Ecological Applications, 24(7), 2014, pp. 1596–1607

Urban warming trumps natural enemy regulation of herbivorous pests

ADAM G. DALE[1] AND STEVEN D. FRANK

North Carolina State University, Campus Box 7613, Raleigh, North Carolina 27695 USA

Abstract. Trees provide ecosystem services that counter negative effects of urban habitats on human and environmental health. Unfortunately, herbivorous arthropod pests are often more abundant on urban than rural trees, reducing tree growth, survival, and ecosystem services. Previous research where vegetation complexity was reduced has attributed elevated urban pest abundance to decreased regulation by natural enemies. However, reducing vegetation complexity, particularly the density of overstory trees, also makes cities hotter than natural habitats. We ask how urban habitat characteristics influence an abiotic factor, temperature, and a biotic factor, natural enemy abundance, in regulating the abundance of an urban forest pest, the gloomy scale, (*Melanaspis tenebricosa*). We used a map of surface temperature to select red maple trees (*Acer rubrum*) at warmer and cooler sites in Raleigh, North Carolina, USA. We quantified habitat complexity by measuring impervious surface cover, local vegetation structural complexity, and landscape scale vegetation cover around each tree. Using path analysis, we determined that impervious surface (the most important habitat variable) increased scale insect abundance by increasing tree canopy temperature, rather than by reducing natural enemy abundance or percent parasitism. As a mechanism for this response, we found that increasing temperature significantly increases scale insect fecundity and contributes to greater population increase. Specifically, adult female *M. tenebricosa* egg sets increased by approximately 14 eggs for every 1°C increase in temperature. Climate change models predict that the global climate will increase by 2–3°C in the next 50–100 years, which we found would increase scale insect abundance by three orders of magnitude. This result supports predictions that urban and natural forests will face greater herbivory in the future, and suggests that a primary cause could be direct, positive effects of warming on herbivore fitness rather than altered trophic interactions.

Key words: Acer rubrum; *climate change; enemies hypothesis;* Melanaspis tenebricosa; *pest abundance; temperature; urban ecology; urban forest; urban heat island.*

INTRODUCTION

Trees are essential to urban habitats because they provide ecosystem services such as air filtration, temperature reduction, carbon sequestration, and enhanced aesthetic value (Oke et al. 1989, Nowak and Dwyer 2000, Dawe 2011) that improve human health (Donovan et al. 2013). Unfortunately, herbivorous arthropods are often more abundant on urban than rural trees (Hanks and Denno 1993*a*, Speight et al. 1998, Raupp et al. 2010), reducing tree health (Zvereva et al. 2010) and the ecosystem services they provide. However, the factors that increase herbivore abundance in urban areas are not well understood (Raupp et al. 2010).

For decades, ecologists have debated the importance of abiotic and biotic factors in regulating herbivore abundance and distribution (Hunter et al. 1992). Andrewartha and Birch (1948) proposed that abiotic factors, such as rainfall, temperature, and humidity regulate herbivore distribution. In contrast, Hairston et al. (1960) argued for the importance of biotic factors such as predation and parasitism. Most research on herbivores in urban environments has focused on the hypotheses of Hairston et al. (1960), attributing increased herbivore abundance on urban plants to ineffective biological control by natural enemies (Frankie and Ehler 1978, Kahn and Cornell 1989, Hanks and Denno 1993*a*, Shrewsbury and Raupp 2000, 2006, Tooker and Hanks 2000). However, the influences of abiotic components of urban environments on herbivores, such as the urban heat island effect, have not been examined. In this study, we investigate how heat, a ubiquitous abiotic factor in cities, and natural enemies, a biotic factor, affect scale insect fitness and abundance on urban street trees. The relative influence of natural enemies and urban heat on pest populations is of direct relevance to management of these trees because the management implications differ depending on which factor is most important. As cities expand and the global climate changes, the extent of urban warming will increase and natural areas will experience warming similar to that of cities; therefore, temperature may be

Manuscript received 19 October 2013; revised 21 February 2014; accepted 24 February 2014. Corresponding Editor: J. M. Marzluff.

[1] E-mail: agdale2@ncsu.edu

highly important and influential in both urban and natural habitats.

The enemies hypothesis predicts that increased habitat complexity will support more natural enemies, which then more intensively regulate herbivore populations (Root 1973). This prediction is consistent with the importance of biotic regulation proposed by Hairston et al. (1960) and has been supported by studies in natural (Maron and Harrison 1997, Hawkins et al. 1999), agricultural (Letourneau 1987, Bianchi et al. 2006), and urban landscapes (Hanks and Denno 1993*a*, Shrewsbury and Raupp 2000, 2006, Tooker and Hanks 2000, Frank and Shrewsbury 2004). Specifically, in urban landscapes Shrewsbury and Raupp (2006) used a vegetation structural complexity index to rate urban yards as simple or complex based on the amount and frequency of vegetation. They found that azalea lace bug, *Stephanitis pyrioides* (Scott) (Hemiptera: Tingidae), abundance was greater in yards with simple vegetation, compared to yards with complex vegetation. This greater pest abundance was attributed to lower predator abundance in simple urban yards. Shrewsbury and Raupp (2000) also found that sun exposure was greater in simple yards and one of the best predictors of lace bug abundance. Others have associated greater pest abundance and damage with sun exposure in natural (Louda et al. 1987, Moore et al. 1988) and urban habitats (Kahn and Cornell 1989). Direct sun exposure increases temperature yet the effect of habitat complexity on natural enemies has never been separated from habitat effects on temperature.

Urban habitats are up to 10°C warmer than surrounding rural habitats (Oke 1973, Kim 1992) as a result of anthropogenic heat sources, increased impervious surface, and reduced vegetation cover (Nowak and Dwyer 2000). As vegetation cover is reduced, it is either replaced by or exposes impervious surfaces (Nowak and Greenfield 2012), which absorb and reradiate heat from solar radiation and anthropogenic heat sources (Oke et al. 1989) resulting in what is referred to as an urban heat island effect. Warmer temperatures can decrease arthropod development time and increase survival and fitness (Kozlowski 1992, Berger et al. 2008). Therefore, increased herbivore abundance in urban habitats may be attributable to temperature effects on arthropod physiology. Only one study has directly examined the influence of heat on arthropod pest abundance in urban habitats: Meineke et al. (2013) found that soft scale insect (Hemiptera: Coccidae) abundance varied 13-fold across a 2.4°C urban temperature gradient. However, this study focused on the effects of temperature without directly addressing the cause of temperature differences among study sites. Our goal is to separate the effects of habitat complexity on temperature from its well-documented effects on natural enemies, to examine the relative importance of abiotic and biotic factors in regulating pest abundance on urban trees.

Over a century ago, Metcalf (1912) documented greater abundance of gloomy scale, *Melanaspis tenebricosa* (Comstock) (Hemiptera: Diaspididae), on urban street trees, compared to rural street trees in Raleigh, North Carolina, USA. Since then, in concert with the loss of elm and chestnut trees to pests, maples have become one of the most commonly planted genera of street trees in eastern North America (Raupp et al. 2006). *Melanaspis tenebricosa* persists as the most important pest of red maple in the southeastern United States but is rarely found on trees outside of urban areas (Metcalf 1922, Frank et al. 2013). The injurious effects of *M. tenebricosa* feeding on tree health are apparent and widespread in urban habitats (Frank et al. 2013) but the forces driving increased abundance are not well understood.

