed on uncaged leaves) – ln(proportion of prey removed on caged leaves). To test our prediction that native landscapes would have more egg predation we analyzed the same a priori linear mixed effects model for predation as we did for herbivory and natural enemies with treatment as a predictor. We used model validation diagnostic plots in R to detect and test for violations of linear regression assumptions for all models. 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.
Results

Herbivory

Chewing herbivory was two times greater in native plots when compared to exotic plots in 2018 (p<0.001, marginal \( R^2 = 0.10 \), conditional \( R^2 = 0.94 \)) such that for every 1 cm\(^2\) of leaf missing due to chewing herbivory in exotic plots there was 2 cm\(^2\) of leaf missing in native plots ([Est +/- SE] 0.31 +/- 0.86). In 2018, herbivory was significantly greater on native than exotic maple trees (Acer spp.) (p<0.05, [Est +/- SE] 0.28 +/-0.10) and redbud trees (Cercis spp) (p<0.05, [Est +/-SE] 0.48 +/-0.13), while oak trees (Quercus spp) had no difference in herbivory between treatments in 2018 (Fig. 2). Herbivory was not different between native and exotic plots in 2017 (Fig. 2). Total leaf area sampled was greater in native plots in 2018 (p<0.01) ([Est +/- SE] 0.16 +/- 0.054) but not in 2017, and surface area was not a significant predictor of herbivory in either year. Genus and interactions between genus and treatment were not significant in either year. Treatment was not a significant predictor of LDI in 2017 or 2018. However, genus was a significant predictor of LDI in 2018. 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 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.

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. However, natural enemy diversity was greater in native plots in both 2017 (p<0.05, 0.16 +/- 0.08) and in 2018 (p<0.001, 0.24 +/- 0.06) (Fig. 3) (Supplementary Table 1). Natural enemy species richness was greater in native plots compared to exotic plots in 2018 (p<0.01, 0.61 +/- 0.21), but not in 2017. Although treatment was a significant predictor of natural enemy diversity in 2017 (marginal R² = 0.05, conditional R²=0.99) and 2018 (marginal R²=0.08, conditional R²=0.99), and of richness in 2018 (marginal R²=0.05, conditional R²=0.99), it was generally weak at explaining variation in responses (Supplementary Table).

Tree and shrub genus was a significant predictor of natural enemy abundance in both years and a significant predictor of richness in 2017. 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. In 2017 Quercus had the greatest richness of natural enemy genera and was significantly more species rich than Viburnum and Liriodendron.

Significant interactions between treatment and genera in 2018 revealed that some genera were more affected by treatment (i.e. plant origin) than others. In 2018 Liriodendron and Viburnum stood out from other genera because their congeners were statistically different. When compared to exotic congeners, native Liriodendron had greater natural enemy diversity (p<0.01, 0.48 +/- 0.14) and richness (p<0.001, 1.58 +/- 0.31). Native Viburnum also had greater natural enemy diversity (p<0.001, 0.64 +/- 0.09) and richness (p<0.001, 2.42 +/- 0.36). Thus, native Liriodendron and native Viburnum congeners contributed to the positive effect of native treatment on both natural enemy diversity and richness on landscape plots in 2018.

In community analysis, natural enemy communities in native and exotic plots did not differ in either year (p>0.05) (Fig. 4). 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, nantids, dabids, Dermaptera, and reduviids (Supplementary Table).

*Spider biomass*

Spider dry weight 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 dry weight of spiders and had significantly more spider biomass than *Cercis* (p<0.01), *Liriodendron* (p<0.05), and *Catalpa* (p<0.05) (Fig. 5).

*Predation*

Uncaged leaves had three times as many eggs missing after 24-hours than caged eggs (p<0.001, Est. +/- SE, 3.72 +/- 0.787) (Fig.6), indicating significant predation. Contrary to our predictions, native plots did not have more egg predation than exotic plots (Fig. 6). Egg predation also did not differ among tree genera.

