Urban forest fragments buffer trees from warming and pests

Lawrence C. Long [a,*], Vincent D'Amico [b], Steven D. Frank [a]

[a] *Department of Entomology and Plant Pathology, North Carolina State University, Raleigh, NC 27607, USA*
[b] *U.S. Forest Service, Northern Research Station, 531 S. College Ave, Newark, DE 19716, USA*

HIGHLIGHTS

- Trees in urban forest fragments are cooler than trees in ornamental landscapes.
- Pest density lower in urban forest fragments than landscapes of a mid-latitude city.
- Urban forest fragments protect trees from urban heat island and concomitant pests.
- Lower pest density in high-latitude than mid-latitude city due to background climate

GRAPHICAL ABSTRACT
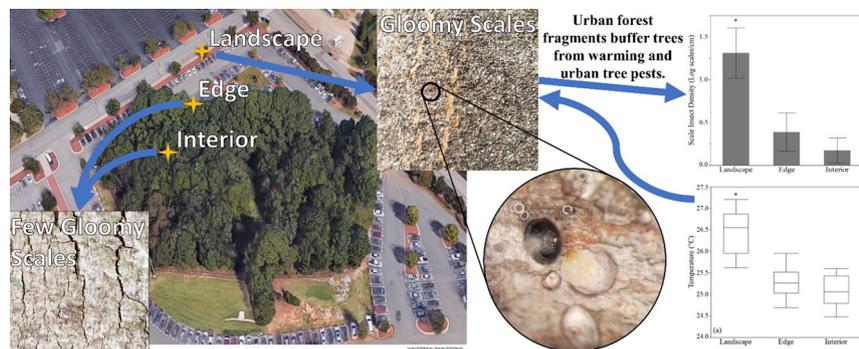
ARTICLE INFO

ABSTRACT

Trees are important components of urban landscapes because of the ecosystem services they provide. However, the effects of urbanization, particularly high temperatures, can benefit chronic insect pests and threaten ecosystem services offered by urban trees. Urban forest fragments are an often-overlooked component of the greater urban forest which may help to mitigate the damaging effects of urbanization. *Melanaspis tenebricosa* (gloomy scale) is a common pest of *Acer rubrum* (red maple) that becomes more abundant because of the urban heat island effect. We conducted observational and manipulative field experiments to test the hypothesis that trees in urban forest fragments would be cooler than those in surrounding ornamental landscapes and would thus have fewer *M. tenebricosa*, particularly in a hot mid-latitude city. Trees in forest fragments were 1.3° cooler and had three orders of magnitude fewer *M. tenebricosa* than trees in ornamental landscapes in Raleigh, NC USA. However, there was no difference in *M. tenebricosa* density between forest and landscape trees in Newark, DE and Philadelphia, PA USA which are 3.95 degrees of latitude higher, and nearer to the northern range extent. Trees in landscapes and forest fragments did not differ in predawn water potential, a measure of water stress, but likely differed in soil composition and moisture. We used potted trees to control for these differences and found that *M. tenebricosa* density still increased three times more in landscapes than forests suggesting temperature and not tree stress is the dominant factor. Taken together our results indicate two things. First, that trees growing in urban forest fragments are buffered from a chronic urban tree pest due to lower temperatures. Second, that temperature-driven differences in *M. tenebricosa* density which we saw in Raleigh could predict future density of the pest in higher latitude cities as the climate warms.

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1. Introduction

Urban forests provide many ecosystem services important for maintaining environmental health and human well-being (Mullaney et al.,

* Corresponding author.
E-mail address: lclong2@ncsu.edu (L.C. Long).

2015a). However, urban trees are often under abiotic stress and have severe pest infestations (Frankie and Ehler, 1978; Raupp et al., 2010) that can reduce ecosystem services (Meineke et al., 2016). So, it is important to understand how stressors associated with urban environments and warming climate will affect urban trees. The urban heat island effect is caused by impervious surfaces that absorb solar radiation and emit heat, thus intensifying temperatures in cities (Oke, 1973; Oke et al., 1989; Taha, 1997) and contributing to tree stress (Cregg and Dix, 2001). Impervious surfaces also increase tree stress by reducing soil moisture (Savi et al., 2015) and increasing vapor pressure deficit which reduces photosynthetic water use efficiency (Oke et al., 1989; Lahr et al., 2018a). The urban heat island effect can benefit arthropod pests directly by increasing survival, fecundity, or rate of development (Hart et al., 1986; Cregg and Dix, 2001; Sperry et al., 2001; Meineke et al., 2013; Dale and Frank, 2014a), or indirectly by increasing host plant stress and quality for pests (Hanks and Denno, 1993; Hanks et al., 1999; Huberty and Denno, 2004), or reducing top-down control by natural enemies (Meineke et al., 2014).

Trees that are growing in managed landscapes such as residential neighborhoods, parking lots, and street medians make up a relatively small proportion of urban tree cover (McPherson, 1998). Urban forests also contain trees that are clustered together in small unmanaged patches. These urban forest fragments are commonly found in city parks and preserves, or they are remnants of larger rural forests that were left behind after development. They may also form because of ecological succession on vacant land (Riley et al., 2018) and in urban areas that are difficult to maintain. Trees growing in these situations account for nearly 54% of urban tree coverage in a large city in the Midwestern U.S. (Nowak, 1994). This is a substantial contribution given that the same study found that trees covered only 11% of the total urban land area (Nowak, 1994).

