

## Urbanization drives unique latitudinal patterns of insect herbivory and tree condition

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**Abstract**

Urban landscapes are characterized by high proportions of impervious surface resulting in higher temperatures than adjacent natural landscapes. In some cities, like those at cooler latitudes, trees may benefit from warmer urban temperatures, but trees in many cities are beset with problems like drought stress and increased herbivory. What drives patterns of urban tree health across urbanization and latitudinal temperature gradients? In natural systems, latitude-herbivory relationships are well-studied, and recent temperate studies have shown that herbivory generally increases with decreasing latitudes (warmer temperatures). However, the applicability of this latitude-herbivory theory in already-warmed urban systems is unknown. In this study, we investigated how the interaction of urbanization, latitudinal warming, and scale insect abundance affected urban tree health. We predicted that trees in warmer, lower latitude cities would be in poorer health at lower levels of urbanization than trees at cooler, higher latitudes due to the interaction of urbanization, latitudinal temperature, and herbivory. To evaluate our predictions, we surveyed the abundance of scale insect herbivores on a single, common tree species *Acer rubrum* in eight US cities spanning 10° of latitude. We estimated urbanization at two extents, a local one that accounted for the direct effects on an individual tree, and a larger one that captured the surrounding urban landscape. We found that urban tree health did not vary with latitudinal temperature but was best predicted by local urbanization and herbivore abundance. We did not observe increased herbivore abundance in warmer, lower latitudes cities, but instead herbivore abundance peaked in the mid latitudes of our study. This study demonstrates that urban landscapes may deviate from classical theory developed in natural systems and reinforces the need for research reconciling ecological patterns in urban landscapes.

**Keywords:** urban ecology, herbivory, urban forest

## Introduction

Trees provide many important services in both natural and urban ecosystems, including habitat provisioning for other species, regulating climate, filtering air and water, and sequestering carbon (Bolund and Hunhammar 1999). High temperatures can negatively affect tree health and reduce these services by reducing photosynthesis and growth (Way and Oren 2010, Meineke et al. 2016). Temperatures are increasing globally but the effects may be particularly acute in cities where impervious surfaces yield higher temperatures than surrounding rural areas (Oke 1988). These temperature differences, typically 2-3°C, are analogous to those predicted from global change for natural areas at the same latitudes in 50-100 years in the eastern USA (Kunkel et al. 2013, Youngsteadt et al. 2017, Lahr et al. 2018). Understanding the consequences of rising temperatures due to urbanization and climate change on tree health and functioning is crucial to preserving tree-provided services.

The strong relationship between latitude, temperature, and thermal tolerance could provide insight into the potential consequences of warming on plants and animals (Addo-Bediako et al. 2000, Sunday et al. 2014, Diamond et al. 2017, O'Sullivan et al. 2017). As a result of living in a warmer and less variable climate, many plants (Doughty and Goulden 2009, Way and Oren 2010) and animals (Deutsch et al. 2008, Khaliq et al. 2014) at lower latitudes live closer to their physiological thermal maxima and have narrower tolerances for temperature changes than those further from the equator. Therefore, small temperature increases at warmer latitudes likely have stronger and more negative effects than the same magnitude increases at higher, cooler latitudes, which may be positive or neutral (Diamond et al. 2017, Youngsteadt et al. 2017). Moreover, trees have species-specific photosynthetic rates that are optimized within certain temperature ranges (O'Sullivan et al. 2017) and when temperatures are outside of this range, photosynthetic rate can abruptly decline (Knight and Ackerly 2002). Higher temperatures increase water demand and drought stress if sufficient water is not available (Williams et al. 2012), which can reduce photosynthesis through stomatal closure or xylem cavitation (Schymanski et al. 2013), and can lead to eventual plant death (Allen et al. 2010). Thus, trees at higher, cooler latitudes may benefit from urban or global warming (Ibanez et al. 2010, Way and Oren 2010, Peñuelas et al. 2011), whereas trees at lower, warmer latitudes may become too warm resulting in greater stress and less growth, as plant processes reach physiological limits (Crumpacker et al. 2010, Bowman et al. 2014).

