



# Effects of temperature and habitat complexity on an urban tree pest (*Tinocallis kahawaluokalani*), natural enemies, and predation services in the city

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## 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 tree pest, crape myrtle aphid (*Tinocallis kahawaluokalani*), natural enemies, and egg predation services on crape myrtles in the city. 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 affect one species of piercing-sucking herbivore, 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, yet decreases natural enemy density and egg predation services on street trees, we collected data on crape myrtle trees in Raleigh, NC 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 and plant water potential. Aphid density decreased with hotter urban temperatures. However, natural enemies and egg predation were not affected by temperature. Natural enemy density was most correlated with local structural complexity. Together these findings suggest that increasing local structural complexity around trees may be a way to support natural enemies on both cool and hot urban trees. Our findings also emphasize the need for similar studies that evaluate temperature effects on common tree pests to help landscape managers prioritize pest targets for pest control in a warmer and more urban world.

**Keywords** Biological control · Aphids · Natural enemies · Urban trees · Urban heat island

## Introduction

Trees in urban landscapes provide many services, such as atmospheric cooling, beautification, and carbon sequestration (Nowak and Dwyer 2000; Meineke et al. 2016). Unfortunately, urban trees often have more pests than trees in natural areas (Hanks and Denno 1993; Raupp et al. 2010; Long et al. 2019). Pests can reduce tree aesthetics and

ecosystem services and may require insecticide applications or other costly maintenance (Dreistadt et al. 1990; Raupp et al. 1992; 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 (Hanks and Denno 1993; Tooker and Hanks 2000; Burkman and Gardiner 2014). Furthermore, pest densities on city plants 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 developmental rate, fecundity, and survival (Zvereva and Kozlov 2006; Meineke et al. 2013; Dale and Frank 2014). Overall, the combined negative effects of urbanization on natural enemies and positive effects of hotter urban temperatures on pests may reduce the potential for biological control in urban areas. However, little work has explored if high urban temperatures alter natural enemies communities or diminish efficacy of biological control. Understanding effects of temperature on pests and

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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 herbivore performance by increasing survival, developmental rate, weight gain, and fecundity, for a number of different feeding guilds, including mining, chewing, and sucking guilds (Zvereva and Kozlov 2006; Raupp et al. 2010). More impervious cover or less vegetation immediately around trees can increase temperature within tree canopies, where pests feed, and benefit pest fitness (Meineke et al. 2013; Dale and Frank 2014). For example, less overstory and understory immediately around red maples in Raleigh, NC, USA correlated with higher canopy temperature and greater *Melanaspis tenebricosa* fecundity and abundance (Dale and Frank 2014). High densities of other piercing-sucking pests on urban trees have also been attributed to hotter urban temperatures (Kropczynska et al. 1988; Schneider et al. 2000; Meineke et al. 2013). For example, *Eotetranychus 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 can be worsened by high temperatures and the additive effect of plant water stress and temperature can also affect herbivorous pests, although the consequences of plant water stress and its interaction with temperature varies by taxa (Hanks and Denno 1993; Koricheva et al. 1998; Huberty and Denno 2004; Dale and Frank 2017; Meineke and Frank 2018). For example, aphid densities often decrease with plant water stress, a phenomenon attributed to low turgor pressure, which makes phloem more difficult to access (Huberty and Denno 2004).

Natural enemies can vary in their response to hot urban temperatures. 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 (McKinney 2008; Faeth et al. 2011), which is in turn a major driver of natural enemy abundance and diversity (Pimental 1961; Root 1973; Shrewsbury and Raupp 2006; Raupp et al. 2010). Many studies have linked greater habitat complexity, in terms of 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 (Hanks and Denno 1993; Shrewsbury and Raupp 2006; Philpott and Bichier 2017; Rocha et al. 2018). For the purposes of this manuscript we define habitat complexity as structural complexity, or how densely different layers of vegetation, such as turf, groundcover, shrubs, understory, and overstory fill a habitat. The negative relationship between habitat complexity and impervious surface, which increases

temperature, suggests a potential for interaction between these variables in their effects on natural enemies (McKinney 2008). Thus, natural enemies may be more abundant 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). However, effects of temperature and vegetation likely vary among arthropods with different diets, in different feeding guilds, of different sizes, and with different dispersal behaviors, and could change natural enemy community structure and biological control. For example, greater mortality of *Stephanitis pyrioides* on azaleas in more complex habitats was attributed to more generalist natural enemies, which were present because of greater access to alternative prey resources (Shrewsbury and Raupp 2006). Alternatively, *Stethoconus japonicus*, the specialist natural enemy of *S. pyrioides*, was more abundant in less complex habitats where *S. pyrioides* was also more abundant (Shrewsbury and Raupp 2006). Although temperature was not explored in this system, greater light exposure, and thus potentially higher temperature, in less complex habitats in this system correlated with more *S. pyrioides* on azaleas (Shrewsbury and Raupp 2000). Few studies have assessed if temperature explains the presence of more natural enemies in structurally complex habitats in hot urban spaces, an area we hope to explore with this research.