Trees growing in urban forest fragments may also be cooler because they are not surrounded by impervious surface. The formation of 'cool islands' by forest fragments within large urban areas are evidence for this (O'Brien et al., 2012; Chen et al., 2014). Thus, trees in urban forest fragments may be buffered from heat-related stress and pest infestations. Understanding if trees in urban forest fragments have fewer pests than landscape trees and untangling the mechanisms which contribute to differences in pest abundance will inform management of trees in both situations.

Gloomy scale, *Melanaspis tenebricosa* (Comstock), (Hemiptera: Diaspididae), is an important pest of red maple (*Acer rubrum* L.) trees in the southeastern United States (Metcalf, 1912; Frank et al., 2013) and *A. rubrum* are among the most common trees planted in cities and growing in forests throughout the eastern United States (Iverson and Prasad, 1998; Raupp et al., 2006). *Melanaspis tenebricosa* is native to North America and feeds on parenchyma cells of tree branches and trunks (Beardsley and Gonzalez, 1975). Infestation of trees by *M. tenebricosa* causes branch dieback and heavy infestations cause tree mortality (Metcalf, 1922; Frank et al., 2013). Our observations and those of Metcalf (1912) >100 years ago show that *M. tenebricosa* density is high on urban street and landscape trees but low on nearby rural trees. The abundance of *M. tenebricosa* was more than three orders of magnitude greater on *A. rubrum* street trees across a 2 °C urban warming gradient due to greater scale fecundity and population growth (Dale and Frank, 2014b, 2017) on warm trees. *Melanaspis tenebricosa* produced 17% more embryos on watered vs. unwatered trees over the same 2 °C gradient and was 1.5 times more fecund on hot and dry *A. rubrum* than cool trees that received frequent supplemental water (Dale and Frank, 2017) suggesting an additive effect of drought and temperature. As such, heat is a primary factor affecting the abundance of *M. tenebricosa* and other scale insects on urban and rural trees but drought may also play a role (Meineke et al., 2013; Dale and Frank, 2014a, 2014b; Youngsteadt et al., 2014; Meineke and Frank, 2018).

Scale insects are ideal organisms for studying temperature effects on arthropod populations because they are sessile and cannot leave a host plant under stressful conditions. Thus, they are subject to the total complement of abiotic and biotic factors affecting them and the host on which they live. If trees in urban forest fragments are buffered from the urban heat island effect and other stressors associated with urbanization such as reduced water availability and soil compaction (O'Brien et al., 2012; Chang and Li, 2014; Mullaney et al., 2015a, b; Song et al., 2015) it follows that they should have fewer *M. tenebricosa*, greater physiological function, and heightened longevity. Therefore they would offer more ecosystem services such as greater carbon sequestration (Meineke et al., 2016). Since *M. tenebricosa* fecundity and abundance increases with temperature, we asked if *M. tenebricosa* density would be greater on *A. rubrum* growing in urban landscapes than those in urban forest fragments due to warmer temperature of landscape trees. We tested this hypothesis with three experiments. First, with a series of observational experiments, we measured tree canopy temperature, water stress, *M. tenebricosa* density, and natural enemy abundance on *A. rubrum* trees growing in urban landscapes and nearby urban forest fragments. Natural enemies are affected by habitat complexity, which differs between urban landscapes and urban forest fragments (Hanks and Denno, 1993; Tooker and Hanks, 2000) so it was important, and novel, to compare abundance of *M. tenebricosa* natural enemies in urban landscapes and forest fragments. Second, we used a manipulative experiment to isolate the effects of temperature from soil and other environmental conditions by measuring the change in *M. tenebricosa* density on potted *A. rubrum* saplings placed in the same urban landscapes and forest fragments. Third, to further test the hypothesis that *M. tenebricosa* increases with temperature, we compared *M. tenebricosa* density in landscapes and forest fragments of a mid-latitude city to those of a cooler urban area that lies 3.95 degrees of latitude higher. Latitude, a major predictor of background climate, coupled with urban heat island effect are the main factors which contribute to the temperature of an urban area. Again, we predicted that landscape trees would have more *M. tenebricosa* than urban forest fragment trees. By comparing urban areas from differing background climates, we also create a scenario analogous to future climate change whereby conditions in the mid-latitude city could predict future pest abundance in the high-latitude urban area. We also predicted that *A. rubrum* in the mid-latitude city, would have more *M. tenebricosa* overall than trees in the cooler, higher-latitude urban area. Urban trees are an important part of the landscape in most cities (Nowak et al., 2001). It is critical to understand how urban forest fragments, a major component of the urban forest, buffer trees and their services from urban heat and warming global climate.