*Discussion*

Better understanding of how the plants we install in urban landscapes affect arthropod communities can help us design landscapes that protect aesthetics and plant health while also providing valuable resources for urban wildlife. Our study highlights that whether an ornamental landscape is native or exotic plays a weak role in the structuring of invertebrate natural enemy
communities. Contrary to our prediction, native ornamental landscapes did not have more natural enemies or spider biomass. Furthermore, native treatment was a weak predictor of natural enemy richness and diversity. Leaf damage index values also did not differ in native and exotic ornamental landscapes in either year, and were actually greater on exotic oaks in 2018. Our results support other findings that have shown variability in herbivory among plant species and congeners (Pearse and Hipp 2009, Frank 2014). Overall our findings suggest that plant origin may play less of a role in structuring natural enemy communities and affecting herbivory on ornamental landscapes than previously thought. Our project revealed greater similarities than differences between native and exotic ornamental landscapes with regard to natural enemies and pest management.

Lower herbivory on introduced exotic plants has been well documented in both ornamental (Frank 2014, Matter et al. 2012, Tallamy et al. 2010, Tallamy 2004) and exotic invasive studies (Keane and Crawley 2002, Carpenter and Cappuccino 2005, Schierenbeck et al. 1994, Williams and Sahli 2016, Lieurance and Cipollini 2013). In keeping with this previous research, we found that plants in native ornamental landscapes had more leaf area lost due chewing herbivory than plants in exotic ornamental landscapes in 2018. Although we did not quantify herbivore density, more herbivory in native plots in our study is likely the result of more chewing herbivores (Proches et al. 2008, Heleno et al. 2009, Burghardt et al. 2009, 2010, Perre et al. 2011). In 2017 we did not find a significant difference in leaf area missing on plants in native and exotic ornamental landscapes. Discrepancy in results could be attributed to sampling frequency, given that we only sampled for herbivory once in 2017 at the end of the season and we sampled four times throughout the season in 2018. Despite the discrepancies between years in leaf area lost, leaf damage index values did not differ on native and exotic congeners in either
year, meaning that a similar number of leaves had damage in native and exotic plots. In fact, exotic oak congeners had on average higher 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 (Raupp et al. 1992, Raupp et al. 1988, Larew et al. 1984, 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. 1992, Raupp et al. 1988). In addition to exotic 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 plot treatment in 2018. In 2017 LDI values were on average higher, again likely the result of lower sampling frequency, but still low, 14% in exotic plots and 28% in native plots. Our research, coupled with work that has found that chewing herbivory is lower in urban landscapes compared to natural areas (Moreira et al. 2019, Nuckols and Connor 1995, Raupp et al. 2010), may suggest that planting the exotic tree and shrub species used in this study may not be particularly advantageous for homeowners.

However, not all congeners are equal in how much leaf area is lost to chewing herbivory. For example, native *Acer* and *Cercis* had significantly more herbivory than their exotic congeners, whereas there was no difference between *Quercus* congeners. This difference may be explained by evolutionary history or the insect communities often associated with different plant genera. For example, more distantly related congeners of oaks had greater discrepancy in herbivory than more closely related oak congeners (Pearse and Hipp 2005). In our study *Quercus robur* and *Quercus alba*, the two oak congeners that did not significantly differ in
herbivory, are more closely related than *Cercis canadensis* and *Cercis chinensis*, the two redbud congeners in our study that had the greatest difference in herbivory (Greenstone et al. 2017, Manos and Stanford 2001, Donoghue et al. 2001). Similarly, native *Cercis canadensis* had twelve times more herbivory than *Cercis chinense* in ornamental landscapes in North Carolina (Frank 2014). However, insect communities associated with plant genera may also explain herbivory differences, or lack thereof. For example, the robust herbivore communities of oaks are well documented (Southwood et al. 2005). In a comparison of native oaks and exotic oaks, Southwood et al. found that, although densities of herbivore species were lower on exotic oaks, they were still relatively high. Thus, herbivory may still remain high on exotic oaks given high background numbers of herbivores. Overall our results highlight the variability in chewing herbivory among species and congeners, and show that some exotic congeners may be better than others for landscape managers seeking to reduce herbivore damage in landscapes.