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 aphids (*Tinocallis kahawaluokalani*) (Frank 2019). *T. kahawaluokalani* can be found throughout much of the range of crape myrtles, and therefore, is an important management consideration for landscape and nursery managers (Mizell et al. 2002; Chappell et al. 2012). This specialist herbivore, which was co-introduced with its host and eats 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: Anthochoridae), damsel bugs (Hemiptera: Nabidae) and syrphid flies (Diptera: Syrphidae) (Mizell and Schifauer 1987; Mizell 2007). 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 urban crape myrtles surrounded by high amounts of impervious cover (Parsons and Frank 2019). Since impervious surface cover increases canopy temperature of urban trees (Dale and Frank 2014; Dale et al. 2016), temperature may directly increase *T. kahawaluokalani* density by increasing developmental rate and fecundity.

We predict that canopy temperature and habitat complexity play important roles in the regulation of *Tinocallis kahawaluokalani*, natural enemies, and predation services on crape myrtle trees in urban areas. We predict that plant water stress also affects *T. kahawaluokalani* densities and that temperature and plant water stress together are key predictors of *T. kahawaluokalani* abundance. In our study we tested our predictions with the following hypotheses: 1) aphid abundance will increase as canopy temperature increases but less so on trees in structurally complex habitats; 2) natural enemy density and predation rates will decline as canopy temperature increases but less so on trees in structurally complex habitats 3) experimental increases in temperature will increase aphid fecundity and population growth; and 4) the highest densities of aphids will be found on hot trees that are less water stressed when compared to other trees in the study area. With these hypotheses we thus assume that an interaction exists between temperature and local structural complexity for both aphid and natural enemy responses. To test our hypotheses, we measured temperature, plant water potential, and local structural complexity around urban crape myrtle trees in Raleigh, NC and examined their effect on *T. kahawaluokalani* density, natural enemies, and estimated predation rate in the field. Then, we conducted lab experiments to determine how temperature affects aphid fecundity and population growth. Our study is valuable in understanding how urban temperatures may differentially affect tree pests, natural enemies, and predation services, and explores if increasing habitat complexity immediately around trees may be a means to reduce pests and improve biological control services on city trees.

## Methods

### Study sites

This study was conducted on North Carolina State Campus in Raleigh, NC, USA from May–August 2018. We randomly selected 33 crape myrtles (*Lagerstroemia indica x fauriei* ‘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 (Fig. S1). Trees were at least 100 m 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. Instead we adapted methods from Meineke et al. (2016) and set iButtons to record temperature at 3-h intervals and only used sunset temperatures between 1800 and 2100 h for analyses. Direct sunlight on iButtons can cause spikes in readings, which may not be representative of overall canopy temperatures. Thus, 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). However, mid-day averages were also calculated to compare which set of averages were better at predicting aphid abundance.

### Measuring plant water potential

To assess tree water stress pre-dawn (2:00 am–6:30 am) xylem water potential was measured using a pressure chamber (PMS Instrument Company, Albany, OR) (Dale and Frank 2017; Long et al. 2019). A growing number of urban studies are using pre-dawn measurements to assess plant water potential of street trees (Levinsson et al. 2015; Savi et al. 2015; Long et al. 2019). 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, 15–20 cm in length, from the canopies of study trees approximately 4–6 m 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 (2000). Temporary grids of 10 × 10 m 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 m 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 10 × 10 m grid space, each vegetation strata was identified and scored as present or absent in each 1 × 1 m 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 1 × 1 m square therefore was 5. Similarly, the maximum number of squares any one vegetation layer occupied was 100, meaning the vegetation layer occupied all 1 × 1 m 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 1 × 1 m 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 to 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 2019) that concluded that  $H'$  values explained more variation in aphid and natural enemy abundance than total structural complexity index values. For example, models with Shannon  $H'$  values explained 10–15% more variation in natural enemy abundance in previous work when compared to models with total structural complexity (Parsons and Frank 2019).

## 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 three times 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.

Because a main focus of our study was to broadly assess temperature effects on natural enemies in street tree canopies, we identified and counted all natural enemies in samples, even if they were not known predators of *T. kahawaluokalani*.