2. Materials and methods

2.1. Temperature, water stress, M. tenebricosa density, and natural enemy variation

To determine how the location of an urban tree affects canopy temperature, water stress, *M. tenebricosa* abundance, and natural enemies, we selected 77 *A. rubrum* in Raleigh, North Carolina, USA growing in landscapes ($n = 23$), forest fragment edges ($n = 27$), or forest fragment interiors ($n = 27$). Tree locations, therefore, lie along a gradient of possible exposure to the urban heat island effect such that trees in forest fragments likely had the least exposure, even though all fragments were in highly urbanized areas. Specifically, we define urban forest fragments as any space within an urban area which contains trees >5.0 cm in diameter at breast height, and is not being actively managed (e.g. cultivation, mowing, or raking of the understory or pruning of the trees themselves). All landscape trees were planted within 50 m of an urban forest fragment. Fragment edge trees were rooted within 2.5 m of a forest edge and their crown extended outside of the continuous forest canopy. We included fragment edge trees in our design as an intermediate location because trees growing there may be subject to some of the same stressors as trees planted in landscapes, but they may also be

buffered from urban stressors because of their proximity to the forest fragment. Fragment interior trees were rooted >2.5 m inside the forest edge and their crowns were surrounded by other tree crowns. Study trees were distributed across 0.04 degrees latitude and 0.05 degrees longitude (from 35°48′10.22″N, 78°43′6.61″W to 35°45′36.00″N, 78°39′50.17″W). Urban forest fragments ranged in area from 0.18 ha to 12.13 ha with an average area of 2.17 ha ($\pm$0.74 ha).

To determine how tree location affects canopy temperature, we recorded temperature at 4-hour intervals from May 26, 2016 to September 26, 2016 with Thermochron iButton data loggers DS1921G (Dallas Semiconductor, Dallas, TX). To avoid inflated temperature readings caused by exposure to direct sunlight, the data loggers were positioned in the lower canopy of a subset ($n = 16$ per location) of our study trees. Temperature readings were averaged across the 123 active days to obtain the mean temperature of each tree and analyzed with ANOVA specifying average temperature as the response and tree location as the predictor. Tukey's HSD was used for means comparison. These and all other analyses were conducted using JMP ('JMP® Pro, Version 13.0.0. SAS Institute Inc., Cary, NC, 1987–2007') statistical software.

We measured pre-dawn xylem water potential to assess tree water stress using a Scholander type pressure chamber (PMS Instrument Company, Albany, OR). In the same subset of study trees used to measure temperature, we pruned two 15 cm twigs with leaves intact from opposite sides of each tree canopy on the morning of August 12, 2016. Within 5 min of being abscised, the twigs were placed one at a time into the pressure chamber for measurement. Upon gradual pressurization of the twig we recorded the value at which water was released from the xylem and the mean of the two twig measurements per tree was taken to obtain an average water potential per tree. ANOVA was used to test for differences in water potential among landscape, fragment edge, and fragment interior trees where average tree water potential was specified the response variable and tree location the predictor.

We quantified *M. tenebricosa* density by randomly pruning two 30 cm long twigs from opposite sides of each tree canopy between 28 January and 25 February 2016. All live scales were counted on each twig and the sum was divided by 30 cm to obtain *M. tenebricosa* density. The densities of the two twigs per tree were averaged for a measure of tree-level *M. tenebricosa* density, expressed as *M. tenebricosa*/cm. A subset of the trees ($n = 17$ landscape, n = 17 fragment edge, and $n = 17$ fragment interior) were sampled again in the same manner between 9 and 15 December 2016. *M. tenebricosa* are univoltine and overwinter as adults (Miller and Davidson, 2005) so this sampling scheme captured the 2015 and 2016 generations. Scale density failed to meet the assumptions of normality and homogeneity of variance. We tested for differences in scale density among tree locations with the non-parametric Kruskal-Wallis test where *M. tenebricosa* was specified as the response variable and tree location the predictor variable. We used Steel-Dwass posthoc significance tests ($a = 0.05$) to assess multiple comparisons between tree locations.

We compared abundance of parasitoids from three families previously shown to parasitize *M. tenebricosa* (Dale and Frank, 2014b), among landscape, fragment edge, and fragment interior trees by hanging 7.6 × 12.7 cm yellow sticky cards (Olson Products, Medina, OH, USA) in the lower canopy of the subset of our study trees. Some sticky cards went missing and thus could not be used in the analysis. Sticky cards that were visibly damaged or tampered with were also removed from the analysis. Sticky cards were exchanged every 2 weeks while *M. tenebricosa* parasitoids were active from May 18 to June 7, 2016. We tested for overall parasitoid abundance among tree locations using a Kruskal-Wallis test where the total number of parasitoids captured per tree was specified as the response variable and tree location the predictor variable. We used the Steel-Dwass method for post-hoc comparison of parasitoid abundance among locations ($a = 0.05$).

2.2. Separating the effects of temperature from other environmental factors affecting M. tenebricosa

To control for effects of soil conditions (e.g., type, nutrition, compaction, moisture) that may differ between landscapes, forest fragment edges, and interiors, we measured *M. tenebricosa* density on potted *A. rubrum*. Saplings were planted in 15-liter nursery pots with composted bark and sand nursery mix (Parker Bark, Rose Hill, NC, USA). Most urban landscape trees are planted cultivars but since we had no way of knowing which cultivars were used in the Raleigh landscape, we used saplings of three common cultivars (*Marmo, Summerset, Red Sunset*). Saplings were infested with *M. tenebricosa* in May 2014. Infestation consisted of fastening *M. tenebricosa*-infested twigs to the stem and allowing first-instar nymphs to settle on the sapling's stem as they emerged. Because of the difficulty of infestation and to ensure even distribution of *M. tenebricosa*, the saplings were also placed beneath a grove of *M. tenebricosa* infested maples where first instar nymphs could rain onto the saplings. In July 2014, all saplings were moved to a nursery pad and watered with drip irrigation for two growing seasons which also permitted two generations for *M. tenebricosa* populations to build. On May 18, 2016, more composted bark mulch was added to the surface of each pot and water retaining polymer gel crystals (BioPlex Organics Plant Survival Solutions, Joy, PA, USA) were mixed with the medium according to label specifications for potted containers.