Although native plants can support greater herbivore biomass in ornamental landscapes (Burghardt and Tallamy 2009, Narango et al. 2017), little is known about plant origin effects on natural enemy 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 density 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 (Greenstone et al. 2017, Fiedler and Landis 2007, Southwood et al. 2005). Biomass of predators was almost double on native oaks when compared to exotic congeners (Southwood et al. 2005). Heleno et al. (2009) found that forests that had been invaded by exotic plants had a decrease in
overall insect biomass, but they did not separate natural enemy biomass from overall biomass. Although plant origin did not have an effect on spider biomass in our study, genus was predictive of biomass. *Hydrangeas* had the most biomass of all genera and significantly more biomass than *Cercis, Liriodendron*, and *Catalpa*. Likely this difference can 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 (Fiedler and Landis 2007, Frank and Shrewsbury 2004, Landis et al. 2000, Braman et al. 2002, Lee and Heimpel 2005). Overall our results suggest that plant origin may have little effect on natural enemy biomass. Furthermore, in light of recent work on effects of plant origin on herbivore biomass (Burghardt and Tallamy 2009, Narango et al. 2017), our results suggest that not all trophic levels are affected similarly by plant origin. Certain plant traits, however, such as a long flower period that may provide alternative nectar and pollen resources, greater architectural complexity that may provide refugia from predators, or fewer mechanical plant barriers that may promote oviposition, among other traits, may play more important roles in increasing invertebrate natural enemy biomass available to higher trophic levels.

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. The compositional turnover in the herbivore community that occurs on exotic plants from more specialist herbivores to generalist herbivores (Carvalheiro et al. 2010, Burghardt and Tallamy 2013, 2015) can have an effect on species abundance and diversity at higher trophic levels. For example, lower parasitoid richness and abundance have been found in forested and
disturbed landscapes that have been invaded by exotic plants, due to the decrease in native plant species and specialist herbivore hosts (Peralta et al. 2018, Carvalheiro et al. 2010). Similarly, overall lower natural enemy diversity in exotic plots in our study may have resulted from a lower diversity of herbivores on exotic congeners (Peralta et al. 2018, Carvalheiro et al. 2010, Burghardt and Tallamy 2013, 2015). However, in our system, blooming of shrubs may 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. Blooming can increase abundance and diversity of natural enemies (Fiedler and Landis 2007, Frank and Shrewsbury 2004, Landis et al. 2000, Braman et al. 2002, Lee and Heimpel 2005), and thus may have contributed in the differences in natural enemy diversity between native and exotic plots. *Liriodendron* and *Viburnum* were the only congeners that significantly differed among all the genera sampled in 2018 and contributed largely to the differences in diversity between landscape types. Although bloom time mismatch was a consideration for *Viburnum*, it was not for *Liriodendron*, which had passed peak bloom in both native and exotic plots during the time of collection. Coccinellids and Neuropterans were in high numbers on native *Liriodendron* and responsible for much of the discrepancy in natural enemy diversity between native and exotic *Liriodendron*. Native *Liriodendron* is famously known for its heavy infestations of *Illinoia liriodendri*, which are common during the time of year when we were sampling. High densities of *Illinoia liriodendri* often attract high densities of lady beetles and lacewings (Dreistadt and Dahlsten 1988). Thus, although we did not sample aphid populations on *Liriodendron*, we suspect the greater species diversity on native Liriodendron to be attributed to high availability of
aphid prey. Overall, blooming traits and host prey availability may play important roles in
supporting robust natural enemy communities on ornamental landscapes.

