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Urban warming reduces aboveground carbon storage

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A substantial amount of global carbon is stored in mature trees. However, no experiments to date test how warming affects mature tree carbon storage. Using a unique, citywide, factorial experiment, we investigated how warming and insect herbivory affected physiological function and carbon sequestration (carbon stored per year) of mature trees. Urban warming increased herbivorous arthropod abundance on trees, but these herbivores had negligible effects on tree carbon sequestration. Instead, urban warming was associated with an estimated 12% loss of carbon sequestration, in part because photosynthesis was reduced at hotter sites. Ecosystem service assessments that do not consider urban conditions may overestimate urban tree carbon storage. Because urban and global warming are becoming more intense, our results suggest that urban trees will sequester even less carbon in the future.

1. Background

Trees are critical components of nearly every ecosystem on Earth. They regulate local [1] and global climates [2–4], filter air [5] and water [6], and provide habitats for a large proportion of known biodiversity [7]. One of the most important services trees provide is carbon storage. During photosynthesis, trees take up CO_2 from the atmosphere and incorporate its components into their tissues. By doing so, they reduce CO_2 concentrations in the atmosphere and future climate warming. Despite considerable research on how climate change will affect trees and the services they provide [8–10], predictions remain contradictory, in part because experiments on mature trees are rare. Further, no experiments have tested how mature trees respond to warming, a key component of climate change.

Net effects of future warming on temperate trees remain uncertain. Theoretically, warming could directly reduce tree growth and, thus, carbon storage by intensifying water stress [11], reducing photosynthesis or both [12]. Warming could increase growth by extending growing seasons [13]. Warming could also indirectly decrease tree growth by increasing herbivorous arthropod abundances [14]. Outbreaks of herbivorous pests, such as the pine processionary moth [15] and the mountain pine beetle [16], have become more frequent due to climate change, sometimes turning forests from carbon sinks into carbon sources by killing trees [17]. However, chronic herbivory—sub-lethal feeding by native arthropods throughout trees' lives, typically in low abundances—has rarely been studied. This is despite the fact that most tree species worldwide have chronic herbivores such as many scale insect and aphid species, several of which are already more abundant due to warming [14,18].

Urban forests provide a unique opportunity to determine the effects of recent, rapid warming on mature trees. In many cities, the urban heat island effect, or 'urban warming,' is comparable in magnitude to warming expected globally in the next century [19]. Urban warming is caused by hard surfaces that absorb radiation from the sun and emit it as heat [20]. Because these hard surfaces are patchily distributed, cities are thermal mosaics [21,22]. These mosaics provide ready-made experiments, in which trees have been planted and then subjected to a variety of thermal environments. Further, trees in the hottest parts of cities

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are often infested with chronic herbivores that are rare in rural forests and cooler parts of cities, but become pests due to urban warming. For example, urban warming increases densities of two native scale insect species that survive better [23] and produce more eggs [24,25] at hotter urban sites.

To determine how warming affects urban tree function and growth, we conducted a 3-year, factorial experiment across a range of urban warming intensities. Across this temperature range, we treated some trees with horticultural oil to reduce chronic herbivore abundance, separating direct effects of warming on tree physiology from indirect effects through herbivores. First, we measured how warming affected tree growth. To identify the mechanisms by which warming affected tree growth, we measured leaf gas exchange and water stress. Our study is the first to use urban habitats to measure how warming affects the function of mature trees and to scale these effects up to an entire city.

2. Material and methods

(a) Study system

Our focal tree species, willow oak *Quercus phellos*, is one of the largest, most commonly planted shade tree species in the eastern USA. Its most common arthropod pest species is the oak lecanium scale insect *Parthenolecanium quercifex*. *Parthenolecanium quercifex* is univoltine. In spring, females feed on phloem sap from branches and produce up to 3000 eggs per female (E Meineke, S Frank 2013, unpublished data). Newly hatched nymphs move to leaves to feed during summer and return to branches before leaf fall to overwinter. In general, scale insects can reduce tree growth by feeding on sap and by promoting sooty mould on leaves, which blocks leaf light interception and photosynthesis [26].

(b) Study design

Raleigh, NC, has a humid, subtropical climate and is located at 35.77° N 78.64° W. As in Youngsteadt *et al*. [21], we used a Landsat infrared layer of surface temperature in 7 April 2011 to choose our study sites. Each 30-m pixel in this image incorporates temperatures of built structures, land and vegetation; the image identifies sites that are likely to be overall hotter or cooler. We overlaid a map of Raleigh street trees provided by the Parks, Recreation and Cultural Resources Department with the thermal image and chose 10 relatively hot sites (above median temperature of all pixels containing street trees) and 10 relatively cool sites, each of which contained two willow oak trees less than 30 m apart. The mean (±s.e.m.) study tree diameter at breast height (DBH) was 20.9 ± 1.2 cm (see electronic supplementary material, figure S1*a* for a histogram of all trees.)