All *M. tenebricosa* within a 30 cm section of stem beginning 10 cm above the potting medium, on each sapling were counted using an Optivisor, DA-4/LX-4 (Donegan Optical Company, Lenexa, KS, USA). Potted saplings were deployed in the field by staking the pots within 1 m of the trunks of 16 trees per location ($N = 48$). Scale-free saplings ($N = 24$) were paired with half of the infested saplings to measure the number of *M. tenebricosa* scales that colonized potted saplings by raining down from the mature tree. The scale-free saplings underwent the same treatment as infested saplings but were stripped of all *M. tenebricosa* by visual inspection and hand removal prior to placement in the field. Once deployed the saplings each received 7.5 l of water twice per week which was sufficient to keep the water retaining polymer gel crystals hydrated at all locations. *Melanaspis tenebricosa* were counted again on the same 30 cm section of stem after 15 weeks in the field on September 9, 2016. The final *M. tenebricosa* density was log transformed and we used ANCOVA to determine how sapling location affected final *M. tenebricosa* density. We specified final *M. tenebricosa* density as the response variable and location as the fixed predictor. Initial *M. tenebricosa* density was specified as a covariate to determine if the final density of *M. tenebricosa* among tree locations was influenced by the initial density. Separately, ANOVAs were used to determine if initial or final *M. tenebricosa* density varied among cultivars, where initial and final densities were specified as response variables and cultivar the predictor variable. ANOVA was also used to determine if colonization of scale-free potted saplings varied among locations where final density of *M. tenebricosa* is the response and tree location is the fixed predictor. Tukey's HSD was used for post-hoc comparison of group means when significant differences were found among tree locations for any of the analyses in this experiment.

2.3. Effect of background temperature on M. tenebricosa abundance

To determine the effect of background temperature on *M. tenebricosa,* we compared scale abundance for trees from Raleigh, North Carolina USA to trees from Newark, Delaware and Philadelphia, Pennsylvania USA. By comparing *M. tenebricosa* abundance across fragment interior, edge, and landscape trees at a higher latitude we mimicked the Raleigh experiment in which we examined *M. tenebricosa* density across the gradient of urban tree locations. Newark-Philadelphia study trees were distributed across 0.48 degrees of latitude (from 39°36′40.28″N, 75°43′19.85″W to 40°05′23.07″N, 74°59′09.62″W) and 0.61 degrees of longitude (from 39°40′32.14″N, 75°46′49.74″W

W to 40°05′23.07″N, 74°59′09.62″W). Sites in Newark, DE and Philadelphia, PA were part of the University of Delaware's FRAME program (Forest Fragments in Managed Ecosystems; https://sites.udel.edu/frame; (Handley et al., 2015)) and because of the similarity of latitude, longitude, and average annual temperature will henceforth be referenced as a single urban area called Newark-Philadelphia.

We selected 71 *A. rubrum* divided among planted landscape ($n =$ 24), fragment edge ($n =$ 23) and fragment interior (n = 24) in Newark-Philadelphia. *M. tenebricosa* density on trees in Newark-Philadelphia were quantified using the methods outlined in Section 2.1. Sampling in Newark-Philadelphia occurred from 4 to 7 November 2016 and was compared to the December 2016 sampling in Raleigh. To determine the effect of background temperature on *M. tenebricosa*, we compared scale density for trees from Raleigh to trees from Newark-Philadelphia using a generalized linear model. We specified *M. tenebricosa* density as the response and tree location, city, and their interaction as predictors. By including the interaction between city and tree location we were able to determine if *M. tenebricosa* responded differently to tree location in each urban area. Because *M. tenebricosa* density was over-dispersed we elected to fit it to a negative binomial distribution (White and Bennetts, 1996; Lindén and Mäntyniemi, 2011).

3. Results

3.1. Temperature, water stress, M. tenebricosa density, and natural enemy variation

The mean temperature across all trees ranged from 24.4 °C to 27.2 °C. Mean temperature of planted landscape trees was greater than fragment edge trees by 1.2 °C and greater than fragment interior trees by 1.3 °C ($P < 0.001$, $F_{2,45} = 58.44$) (Fig. 1). Pre-dawn water potential ranged from −0.4 to −1.2 MPa with mean of −0.6 MPa but did not differ among planted landscape, fragment edge, or fragment interior trees ($P = 0.27$, $F_{2,45} = 1.32$) (Fig. 1).