Predation of *H. zea* eggs did not differ in native and exotic plots. Similarly, Cornelius et al. (2016) found that predation and parasitism of *Halyomorpha halys* eggs did not differ on the basis of plant origin. Common predators of *H. zea* eggs are primarily generalist natural enemies, such as many of those found in our beat samples, including Nabids, Coccinellids, *Orius insidiosus*, and Opiliones, among others (Gardiner et al. 2014, Nuessly and Sterling 1994, Pfanannenstiel and Yeargan 2002). Egg predation of *H. zea* eggs can be affected by plant type, time of season, time of day, and pollen and alternative food availability, among other factors (Pfanannenstiel and Yeargan 200). Similarities in natural enemy abundance and spider biomass among plots may explain similar predation responses, and indicate that predatory function may be maintained despite plant origin.

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, Herms 2002, Raupp et al. 2010). 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 enemies and biocontrol services, an area of concern given previous research documenting the reduction of herbivore abundance and diversity on exotic ornamental plants (Burghardt and Tallamy 2013, 2015). Our study fills these gaps in the research, and it sheds light on how both native and exotic ornamental landscapes provide valuable pest management services. Our research also suggests that exotic ornamental landscapes may support comparable levels of natural enemy biomass to native ornamental landscapes. Overall, herbivory, natural enemy abundance, and biomass were similar on native
and exotic landscapes. In conclusion, native ornamental landscapes are more similar than different to exotic ornamental landscapes, with regard to the natural enemy communities they support and the pest management services they provide. Our study demonstrates that special plant traits, such as long bloom periods, may overall play a more important role than plant origin in ornamental landscapes in supporting robust communities of natural enemies. Furthermore, some congeners, such as *Quercus*, are more similar in the natural enemies they support. Choosing exotic congeners that are more similar to native congeners in the natural enemies they support and selecting plants with special plant traits attractive to natural enemies may be two ways that landscape designers can support robust natural enemy communities and pest control services on ornamental landscapes. Overall, our study helps inform landscape design that provides more biomass available to urban wildlife and bolsters pest control services on city landscapes.
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Faith, D. P., Minchin, P. R., and Belbin, L. 1987. ‘Compositional dissimilarity as a robust measure of ecological distance’, Vegetatio, 69: 57–68


Proches S, Wilson JRU, Richardson DM, Chown SL. 2008. Herbivores, but not other insects, are


Figure 1. Landscape planting plan for native and exotic plot treatments.
**Figure 2.** 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. In 2017, native Acer in one of the plots was not sampled, as the tree was in poor condition. Thus, a box plot is not available for native Acer in 2017.
Figure 3. Natural enemy diversity in native and exotic plot treatments in (a) 2017 and (b) 2018. The boxplots 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.
Figure 4. 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. Blue triangles outline exotic plot communities, while red triangles outline native plot communities. Overlapping triangles or touching triangles are good indicators that communities do not differ from one another. Individual plot names are in black. Points of the triangles signify plot communities. Plot communities closer together in the ordination space mean that they are more similar in their composition. Natural enemy groups are indicated in red lettering.
**Figure 5.** Differences in spider dry weight 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. Asterisks indicate significant differences. Hydrangea had significantly more spider biomass than Catalpa, Cercis, and Liriodendron.

**Figure 6.** 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 hours. 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 hours than caged treatments, indicating predation.
APPENDICES
Appendix A