To remove scale insects and other small, soft-bodied chronic herbivores, we used a mist blower (model: 451, Solo, Newport News, VA, USA) to treat one tree per site with horticultural oil (SuffOil-X, BioWorks, Victor, NY, USA) on seven dates (March, July and September 2013; February, March, April and May 2014). We applied the oil until leaves were wet, using a concentration of 2 l per 100 l of water in March 2013, September 2013, February 2014 and March 2014, and 1 l per 100 l of water in July 2013, April 2014 and May 2014. Our treatments created a split plot design with temperature as the whole plot factor and oil as the split plot factor.

To measure air temperature in the tree canopies, we installed one iButton Thermocron data logger (model: DS1921G, precision: 0.5°C, accuracy: ±1.0°C, Dallas Semiconductor, TX, USA) on the northern, bottommost branch of one tree per site. We placed iButtons below branches to reduce sun exposure associated with malfunctions in other studies [24]. iButtons were housed in wall mounts (Dallas Semiconductor of Dallas, TX) inside 2.54-cm deep plastic cups to protect them from precipitation and direct sun.

At our study site Raleigh, NC, USA, willow oak is living far below its thermal maximum, as its range extends across much of the southern USA. Therefore, we predicted that warming would enhance growth rates in trees treated for herbivores at hotter sites. By contrast, we expected that cooler trees would grow less overall and would benefit from the insecticide treatment less because they had lower baseline herbivore abundances [22].

(c) Herbivore abundance

We provide a timeline (electronic supplementary material, table S1) of when all response variables for this study were measured. To determine which arboreal herbivores were most abundant, and, therefore, had the potential to act as pests, we used a funnel beat sampler [27] in August 2013 and 2014. The sampler is a 30.5-cm diameter funnel attached to a 2.5-m pole, with a hinged lid that beats arthropods from foliage into the funnel, where they fall into alcohol in a sampling jar fixed to the bottom of the funnel. We sampled foliage along the lowest part of crowns of study trees in 12 locations. Arthropods were stored in 95% ethanol and identified to the lowest taxonomic level possible without dissections or slide mounts (usually family or genus) under a dissecting microscope.

To determine how herbivores responded to temperature, we did more targeted counts of the two most abundant herbivore taxa from funnel beat samples, *Parthenolecanium* scale insects and spider mites (see Results). Both of these groups include chronic herbivores that live on leaves or stems their entire lives. To measure their abundances, we collected one 30.5 cm branch from each cardinal direction of the bottom, outer canopy of each study tree in August 2013 and June 2014. On these dates, we counted *Parthenolecanium* scale insects on five leaves per branch using a dissecting microscope. In March 2015, we collected, then counted overwintering *Parthenolecanium* scale insects on twelve 30.5-cm branches from the bottom, outer canopy of each study tree. Because *P. quercifex* and its congener *P. corni* are both willow oak residents, are indistinguishable in nymphal stages, and feed on the same part of trees (phloem), counts of these species are pooled. In August 2013, we counted spider mites on the same leaves on which we counted *Parthenolecanium*.

(d) Photosynthesis

We measured gas exchange and fluorescence with a LI-6400XT Portable Photosynthesis System equipped with a 6400-40 leaf-chamber fluorometer (LI-COR, Inc., Lincoln, Nebraska). We measured maximum light-saturated photosynthesis (hereafter 'photosynthesis') and conductance on three full-sun leaves with no chewing damage on three severed branches in floral picks [28]—i.e. conical, water-filled containers—per study tree between 08.00 and 13.00 from 7–19 July, 2014, on sunny, dry days. To prepare branches, we severed them from the tree, immediately re-cut them underwater, and, still underwater, inserted them in floral picks. During gas-exchange measurements, we held leaf-chamber CO_2 concentration at 400 µmol mol^{-1}, vapour pressure deficit between 1 and 2 kPa, block temperatures at 30°C, and used a saturating light intensity of 1200 µmol photons m^{-2} s^{-1}. To determine if water deficits affected gas exchange, we used a pressure chamber (model: 1505D, PMS Instrument Company, Albany, OR, USA) to measure branch water potential on the same days and at the same time during which we measured gas exchange. We haphazardly collected three bottom, outer branches from the north side of each tree, pressurized those branches and recorded the pressure required to release water from the xylem.

We measured the maximum quantum efficiency of photosystem II (Fv/Fm), a common measurement of plant stress [29], on the same days we measured gas exchange. We cut three branches per tree,

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immediately re-cut branches under water, and then put them in floral picks. Leaves were dark-adapted in a cooler with ice packs (which cooled the air but did not contact leaves) for at least 4 h. We measured Fv/Fm on three leaves per tree in a darkroom.