## Predation experiments

Sentinel *Helicoverpa zea* eggs were used as factitious prey items to assess predation services on crape myrtles (Nuessly and Sterling 1994; Pfannenstiel and Yeorgan 2002; Gardiner et al. 2014). Although measuring predation of *H. zea* eggs cannot be equated with measuring the predation of *T. kahawaluokalani*, it provides some indication of predation by natural enemies on street trees, an area of work that has rarely been studied in urban areas, and a primary focus of this study. Frozen *H. zea* eggs were purchased from Frontier Agricultural Sciences (Newark, DE). Eggs were received frozen on mesh cloth from which we cut 1 × 1 cm 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 1 × 1 cm 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 4 cm plastic tube, and a mesh top. The other square was uncaged (Fig. 1). After 24 h 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-l pots in climate-controlled growth chambers



**Fig. 1** Caged and uncaged treatments in predation experiments. **a** Uncaged treatments of *H. zea* eggs on an egg cloth attached to a leaf on a study tree. **b** Caged treatments of *H. zea* eggs on a leaf attached to a study tree

on NC State campus. Aphids were collected in the field from Natchez' crape myrtles and transferred to trees in the lab to start colonies. 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  $26^{\circ} \pm 1^{\circ}\text{C}$ ,  $29^{\circ}\text{C} \pm 1^{\circ}\text{C}$ , and  $32^{\circ}\text{C} \pm 1^{\circ}\text{C}$  during day time hours and  $21^{\circ}\text{C}$ ,  $24^{\circ}\text{C}$ , and  $27^{\circ}\text{C}$  during night hours. Day hours extended from 6:00–20:00 (14-h day/10-h 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 n.d.). Aphid colonies were reared for 2 weeks. 25 cm 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 h for eight days to record the number of nymphs produced. Trials were terminated at eight days because all adults in the  $32^{\circ}\text{C}$  chamber died. The experiment was performed twice. Colony trees were rotated among chambers and acclimated to chambers for 48 h 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-l 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 trees 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. We removed clip cages after a week to prevent crowding, which can affect

population growth. 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 were performed in R Version 3.4.3 (R Core Team 2017). Statistical model analyses were performed to test a priori hypotheses and explore predictor relationships with responses and interactions among variables (Table 1, Table S1).

Responses for model analyses included number of aphids and natural enemies collected on collection day and predation effect size. We used generalized linear mixed effects models with negative binomial distribution to account for overdispersion, as the variance was larger than the mean in both responses (Zuur et al. 2009, 2010). We chose to analyze our data with generalized linear models with a negative binomial distribution because these models are appropriate for highly overdispersed count data, such as ours, particularly when compared to models with other distribution types, such as Poisson, or linear models with log transformed responses (Zuur et al. 2009, 2010). Predation effect size was calculated using methods from Philpott and Bichier (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-h 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. Generalized linear mixed effects models with negative binomial distribution incorporating random effect terms for tree and date were used to account for design, using the *lme4* package in R (Bates et al. 2015). 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 all models in analyses. We also report AICc (Akaike information criterion adjusted for small sample size) for each model to demonstrate how well models explain variation in response when compared to other models in the candidate set (Burnham and Anderson 2002). We used Moran's I correlation coefficient to test for independence of observations and detect if spatial autocorrelation was present for models using the DHARMA package in R

**Table 1** Aphid models. Outputs for generalized linear mixed effect models with negative binomial distribution. Bold indicates predictors with significance ( $p < 0.05$ ). AICc values are reported for each model. Models with lower AICc values are better than models with higher AICc values at explaining variation in response with the least number of parameters. \*Indicates models that test a priori hypotheses

Aphid Models		Marginal R <sup>2</sup>	AICc	df*	Est.	SE	z-value	p
MODEL1*	Intercept	0.26	884.3	149	12.257	1.552	7.894	<0.001
	Temp				-0.397	0.055	-7.140	<0.001
MODEL2	Intercept	0.08	919.9	149	0.155	0.322	0.483	0.629
	Local Veg.				<b>1.154</b>	<b>0.363</b>	<b>3.177</b>	<0.01
MODEL3	Intercept	0.04	924.7	149	<b>2.736</b>	<b>0.783</b>	<b>3.493</b>	<0.001
	Water Potential				<b>6.908</b>	<b>3.177</b>	<b>2.174</b>	<0.05
MODEL4	Intercept	0.30	883.2	147	11.766	8.608	1.367	0.172
	Water Pot.xTemp				0.3507	1.248	0.281	0.779
MODEL5*	Intercept	0.40	871.3	147	<b>21.045</b>	<b>3.676</b>	<b>5.724</b>	<0.001
	Local Veg.				-0.113	0.043	-2.642	<0.01
	Temp.				-0.746	0.133	-5.6	<0.001
	Local Veg.xTemp				<b>0.004</b>	<b>0.0015</b>	<b>2.906</b>	<0.01
MODEL6	Intercept	0.34	877.1	148	<b>11.470</b>	<b>1.568</b>	<b>7.311</b>	<0.001
	Local Veg.				<b>1.149</b>	<b>0.355</b>	<b>3.232</b>	<0.01
	Temp.				<b>-0.401</b>	<b>0.056</b>	<b>-7.141</b>	<0.001
MODEL7*	Intercept	0.30	881.1	148	<b>14.137</b>	<b>.761</b>	<b>8.027</b>	<0.001
	Water Pot.				<b>7.459</b>	<b>3.100</b>	<b>2.406</b>	<0.05
	Temp.				<b>-0.399</b>	<b>0.055</b>	<b>-7.184</b>	<0.001
MODEL8	Intercept	0.09	921.2	147	0.233	1.673	0.139	0.889
	Water Pot.x Local Veg				6.321	7.614	0.830	0.406
MODEL9	Intercept	0.09	919.8	148	1.417	0.871	1.627	0.103
	Water Pot.				4.660	3.033	1.537	0.124
	Local Veg.				<b>0.998</b>	<b>0.372</b>	<b>2.680</b>	<0.01
MODEL10	Intercept	0.42	876.1	143	<b>19.167</b>	<b>6.976</b>	<b>2.748</b>	<0.01
	WaterxTempxVeg				-1.079	0.687	-1.571	0.116