We examined the contributions of impervious surface groundcover, coarse vegetation groundcover, and local vegetation structural complexity to temperature and natural enemy abundance, and, in turn, the influence of temperature and natural enemy abundance on *M. tenebricosa* abundance. Our hypothesis was that simple habitats with more impervious surface cover and less vegetation cover would be warmer and have greater *M. tenebricosa* abundance than more complex habitats with less impervious surface cover. To identify mechanisms by which warming could increase scale insect abundance we examined the relationship between temperature and *M. tenebricosa* parasitism, fecundity, and population increase. Our hypothesis was that parasitism would not be affected by temperature but that *M. tenebricosa* fecundity and population growth would increase as temperature increased.

METHODS

Study system and species

Red maples (*Acer rubrum*) are deciduous trees indigenous to the eastern United States (Nesom 2006). *Melanaspis tenebricosa* is a key native pest of red maple trees in the southeastern United States (Metcalf 1922). These scale insects live on the trunk and branches (Fig. 1) of maple trees, where they extract fluids from within woody tissues (Metcalf 1922, Frank et al. 2013). They are univoltine and overwinter as mated adult females, with immature stages active for 6–8 weeks beginning in late spring (Metcalf 1922). Scales accumulate on the bark, causing discoloration, premature leaf drop, branch dieback (see Plate 1), and occasionally tree death (Metcalf 1922, Frank et al. 2013). There are several predators that attack immature stages of armored scale including: Coccinellidae (Coleoptera), Dolichopodidae (Diptera), Syrphidae (Diptera), Anthocoridae (Hemiptera), Geocoridae (Hemiptera), Chrysopidae (Neuroptera), and Hemerobiidae (Neuroptera) (Drea and Gordon 1990). Gloomy scales are also parasitized by at least five species of parasitoid wasps from the families Aphelinidae, Encyrtidae, and Signiphoridae (Miller and Davidson 2005; A. G. Dale and S. G. Frank, *unpublished data*).

FIG. 1. Photographs of a *Melanaspis tenebricosa*-infested red maple tree in an urban landscape. Close-up of a twig heavily infested with *M. tenebricosa* (left). Red maple street tree located in a simple urban habitat composed of turf and impervious surface in Raleigh, North Carolina, USA (right).

Study sites

We conducted field studies on red maple trees at 26 sites throughout the Raleigh, North Carolina metropolitan area. Study sites varied across a gradient of vegetation and ground cover from a parking lot tree planted in 16 m^2 of soil, to street trees in turf planting strips (Fig. 1) and trees in residential front lawns. Sites were selected using a thermal map constructed from surface temperature measurements in band 6 of Landsat-5 World Reference System 2 (WRS-2) path 16, row 35 images acquired on 18 August 2007 (Fig. 2; Meineke et al. 2013). We overlaid a map of red maple locations (provided by the Raleigh Parks and Recreation Department) in ArcMap (ArcGIS Desktop 10; ESRI, Redlands, California, USA) and selected 13 red maples within relatively hot sites and 13 within relatively cool sites of the thermal map (Fig. 2).

Vegetation structural complexity

We define vegetation structural complexity as an index of the amount and structure of vegetation at each study site based on the frequency of vegetation in three-dimensional space (Erdelen 1984, Shrewsbury and Raupp 2000). We quantified three-dimensional vegetation structural complexity around each study tree using methods described by Shrewsbury and Raupp (2000). With the tree in the center, we measured and marked a 10 × 10 m area around each study tree. The vertical dimension of this area consists of five vegetation strata layers, creating a 500-cubic-unit grid. These layers are ground cover (e.g., turf, English ivy), annuals/perennials, shrubs, understory tree species, and overstory tree species (Shrewsbury and Raupp 2000). We recorded immature overstory tree species as part of the understory. We assigned each box within the grid a 1 or 0 based on the presence or absence of vegetation. Ratings could reach a maximum of 500, representing the most structurally complex vegetation. Vegetation complexity ratings measure the quantity of vegetation in a habitat but do not account for the distribution of vegetation among strata. As a second measure of structural complexity, we used Shannon's diversity index to calculate an index of vegetation complexity at each site (Primer v6; PRIMER-E, Lutton, Ivybridge, UK). Using this index, we treated vegetation strata as a "species" and box counts within each strata as "abundance." In addition to including total structural complexity scores in our path analysis we analyzed the correlation between each strata and *M. tenebricosa* abundance and mean site temperature to assess the importance of each strata.

Ground cover

To examine the habitat around each study site on a larger scale, we analyzed the ground cover around each tree in ArcMap (ArcGIS10) using impervious surface and coarse vegetation groundcover data in Raleigh, North Carolina (Bigsby et al. 2013). Bigsby et al. (2013) delineated six groundcover types at a 1-m resolution, which included tree, water, road, building, grass, and bare-ground classifications. We used impervious surface and coarse vegetation cover because these classifications comprised greater than 97% of the groundcover within 100 m of each of our study trees. Impervious surface includes building footprints as well as pavement and