(e) Growth

We measured DBH of each tree 1.4 m above the ground in March 2014, October 2014 and June 2015. Trees were marked with a permanent marker to ensure they were measured in the same place on each date. Because the growing season is between April and October in our study region, our goal was to capture total yearly growth in 2014 and delayed effects of the 2014 temperatures [30] on spring growth in 2015. We used DBH to calculate basal area (πr^2) and basal area growth (difference between starting and ending basal area) in 2014 and 2015, the years after the oil treatment was implemented. Branch growth reacts immediately to abiotic stressors [31] and is, therefore, a useful measurement of tree responses to environmental change. To determine stem growth in 2014 and 2015, we collected 12 branches from the bottom, outer branches of each study tree in March 2015. To determine spring growth in 2015, we measured branches from apical tips to terminal bud scars. To determine total 2014 growth, we measured stems from the terminal bud scar to the penultimate bud scar.

(f) Carbon sequestration

Because both herbivores and warming affected tree growth, we wanted to determine the extent to which each of these stressors reduced carbon sequestration. To do this, we first used a species-specific allometric equation for willow oak [32] to estimate aboveground dry weight for study trees in March and October 2014. Then, we used methods in Nowak *et al.* [33] to estimate total carbon storage per tree from dry weights. The total carbon sequestered by our study trees in 2014 was calculated as the difference between March and October carbon storage estimates.

To estimate how urban warming affected carbon sequestration by willow oaks across our entire focal city, we used the same thermal map and tree inventory that was used to select study sites. From this map, we extracted surface temperatures at all city-owned willow oaks in Raleigh (3333 trees). We then determined the relationship between mean growing season air temperatures (April to October) and surface temperatures at our study sites using simple linear regression. We used the resulting regression to project 2014 air temperatures at all willow oak trees in the tree inventory, i.e. all willow oaks managed by the local, municipal government. (Projected air temperatures averaged 24.3°C, range 23.4–25.5°C.) We used multiple regression to model the relationship between air temperatures at our study sites, tree DBH at the beginning of the growing season, and estimated carbon sequestration. We then used this regression equation (carbon sequestration (kg) = a*projected air temperature (C) + b*DBH (cm) + intercept) to estimate total carbon sequestration by willow oaks in the tree inventory. We then set air temperatures to the lowest observed value in 2014 at our study sites (23.4°C) to estimate carbon sequestration by willow oaks with minimum urban warming. The difference between these two sequestration estimates (based on observed urban warming and minimum urban warming) represents the estimated amount of carbon sequestration lost due to urban warming intensification. To determine upper and lower bound carbon estimates, we calculated carbon sequestration using the upper (mean + s.e.) and lower (mean − s.e.) slope estimates associated with urban warming at all 3333 trees (electronic supplementary material, table S3).

While we could not directly estimate the effects of herbivory on biomass, we could determine the proportion of total tree biomass in tissues affected by herbivores, i.e. new branch biomass. We used a genus-specific allometric equation [34] to estimate total new branch biomass in each of our study trees. We used the same methods as above to convert branch biomass to carbon storage. Then, we calculated the proportion of total tree biomass stored in new branches as an estimate of the carbon stored in tissues subject to growth reduction by *Parthenolecanium* scale insects.

(g) Analyses

We performed all analyses in RStudio [35]. The iButtons recorded unreasonably high midday temperatures (45°C+). We thought this to be associated with solar radiation heating iButtons directly, such that measurements did not represent air temperatures [36]. To avoid biases introduced by these readings, we extracted temperatures between 18.00 and 20.00 h and used these in all downstream analyses. These temperatures represent the urban heat island effect, which rises steadily after 15.00 and levels off around 20.00 h [37], without capturing confounding effects of solar radiation. We calculated average temperatures in the *plyr* package [38] during spring and/or summer months we thought most biologically relevant to each response variable. Details about thermal predictors included in each analysis are located in electronic supplementary material, table S2. In 2013, iButtons failed at two sites, and, in 2014, an iButton failed at one site. These sites were discarded from analyses. In 2014, an additional site was removed from the study due to a dissatisfied homeowner.

Parthenolecanium scale insects and spider mites (Acari: Tetranychidae) were the most common herbivorous arthropods. We analysed their abundances relative to temperature and oil treatment with mixed effects models specified to fit the probability distributions associated with each response. In all analyses, we used linear models when possible and moved to more complex models (generalized linear models) when necessary. In all models, temperature and oil treatment (yes/no) were specified as fixed effects and site was specified as a random effect. We modelled *Parthenolecanium* scale insect and spider mite abundance from 2013 using generalized linear mixed effects models (GLMER) with Poisson distributions and log link functions in the *lme4* package. In these models, we included sample identity as a random effect to correct overdispersion. We modelled *Parthenolecanium* scale insect abundance from 2014 and 2015 (log + 1) using linear mixed effects models (LME) in the *nlme* package [39]. We did not record temperatures in 2015. Therefore, we used growing season temperatures in 2014 as a predictor of *Parthenolecanium* scale insect abundance in 2015. All R^2 values were derived from formulae for marginal and conditional R^2.