Supplementary Tables

Supplementary Table S1: Candidate model set used in model selection process

<table>
<thead>
<tr>
<th>Model name</th>
<th>Formula</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Coarse Veg. (100m) + Cluster + CrownVolume)</td>
<td>mothership</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Coarse Veg. (100m) + Cluster + CrownVolume + Temperature)</td>
<td>mothership2</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H'))</td>
<td>modelA</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Percent Coarse Veg. (100m))</td>
<td>modelB</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Coarse Veg. (20m) + Cluster + CrownVolume)</td>
<td>modelC</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Cluster + CrownVolume)</td>
<td>modelD</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Percent Coarse Veg. (100m) + Temperature)</td>
<td>modelE</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Coarse Veg. (20m) + Cluster + CrownVolume + Temperature)</td>
<td>modelF</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Temperature)</td>
<td>modelG</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Cluster + CrownVolume + Temperature)</td>
<td>modelH</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Percent Impervious (100m) * Local Veg. Complexity (H'))</td>
<td>modelI</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Temperature + Percent Impervious (100m) * Local Veg. Complexity (H'))</td>
<td>modelJ</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Percent Impervious (100m) * Local Veg. Complexity (H'))</td>
<td>modelK</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m) + Local Veg. Complexity (H') + Cluster + CrownVolume + Percent Impervious (100m) * Local Veg. Complexity (H'))</td>
<td>modelL</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Impervious (20m) * Local Veg. Complexity (H'))</td>
<td>modelM</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (20m) + Local Veg. Complexity (H') + Percent Impervious (20m) * Local Veg. Complexity (H') + Temperature)</td>
<td>modelN</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Local Veg. Complexity (H'))</td>
<td>modelO</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (100m))</td>
<td>modelP</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Percent Impervious (20m))</td>
<td>modelQ</td>
<td></td>
</tr>
<tr>
<td>lm(Log10 Nat En. Abundance ~ Aphid Abundance (Log10))</td>
<td>modelR</td>
<td></td>
</tr>
</tbody>
</table>

*The same models were run with Aphid Abundance as the response.
*All models with temperature were left out of the 2016 model selection process, as no temperature data existed for 2016.
Supplementary Table S2. Distribution of vegetative strata among trees

<table>
<thead>
<tr>
<th>Vegetation Strata</th>
<th>Percentage of trees with strata</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turf</td>
<td>57.57%</td>
</tr>
<tr>
<td>Herbaceous</td>
<td>42.42%</td>
</tr>
<tr>
<td>Shrub</td>
<td>57.57%</td>
</tr>
<tr>
<td>Understory</td>
<td>100%*</td>
</tr>
<tr>
<td>Overstory</td>
<td>24.24%</td>
</tr>
</tbody>
</table>

*All sites had understory, because study trees were understory trees.

Supplementary Table S3. Top models describing aphid abundance in 2016 and 2017. Models with deltaAIC<2.

Supplementary Table S4. Top models describing natural enemy abundance in 2016 and 2017. Models with deltaAIC<2.
**Supplementary Table S5. Natural enemy groups in 2016 and 2017, expressed in proportions.**

<table>
<thead>
<tr>
<th></th>
<th>2016</th>
<th>2017</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n=1359</td>
<td>n=700</td>
</tr>
<tr>
<td>Parasitoids</td>
<td>0.036</td>
<td>0.017</td>
</tr>
<tr>
<td>Coccinellidae</td>
<td>0.079</td>
<td>0.050</td>
</tr>
<tr>
<td>Chrysopidae</td>
<td>0.042</td>
<td>0.023</td>
</tr>
<tr>
<td>Phlaeothripidae</td>
<td>0.057</td>
<td>0.053</td>
</tr>
<tr>
<td>Orius insidiosus</td>
<td>0.350</td>
<td>0.473</td>
</tr>
<tr>
<td>Spiders</td>
<td>0.431</td>
<td>0.371</td>
</tr>
<tr>
<td>Staphylinidae</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Nabidae</td>
<td>0.004</td>
<td>0.009</td>
</tr>
<tr>
<td>Opiliones</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>Dermaptera</td>
<td>0.001</td>
<td>0.001</td>
</tr>
</tbody>
</table>

*Anything below 1% was excluded from analyses and model selection
*Parasitoids were also excluded from analyses because *T. kahawaluokalani* have no known parasitoid
Supplementary Table S6. Natural enemy groups in 2016 on sticky cards, expressed in proportions.