Melanaspis tenebricosa density across all trees in Raleigh, NC in January 2016 ranged from 0 to 18.5 scales/cm. Its density was greater ($P < 0.001$, $X^2 = 46.53$) by three orders of magnitude on landscape trees than on either fragment edge or fragment interior trees. *Melanaspis tenebricosa* were found on 92.5% of the landscape trees but only on 11.1% of fragment edge trees and 18.5% of fragment interior trees. We found a similar pattern the next generation in December 2016 when *M. tenebricosa* density ranged from 0 to 28.8 scales/cm and was greater ($P < 0.001$, $X^2 = 26.88$) on landscape trees than on either fragment edge or fragment interior trees (Fig. 2). *M. tenebricosa* was again present on more of the landscape trees (94.4%) than forest fragment edge (33.3%) or interior trees (29.4%). Parasitoids were four times more abundant

in landscape trees than either fragment edge, or fragment interior trees ($P < 0.001$, $X^2 = 13.59$; Fig. 3).

3.2. Separating the effects of temperature from other environmental factors affecting M. tenebricosa

Final *M. tenebricosa* density was greater on saplings paired with landscape trees than saplings paired with either fragment edge or fragment interior trees ($P = 0.005$, $F_{2,40} = 6.17$) (Fig. 4). As expected, initial *M. tenebricosa* density had a significant effect on final *M. tenebricosa* density ($P < 0.001$, $F_{1,40} = 22.06$). However, there was no significant interaction between sapling position and initial *M. tenebricosa* density ($P = 0.204$, $F_{2,40} = 1.65$). Cultivar had no significant impact on the initial ($P = 0.70$, $F_{2,43} = 0.36$) and final density ($P = 0.71$, $F_{2,43} = 0.35$) of *M. tenebricosa*. Colonization of initially uninfested saplings was low (0.3 ± 0.1 SEM *M. tenebricosa*/cm) and did not differ among trees in landscape, edge, or interior locations ($P = 0.27$, $F_{2,21} = 1.39$) suggesting that colonization of potted saplings due to dispersal of first-instar *M. tenebricosa* from landscape and fragment trees was negligible during the time saplings were deployed.

### 3.3. Effect of background temperature on M. tenebricosa abundance

The density of *M. tenebricosa* was 15 times greater on landscape trees in Raleigh than in Newark-Philadelphia (Fig. 5). *Melanaspis tenebricosa* density across all Newark-Philadelphia trees in November 2016 ranged from 0 to 4.89 scales/cm with mean 0.16 (± 0.1) scales/cm and did not differ ($P = 0.08$, $X^2 = 5.1$) among tree locations (Fig. 2). *Melanaspis tenebricosa* were found on 62.5% of the landscape trees in Newark-Philadelphia but only on 26.1% of fragment edge trees and 33.3% of fragment interior trees. The generalized linear model of scale density showed that main effects of tree location and city each had a significant effect on scale density (Wald $X^2 = 56.19$, $P < 0.001$ and Wald $X^2 = 45.74$, $P < 0.001$ respectively). We found a significant interaction between tree "location" and "city" which suggests that *M. tenebricosa* responded differently to tree location (landscape, fragment edge, fragment interior) in each city (Wald $X^2 = 16.28$, $P < 0.001$) (Fig. 5).

4. Discussion

Understanding how tree pests respond to warming in different parts of the urban forest is vital to protecting the ecosystem services offered by trees as cities expand and the climate warms. Urban trees in managed landscapes such as residential neighborhoods, industrial areas, and business complexes are subject to infestation by pests that are less common in rural forests (Metcalf, 1922; Raupp et al., 2010;
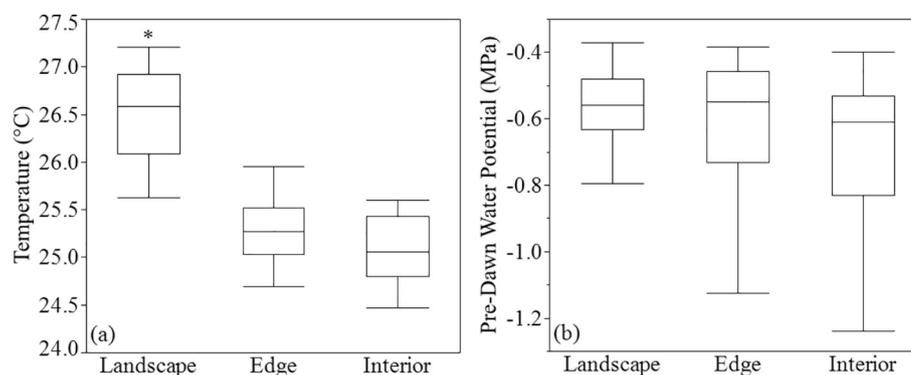
Fig. 1. The effects of tree location on canopy temperature and water potential are illustrated using boxplots to demonstrate the range of values obtained. The median of the data range is marked by the line which divides each box. Boxes represent the interquartile range and upper and lower whiskers represent data outside the middle 50% of observations. Asterisks indicate significant differences from Tukey HSD tests. (a) The average canopy temperature of urban landscape trees ($n = 16$) was significantly greater than it was for trees growing at urban forest fragment edge ($n = 16$) or interior ($n = 16$). (b) The average predawn water potential did not differ among urban landscape (n = 16), urban forest fragment edge (n = 16) or interior trees (n = 16).
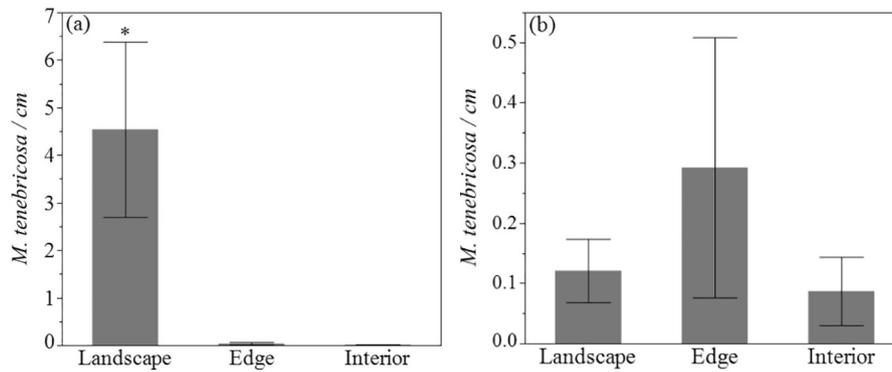
Fig. 2. The effect of tree location on mean *Melanaspis tenebricosa* density. (a) In December 2016, planted landscape trees ($n = 17$) had three orders of magnitude more *M. tenebricosa* than fragment edge (n = 17) or fragment interior ($n = 17$) trees in Raleigh, NC. (b) There was no difference in *M. tenebricosa* density among planted landscape ($n = 24$), fragment edge (n = 23), and fragment interior (n = 24) trees in the Newark-Philadelphia urban area during November 2016. Asterisks indicate significant differences ($P < 0.05$) derived from post-hoc Steel-Dwass all pairs test. Error bars represent ± 1 standard error of the mean.