We analysed all gas-exchange measurements and Fv/Fm with LME with temperature and oil treatment as fixed effects and tree nested within site (for gas exchange) or branch nested within tree nested within site (for Fv/Fm) as random effects. We $1/x$ transformed fluorescence (Fv/Fm) to improve residuals. To determine if water deficits drove gas exchange, we tested for a correlation between water potential and light-saturated photosynthesis using simple linear regression.

To determine how temperature and insect removal affected tree growth, we used LME with branch growth and basal area growth in each year as responses and temperature and oil treatment as fixed effects in the *nlme* package. For basal area growth, we specified site as a random effect, and for branch growth we specified tree nested within site as a random effect. Trees with bigger original DBH grow more in other systems [40,41], so we included original basal area as a covariate in the model for basal area growth. Because basal area growth and photosynthesis were lower due to warming, and branch growth tended to be lower though was not significantly affected by warming, we wanted to test if photosynthetic declines drove growth declines. To do this, we used simple linear regressions with mean photosynthesis per tree as the predictor and basal area and branch growth from 2015 as responses.

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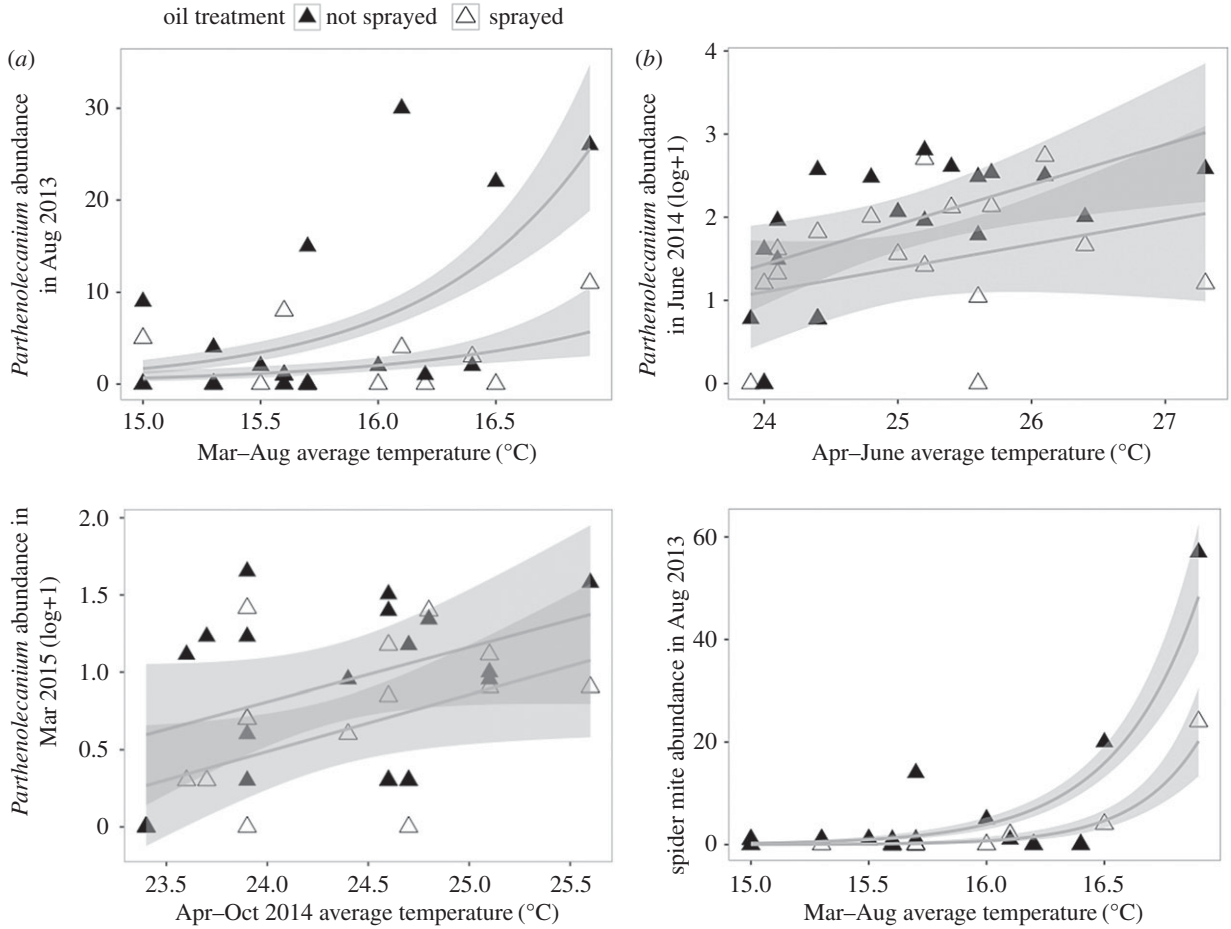

Figure 1. Urban warming increased chronic herbivore abundance, and oil treatments reduced chronic herbivore abundance. The two most common herbivorous arthropods on street trees in Raleigh, NC, USA, (*a–c*) oak lecanium scales (Coccidae: *Parthenolecanium* scale insects) and (*d*) spider mites (Tetranychidae) and were more abundant at hotter urban sites and less abundant due to oil treatments. Lines are means. Grey areas are 95% CIs.