All models had conditional R<sup>2</sup> values of 0.95

For non-significant interactions, only estimates for the intercept and interaction term are displayed

\*Residual degrees of freedom

(Hartig 2019). Lastly, we assessed residual plots in R with the DHARMA package to check linear assumptions of all models.

We tested our a priori hypotheses and interactions among variables (Table 1). For aphids, the models used to test our a priori 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 natural enemies and predation, the models used to test our a priori 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.

### 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. Aphid fecundity and population growth was evaluated with a non-parametric Kruskal-Wallis

test, as aphid density failed to meet the assumptions of normality and homogeneity of variance. 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

From May–August average mid-day temperatures ranged from 20.25–37.75 °C and sunset temperatures ranged from 20.75–35.5 °C. Average sunset temperatures calculated for one-week prior to collection dates were most correlated with aphid abundance (marginal  $R^2 = 0.23$ ) when compared to 2-week mid-day (marginal  $R^2 = 0.12$ ) and sunset averages (marginal  $R^2 = 0.09$ ) and one-week mid-day averages (marginal  $R^2 = 0.21$ ). Therefore, average sunset temperatures for the week prior to collection date of aphids were used in all aphid models. Similarly, average sunset temperatures for the week prior to the collection date of natural enemies were 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 to 1.43 ([mean  $\pm$  SD]  $0.77 \pm 0.38$ ). 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  $-0.17$  MPa to  $-0.36$  MPa ([mean  $\pm$  SD]  $-0.245 \pm 0.046$ ). No significant correlations existed among the predictors: local structural complexity, drought, and temperature (Pearson Product Correlation  $p > 0.05$ ), and local structural complexity was also *not* predictive of canopy temperature.

### Temperature effects on aphid abundance

Temperature significantly explained some variation in aphid abundance ( $p < 0.001$ , marginal  $R^2 = 0.26$ ). However, aphid density decreased with hotter canopy temperatures (Table 1), which was not expected. For every degree increase in temperature, aphid density decreased by 0.40 aphids. Thus, our first a priori hypothesis that aphids would increase with temperature was not supported. The interaction between local structural complexity and temperature was significant ( $p < 0.01$ ), meaning that the effect of temperature on aphids depended on local structural complexity. However, in the presence of this interaction overall aphid abundance still decreased as temperature increased. Furthermore, the effect size of this interaction was almost negligible ([Est.  $\pm$  SE]  $0.004 \pm 0.002$ ). Thus, our second a priori hypothesis that the positive effect of temperature on aphid abundance would be reduced in more complex habitats was not supported. Our last hypothesis that hotter trees that

were less stressed would have more aphids was not supported (Table 1). Although temperature and water potential were significant predictors of aphid abundance, and although aphids were more abundant on less stressed trees, aphids were less abundant on hot trees (Table 1). Individually water potential was a significant predictor of aphid density ( $p < 0.05$ ), although it only explained 4% of the variation in aphid response (marginal  $R^2 = 0.04$ ) (Table 1). Aphid density decreased as water potential decreased, meaning that more water stressed trees had fewer aphids (Table 1). Lastly, natural enemy abundance was not a significant predictor of aphid density ( $p > 0.05$ ).

### Temperature effects on natural enemy abundance

Temperature was a significant negative predictor of natural enemy abundance, thus supporting our first a priori hypothesis ( $p < 0.001$ ) (Table 2). However, the goodness of fit for this model was poor compared to other models in the candidate set (marginal  $R^2 = 0.01$ ). In support of our second a priori hypothesis, local structural complexity was a significant and positive predictor of natural enemies ( $p < 0.01$ ) and explained 12% of variation in natural enemy response (marginal  $R^2 = 0.12$ ) (Table 2). Our last hypothesis was not supported, as the interaction of temperature with local structural complexity was not significant, suggesting that the effect of local structural complexity on natural enemies did not depend on temperature. Aphid abundance was not a significant predictor of natural enemy abundance ( $p > 0.05$ ).