<table>
<thead>
<tr>
<th>2016</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinellidae</td>
<td>0.03908795</td>
<td></td>
</tr>
<tr>
<td>Chrysopidae</td>
<td>0.00651466</td>
<td></td>
</tr>
<tr>
<td>Phaeolethriptidae</td>
<td>0.3786645</td>
<td></td>
</tr>
<tr>
<td>Reduvididae</td>
<td>0.01140065</td>
<td></td>
</tr>
<tr>
<td>Orius</td>
<td>0.25488599</td>
<td></td>
</tr>
<tr>
<td>Spiders</td>
<td>0.07736156</td>
<td></td>
</tr>
<tr>
<td>Dolichopidae</td>
<td>0.18322476</td>
<td></td>
</tr>
<tr>
<td>Predatory Hymenoptera</td>
<td>0.00977199</td>
<td></td>
</tr>
</tbody>
</table>

*Parasitoids made up 71.1% of all natural enemies but were not included in analyses, as there are no known parasitoids of CMA.
*Percentages above based on total natural enemy numbers excluding parasitoids. n=4254 with parasitoids.

Supplementary Table S7. Predictors explaining abundance of natural enemy groups on sticky cards. Predictors are only reported with importance values above 0.5.

<table>
<thead>
<tr>
<th>2016</th>
<th>Predictor</th>
<th>Importance Value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Lady Beetle Abundance</td>
<td>Na</td>
</tr>
<tr>
<td></td>
<td>Larving Abundance</td>
<td>Na</td>
</tr>
<tr>
<td></td>
<td>Predatory Thrip Abundance</td>
<td>0.77982077</td>
</tr>
<tr>
<td></td>
<td>Local Veg (Ht)</td>
<td>0.69425037</td>
</tr>
<tr>
<td></td>
<td>Imp (100m)</td>
<td>0.64425037</td>
</tr>
<tr>
<td></td>
<td>Orius Abundance ***</td>
<td>0.99358261</td>
</tr>
<tr>
<td></td>
<td>Local Veg (Ht)</td>
<td>0.80467791</td>
</tr>
<tr>
<td></td>
<td>Imp (100m)</td>
<td>0.80467791</td>
</tr>
<tr>
<td></td>
<td>Spider Abundance *</td>
<td>Na</td>
</tr>
<tr>
<td></td>
<td>Dolichopidae</td>
<td>Na</td>
</tr>
</tbody>
</table>

NA* No importance values above 0.5.
***Model selection with Orius was analyzed again with an adjusted data set, excluding four trees. The same predictors were most important. Importance values for local vegetation and impervious cover at 100m were 0.54 and 0.53 respectively.
Supplementary Table S8. Importance values for predictors of aphid predation. Importance values were calculated in the model selection process. Importance values in bold are above 0.5. Importance values indicate the probability that a predictor will be selected in the top models given a candidate model set.

<table>
<thead>
<tr>
<th>Year</th>
<th>Response</th>
<th>Predictor</th>
<th>Importance Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2016</td>
<td>Predation (% of Aphids Eaten)</td>
<td>Local Veg (H)</td>
<td>0.615</td>
</tr>
<tr>
<td></td>
<td></td>
<td>impervious (100m)</td>
<td>0.437</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Start Count</td>
<td>0.397</td>
</tr>
<tr>
<td></td>
<td></td>
<td>impervious (20m)</td>
<td>0.255</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Local Veg; impervious (100m)</td>
<td>0.204</td>
</tr>
<tr>
<td>2017</td>
<td>Predation (% of Aphids Eaten)</td>
<td>impervious (20m)</td>
<td>0.918</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Local Veg (H)</td>
<td>0.186</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Local Veg; impervious (20m)</td>
<td>0.124</td>
</tr>
<tr>
<td></td>
<td></td>
<td>impervious (100m)</td>
<td>0.039</td>
</tr>
</tbody>
</table>
Supplementary Figure S1. Local structural complexity around study trees. To the left is a site with local structural complexity Shannon H’ value of 0. To the right is a site with a high structural complexity, as lots of different layers of vegetation surround the tree. In this picture you can see a shrub layer, an herbaceous layer, as well as a canopy and understory layer of vegetation within 5 meters of the study tree. This site had a local structural complexity Shannon H’ value of 1.16.