In addition to temperature-related physiological stress, many studies have demonstrated that herbivory is positively correlated with decreasing latitudes (e.g., Lim et al. 2015, Baskett and Schemske 2018). However, the consistency of latitude-herbivory patterns is an area of active debate (e.g., Moles et al. 2011, Anstett et al. 2016). Some recent latitude-herbivory studies have yielded equivocal results, with some studies finding no, hump-shaped, or positive latitude-herbivory patterns (Moreira et al. 2015, Nunes et al. 2016). These contrasting patterns have been reviewed (e.g., Anstett et al. 2016), and one potential source of the ambiguity of these patterns is the lack of a consistent methodology. However, there is growing support for these classic latitude-herbivory patterns in the northern hemisphere (Zhang et al. 2016, Baskett and Schemske 2018), but see Kozlov and Klemola (2017) and Zhang et al. (2017) for a discussion on these patterns. Importantly, heat and drought stress can also increase herbivore fitness (e.g., Dale and Frank 2017) and make trees more susceptible to herbivory by increasing their nutritive value for herbivores (Mody et al. 2009), reducing defensive compounds (Mattson and Haack 1987), or both (Herms and Mattson 1992).

In fact, urban warming, such as that associated with impervious surface, increases herbivory similarly to the pattern we would expect with latitudinal warming and in ways that are similar to climate warming (Youngsteadt et al. 2014, 2017). For example, 2°C of urban warming significantly increases the abundance of herbivorous mites and scale insects (Meineke et al. 2013, Dale and Frank 2014a); each of which are associated with trees in poorer condition (Dale and Frank 2014b, Meineke and Frank 2018). This pattern is similar for these same scale insects in natural forests during natural warming and cooling cycles (Youngsteadt et al. 2014). Moreover, synergistic effects between the UHI and latitudinal temperature have been shown for arthropods (e.g., increased abundance at higher latitudes) (Youngsteadt et al. 2017) and trees (e.g., longer growing seasons) (Dallimer et al. 2016). While latitudinal patterns of both temperature and herbivory are well studied in natural ecosystems, we do not know how well this ecological theory applies in cities. Thus, based on classic latitudinal patterns of thermal tolerance and herbivory (Dobzhansky 1950, Janzen 1967, Levin 1976, Coley and Barone 1996), urban trees at lower latitudes may face a combined effect of greater heat stress and herbivory with warming, whereas more poleward trees may benefit and even become more resistant to herbivores (Bale et al. 2002).

Using latitude-herbivory patterns as a prediction source, we sought to determine the relative contributions of impervious surface, herbivore abundance, latitudinal temperature, and their interactions on urban tree condition and to also identify if the size

and estimation method of impervious surface cover at planting sites affects their ability to describe tree condition. Our motivations are threefold. First, we aim to reconcile the relevance of ecological theory to wholly contrived ecosystems. Second, testing the effects of urban and latitudinal warming on an urban tree is valuable to improve management of urban forests and the ecosystem services they provide; and third, this work furthers the use of cities as experimental proxies for climate change. We predicted that, at a given amount of impervious surface (e.g., 50%), urban trees at warmer, lower latitudes would be more likely to be in poorer condition and with greater herbivore load when compared to trees in similar urban conditions at cooler, higher latitudes with fewer herbivores. Due to the different possible scale-dependent mechanisms of how impervious surface could affect tree condition and herbivore abundance (e.g., tree water stress, natural enemy abundance, scale fitness (Dale and Frank 2014a, 2017, Meineke and Frank 2018)), we predicted that the effects of impervious surface on tree condition would vary based on spatial extent and estimation technique. We predicted that a smaller, field-based estimate would be more robust, given its ability to account for the conditions that directly affect a tree and, thus, its herbivores than a larger, remotely-sensed estimate.