3. Results

(a) Herbivore abundance

Parthenolecanium scale insects and spider mites were the most abundant herbivorous arthropods in funnel beat samples when counts are summed over both years (electronic supplementary material, figure S2). Together, they made up over 65% of herbivores captured in funnel beat samples. In all years, hotter sites had significantly more *Parthenolecanium* scale insects (2013, figure 1*a*, Wald $Z = 1.62$, $p = 0.043$; 2014, figure 1*b*, $F_{1,16} = 4.88$, $p = 0.042$; 2015, figure 1*c*; $F_{1,16} = 4.74$, $p = 0.045$), such that the hottest site had seven times more *Parthenolecanium* scale insects on average than the coolest site at which we detected *Parthenolecanium* scale insects. Trees treated with oil had half as many *Parthenolecanium* scale insects on average than untreated trees ($p < 0.05$ in all years; for detailed statistics, see electronic supplementary material, table S2). Similarly, hotter trees had up to 56 times more spider mites than the cooler sites; (figure 1*d*, Wald $Z = 2.14$, $p = 0.003$), and trees treated with oil had one-third as many spider mites than untreated trees ($p < 0.001$; electronic supplementary material, table S2).

(b) Photosynthesis

Light-saturated photosynthesis (figure 2*a*; $F_{1,16} = 4.79$, $p = 0.044$) and conductance ($F_{1,16} = 5.53$, $p = 0.032$) declined linearly with warming but were not affected by oil treatments ($p > 0.05$; detailed statistics in electronic supplementary material, table S2). Knowing that photosynthesis and conductance declined with warming, we wanted to know the extent to which water relations drove photosynthesis. To determine the relationship between these responses, we used simple linear regression. We found that light-saturated photosynthesis and conductance were highly and positively correlated (electronic supplementary material, figure S3; $F_{1,14} = 144.46$, $p < 0.0001$), such that trees with higher conductance also photosynthesized more. Although tree water deficits ranged from mild to moderate (PMS Instrument Company Guide) with stem water potential measurements ranging from −0.91 to −2.46 MPa, mid-morning water potential was unrelated to light-saturated photosynthesis ($F_{1,36} = 0.03$, $p = 0.865$). Neither warming ($F_{1,16} = 1.09$, $p = 0.311$) nor oil treatment ($F_{1,17} = 1.04$, $p = 0.322$) affected fluorescence (Fv/Fm).

(c) Growth

As expected, basal area growth rates were higher for trees with larger basal areas at the beginning of each year (2014: $F_{1,16} = 15.62$, $P = 0.011$, 2015: $F_{1,16} = 5.15$, $P = 0.037$). Urban warming was associated with less basal area growth in both years (2014: figure 2*b*, $F_{1,16} = 5.36$, $p = 0.034$; $F_{1,16} = 5.87$, $p = 0.028$). Lower light-saturated photosynthetic rates were associated with smaller basal area growth (figure 2*c*; $F_{1,34} = 7.99$, $p = 0.008$). Oil treatments did not affect basal area growth (2014: $F_{1,16} = 0.34$, $p = 0.566$, 2015: $F_{1,16} = 0.01$, $p = 0.908$). In contrast with basal area growth, 2015 branch growth was not affected by warming ($F_{1,16} = 2.03$, $p = 0.173$), oil treatments ($F_{1,17} = 2.56$,