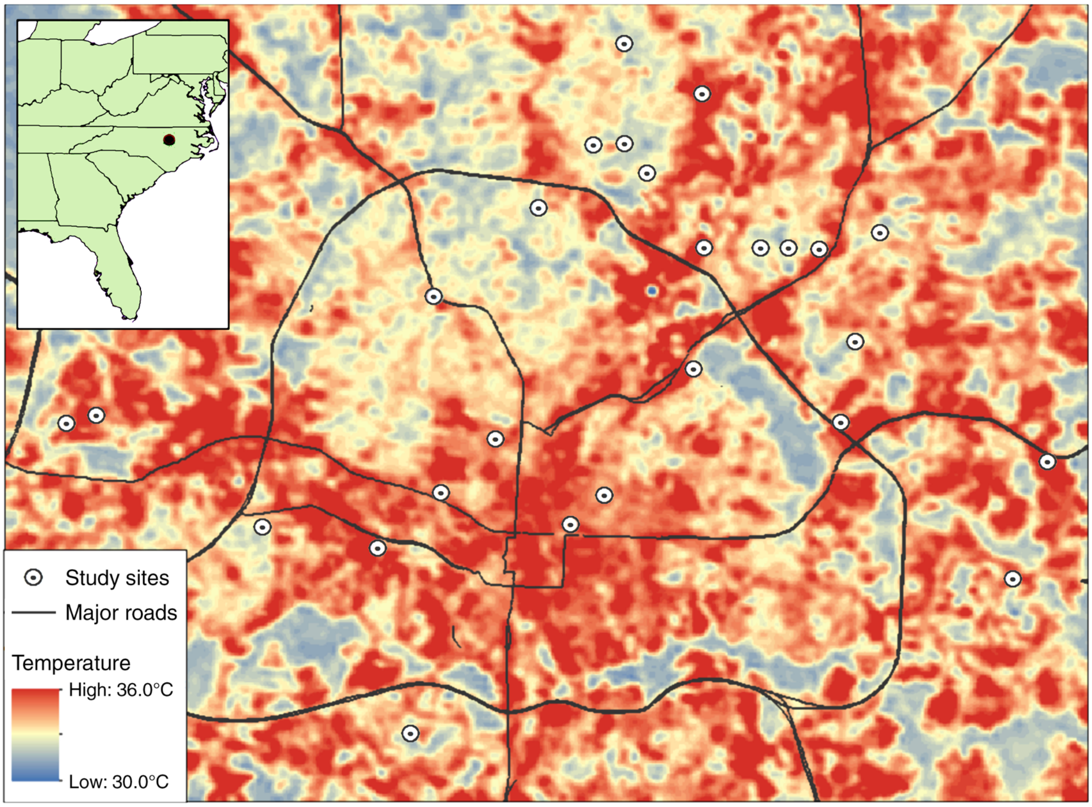

FIG. 2. Thermal map of surface temperature measurements in the Raleigh, North Carolina metropolitan area on 18 August 2007. Temperatures range from 30°C to 36°C, designated by the darkest blue and red regions, respectively. White circles with black dots indicate selected red maple study sites. Inset map in the upper left corner illustrates the regional location of Raleigh, North Carolina in the southeastern United States.

asphalt such as parking lots, roads, and sidewalks. Coarse vegetation includes large, woody flora such as shrubs and trees, which are supportive of pest and natural enemy populations and were the most important vegetation strata in predicting site temperature and scale insect abundance at the local scale. Each classification was represented as a shape file in ArcMap (ArcGIS10), along with a shape file of our 26 trees as points. We created a buffer zone around each tree with a radius of 100 m (Sperry et al. 2001), calculated the total area of each groundcover within the buffer zone, and divided by the total area of the buffer zone to determine percent groundcover type around each tree.

Melanaspis tenebricosa *abundance*

To measure *M. tenebricosa* abundance, we pruned one haphazardly selected 0.15 m terminal twig from each of four cardinal directions on each of our 26 study trees using a 3.66 m pole pruner. We collected twigs on four dates in 2012 when scales were active (5 and 20 April; and 3 and 18 May) and examined them under a dissecting microscope to record scale abundance and life stage per 0.6 m length of twig.

Natural enemy abundance

Using methods similar to Raupp et al. (2001), we surveyed the abundance of flying natural enemies at each of our study sites with 7.6 × 12.7 cm yellow sticky cards (Olson Products, Medina, Ohio, USA). We hung sticky cards in the lower canopy of each tree and replaced them every two weeks from April through July 2012.

To determine which parasitoids were attacking *M. tenebricosa*, we collected 0.5 m scale-infested twigs, placed them in vials with a cotton ball stopper, and kept them in an environment chamber at 27° ± 0.5°C (mean ± SE) (Percival Scientific, Perry, Iowa, USA). We collected emerged parasitoids, preserved them in 80% ethanol, and identified them to genus. After this, we could distinguish between parasitoids that attack *M. tenebricosa* and other parasitoids present at each site. We recorded the abundance of these *M. tenebricosa* parasitoids collected on yellow sticky cards.

To determine predator abundance, we counted and identified to family all generalist predators that were collected on yellow sticky cards and known to feed on scale insects.

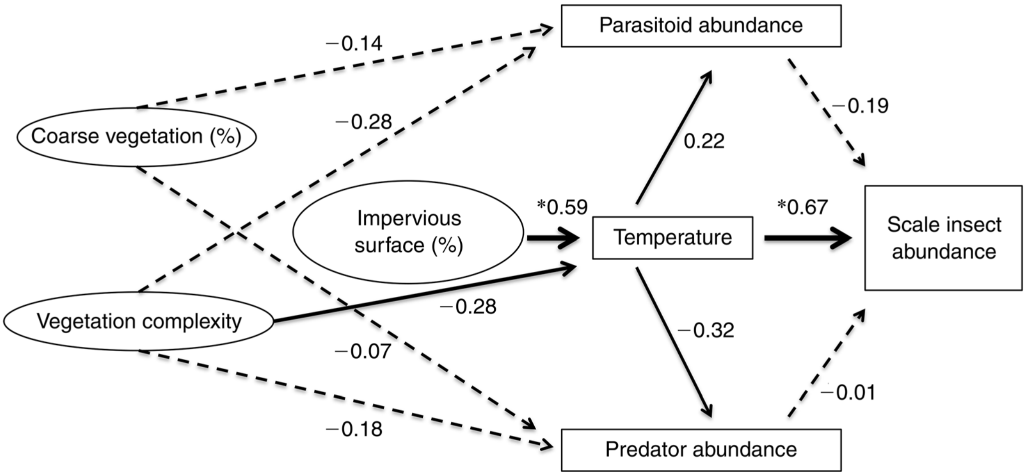

FIG. 3. Model 3 path diagram illustrating the direct effects of each exogenous (circles) and endogenous (rectangles) variable in our study system. Dashed arrows show the hypothesized direct biotic effects (enemies hypothesis) regulating *M. tenebricosa* abundance. Solid arrows show the hypothesized direct abiotic effects (temperature) regulating *M. tenebricosa* abundance. Asterisks indicate relationship is significant ($P < 0.05$).

Tree canopy temperature

Thermal mapping gave approximate site surface temperatures on 18 August 2007. To determine actual tree canopy temperatures, we placed iButton thermochron (Dallas Semiconductor, Dallas, Texas, USA) remote temperature loggers within the canopy of each study tree. Using methods similar to Meineke et al. (2013), we placed thermochrons in iButton wall mounts (Dallas Semiconductor) within 59-mL portion containers (Dart Container Corporation, Mason, Michigan, USA) and fastened them to the undersides of branches approximately 4.5 m above ground using zip ties. iButtons recorded the temperature every hour from April 2012 to April 2013. Due to loss of iButtons, complete 12-month temperature readings were only available for 22 of the 26 sites. Therefore, we used seven months for which all sites had complete data. These months, in chronological order from 2012 to 2013, are June, July, August, September, February, March, and April.

Path analysis

We hypothesize causal pathways that include direct and indirect contributions of biotic and abiotic factors to *M. tenebricosa* abundance (Fig. 3). Based on this hypothesis, we constructed path diagrams and conducted a path analysis (Grace 2008) using PROC CALIS (SAS 9.3; SAS Institute 2013). We fitted three potential models including different combinations of exogenous and endogenous variables and their potential associations but selected one for analysis. We chose this model based on concurrence with our a priori hypothesized associations and variables of interest in addition to goodness of fit indices, Akaike information criterion (AIC), Schwarz Bayesian criterion (SBC), and model parsimony. We did not use chi-square values for goodness of fit because our variables are not independent and identically distributed. Our model predicts that habitat characteristics influence natural enemy abundance and site temperature, both of which influence scale insect abundance (Fig. 3) based on the enemies hypothesis and our temperature hypothesis, respectively. We treated vegetation structural complexity (local scale) and percent groundcover type (landscape scale) as continuous, exogenous, variables influencing site temperature, predator abundance, and parasitoid abundance (Fig. 3). Temperature, predator abundance, parasitoid abundance, and scale insect abundance were treated as endogenous variables with the former three contributing to scale insect abundance (Fig. 3). We repeated the above analyses replacing the vegetation structural complexity rating with Shannon's *H* indices for complexity.