## Methods

### *Study organisms*

We selected *Acer rubrum* L. as our study tree species because it can thrive across a wide range of environmental conditions (Abrams 1998), has one of the longest continuous geographic distributions (> 2,500 km) on the North American Atlantic coast (Burns and Honkala 1990), and is a ubiquitously planted tree in the eastern USA (Raupp et al. 2006). In urban landscapes, *A. rubrum* is particularly prone to scale insect herbivory (Frank et al. 2013). Scale insects are found on the trunk and branches of *A. rubrum* and use specialized mouthparts to feed on sap or parenchyma cells of the tree host. Severe infestations can lead to branch dieback, canopy thinning, and eventual tree death (Frank et al. 2013). Our study cities span the southern portion of the *A. rubrum* range, where it has a primary scale insect pest, *Melanaspis tenebricosa* (Comstock), the gloomy scale. *Melanaspis tenebricosa* is a native herbivore of *A. rubrum* and has been reported to occur in the eastern USA from Delaware to Florida and as far west as Texas. *Melanaspis tenebricosa* are univoltine and overwinter as adult females throughout our study area. Other common scale insect (*Coccoidea*) herbivores of *A. rubrum* in our study area include armored scales such as the oystershell scale (*Lepidosaphes ulmi*

(Linnaeus)) and Japanese maple scale (*Lopholeucaspis japonica* (Cockerell)), and soft scales such as calico scale (*Eulecanium cerasorum* (Cockerell)) and cottony maple scale (*Neopulvinaria innumerabilis* (Rathvon)). Notably, native scale insects have been found at much greater abundances on urban trees as compared to forest trees for more than 100 years in the USA (Putnam 1880, Metcalf 1912). Moreover, historical abundances of *M. tenebricosa* on *A. rubrum* in natural areas were positively correlated with warmer temperatures (Youngsteadt et al. 2014).

### *Study cities*

We visited eight cities in the eastern USA (Asheville, NC, Atlanta, GA, Charlotte, NC, Gainesville, FL, Knoxville, TN, Newark, DE, Raleigh, NC, and Savannah, GA) that encompassed the southern distribution of *A. rubrum* and the known latitudinal extent of *M. tenebricosa* (Table 1). Study cities spanned approximately 10° of latitude (Supplementary material Appendix A Fig A1) and differed by 7.4 °C in mean annual temperature (Newark, DE – Gainesville, FL). For cities with tree inventories, *A. rubrum* individuals were randomly selected using a GIS and for cities without inventories (Newark, DE and Gainesville, FL), we haphazardly selected individuals from planting locations identified by local cooperators. We selected 30-36 study trees per city (n=263; Table 1). The mean minimum distance between study trees was 299 ±47 (SE) m. The mean area containing the sampled trees in each city was 63 ±18 km<sup>2</sup>. Our field campaign occurred October 2016 – February 2017; we selected this sampling period because all scale individuals were on twigs and not reproducing, allowing for a consistent census of the whole population across cities with just one sampling effort. All study trees were at least 10 cm diameter at breast height (DBH) and considered to be established based on the stem size difference between typical *A. rubrum* caliper sizes at time of transplanting and the tree size at time of this study (Watson 2005).

### *Tree condition and herbivore abundance*

We evaluated the condition of each study tree. Arboricultural tree condition ratings are a commonly used metric to estimate the overall health of municipal and other planted trees (Roman et al. 2013). The condition of each tree was recorded as Good or Poor as determined by the classification methods outlined in Table A1 (Supplementary material Appendix A). Study trees were assigned condition ratings before accessing herbivore abundance or estimating the proportion of impervious surface adjacent to the tree. We

also measured DBH (cm) for each tree, as stem size and growth and, hence, tree condition, can be affected by environmental stressors (Dobbertin 2005).

To determine scale insect abundance, we pruned 2-4 haphazardly selected terminal twigs, that were at heights at which one could not see if scales were present to reduce bias, from each tree using a pole pruner. We initially collected two twigs per tree for the first trees sampled (n=40), after which we updated our collection protocol to sample four twigs per tree. We excised the most recent season of growth from each twig (identified from most recent terminal bud scar) and retained 30 cm of previous growth. We used a dissecting microscope to count live scale insects. Scale counters were naïve to our hypotheses and the origin city of the twig samples to limit bias. We recorded mean scale insect abundance per scale species per tree per 15 cm. Scale insect abundances were averaged across all species (i.e., total herbivore abundance) and  $\log_{10}(x+1)$  transformed prior to analyses. Studying one tree species and one guild of herbivore with a life history that includes minimal dispersal and non-leaf feeding allowed us to census herbivore abundance with one timepoint across a latitudinal gradient.