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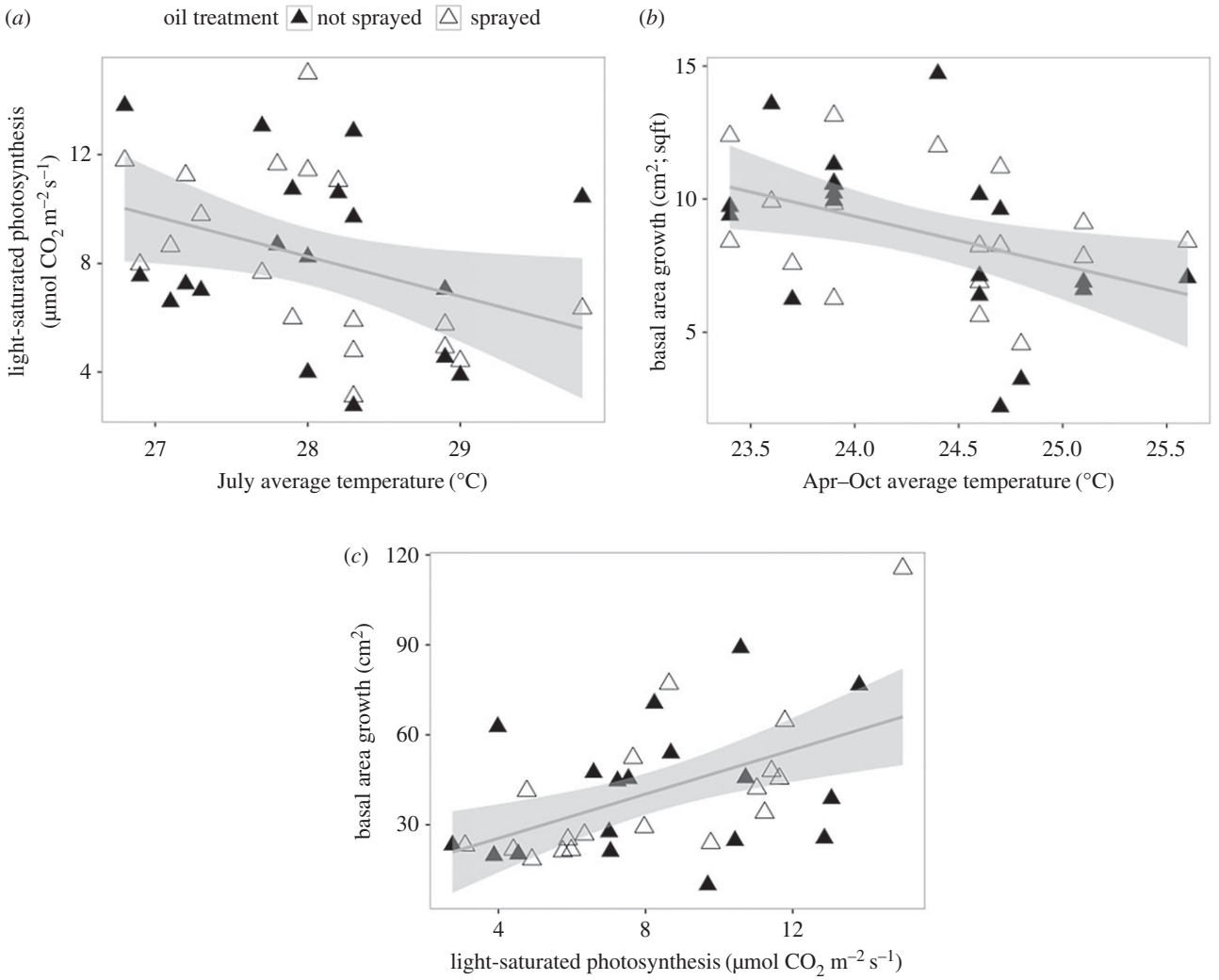

Figure 2. Urban warming reduced basal area (trunk) growth. Warming reduced (*a*) light-saturated photosynthesis and (*b*) basal area growth in 2014 (shown) and 2015. (*c*) Light-saturated photosynthesis and basal area growth were related, such that lower photosynthetic rates at hot sites decreased growth. Lines are means. Grey areas are 95% CIs.

$p = 0.128$), or photosynthesis ($F_{1,34} = 0.55$, $p = 0.795$). In 2014, branch growth was not significantly affected by warming ($F_{1,16} = 0.07$, $p = 0.795$) but was increased by herbivore removal ($F_{1,17} = 4.60$, $p = 0.047$). In summary, warming decreased basal area growth, and this effect was probably mediated by reduced photosynthesis. Arthropod pests did not affect basal area growth, but did reduce branch growth.

(d) Carbon sequestration

Because we found that urban warming reduced growth of our study trees, we scaled these effects up to estimate how urban warming affected carbon storage by municipal trees of our study species in Raleigh. We used a regression equation (carbon sequestration (kg; sqrt transformed) = *a**projected air temperature (C) + *b**DBH (cm) + intercept; $a = -0.67 \pm 0.27$ (mean ± s.e.), $b = 0.12 \pm 0.02$; adjusted $R^2 = 0.67$; $p < 0.0001$) to scale the effects of urban warming on carbon sequestration of our study trees to all of the willow oaks in the Raleigh tree inventory. Detailed statistics for this model are in electronic supplementary material, S3. Total tree and branch dry weights, respectively, are detailed in electronic supplementary material, figure S1*b*,*c*.