Percent parasitism of M. tenebricosa

To examine the efficacy of parasitoids across study sites, we collected 4.8 m of scale-infested twigs from the canopy of each study tree and placed them in a rearing tube. Using methods adapted from Tooker and Hanks (2000), we constructed rearing tubes out of cardboard mailing tubes and placed a clear glass vial in the cap at one end. This end had a light source so that emerging parasitoids would fly into the vial. Every two weeks, over a 12-week period, we collected, counted, and identified parasitoids from the tubes. Percent parasitism was calculated for each site by dividing the number of parasitoids that emerged by mean scale insect abundance per 4.8 m of twig as previously determined per 0.6 m length of twig. The rearing tube percent parasitism distribution followed a zero-inflated Poisson distribution so we analyzed the data using PROC GENMOD ZEROMODEL in SAS 9.3 (SAS Institute 2013).

TABLE 1. Correlations between each vegetation structural complexity strata predicting mean tree canopy temperature and mean *Melanaspsis tenebricosa* abundance.

	Seven-month mean temperature			Mean *M. tenebricosa* abundance		
Vegetation strata	df	*r*	*P*	df	*r*	*P*
Ground cover	24	0.10	0.61	24	0.05	0.82
Annuals/perennials	24	0.32	0.11	24	0.32	0.11
Shrubs	24	0.08	0.69	24	0.12	0.57
Understory tree	24	0.62	0.0007	24	0.41	0.04
Overstory tree	24	0.49	0.01	24	0.42	0.03
Total complexity	24	0.57	0.002	24	0.40	0.045
Shannon's *H*	24	0.49	0.01	24	0.47	0.02

Notes: Degrees of freedom (df) = $N - 2$, where N is number of plots. Correlation coefficient (r) and P indicate strength of correlation and significance, respectively.

As a second measure of percent parasitism, we collected scale-infested twigs on 18 December 2012 and examined them for parasitized *M. tenebricosa*. We removed scale covers and recorded the presence of a parasitized scale insect, parasitoid larva, parasitoid pupa, or parasitoid adult. We calculated percent parasitism at each site by dividing the number of parasitized scales by the number of scales examined. The distribution of the data also followed a zero-inflated Poisson distribution so we analyzed the data using PROC GENMOD ZEROMODEL (SAS 9.3).

Melanaspsis tenebricosa *fecundity and population increase*

To determine if temperature affects scale insect fecundity, we dissected eight gravid adult females per site on four dates in 2013: 1, 16, and 23 April, and 12 May. We selected two females per twig among four twigs collected from each tree. We placed eggs from dissected females on a glass microscope slide and counted them under a phase-contrast compound light microscope. *Melanaspis tenebricosa* eggs were hatching at cold and hot sites on the final sampling date, indicating the end of egg development. We constructed a model treating mean egg count per female per site and mean seven-month temperature as continuous variables and examined their relationship using simple linear regression (JMP, version 10; SAS Institute, Cary, North Carolina, USA).

We also calculated the ratio of recently developed live *M. tenebricosa* adult females in December 2012 to live adult females prior to egg hatch in April 2012 as a measure of population increase across one generation. We treated population increase ratios as continuous response variables correlated with seven-month mean temperature (JMP, Version 10).

Larger female insects often produce eggs earlier in development, are more fecund, and survive better than smaller females (Kozlowski 1992, Berger et al. 2008). As a general measure of fitness, we determined body length of adult female *M. tenebricosa* from the pygidium to the anterior end of eight individuals from each study site on four dates in 2013: 1, 16, and 23 April, and 12 May. As in the fecundity survey, we selected two females per twig among four twigs collected from each tree. We treated mean body size as a continuous response correlated with seven-month mean temperature using simple linear regression (JMP, Version 10).

RESULTS

Habitat analysis

Vegetation structural complexity ratings ranged from 42 to 315 out of 500 (178 ± 66.3 [mean ± SD]) and were distributed across two to five vegetation strata. Shannon's *H* vegetation structural complexity indices ranged from 0.31 to 1.44 (0.93 ± 0.28 [mean ± SD]). Individually, understory and overstory strata significantly predicted site temperature and *M. tenebricosa* abundance (Table 1), providing further support for our coarse vegetation groundcover analysis. We used total vegetation structural complexity in our path analysis for statistical power and because it equally predicts site temperature and *M. tenebricosa* abundance while including all other strata (Table 1). Impervious surface cover ranged from 3.95% to 78.5% with a mean of 33.6% (± 22.9) and coarse vegetation cover ranged from 13.1% to 94.6% with a mean of 52.4% (± 29.2).

Arthropod abundance

Mean *M. tenebricosa* abundance includes all life stages and ranged from 0 to 2241 live individuals per 0.6 m of twig with a mean of 444.0 (± 683.7).

We identified five parasitoid wasp morphotypes as natural enemies of *M. tenebricosa*. Four of these were identified to genus and one was identified to subfamily. These were *Signiphora* (Signiphoridae), *Encarsia* (Aphelinidae), *Ablerus* (Aphelinidae), *Coccidoctonus* (Encyrtidae), and Coccidoxinoides (Encyrtidae). Of these, *Signiphora*, *Encarsia*, and *Ablerus* were collected on yellow sticky cards. Over 94% of all gloomy scale parasitoids collected on sticky cards were *Encarsia* spp. However, all three genera were included in the metric of parasitoid abundance used in the path analysis.

We identified generalist predators in the families Aleothripidae, Anthocoridae, Chrysopidae, Coccinellidae, Dolichopodidae, Forficulidae, Geocoridae, Phlaeothripidae, and Syrphidae on yellow sticky cards. We also

TABLE 2. Model fit indices used to help determine the best model for path analysis.

Model	*N* var.	*N* par.	GFI	Adjusted GFI	AIC	SBC	BCFI	RMSEA
1	7	21	0.77	0.06	77.54	103.96	0.76	0.40
2	6	18	0.86	0.02	52.7	75.35	0.74	0.43
3	7	21	0.82	0.29	67	93.42	0.85	0.32

Notes: Abbreviations are *N* var., number of variables; *N* par., number of parameters; GFI, goodness-of-fit index; AIC, Akaike information criterion; SBC, Schwarz Bayesian criterion; BCFI, Bentler comparative fit index; RMSEA, root mean square error of approximation. The adjusted GFI is a goodness-of-fit index that is adjusted for the degrees of freedom of the model.

recorded spiders (Araneae) and one specialist predator, the scale picnic beetle, *Cybocephalus nipponicus* (Coleoptera: Nitidulidae).

Tree canopy temperature

Seven-month mean hourly tree canopy temperature ranged from 18.26°C to 20.12°C with a mean of 19.17°C (± 0.44°C).