Youngsteadt et al., 2014). Higher urban temperatures result in greater survival and fecundity and are often the mechanism for this disparity (Meineke et al., 2013; Dale and Frank, 2014a, 2017). As such, scale insects and other urban tree pests may be indicators of changing climate and studies of their response to the urban heat island effect are valuable for predicting future threats to urban and rural trees (Youngsteadt et al., 2017; Lahr et al., 2018b). Because trees in urban forest fragments and landscapes are subject to the urban heat island effect and many of the same biotic and abiotic factors (Hanks and Denno, 1993; Tooker and Hanks, 2000) one may not expect to find differences in temperature or pest abundance. However, we show that *A. rubrum* trees growing in urban forest fragments are on average 1.3 °C cooler and have three orders of magnitude fewer *M. tenebricosa* than trees growing in managed landscapes of a mid-latitude city in the southeastern USA.

The dominant effect of temperature over natural enemies and plant stress is supported by our potted tree experiment in which *M. tenebricosa* increased three times more in hot landscape trees than cool forest fragment trees, when both were kept watered to protect against drought stress. Moreover, we found greater overall density of *M. tenebricosa* in the warmer climate of our mid-latitude city, compared with the cooler climate of the higher latitude city. Ours is the first study to demonstrate that urban forest fragments mitigate the urban heat

island effect on trees and thereby reduce tree pest abundance in a warm, mid-latitude city.

The urban heat island effect causes drought stress in urban trees by reducing soil moisture and increasing vapor pressure deficit (Cregg and Dix, 2001). Drought stressed plants require greater negative pressure to draw water from the roots through their xylem (Scholander et al., 1965). We did not find a difference in pre-dawn water potential among landscape and forest fragment trees which suggests that drought stress did not contribute to the differences in *M. tenebricosa* densities that we observed. Moreover, the water potential values we observed did not reach levels known to cause physiological impairment in woody angiosperms (Urli et al., 2013; Yin and Bauerle, 2017) thus, the trees were not suffering from chronic drought at the time of our data collection. Since drought stress did not differ among tree locations, it is likely that other factors regulate *M. tenebricosa* within urban areas.