#### *Environmental variables*

For each study tree location, we estimated the adjacent impervious surface using two methods. First, we estimated impervious surface at a 20 m (0.001 km<sup>2</sup>) spatial extent (Imp20). For Imp20 estimates, we employed the ‘Pace-to-Plant’ technique, which is a manual, pace-counting method to estimate impervious surface on site within a ~20 m radius of a tree at an approximately 1 m<sup>2</sup> resolution (Dale et al. 2016). The proportion of impervious surface cover at this spatial extent is a good predictor of urban *A. rubrum* condition at a 1 m<sup>2</sup> resolution (Dale et al. 2016, Just et al. 2018). However, data at this fine resolution are not universally available and are computationally cumbersome. We also estimated the proportion of impervious surface cover within a larger, 125 m radius (0.049 km<sup>2</sup>; Imp125) of the tree using remotely-sensed data. For our Imp125 analyses, we used the more readily accessible and widely used National Land Cover Database Percent Developed Imperviousness dataset which has a resolution of 30 m<sup>2</sup> (Xiam et al. 2011). We calculated the mean proportion of impervious cover with the *extract* function from the *raster* package in R. Some of the 125 m extents overlapped for our study trees, but the overlap of these predictor terms did not violate the assumption of independence of our response variable (Zuckerberg et al. 2012). Latitudinal climate data for each study tree location was derived from the PRISM Climate Group’s 30-yr normals



temperature grids (800 m<sup>2</sup>) (Di Luzio et al. 2008). For each tree, we calculated three temperature variables with the *extract* function: the mean minimum winter temperature (December, January, February), the mean maximum summer temperature (June, July, August), and the difference between winter and summer temperature.

### *Statistical analyses*

All statistical analyses were performed in R version 3.5.1. We used binomial logistic regression, *glm* function of the *stats* package, for all tree condition modeling, where tree condition was the dependent variable. We used ROC analyses from package *pROC* to assess model fit (function *roc*) using the ‘Area Under the Curve’ (AUC) test statistic (Robin et al. 2011). We calculated the relative importance weight (RIW) of each predictor term in our GLM models, which describes the relative amount of explained variance attributed to a given term (Tonidandel and LeBreton 2011). We initially modeled tree condition using a generalized linear mixed-effects model (function *glmer* in package *lme4* (Bates et al. 2015)) with city identity as a random group intercept. However, this additional group-level variation was near zero and, thus, did not justify an additional group-level random effect to explain the observed variation. As such, we opted to use the more parsimonious approach described above.

To detect the effects of latitudinal temperature, herbivore abundance, impervious surface, and their interactions on tree condition, we began by constructing a model with the following terms: Temperature, Impervious Surface (Imp20 or Imp125), Herbivore Abundance, DBH, Temperature × Impervious Surface, Temperature × Herbivore Abundance, Impervious Surface × Herbivore Abundance, and Impervious Surface × Temperature × Herbivore Abundance. This procedure was completed for each temperature variable separately. The interactions between impervious surface, temperature, and herbivore abundance were the primary terms of interest with respect to our predictions. We assessed non-interaction terms for both full models for multicollinearity using the *vif* function from package *car* (Fox and Weisberg 2011; *VIF* ≤ 1.5).