Path analysis

All three potential path models fit well and displayed similar associations between variables (see Appendices A and B); however, we present the one that fully tests our a priori hypotheses and includes all measured variables (Table 2, Fig. 3). Results for each model suggest that only impervious surface and temperature are significantly associated with and significantly predict *M. tenebricosa* abundance. Replacing vegetation structural complexity with Shannon's H indices in the analysis produced the same significant relationships between impervious surface, temperature, and scale insect abundance corroborating the strength of these responses (see Appendix C). For all models, all nonsignificant path coefficients exhibit minor to no difference in coefficient values and in all cases do not change significance. In addition, goodness-of-fit indices were acceptable for all models and close enough to one another to permit selection of any model based on these values (Table 2). As such, we chose the full model that most completely represents our hypotheses and the linear relationships between variables. We found no evidence of nonlinearity in the relationship between explanatory and response variables in our model. Direct effect path coefficients represent the direct contribution of an explanatory variable to the response variable when keeping all other variables constant (Fig. 3). Indirect effects represent the effect of an explanatory variable on a response through its effect on other variables. The total effects equal the sum of direct and indirect effects and represent the total contribution of an explanatory variable to a response (Table 3).

The strongest effect in our path model was the total positive effect of mean temperature on *M. tenebricosa* abundance ($t = 4.62$, $P < 0.0001$; Table 3). The total effect of percent impervious surface cover was significantly positively associated with mean temperature ($t = 4.45$, $P < 0.0001$; Table 3), which is consistent with other studies associating ground cover and temperature (Oke 1973, Hart and Sailor 2009, Jenerette et al. 2011). Impervious surface was also significantly positively associated with *M. tenebricosa* abundance ($t = 3.08$, $P = 0.002$) due to its strong, positive association with temperature (Table 3). To the extent that it showed a trend, vegetation structural complexity was negatively, but not significantly associated with mean temperature, almost certainly due to its inverse relationship with impervious surface cover. However, this trend disappeared when Shannon's *H* indices were included in the path analysis. There was no correlation between habitat complexity and natural enemies or natural enemies and *M. tenebricosa* abundance (Table 3). No other exogenous or endogenous variables had significant direct, indirect, or total effects on one another in our path model.

Percent parasitism of M. tenebricosa

Rearing tube percent parasitism was low with a mean of 0.72% ranging from 0 to 4.4% and was not related to seven-month mean temperature (Wald $\chi^2 = 0.07$, df = 1, $P = 0.79$), vegetation complexity (Wald $\chi^2 = 0.01$, df = 1, $P = 0.91$), or coarse vegetation cover (Wald $\chi^2 = 0.05$, df = 1, $P = 0.82$). Percent parasitism of *M. tenebricosa* determined by removing scale covers was slightly higher, ranging from 0 to 12.5% with a mean of 2.22% but also not related to temperature (Wald $\chi^2 = 0.01$, df = 1, $P = 0.93$), vegetation complexity (Wald $\chi^2 = 0.00$, df = 1, $P = 0.96$), or coarse vegetation cover (Wald $\chi^2 = 0.01$, df = 1, $P = 0.94$).

Melanaspis tenebricosa *fecundity and population increase*

Simple linear regression revealed the strongest association between mean egg count per female and seven-month temperature on the first sampling date ($R^2 = 0.72$, $P < 0.0001$; Fig. 4A). On the final date there was still a significant positive correlation between mean egg count per female and seven-month temperature ($R^2 = 0.20$, $P = 0.04$; Fig. 4D). In addition, the slope of the regression equation was greatest for the final survey date ($y = 14.46x - 231$; Fig. 4D), suggesting the strongest effect of temperature on egg count.

The ratio of second-generation adults to first-generation adults was significantly positively correlated with seven-month site temperature ($R^2 = 0.32$, $P = 0.02$; Fig. 5A). There was also a significant positive association

TABLE 3. Total (direct + indirect) effects of explanatory variables (side headings) on response variables.

Variables	Total effect	SE	*t*	*P*
Mean temperature				
Mean temperature	0	0	0	0
Parasitoid abundance	0.22	0.25	0.86	0.39
M. tenebricosa abundance	0.63	0.14	4.45	**<0.0001**
Predator abundance	−0.32	0.29	−1.08	0.28
Parasitoid abundance				
Mean temperature	0	0	0	0
Parasitoid abundance	0	0	0	0
M. tenebricosa abundance	−0.19	0.18	−1.08	0.28
Predator abundance	0	0	0	0
Predator abundance				
Mean temperature	0	0	0	0
Parasitoid abundance	0	0	0	0
M. tenebricosa abundance	−0.008	0.16	−0.05	0.96
Predator abundance	0	0	0	0
Percent coarse vegetation				
Mean temperature	0	0	0	0
Parasitoid abundance	−0.14	0.23	−0.58	0.56
M. tenebricosa abundance	0.03	0.06	0.48	0.63
Predator abundance	−0.18	0.27	−0.66	0.51
Percent impervious surface				
Mean temperature	0.59	0.13	4.62	**<0.0001**
Parasitoid abundance	0.13	0.15	0.84	0.40
M. tenebricosa abundance	0.38	0.12	3.08	**0.002**
Predator abundance	−0.19	0.18	−1.04	0.30
Vegetation complexity				
Mean temperature	−0.28	0.14	−1.93	*0.05*
Parasitoid abundance	−0.34	0.18	−1.84	*0.07*
M. tenebricosa abundance	−0.12	0.11	−1.08	0.28
Predator abundance	0.01	0.22	0.06	0.95

Notes: Total effect, SE, *t*, and *P* value are listed per cell. Effects indicate the magnitude of the explanatory variable's effect on the response; *t* values are representative of the importance of the relationship. Values in boldface type are significant ($P < 0.05$) and values in italics are nearly significant.

between seven-month site temperature and body size ($R^2 = 0.44$, $P = 0.0008$; Fig. 5B).

DISCUSSION

For over a century, scientists have observed greater pest abundance on urban trees compared to trees in natural habitats (Putnam 1880, Metcalf 1912). We found that *M. tenebricosa* abundance increased in response to urban heat, supporting our hypothesis that the abiotic factor, temperature, is more important than the biotic factors we measured. Trees in the hottest urban habitats had three orders of magnitude more *M. tenebricosa* than the trees in the coldest urban habitats; some had up to 2241 individuals per 0.6 m of twig. We conclude that in our study, urban habitat characteristics such as high impervious surface cover increase herbivore abundance by making the habitat warmer, rather than less suitable for natural enemies as proposed in other studies. As urban areas become warmer and continue to expand, the direct abiotic effects of warming on herbivore fitness, particularly scale insects, may be greater than the effects of warming on trophic interactions.