Individual natural enemy groups had different responses to temperature. Temperature had a significant and positive effect on spiders ( $p < 0.05$ , [Est.  $\pm$  SE]  $0.19 \pm 0.080$ ), while it had a significant and negative effect on *Orius insidiosus* ( $p < 0.001$ , [Est.  $\pm$  SE]  $-1.9 \pm 0.425$ ) and neuropterans ( $p < 0.001$ , [Est.  $\pm$  SE]  $-1.38 \pm 0.142$ ). All other natural enemy relationships with temperature were nonsignificant.

### Temperature effects on egg predation

Caged treatments had significantly more *H. zea* eggs than uncaged treatments after 24-h, indicating significant predation ( $p < 0.001$ , [Est.  $\pm$  SE]  $1.12 \pm 0.160$ ) (Fig. 2). However, none of the tested a priori models were good at explaining variation in predation effect size (Table 3). Natural enemy abundance was also not a significant predictor of egg predation ( $p > 0.05$ ).

### 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. 3). Trials were terminated at eight days because all adults in the 32 °C chamber died.

**Table 2** Natural enemy models. Outputs for generalized linear mixed effect models with negative binomial distribution. Bold indicates predictors with significance ( $p < 0.05$ ). AICc values are reported for each model. Models with lower AICc values are better than models

with higher AICc values at explaining variation in response with the least number of parameters. \*Indicates models that test a priori hypotheses

Natural Enemy Models		Marginal R <sup>2</sup>	AICc	df*	Est.	SE	z-value	p
MODEL1*	Intercept	0.01	495.7	88	<b>3.603</b>	<b>0.001</b>	<b>1980.8</b>	<b>&lt;0.001</b>
	Temp				<b>-0.073</b>	<b>0.001</b>	<b>-44.79</b>	<b>&lt;0.001</b>
MODEL2*	Intercept	<b>0.122</b>	<b>488.3</b>	88	<b>0.944</b>	<b>0.201</b>	<b>4.685</b>	<b>&lt;0.001</b>
	Local Veg.				<b>0.695</b>	<b>0.225</b>	<b>3.082</b>	<b>&lt;0.01</b>
MODEL3	Intercept	0.007	496.5	88	<b>1.847</b>	<b>0.001</b>	<b>1022.7</b>	<b>&lt;0.001</b>
	Water Potential				<b>1.507</b>	<b>0.001</b>	<b>835.2</b>	<b>&lt;0.001</b>
MODEL4	Intercept	0.02	499.5	86	<b>-2.474</b>	<b>0.001</b>	<b>-1358.4</b>	<b>&lt;0.001</b>
	Water Pot.				-25.460	0.001	-13,988	<b>&lt;0.001</b>
	Temp.				0.149	0.001	91.31	<b>&lt;0.001</b>
	Water Pot.xTemp				<b>0.931</b>	<b>0.001</b>	<b>510.57</b>	<b>&lt;0.001</b>
MODEL5*	Intercept	0.13	492.1	86	2.899	4.69	0.618	0.536
	Local Veg.xTemp				0.007	0.184	0.042	0.967
MODEL6	Intercept	0.13	489.8	87	2.72	1.902	1.430	0.152
	Local Veg.				<b>0.676</b>	<b>0.224</b>	<b>3.009</b>	<b>&lt;0.01</b>
	Temp.				-0.060	0.064	-0.938	0.348
MODEL7	Intercept	0.02	497.5	87	<b>4.028</b>	<b>0.001</b>	<b>2213.4</b>	<b>&lt;0.001</b>
	Water Pot.				<b>1.602</b>	<b>0.001</b>	<b>881.6</b>	<b>&lt;0.001</b>
	Temp.				<b>-0.07</b>	<b>0.001</b>	<b>-45.47</b>	<b>&lt;0.001</b>
MODEL8	Intercept	0.17	490.0	86	<b>2.705</b>	<b>1.191</b>	<b>2.271</b>	<b>&lt;0.05</b>
	Water Pot.x Local Veg				-8.951	5.323	-1.681	0.092
MODEL9	Intercept	0.122	490.6	87	0.933	0.559	1.668	0.095
	Water Pot.				-0.040	1.978	-0.021	0.983
	Local Veg.				<b>0.696</b>	<b>0.231</b>	<b>3.015</b>	<b>&lt;0.01</b>
MODEL10	Intercept	0.19	497.5	82	36.465	32.63	1.117	0.264
	WaterxTempxVeg				5.939	4.845	1.226	0.220