Supplementary Figure S2. Measuring local structural complexity. Local structural complexity was measured using methods from Shrewsbury and Raupp 2000, in which a 10mx10m grid was placed around trees and number of vegetation strata were counted in each 1mx1m grid square.
Supplementary Figure S3. Effects of local structural complexity and natural enemy abundance. Linear models indicated that local structural complexity was a predictor of natural enemy abundance ($R^2 = 0.18$ (2016), $R^2 = 0.17$ (2017)). Structural complexity is quantified via the Shannon Index. Above are plots for (a) 2016 and (b) 2017 highlighting natural enemy response against structural complexity within 10mx10m grid around trees. Shaded areas represent 95% confidence intervals.
Appendix B

Supplementary Tables

Supplementary Table 1. Candidate model set.

<table>
<thead>
<tr>
<th>Model</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>model1</td>
<td>Imel(TransAph-AphidsSunTemps1wk,random==1</td>
</tr>
<tr>
<td>model2</td>
<td>Imel(TransAph-Percentimp,random==1</td>
</tr>
<tr>
<td>model3</td>
<td>Imel(TransAph-H,random==1</td>
</tr>
<tr>
<td>model4</td>
<td>Imel(TransAph-DroughtStressMPA,random==1</td>
</tr>
<tr>
<td>model5</td>
<td>Imel(TransAph-AphidsSunTemps1wk+DroughtStressMPA+DroughtStressMPA*AphidsSunTemps1wk,random==1</td>
</tr>
<tr>
<td>model6</td>
<td>Imel(TransAph-AphidsSunTemps1wk+DroughtStressMPA,random==1</td>
</tr>
<tr>
<td>model7</td>
<td>Imel(TransAph-AphidsSunTemps1wk*H,random==1</td>
</tr>
<tr>
<td>model8</td>
<td>Imel(TransAph-H+DroughtStressMPA+H*DroughtStressMPA,random==1</td>
</tr>
<tr>
<td>model9</td>
<td>Imel(TransAph-DroughtStressMPA+H<em>AphidsSunTemps1wk+H</em>DroughtStressMPA*AphidsSunTemps1wk,random==1</td>
</tr>
<tr>
<td>model10</td>
<td>Imel(TransAph-Percentimp*DroughtStressMPA,random==1</td>
</tr>
<tr>
<td>model11</td>
<td>Imel(TransAph-Percentimp+H,random==1</td>
</tr>
<tr>
<td>model12</td>
<td>Imel(TransAph-Percentimp+H<em>AphidsSunTemps1wk+AphidsSunTemps1wk+H</em>Percentimp,random==1</td>
</tr>
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</table>
Supplementary Table 2. Multiple linear regression analysis for natural enemy abundance.