Warmer temperatures increase insect metabolic activity, which can increase body size (Ray 1960), while also decreasing development time and increasing fecundity (Yasuda 1983, Kozlowski 1992). *Melanaspis tenebricosa* is univoltine (Metcalf 1922), so shorter generation time does not explain differences in abundance. However, increases in abundance could be due to increases in fecundity. Female *M. tenebricosa* were significantly larger and produced more eggs in warmer than cooler urban habitats. Our first survey for egg set revealed the strongest association between temperature and egg count, suggesting that scale insects at warmer urban sites produce eggs earlier in the season. This association

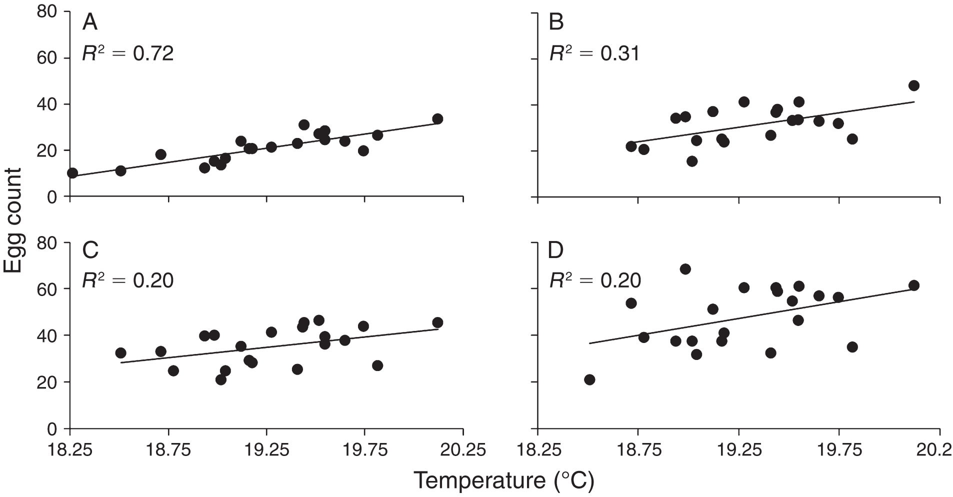

FIG. 4. Relationship between seven-month mean temperature and mean egg count per female on four dates in 2013. (A) 1 April, $y = 12.30x - 215.7$. (B) 16 April, $y = 12.59x - 211.9$. (C) 23 April, $y = 8.871x - 135.8$. (D) 12 May, $y = 14.46x - 231$. All regression models are statistically significant ($P < 0.05$).

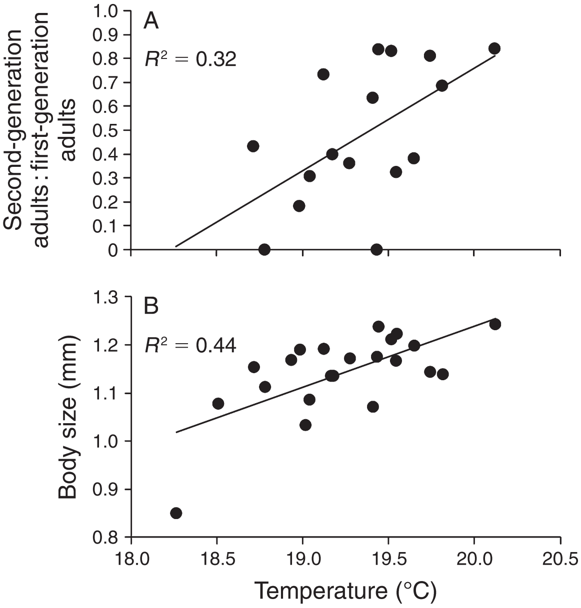

FIG. 5. Relationship between seven-month mean temperature and (A) the ratio of second- to first-generation adult *M. tenebricosa* ($y = 0.428x - 7.79$) and (B) mean adult female *M. tenebricosa* body size ($y = 0.127x - 1.301$). Both regression models are statistically significant ($P < 0.05$).

weakened over time but remained significant and at the time of immature emergence, individual *M. tenebricosa* egg sets increased by approximately 14 eggs for every 1°C increase in temperature. This increase in fecundity is corroborated by an over four times greater population increase on warmer than cooler trees. Thus, greater fecundity provides a feasible mechanism through which warming could increase *M. tenebricosa* population growth and density on urban trees.

Vegetation structural complexity and ground cover did not increase natural enemy abundance or efficacy as predicted by the enemies hypothesis. In fact, we found a nearly significant, negative association between vegetation structural complexity and parasitoid abundance (Table 3). Parasitoid abundance was greater in simpler habitats where scale insect abundance was also high, which is likely explained by a density-dependent response of parasitoids to their herbivore hosts (Holling 1959, 1961, Waage 1983). Percent parasitism was not affected by vegetation structural complexity or ground cover, similarly to Hanks and Denno (1993*a*) who attributed scale insect abundance in simple urban landscapes, in part, to a lack of generalist predators. In our system, *M. tenebricosa* abundance was not associated with generalist predator abundance. Although natural enemies have been shown to regulate scale insects and other pests (Luck and Dahlstein 1975, McClure 1977, Clarke et al. 1992, Raupp et al. 2001), we did not find evidence to support the enemies hypothesis or the role of natural enemies in regulating *M. tenebricosa* abundance.

PLATE 1. A red maple street tree heavily infested with gloomy scale and exhibiting severe branch dieback throughout its canopy. Photo credit: A. G. Dale.

Our results may shed light on other studies that have found a negative relationship between vegetation structural complexity or groundcover and herbivore abundance without identifying a strong biotic mechanism (Hanks and Denno 1993*a*, Shrewsbury and Raupp 2000, Tooker and Hanks 2000). For example, Tooker and Hanks (2000) found greater pine needle scale, *Chionaspis pinifoliae* (Hemiptera: Diaspididae), abundance in simple impoverished habitats near impervious surface cover compared to complex wooded habitats despite higher parasitoid abundance and parasitism in the impoverished habitats. Shrewsbury and Raupp (2000) found that light exposure, most strongly influenced by the overstory tree strata, predicted azalea lace bug abundance better than other habitat components such as plant diversity. Our results suggest that the overstory, as well as the understory tree strata most strongly influence site temperature. It is plausible that, in these and similar studies, the simple urban habitats were warmer than the more complex ones. Herbivorous pest abundance and impervious surface cover have been associated in other studies (Speight et al. 1998, Sperry et al. 2001), but a mechanism behind this was never identified. Our study integrates temperature into existing theory about the effects of habitat and urbanization on biotic interactions.

Plant stress caused by characteristics of urban habitats has been predicted to increase herbivore abundance in some cases by increasing plant nutritional quality, decreasing defense, or both (Mattson 1980, White 1984, Miller et al. 2006). Increasing impervious surface cover can increase plant water stress (Berrang et al. 1985) and temperature (Hart and Sailor 2009). However, water stress has generally been found to reduce survival and abundance of armored scales (Cockfield and Potter 1986, Hanks and Denno 1993*a*, *b*) and other sap feeding insects (Koricheva et al. 1998, Huberty and Denno 2004) and thus does not explain the greater abundance of these pests on urban trees. For example, Hanks and Denno (1993*a*) found that survival of armored scale cohorts decreased on drought-stressed trees and did not explain why there were more scales on stressed urban trees compared to trees in wooded areas. Therefore, we suspect that scale insects at our hot sites thrived in spite of, not because of, host-plant water stress.