All models had conditional R<sup>2</sup> values of 0.63

For non-significant interactions, only estimates for the intercept and interaction term are displayed

\*Residual degrees of freedom

## Temperature effects on population growth

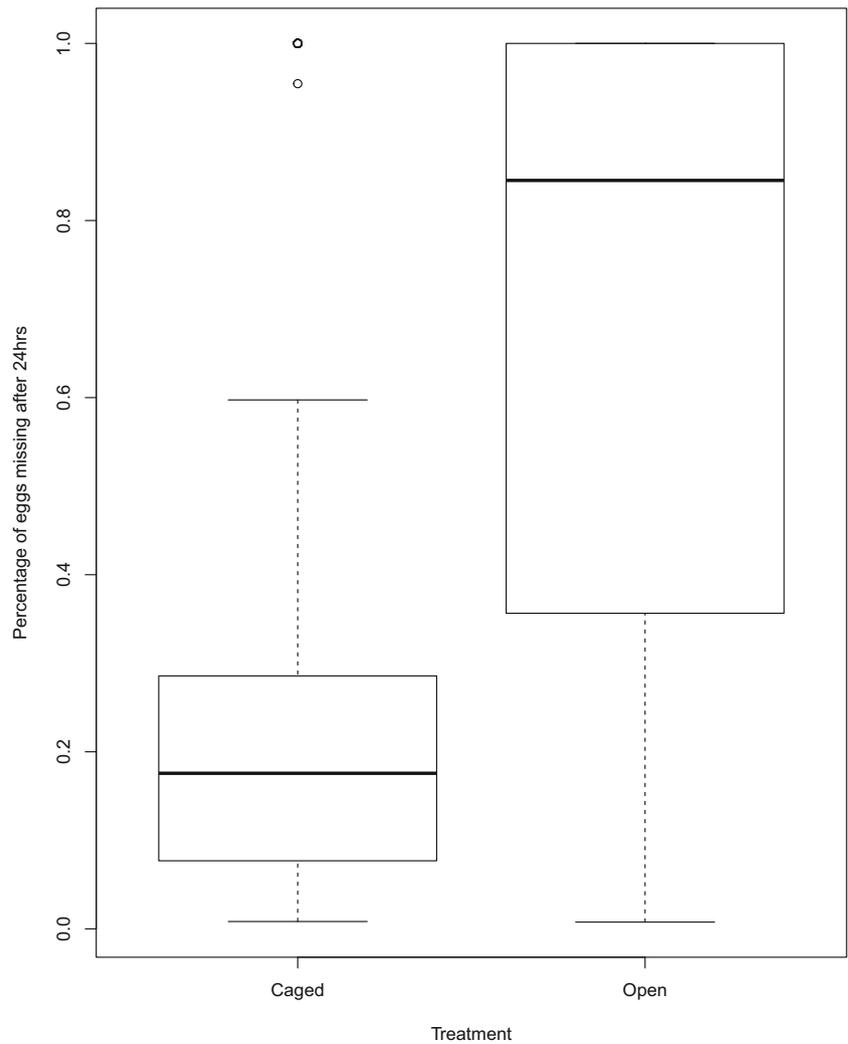
We predicted that population growth would be highest at 32 °C but found that the 29 °C treatment had significantly more aphids than the 26 °C treatment (Dunn Test,  $p < 0.01$ ), and the 32 °C treatment (Dunn Test,  $p < 0.05$ ) (Kruskal-Wallis test,  $p < 0.01$ ) (Fig. 4).

## Discussion

As our world becomes warmer and more urban, understanding how temperature affects pests, 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 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, a result we attribute to the lack of overstory trees present around crape myrtles in our study. Local structural complexity was a significant predictor of natural enemy abundance, and, although temperature had a significant negative effect on natural enemies, this relationship was weak. Together these results indicate that crape myrtles in hot urban areas of Raleigh, NC may be less likely to have high

**Fig. 2** Percentage of *H. zea* eggs missing in caged and uncaged treatments. The boxplots here show the interquartile ranges of percentages of eggs missing after 24 h. The median of the data range is marked by the line that divides boxes. Asterisks indicate significant differences. Open treatments had significantly more eggs missing after 24 h than caged treatments, indicating predation