<table>
<thead>
<tr>
<th>NATURAL ENEMY MODELS</th>
<th>Marginal $R^2$</th>
<th>Conditional $R^2$</th>
<th>df</th>
<th>Est.</th>
<th>SE</th>
<th>t-value</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>MODE1</td>
<td>0.008</td>
<td>0.26</td>
<td>61</td>
<td>1.386</td>
<td>0.722</td>
<td>1.917</td>
<td>0.059</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>61</td>
<td>-0.023</td>
<td>0.024</td>
<td>-0.94</td>
<td>0.35</td>
</tr>
<tr>
<td>MODE2</td>
<td>0.02</td>
<td>0.27</td>
<td>60</td>
<td>1.346</td>
<td>4.256</td>
<td>0.316</td>
<td>0.752</td>
</tr>
<tr>
<td></td>
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<td></td>
<td>60</td>
<td>-0.016</td>
<td>0.146</td>
<td>-0.103</td>
<td>0.913</td>
</tr>
<tr>
<td>MODE3</td>
<td>0.02</td>
<td>0.28</td>
<td>29</td>
<td>0.291</td>
<td>0.173</td>
<td>0.173</td>
<td>0.867</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>29</td>
<td>-0.0344</td>
<td>0.594</td>
<td>-0.057</td>
<td>0.954</td>
</tr>
<tr>
<td>MODE4</td>
<td>0.12</td>
<td>0.28</td>
<td>60</td>
<td>0.85</td>
<td>1.612</td>
<td>0.527</td>
<td>0.599</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>-0.011</td>
<td>0.055</td>
<td>-0.211</td>
<td>0.835</td>
</tr>
<tr>
<td>MODE5</td>
<td>0.12</td>
<td>0.28</td>
<td>60</td>
<td>0.227</td>
<td>1.885</td>
<td>0.295</td>
<td>0.769</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>-0.01</td>
<td>0.065</td>
<td>-0.159</td>
<td>0.873</td>
</tr>
<tr>
<td>MODE6</td>
<td>0.12</td>
<td>0.28</td>
<td>60</td>
<td>1.0786</td>
<td>0.724</td>
<td>1.488</td>
<td>0.141</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>-0.0106</td>
<td>0.024</td>
<td>-0.704</td>
<td>0.493</td>
</tr>
<tr>
<td>MODE7</td>
<td>0.12</td>
<td>0.28</td>
<td>29</td>
<td>0.256</td>
<td>0.088</td>
<td>2.896</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>29</td>
<td>1.925</td>
<td>2.909</td>
<td>0.686</td>
<td>0.495</td>
</tr>
<tr>
<td>MODE8</td>
<td>0.12</td>
<td>0.28</td>
<td>60</td>
<td>0.22</td>
<td>5.567</td>
<td>0.230</td>
<td>0.819</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>29</td>
<td>1.282</td>
<td>5.567</td>
<td>0.230</td>
<td>0.819</td>
</tr>
<tr>
<td>MODE9</td>
<td>0.02</td>
<td>0.28</td>
<td>60</td>
<td>1.457</td>
<td>0.728</td>
<td>1.099</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>60</td>
<td>-0.012</td>
<td>0.024</td>
<td>0.845</td>
<td>0.393</td>
</tr>
<tr>
<td>MODE10</td>
<td>0.15</td>
<td>0.31</td>
<td>29</td>
<td>0.224</td>
<td>0.271</td>
<td>0.824</td>
<td>0.416</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>29</td>
<td>1.315</td>
<td>3.143</td>
<td>0.387</td>
<td>0.707</td>
</tr>
<tr>
<td>MODE11</td>
<td>0.13</td>
<td>0.34</td>
<td>58</td>
<td>-18.824</td>
<td>30.01</td>
<td>-1.879</td>
<td>0.065</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>27</td>
<td>27.344</td>
<td>30.7</td>
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<td>&lt;0.05</td>
</tr>
<tr>
<td>MODE12</td>
<td>0.15</td>
<td>0.34</td>
<td>58</td>
<td>1.4743</td>
<td>0.681</td>
<td>2.162</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

*Models with interactions of predictors excluding temperature were also analyzed in the model selection process.
Appendix C

Supplementary Table 1. Model outputs for natural enemy responses by treatment and genus. Bold indicates models with lower AICc, and the better fit of the two compared models for each response.

<table>
<thead>
<tr>
<th>2017</th>
<th>Predictor</th>
<th>Marginal R</th>
<th>Conditional R</th>
<th>AICc</th>
</tr>
</thead>
<tbody>
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Supplementary Table 2. Percentage of natural enemy groups in beat samples in (a) 2017 and (b) 2018.

(a)

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<tr>
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<td>0.05</td>
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<tr>
<td>Chrysopidae and Hemerobiidae</td>
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<td>Nabidae</td>
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<tr>
<td>Dermaptera</td>
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(b)

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Supplementary Figure 1. Leaf damage index values for 2017 (a) and 2018 (b).