Habitats with greater plant structural complexity or diversity generally have more natural enemies or higher rates of parasitism than simple habitats (Andow, 1991; Langellotto and Denno, 2004) in natural (Roland and Taylor, 1997), agricultural (Root, 1973; Thomas et al., 1991; Landis et al., 2000; Chaplin-Kramer et al., 2011), and urban ecosystems (Tooker and Hanks, 2000; Shrewsbury et al., 2004). Thus, greater natural enemy abundance would be expected in urban forest
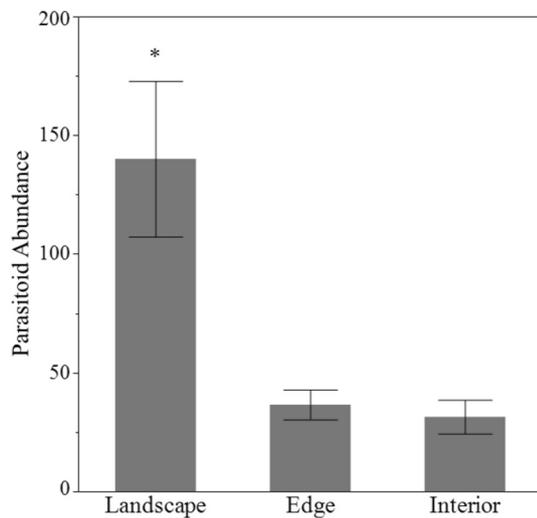
Fig. 3. Effect of tree position on parasitoid wasp abundance. The total number of parasitoid hymenopterans captured on sticky cards from three families (Aphelinidae, Encyrtidae, and Signophoridae) were more numerous in landscape trees ($n = 13$) than either forest fragment edge ($n = 12$) or interior trees (n = 11). Post hoc nonparametric multiple comparisons from Steel-Dwass all pairs test. Asterisks indicate significant differences ($P < 0.05$). Error bars represent ± 1 standard error of the mean.
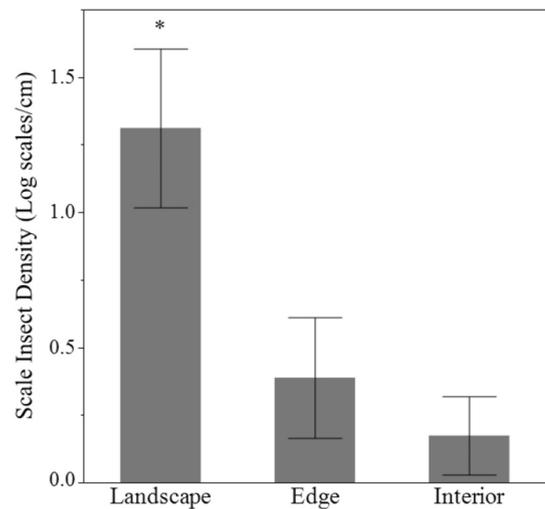
Fig. 4. Effect of tree position on *Melanaspis tenebricosa* density. Potted saplings that were paired with landscape trees ($n = 14$) had higher densities of *M. tenebricosa* than potted saplings paired with forest fragment edge ($n = 16$) or interior trees (n = 16). Asterisks indicate significant differences from Tukey HSD tests ($P < 0.05$). Error bars represent ± 1 standard error of the mean. Two of the potted saplings that were paired with urban landscape trees were destroyed by vandals during deployment.
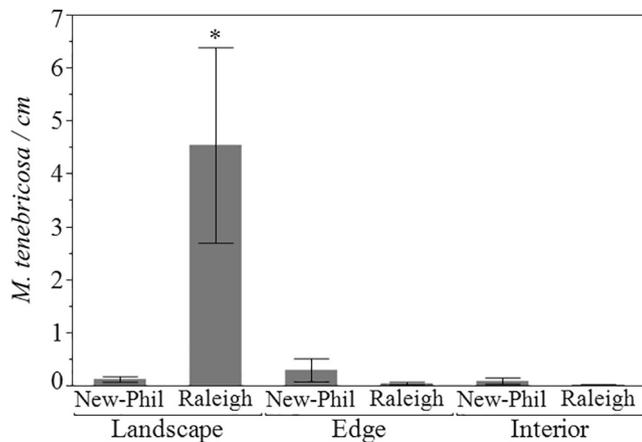
Fig. 5. Effects of tree location on *Melanaspis tenebricosa* density by city. *M. tenebricosa* density was greater on urban landscape trees in the city of Raleigh, NC than urban landscape, urban forest fragment edge, or urban forest fragment interior trees from the Newark-Philadelphia urban area. Asterisks indicate significant differences from Steel-Dwass all pairs test ($P < 0.05$). Error bars represent ± 1 standard error of the mean. Sample sizes for each city and tree location follow – Raleigh: landscape ($n = 17$), Forest fragment edge ($n = 17$), forest fragment interior ($n = 17$). New-Phil abbreviates the Newark-Philadelphia urban area: landscape ($n = 24$), forest fragment edge ($n = 23$), forest fragment interior ($n = 24$).

fragments than landscape trees. However, we captured more *M. tenebricosa* parasitoids from landscape trees, where *M. tenebricosa* were also more abundant, than on forest fragment trees. This suggests that control by natural enemies is less important than temperature in predicting *M. tenebricosa* density. Had natural enemies exerted effective control over *M. tenebricosa* we would have expected lower densities on landscape trees than forest trees. We did not assess generalist predatory arthropods which may also contribute to biological control of scale insects. However, our findings corroborate those of Dale and Frank (2014b), who found that natural enemies do not regulate *M. tenebricosa* in urban landscapes where its fecundity and survival are also greater (Dale and Frank, 2014b, 2017). The results of our observational experiments infer temperature as the driver of *M. tenebricosa* density. However, there are other confounding factors that may exist between sites which we have accounted for in our manipulative experiment.

The results of our manipulative study which paired potted saplings with mature urban trees reinforces that temperature is the main factor that influences scale abundance by controlling for variation in soil moisture, compaction, and nutrition. After a single generation, *M. tenebricosa* density was greater in potted saplings which were paired with warmer landscape trees than in saplings paired with either fragment edge or interior trees. We were also able to control for tree genotype and the possibility that landscape trees, likely cultivars, were simply more susceptible to scales than wildtype forest fragment trees. We found that there was no difference in *M. tenebricosa* density among the three common cultivars we used. Since *M. tenebricosa* density was highest in landscapes for both the observational and manipulative experiments we attribute differences in *M. tenebricosa* density primarily to temperature-driven differences in survival and reproduction (Dale and Frank, 2014b, 2017) rather than differences in tree stress or susceptibility of *A. rubrum* cultivars. We suspect that as background temperatures warm and the urban heat island effect intensifies *M. tenebricosa* densities will increase on *A. rubrum* regardless of their genotype, soil characteristics, or position on the landscape.