Climate change is predicted to affect ecosystems via direct effects on the organisms present and by disrupting trophic interactions (McKinney 2002). Urban trees and their herbivores have lived in warmer temperatures for decades. Our results support the hypothesis that warming increases herbivore, specifically *M. tenebricosa* and likely other scale species, abundance directly, more than by disrupting biotic control by natural enemies. Within the next century, the global climate is projected to increase by 2°–3°C (Meehl et al. 2007, Hansen et al. 2010). The warmest trees in our study were less than 2°C warmer than the coolest trees and had over 2000 more scale insects per 0.6 m of twig. Trees cool urban habitats through transpiration and by providing shade (Oke et al. 1989). Pests decrease these services by reducing plant photosynthesis and growth (Cockfield et al. 1987, Schaffer and Mason 1990, Vranjic and Ash 1997, Zvereva et al. 2010), especially at warmer temperatures (Zvereva et al. 2010). This likely occurs in our system because *M. tenebricosa* feeding causes branch dieback and premature leaf drop (Metcalf 1922, Frank et al. 2013). Although our study was limited to one herbivore pest, our results suggest that as cities become warmer, herbivores will reduce plant health and the ecosystem services they provide. Mitigation of this reduction may include planting trees that are less susceptible to known urban pests (Lacan and McBride 2008) or increasing vegetation complexity in urban habitats to maximize plant ecosystem services.

Acknowledgments

Elsa Youngsteadt and Emily Meineke assisted with data analysis, study design, and provided comments on the manuscript. Rob Dunn, Mike Raupp, Paula Shrewsbury, Kevin McCluney, and Sarah Jandricic provided comments on the manuscript. Consuelo Arellano provided assistance with statistical design and analysis. Sally Thigpen provided tree maps. Andrew Ernst assisted with parasitoid identification. George Washburn and Caitlin Melvin assisted with data collection. The Raleigh Parks, Recreation, and Cultural Resources Department approved this study. This work was supported by a grant from USDA AFRI (2013-02476) to S. D. Frank and by the NCSU Department of Entomology. S. D. Frank was also supported by grants from NSF RAPID (1318655), USDA Southern Region IPM (2010-02678), North Carolina Nursery and Landscape Association, and the Horticultural Research Institute. The project described in this publication was supported by Cooperative Agreement No. G11AC20471 and G13AC00405 from the United States Geological Survey. Its contents are solely the responsibility of the authors and do not necessarily represent the views of the Southeast Climate Science Center or the USGS. This manuscript is submitted for publication with the understanding that the United States Government is authorized to reproduce and distribute reprints for Governmental purposes.

Literature Cited

Andrewartha, H. G., and L. C. Birch. 1948. Measurement of "environmental resistance" in the Australian plague grasshopper. Nature 161:447–448.

Berger, D., R. Walters, and K. Gotthard. 2008. What limits insect fecundity? Body size- and temperature-dependent egg maturation and oviposition in a butterfly. Functional Ecology 22:523–529.

Berrang, P., D. Karnosky, and B. Stanton. 1985. Environmental factors affecting tree health in New York City. Journal of Arboriculture 11(6):185–189.

Bianchi, F. J. J. A., C. J. H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. Proceedings of the Royal Society B 273:1715–1727.

Bigsby, K. M., M. R. McHale, and G. R. Hess. 2013. Urban morphology drives the homogenization of tree cover in Baltimore, MD, and Raleigh, NC. Ecosystems. http://dx.doi.org/10.1007/s10021-013-9718-4

Clarke, S. R., F. Negroni, and G. L. Debarr. 1992. Effects of four pyrethroids on scale insect (Homoptera) populations and their natural enemies in loblolly and shortleaf pine seed orchards. Journal of Economic Entomology 85:1246–1252.

Cockfield, S. D., and D. A. Potter. 1986. Interaction of euonymus scale feeding damage and severe water stress on leaf abscission and growth of *Euonymus fortunei*. Oecologia 71:41–46.

Cockfield, S. D., D. A. Potter, and R. L. Houtz. 1987. Chlorosis and reduced photosynthetic CO_2 assimilation of *Euonymus fortunei* infested with euonymus scale. Environmental Entomology 16:1314–1318.

Dawe, G. F. M. 2011. Street trees and the urban environment. Pages 424–450 *in* I. Douglas, D. Goode, M. C. Houck, and R. Wang, editors. The Routledge handbook of urban ecology. Routledge Taylor and Francis Group e-Library, New York, New York, USA.

Donovan, G. H., et al. 2013. The relationship between trees and human health: evidence from the spread of the emerald ash borer. American Journal of Preventative Medicine 44:139–145.

Drea, J. J., and R. D. Gordon. 1990. Predators. Pages 19–98 *in* D. Rosen, editor. World crop pests: armored scale insects, their biology, natural enemies and control. Volume 4B. Elsevier, Amsterdam, The Netherlands.

Erdelen, M. 1984. Bird communities and vegetation structure: correlations and comparisons of simple and diversity indices. Oecologia (Berlin) 61:277–281.

Frank, S. D., W. E. Klingeman, S. A. White, and A. Fulcher. 2013. Biology, injury, and management of maple tree pests in nurseries and urban landscapes. Journal of Integrated Pest Management 4:1–14.

Frank, S. D., and P. M. Shrewsbury. 2004. Effect of conservation strips on the abundance and distribution of natural enemies and predation of *Agrotis ipsilon* (Lepidoptera: Noctuidae) on golf course fairways. Environmental Entomology 33:1662–1672.

Frankie, G. W., and L. E. Ehler. 1978. Ecology of insects in urban environments. Annual Review of Entomology 23:38–41.

Grace, J. B. 2008. Structural equation modeling for observational studies. Journal of Wildlife Management 72:14–22.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. American Naturalist 94:421–425.

Hanks, L., and R. Denno. 1993*a*. Natural enemies and plant water relations influence the distribution of an armored scale insect. Ecology 74:1081–1091.

Hanks, L., and R. Denno. 1993*b*. The white peach scale, *Pseudaulacaspis pentagona* (Targioni-Tozzetti) (Homotptera: Diaspididae): life history in Maryland, host plants, and natural enemies. Proceedings of the Entomological Society of Washington 95:79–98.

Hansen, J., R. Ruedy M. Sato, and K. Lo. 2010. Global surface temperature change. Review of Geophysics 48:1–29.

Hart, M. A., and D. J. Sailor. 2009. Quantifying the influence of land-use and surface characteristics on spatial variability in the urban heat island. Theoretical and Applied Climatology 95:397–406.

Hawkins, B. A., N. J. Mills, M. A. Jervis, and P. W. Price. 1999. Is the biological control of insects a natural phenomenon? Oikos 86:493–506.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Canadian Entomologist 91:385–398.

Holling, C. S. 1961. Principles of insect predation. Annual Review of Entomology 6:163–182.

Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383–1398.

Hunter, M. D., P. W. Price, N. Jun, U. Park, and P. Us. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Jenerette, G. D., S. L. Harlan, W. L. Stefanov, and C. A. Martin. 2011. Ecosystem services and urban heat riskscape moderation: water, green spaces, and social inequality in Phoenix, USA. Ecological Applications 21:2637–2651.

Kahn, D., and H. Cornell. 1989. Leafminers, early leaf abscission, and parasitoids: a tritrophic interaction. Ecology 70:1219–1226.

Kim, H. H. 1992. Urban heat island. International Journal of Remote Sensing 13:2319–2336.

Koricheva, J., S. Larsson, and E. Haukioja. 1998. Insect performance on experimentally stressed woody plants: a meta-analysis. Annual Review of Entomology 43:195–216.

Kozlowski, J. 1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. Trends in Ecology and Evolution 7:15–19.