Urban warming reduced carbon sequestration of Raleigh, NC willow oaks by 27 tonnes in 2014 (figure 3; detailed statistics are in electronic supplementary material, table S3). This represents a 12% reduction in carbon sequestration due to the direct effects of warming on trees. The effect of herbivores on carbon storage was negligible, as they reduced growth only in new branch tissue, which accounted for a mere 0.45 ± 0.05% (mean ± s.e.m.) of total carbon stored by willow oak trees.

4. Discussion

Urban warming was associated with reduced tree growth, such that citywide carbon sequestration by our focal species was an estimated 12% lower when accounting for the urban heat island effect. Therefore, our results suggest that warming in cities can significantly reduce the extent to which urban forests act as carbon sinks. Current estimates, which do not incorporate warming, probably overestimate carbon storage in cities, where trees are the primary repositories of carbon [42].

A key question is why urban warming reduced tree growth and carbon sequestration. One potential explanation relates to the influence of warming on herbivorous pests. As predicted, urban warming dramatically increased arthropod pest abundance on our study trees. However, experimental removal of pest arthropods through oil treatments successfully reduced their abundance, enabling us to separate the effects of temperature and herbivores on tree growth. These results revealed that

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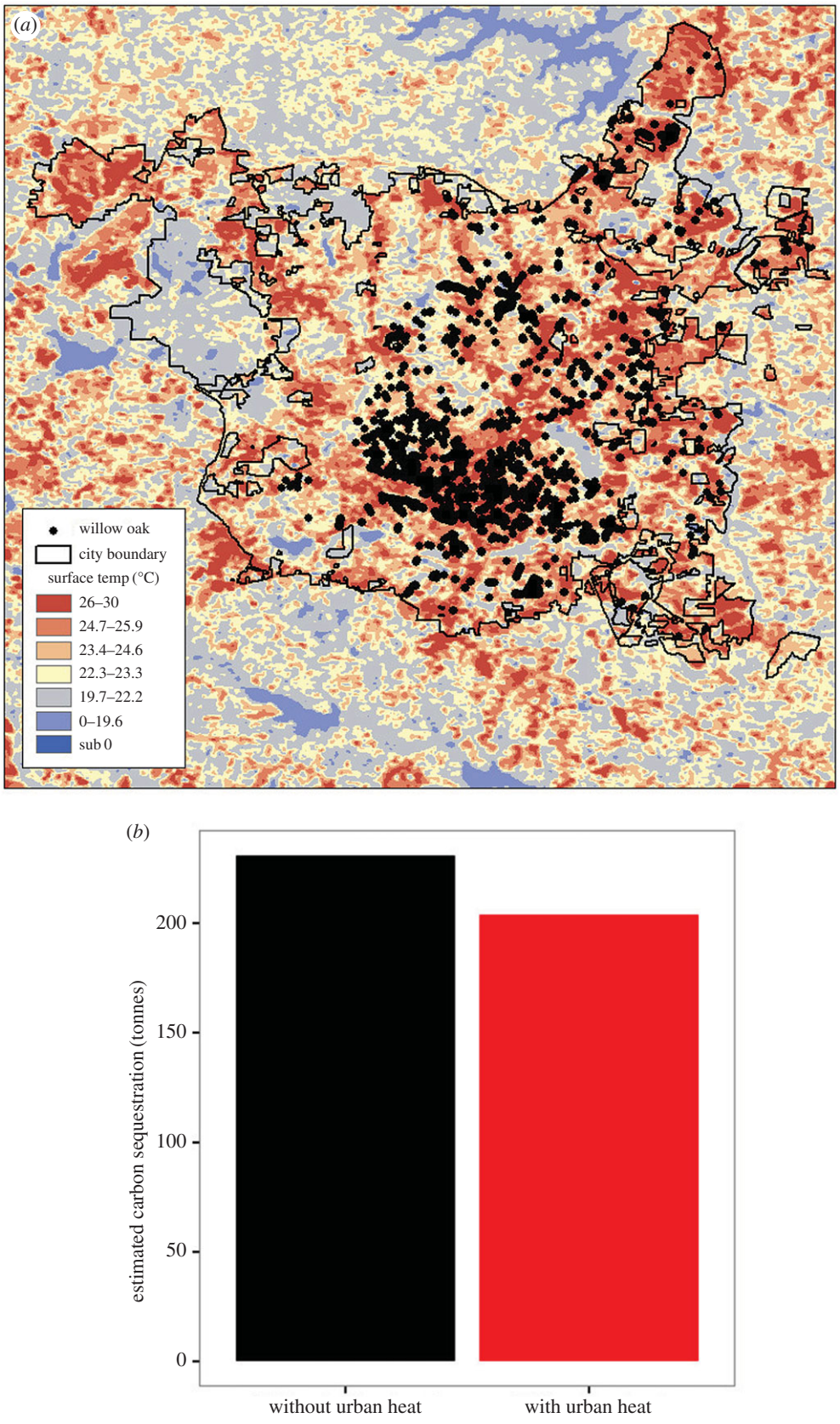

Figure 3. Carbon sequestration estimations across Raleigh, NC, urban heat island. (*a*) Map of willow oak trees. (*b*) Estimated carbon sequestration by willow oak trees with and without the urban heat island effect. (Online version in colour.)

herbivore effects were confined to new branches, and thus, accounted for less than 1% of tree carbon sequestration losses associated with urban warming. Together, our results point to a future in which even trees that are largely unaffected by higher herbivore abundance will store less carbon where warming and other global change factors like urbanization and drought reduce tree growth.