Given that the interaction terms addressing our predictions were not significant (Supplementary material Appendix A Tables A2, A3), we elected to also construct a model for describing tree condition where terms could be sequentially removed to optimize the model. Our initial model contained the following terms: Temperature, Impervious Surface (Imp20 or Imp125), Herbivore Abundance, DBH, Temperature × Impervious Surface, Temperature × Herbivore Abundance, Impervious Surface ×



Herbivore Abundance, and Impervious Surface  $\times$  Temperature  $\times$  Herbivore Abundance. We used log-likelihood ratio tests from the *anova* function from package *car*, testing the full model versus a model reduced by one term and terms were removed from the model if there was no difference in explanatory power between the two models (i.e.,  $P > 0.05$ ). After this exercise, the remaining terms were included in a new reduced model. Again, this procedure was completed for each temperature variable separately. We assessed the remaining terms in both final models for multicollinearity ( $VIF \leq 1.5$ ).

To test for the effect of spatial extent and estimation method on the strength of the relationship between the proportion of impervious surface and *A. rubrum* condition, we compared the model fits (AUC) between models built with Imp20 or Imp125 with the DeLong Method (DeLong et al. 1988), via function *roc.test* in package *pROC* (Robin et al. 2011), which is a non-parametric procedure suitable for comparing the AUCs between non-nested models (Demler et al. 2012).

We used linear mixed-effects modelling (*lmer* function of the *lme4* package) to evaluate the fixed effects of latitudinal temperature and impervious surface (Imp20 or Imp125) on herbivore abundance with city identity a random effect. We created three models, one for each temperature variable, and retained the temperature variable (mean maximum summer temperature) that resulted in the best model fit (i.e., marginal  $R^2$  (Nakagawa and Schielzeth 2013)) for either impervious surface predictor.

## Results

We did not find an effect of the interaction between latitudinal temperature impervious surface, and herbivore abundance (Supplementary material Appendix A Tables A2, A3). Thus, trees at lower latitudes were not more likely to classified as being in poorer condition at lower levels of impervious surface and herbivore abundance as predicted.

The model that best described tree condition ( $AUC = 0.917$ ) included impervious surface cover (Imp20;  $z = 7.13$ ,  $P < 0.001$ ) and herbivore abundance ( $z = 2.50$ ,  $P < 0.001$ ) as predictor terms (Table 2). Of the variation explained by this model, 82% was attributed to impervious surface and 17% to herbivore abundance (Table 2). For this model, a percentage point increase in impervious cover (herbivore abundance held constant) increases the odds (i.e., odds-ratio) of a tree in Good condition being classified as being in Poor condition by 1.10 times (Fig 1). Likewise, a one unit increase in herbivore abundance ( $\log_{10}[x+1]$  scale abundance), increases the odds of a tree being classified as Poor by 2.37 times (Fig 2). We found that the model using the smaller extent and field-estimate of impervious surface (Imp20) had a much better fit ( $AUC =$

0.917 vs 0.801;  $z = 3.93$ ,  $P < 0.001$ ) and lower AIC (170.5 vs 244.1) than when using the Imp125 estimate. Additionally, the relative importance of impervious surface was greater in the smaller extent as compared to the larger extent model (RIW: Imp20 = 0.82 vs Imp125 = 0.62; Table 2). Neither of these models contained latitudinal temperature.

We did not find that urban herbivore abundance increased at warmer, lower latitudes. Instead we found that latitude-herbivory relationship was hump-shaped with greater herbivore abundance in our midlatitude study cities (Tables 1, 3; Supplementary material Appendix A Fig A2). Herbivore abundance was better described by the model with Imp20 as a predictor versus the model with Imp125 (marginal  $R^2 = 0.20$  vs 0.17; Table 3).

## Discussion

We investigated the role of latitudinal temperature, impervious surface cover, and herbivore abundance on the condition of a common street tree, *A. rubrum*, in the eastern USA. We found that for this common urban tree, predictions based on patterns observed in natural systems do not hold, and instead that an anthropogenic factor—impervious surface—was most important for predicting *A. rubrum* condition and, thus, potentially for the sustainability of urban forests and ecological services.