Lacan, I., and J. R. McBride. 2008. Pest vulnerability matrix: a graphic model for assessing the interaction between tree species diversity and urban forest susceptibility to insects and disease. Urban Forestry and Urban Greening 7:291–300.

Letourneau, D. K. 1987. The enemies hypothesis: tritrophic interactions and vegetational diversity in tropical agroecosystems. Ecology 68:1616–1622.

Louda, S. M., P. M. Dixon, and N. J. Huntly. 1987. Herbivory in sun versus shade at a natural meadow-woodland ecotone in the Rocky Mountains. Vegetation 72:141–149.

Luck, R. F., and D. L. Dahlstein. 1975. Natural decline of a pine needle scale (*Chionaspis pinifoliae* [Fitch]), outbreak at South Lake Tahoe, California following cessation of adult mosquito control with malathion. Ecology 56:893–904.

Maron, J. L., and S. Harrison. 1997. Spatial pattern formation in an insect host–parasitoid system. Science 278:1619–1621.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119–161.

McClure, M. S. 1977. Resurgence of the scale, *Fiorinia externa* (Homoptera: Diaspididae) on hemlock following insecticide application. Environmental Entomology 6:480–484.

McKinney, M. 2002. Urbanization, biodiversity, and conservation. BioScience 52:883–890.

Meehl, G. A., et al. 2007. Global climate projections. Pages 809–811 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L. Miller, editors. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Meineke, E. K., R. R. Dunn, J. O. Sexton, and S. D. Frank. 2013. Urban warming drives insect pest abundance on street trees. PLoS ONE 8:e59687.

Metcalf, Z. P. 1912. The gloomy scale, an important enemy of shade trees in North Carolina. Journal of the Elisha Mitchell Scientific Society 28:88–91.

Metcalf, Z. P. 1922. The gloomy scale. Technical Bulletin No. 21. North Carolina Agriculture Experiment Station, Raleigh, North Carolina, USA.

Miller, D. R., and J. A. Davidson. 2005. Armored scale insect pests of trees and shrubs (Hemiptera: Diaspididae). Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Miller, T. E. X., A. J. Tyre, and S. M. Louda. 2006. Plant reproductive allocation predicts herbivore dynamics across spatial and temporal scales. American Naturalist 168:608–616.

Moore, L. V., J. H. Myers, R. Eng, and H. Myers. 1988. Western tent caterpillars prefer the sunny side of the tree, but why? Oikos 51:321–326.

Nesom, G. 2006. Plant guide: red maple. USDA Natural Resources Conservation Service National Plant Data Center and the Biota of North America Program, U.S. Department of Agriculture, Washington, D.C., USA.

Nowak, D. J., and J. F. Dwyer. 2000. Understanding the costs and benefits of urban forest ecosystems. Pages 11–25 *in* J. E. Kuser, editor. Handbook of community and urban forestry in the Northeast. Kluwer, New York, New York, USA.

Nowak, D. J., and E. J. Greenfield. 2012. Tree and impervious cover change in U.S. cities. Urban Forestry and Urban Greening 11:21–30.

Oke, T. R. 1973. City size and the urban heat island. Atmospheric Environment 7:769–779.

Oke, T. R., J. M. Crowther, K. G. McNaughton, J. L. Monteith, and B. Gardiner. 1989. The micrometeorology of the urban forest [and discussion]. Philosophical Transactions of the Royal Society 324:335–349.

Putnam, J. D. 1880. Biological and other notes on Coccidae. Proceedings of the Davenport Academy of Sciences 2:293–347.

Raupp, M. J., A. B. Cumming, and E. C. Raupp. 2006. Street tree diversity in eastern North America and its potential for tree loss to exotic borers. Arboriculture and Urban Forestry 32:297–304.

Raupp, M. J., J. J. Holmes, C. Sadof, P. Shrewsbury, and J. A. Davidson. 2001. Effects of cover sprays and residual pesticides on scale insects and natural enemies in urban forests. Journal of Arboriculture 27:203–215.

Raupp, M. J., P. M. Shrewsbury, and D. A. Herms. 2010. Ecology of herbivorous arthropods in urban landscapes. Annual Review of Entomology 55:19–38.

Ray, C. 1960. The application of Bergmann's and Allen's Rules to the poikilotherms. Journal of Morphology 106:85–108.

Root, R. B. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs 43:95–124.

SAS Institute. 2013. SAS 9.3. SAS Institute, Cary, North Carolina, USA.

Schaffer, B., and L. J. Mason. 1990. Effects of scale insect herbivory and shading on net gas exchange and growth of a subtropical tree species (*Guaiacum sanctum* L.). Oecologia 84:468–473.

Shrewsbury, P. M., and M. J. Raupp. 2000. Evaluation of components of vegetational texture for predicting azalea lace bug, *Stephanitis pyrioides* (Heteroptera: Tingidae), abundance in managed landscapes. Environmental Entomology 29:919–926.

Shrewsbury, P. M., and M. J. Raupp. 2006. Do top-down or bottom-up forces determine *Stephanitis pyrioides* abundance in urban landscapes? Ecological Applications 16:262–272.

Speight, A. M. R., R. S. Hails, M. Gilbert, and A. Foggo. 1998. Horse chestnut scale (*Pulvinaria regalis*) (Homoptera: Coccidae) and urban host tree environment. Ecology 79:1503–1513.

Sperry, C. E., W. R. Chaney, S. Guofan, and C. S. Sadof. 2001. Effects of tree density, tree species diversity, and percentage of hardscape on three insect pests of honeylocust. Journal of Arboriculture 27:263–271.

Tooker, J. F., and L. M. Hanks. 2000. Influence of plant community structure on natural enemies of pine needle scale (Homoptera: Diaspididae) in urban landscapes. Environmental Entomology 29:1305–1311.

Vranjic, J. A., and J. E. Ash. 1997. Scale insects consistently affect roots more than shoots: the impact of infestation size on growth of eucalypt seedlings. Journal of Ecology 85:143–149.

Waage, J. K. 1983. Aggregation in field parasitoids populations: foraging time allocation by a population of *Diadegma* (Hymenoptera: Ichneumonoidea). Ecological Entomology 8:447–453.

White, T. C. R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105.

Yasuda, S. 1983. Effects of thermal conditions on the sex ratio of *Pseudaulacaspis pentagona* (Targioni) (Hemiptera: Diaspididae), at the early stage of ovogenesis and egg batch size. Journal of Sericultural Science of Japan 52:106–109.

Zvereva, E. L., V. Lanta, and M. V. Kozlov. 2010. Effects of sap-feeding insect herbivores on growth and reproduction of woody plants: a meta-analysis of experimental studies. Oecologia 163:949–960.

SUPPLEMENTAL MATERIAL

Appendix A

Model 1 path diagram illustrating the direct effects of hypothesized associations between variables (*Ecological Archives* A024-194-A1).

Appendix B

Model 2 path diagram illustrating the direct effects of hypothesized associations between variables (*Ecological Archives* A024-194-A2).

Appendix C

Path analysis output of total effects using Shannon's diversity index as a measure of vegetation structural complexity (*Ecological Archives* A024-194-A3).