Latitude, in addition to the urban heat island effect, affects the temperature of an urban area such that low latitude cities are warmer than higher latitude cities. Mean annual temperatures for Raleigh and Newark-Philadelphia as measured from weather stations which are centrally located among study sites are 16.1 °C and 13.2 °C respectively. We found that *M. tenebricosa* density was greatest in Raleigh landscapes

which are 2.9 °C warmer than Newark-Philadelphia. Thus, background temperature can alter arthropod abundance directly but relative differences in temperature change how arthropods are affected by warming. For example, at low latitudes urban warming may drastically increase or decrease insect abundance, but at high latitudes the effect of warming is largely positive for temperate arthropods (Youngsteadt et al., 2017). Such was the case for increased voltinism by many European butterfly species (Altermatt, 2010) and for range expansions by *Thaumetopoea pityocampa* (pine processionary moth) (Battisti et al., 2005), and *Dendroctonus ponderosae* (mountain pine beetle) (Janes et al., 2014). In addition, insect winter survival can be higher due to the urban heat island effect (Hart et al., 1986; Miller and Hart, 1987; Robinet et al., 2012). Newark-Philadelphia is near the northern edge of *M. tenebricosa* distribution (Metcalf, 1922) so we expected greater density on landscape trees where *M. tenebricosa* would benefit from warming. However, we found no difference in *M. tenebricosa* density among planted and forest trees so other factors must still be limiting *M. tenebricosa* abundance. For example, there may be a temperature threshold at which *M. tenebricosa* has higher survivorship or gains a physiological advantage which has not yet been met in Newark-Philadelphia. The high and low thermal tolerances of *M. tenebricosa* are not known and more work in this area would help predict the current and future range where it is likely to be a chronic pest of urban trees.

We and others (Dale and Frank, 2014a, 2017; Youngsteadt et al., 2014), have found extreme differences in *M. tenebricosa* abundance across only 1.3–2.0 °C urban temperature gradient. The eastern United States is predicted to warm by 2–3 °C in the next 50–100 years (George et al., 2007) and the average annual temperature difference between Raleigh and Newark-Philadelphia is 2.9 °C. Given that we have isolated temperature as the main factor which predicts *M. tenebricosa* density we can conclude that Raleigh may be an indicator of future pest density in Newark-Philadelphia. Evidence for this comes from Just et al. (2018), who surveyed *M. tenebricosa* abundance in street trees across 10 degrees of latitude in southeastern North America and found a hump-shaped distribution with greatest abundances in mid-latitude cities. To the extent that the urban heat island effect is coupled with background climate and future warming, it is also possible that mid-latitudes will become too warm to support chronic infestations of *M. tenebricosa* and the range of the pest may shift altogether northward. Our study cities likely differed in ways other than background climate, such as total area, human population density, and overall urban intensity. However, southern and midlatitude cities which differ in these factors all show similar relationships between temperature and *M. tenebricosa* abundance (Just et al., 2018) thereby corroborating the role of temperature as the primary driver of *M. tenebricosa* density in the present study.

5. Conclusions

Urban forests reduce air and noise pollution, mitigate stormwater runoff, sequester carbon, and have cultural and recreational value (Bolund and Hunhammar, 1999). More people now live in urban areas than in rural areas (United Nations, 2015) and the land area dedicated to urban sprawl is expected to triple by the year 2030 (Seto et al., 2012). For these reasons, urban trees in the United States have been valued at roughly $2.4 trillion (Nowak et al., 2002) and should be managed to sustain and maximize their benefits. Our work shows that urban forest fragments buffer trees from the urban heat island effect and concomitant stress and pest infestations in a warm mid-latitude city. The same buffering should also enhance the ecosystem services provided by trees (Meineke et al., 2016) growing in forest fragments. Therefore, in addition to preserving forest fragments, municipalities may be able plant trees in clusters to reduce the temperature immediately around trees and strive to increase total canopy cover to shade impervious surfaces and reduce the urban heat island effect city-wide.

We anticipate that future climate warming will result in greater *M. tenebricosa* density in high latitude cities. However, if urban trees can be kept healthy, through altered planting practices or by preserving forest fragments during urban development, they may contribute even more to the urban environment and human well-being. For example, greater tree density creates a cooling effect in urban environments (Ng et al., 2012), which as we have demonstrated, is important for reducing urban tree pest density but also for energy savings (McPherson et al., 2005). Tree density is also correlated with increased public living preference, ties among neighbors, and sense of safety in urban areas (Kuo et al., 1998; Kuo, 2003) such that a few urban forest fragments may have a disproportionately high impact on social as well as ecological services in highly urbanized areas. The current study should stimulate further, more applied, investigations related to urban forest fragments and pest response to the urban heat island effect. For example, our results suggest that it would benefit trees, and subsequently enhance the ecosystem services they provide, to plant them in clusters which mimic urban forest fragments. However, urban space is at a premium and knowing the minimum number of trees, their spacing, and total land area required to reduce pest density and boost tree health would optimize management of urban forest fragments.

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Author's contributions

L.C.L. and S.D.F. conceived of experimental design. L.C.L. collected and analyzed the data. All authors contributed to drafts and gave approval for publication.

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