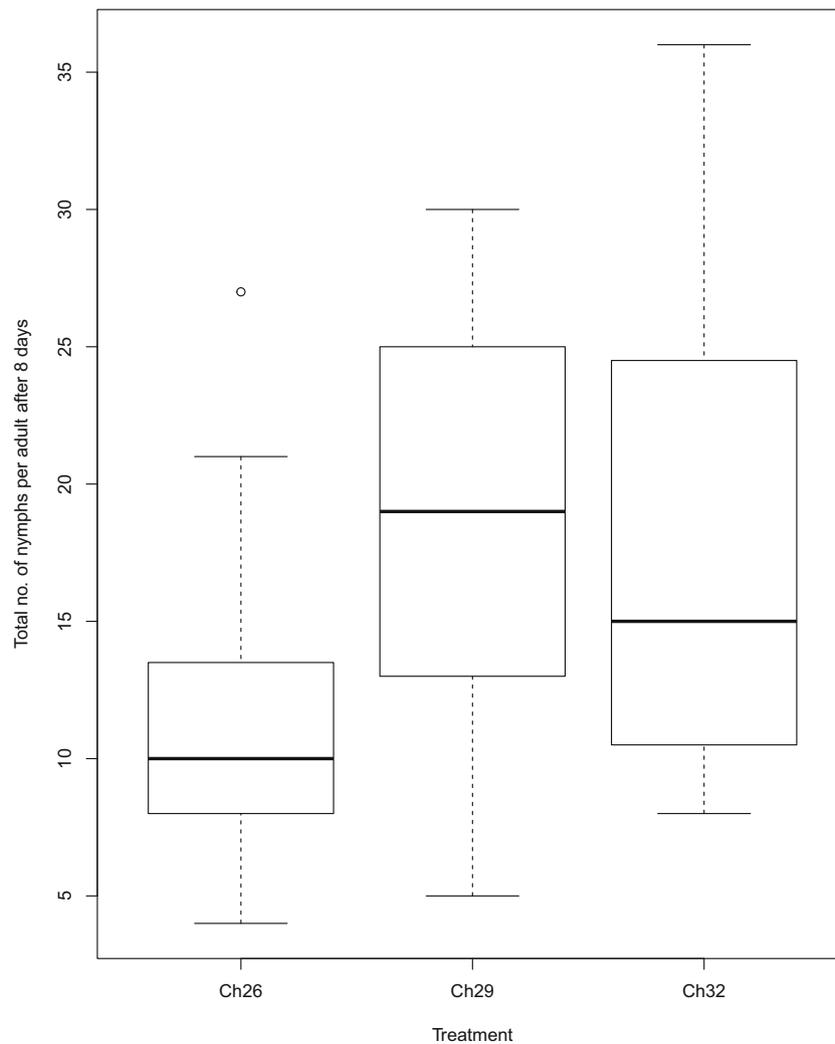
**Table 3** Predation models. Outputs for generalized linear mixed effect models with negative binomial distribution for a priori hypotheses. Bold indicates predictors with significance ( $p < 0.05$ )

Predation Models		Marginal R <sup>2</sup>	AICc	df*	Est.	SE	z-value	p
Model 1		0.002	593.2	189				
	Intercept				-0.198	0.840	-0.236	0.814
	Temperature			0.022	0.028	0.790	0.429	
Model2		0	593.6	189				
	Intercept				<b>0.442</b>	<b>0.123</b>	<b>3.575</b>	<b>&lt;0.0001</b>
	Local Veg.				0.028	0.144	0.196	0.8447
Model3		0.002	597.3	187				
	Intercept				0.139	0.595	0.235	0.815
	Water Pot. x Local Veg.			0.0174	0.017	1.023	0.306	

All models had conditional R<sup>2</sup> values of less than 0

For non-significant interactions, only estimates for the intercept and interaction term are displayed

\*Residual degrees of freedom



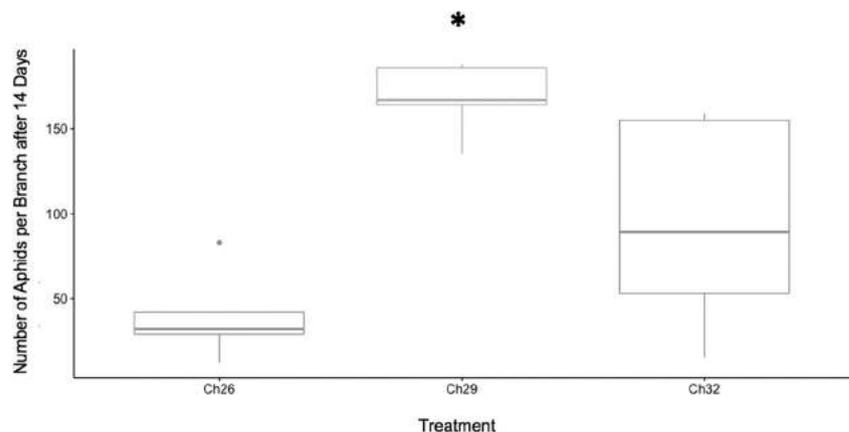
**Fig. 3** Total nymphal production of adults per twig after eight-days at 26 °C, 29 °C, and 32 °C. The boxplots here show the interquartile ranges of aphid nymphs produced after 8 days. The median of the data range is marked by the line that divides boxes. Although more nymphs were

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

densities of *T. kahawaluokalani* and less susceptible to aphid damage than crape myrtles in cooler parts of the city. These results also suggest that increasing structural complexity,

particularly within the understory, shrub, and herbaceous layers around crape myrtles, may be a design solution to bolster natural enemy densities on crape myrtles. Although in our

**Fig. 4** Aphid density on branches 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



study we did not directly assess top-down effects by natural enemies on *T. kahawaluokalani*, our results highlight how hot urban temperatures, a shared element of cities, affects a pest, natural enemies, and one type of predation service on city trees, an area of work that has not been thoroughly explored.