Because our study site is located far north of willow oak's southern range limit, we expected that urban warming would increase its growth. Previous work on mature trees has shown that warming can benefit species at mid to high latitudes, where photosynthesis and other processes necessary for growth and reproduction are temperature limited [8]. Warming can also increase growing season length, leading

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to more growth per season [13]. While these mechanisms could have benefitted the trees in our study system, net effects on tree growth were negative.

We found evidence that less growth at hotter sites was due to water deficits, consistent with drought studies [11]. Stomatal conductance declined linearly with urban warming. Stomatal conductance is regulated by water relations in many tree species, including willow oak [43]. When trees experience water deficits, they close their stomata to reduce water loss through transpiration. We measured water potential concurrently with gas exchange to determine the extent to which urban warming was associated with contemporaneous tree water stress. We did not find that mid-morning water potential was higher (i.e. that tree water stress was greater) in hotter trees. We suggest that future studies could use a direct measurement of tree water deficit, such as predawn water potential, to further explore the relationship between urban warming and tree water stress, as water stress associated with impervious surface cover and restricted rooting space could also reduce tree growth.

Our study represents a conservative view of how further global and urban warming, and resulting herbivory, will affect urban forests. Oak (*Quercus*) contains some of the tree species most resilient to water deficits [44] and disturbance [45] worldwide, and urban tree species are selected for resilience. Of urban oak species, our study species, willow oak, is one of the most resilient, if not the most resilient, to herbivory [46]. Further, our study was located at the northern edge of willow oak's range, where warming should have its least negative effects [12]. More sensitive trees, such as red maple, and trees living at the hotter extremes of their geographical ranges, may have even stronger negative responses to stressors associated with global change.

Carbon storage losses in urban forests should compound over years, leading to even more negative effects on carbon storage. Bigger trees grew more in our study, which is a common pattern across tree species and habitats [40,41]. When urban warming reduces tree growth, it also reduces tree size at the beginning of the next growing season. In turn, smaller trees should grow less in that year, leading to shallower growth trajectories for trees in hotter habitats. These compounded losses could substantially reduce the potential of urban forests to act as carbon sinks. In a recent estimate, trees harboured 97.3% of carbon stored in aboveground urban biomass [42]. Urban forests in our study region, the southeastern USA, store more carbon per hectare than urban forests in any other region, according to the most recent estimate [33]. Willow oak, and species that respond as it does to urban warming, should sequester even less carbon due to the urban heat island effect in more southern cities with stronger urban heat islands, such as Atlanta, GA.

Urban trees face many stressors other than warming, such as impervious surfaces that reduce water entering soil, pollution, restricted rooting spaces and compacted soil. While we could not control for all of these factors, our methods allowed us to determine tree carbon storage across a range of thermal environments within one city. We acknowledge that our results could be partially driven by these other factors, which are often correlated with urban warming. However, combined with measurements of tree physiology, our results suggest urban warming as one mechanism driving carbon storage by urban trees. We expect that warming will have less severe effects in more natural forests, where trees are not subject to other urban stressors that probably exacerbate negative effects of warming on tree growth.

In our study's most conservative interpretation, urban warming was associated with reductions in ecosystem services that contribute to climate regulation [47]. We increasingly rely on urban forests to provide these services as deforestation of more natural forests continues [48] and as more people move to cities where they benefit directly from urban trees. Our results point to a future in which urban habitats will store less carbon due to urban and global warming. Our results also highlight the utility of cities as large-scale natural climate experiments, in which sessile organisms are confined to different thermal environments in close proximity. The range of urban warming they experience parallels the extent of global warming expected regionally, outside the city, over the next several decades. To the extent that urban forests can thereby predict the future of rural forests, our study points to the need for models that incorporate the effects of abiotic and biotic stressors on tree carbon storage.

Ethics. This project was approved by the City of Raleigh Parks, Recreation and Cultural Resources Department.

Data accessibility. Data are available in the Dryad Digital Repository [49].

Authors' contributions. E.M., S.D.F. and R.R.D. conceived of the experiment and designed the study. E.M. and E.Y. collected the data. E.M. identified arthropods and carried out statistical analyses. All authors wrote the paper and gave final approval for publication.

Competing interests. We have no competing interests.

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