Hotter temperatures in urban areas may contribute to higher densities of some species of insect herbivores (Kropczynska et al. 1988; Schneider et al. 2000; Meineke et al. 2013; Meineke et al. 2014; Dale and Frank 2014), 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 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). 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 why densities are low on hot trees. Furthermore, provided that crape myrtle susceptibility to *T. kahawaluokalani* differs by cultivar (Herbert et al. 2009), an exploration of *T. kahawaluokalani* fecundity and population growth under different temperature conditions and on different crape myrtle cultivars, beyond those used in this study, may provide a more comprehensive assessment of temperature effects on this specialist aphid.

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 cover can reduce light exposure and temperature in urban environments on focal plants (Shrewsbury and Raupp 2000; Dale and Frank 2014), and, in our case, may increase climatic refugia for *T. kahawaluokalani* on crape myrtle trees. Given that less than 25 % of the trees in this study were planted under canopy, 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.

Local structural complexity was a significant positive predictor of natural enemy abundance, yet temperature had a weak 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, and not necessarily because of the cooler microclimates they may provide. (Letourneau 1987; Landis et al. 2000; Langellotto and Denno 2004; Shrewsbury and Raupp 2006; Letourneau et al. 2011). Our work concurs with the Enemies Hypothesis (Pimental 1961; Root 1973) and other urban studies that have found that increasing local structural complexity increases natural enemy abundance and top-down control of pests (Shrewsbury and Raupp 2006; Philpott and Bichier 2017). However, more work would need to be done to determine which mechanisms are driving natural enemy abundance in this system. Furthermore, natural enemy groups are affected differently by temperature. For example, 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 a strong 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.

Increasing structural complexity can increase both natural enemy abundance and predation biological control services in urban gardens and ornamental landscapes. For example more local structural complexity in urban gardens resulted in greater biological control of aphids in the California central coast region (Philpott and Bichier 2017). However, landscape-scale habitat complexity 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 et al. 2018). For example, Lowenstein and Minor (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 2019), showed that high structural complexity was one of the best predictors of predation 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; Pfannenstiel 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) 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 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 2019) 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 2019), which may have contributed to similar predation rates on trees across the study area.

Our study highlights the potential effects that hot urban temperatures can have on a pest, natural enemies, and predation services in the canopies of street trees. However, the generalizability of our results may be limited to crape myrtles and cities with a similar climate to Raleigh, NC. Crape myrtles, *T. kahawaluokalani*, and its natural enemies make up a unique model system. Unlike most aphids, *T. kahawaluokalani* has no known parasitoids either in the U.S. or in its native range (Mizell et al. 2002). Researchers of this aphid have speculated this to be consequence of the unique plant chemistries of crape myrtles, particularly present in its alkaloid profile (Riddle and Mizell 2016). One study exploring the effects of a strict *T. kahawaluokalani* diet on *Chrysoperla rufilabris* larvae, found that *Chrysoperla rufilabris* did not develop to adults when exposed to a strict diet of *T. kahawaluokalani* on certain cultivars (Herbert 2009). These findings may suggest why we did not find a relationship between *T. kahawaluokalani* and natural enemy densities on crape myrtles. These findings also suggest that strong plant mediated effects are at play and may limit the extent to which results can be interpreted for other street tree pest-natural enemy complexes.

Our study fills a gap in the research by exploring how temperature affects natural enemies and predation services on street trees, an area of study that has remained largely unexplored. Our study also highlights that, contrary to many previous studies, not all urban tree pests respond similarly to warming temperatures. As the climate gets warmer and cities get bigger, better understanding how pests, natural enemies, and biological control respond to warming on urban trees will be key in implementing effective urban pest management programs. Studies like ours can help identify key priority pest and natural enemy targets, as well as design solutions that can mitigate the effects of pests on urban trees in a warming world.

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**Author's contributions** S.E.P and S.D.F conceived of experimental design. S.E.P. collected and analyzed the data. K.S.S. and A.A.W. collected data for lab experiments. All authors contributed to drafts and gave approval for publication.

## Compliance with ethical standards

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

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