We predicted that the effect of impervious surface and herbivore abundance on *A. rubrum* condition would become more detrimental at lower latitudes where temperatures are warmer. Instead, we found urban tree condition did not vary with latitudinal temperature and found no significant interactions between latitudinal temperature, impervious surface, and herbivore abundance (Supplementary material Appendix A Tables A2, A3). Our results support the primary importance of impervious surface cover as a determinant to tree health. In Raleigh, NC, USA (Dale and Frank 2014b), found that the warmest areas in the city, those with more impervious cover and just 2°C or less of warming, had over twice as many *A. rubrum* individuals in Poor condition than cooler areas. Other research has demonstrated that heat and drought associated with impervious surfaces additively increase *M. tenebricosa* fecundity on *A. rubrum* street trees, providing a potential mechanism for this increased abundance (Dale and Frank 2014a, 2017). We found that tree condition was best described by impervious surface cover, accounting for 82% of the explained variance in our best model (Table 2) and that the likelihood of a tree being classified as being in Poor condition increased by 1.10 times with every percent increase in impervious cover (Fig. 1). Our results suggest

that at least some latitudinal patterns described for natural environments are not present or detectable in urban environments, where the signal of latitudinal temperature in urban landscapes is overwhelmed by the effects of impervious surface cover, especially with regards to tree condition and herbivore abundance.

We also predicted that a smaller urban extent with field-based estimates of impervious surface cover would better describe tree condition, as this extent (Imp20) was more likely to capture the direct effects of urbanization on trees. Our predictions were supported, and we found that this extent was much better at discerning tree condition than remotely-sensed estimates (Imp125), AUC = 0.917 vs 0.802, respectively (Table 2). In the model with Imp20 as a predictor (Table 2), impervious surface accounted for 82% of the explained variance of the model, whereas the Imp125 model only account for 62%. This suggests that more spatially proximate effects of urbanization (e.g., those within a 20 m radius) are the most important for the condition of a planted tree. Impervious surfaces at urban planting sites reduces potential root-accessible soil and can increase drought stress, temperature, and herbivory (Meineke et al. 2016, Dale and Frank 2017). For example, compacted urban soils can reduce root gas exchange and water absorption, which reduces plant hydraulic conductance, photosynthetic capacity, and tree growth (Rahman et al. 2014). Whereas many urban organisms can move about to find refuge from urban stressors, trees are sessile organisms, and when considering an individual tree, perhaps it should not be surprising that their immediate environment is the most important for their overall health. Despite these issues, the 30 m<sup>2</sup> data still have predictive power (Table 2) and are the most readily accessible resolution for remotely-sensed land-cover imagery in the USA (Giri et al. 2013). Moreover, urban landscapes are heterogeneous (Zhou et al. 2017) which suggests that larger spatial extents may be better predictors of the health and functioning of urban forests by encompassing more varied environments (e.g., Nekola and White 1999). Finally, urban forests themselves may reduce impervious surface proportions, which is the most important factor to increase the likelihood of maintaining a tree in Good condition (Table 2).

Contrary to our predictions, we did not observe a linear pattern of increasing herbivore abundance with increasing latitudinal temperature (Table 3, Supplementary material Appendix A Fig A2). Instead, we found that herbivore abundance was a quadratic function of latitudinal temperature (mean maximum summer) and impervious surface cover with peak herbivore abundance corresponding to the mean maximum summer temperatures of the midlatitude locations of our study (including the cities

Asheville, Atlanta, Raleigh, Charlotte, and Knoxville). This herbivory-impervious surface relationship at midlatitudes likely subjects trees in these locations to additional biotic and abiotic stress, ultimately affecting their condition rating. Moreover, herbivore abundance was an important factor for describing tree condition and we found that a one-unit increase in herbivore abundance increased the likelihood of a tree being classified as being in Poor condition by 2.37 times (Fig 2). Like our tree condition analyses, herbivore abundance was also better described by our smaller, field-based estimate of impervious cover (Table 3), again illustrating the importance of direct and immediate stressors for assessing the condition of individual urban trees and their sedentary herbivores.

A recent study (Kozlov et al. 2017) found that leaf area lost to insect herbivory was lower in European cities as compared to nearby rural areas and that the magnitude of the effect of urbanization (population size) on herbivory was independent of latitude. Moreover, they found greater reductions in herbivory with increasing urbanization in large cities ( $\geq 1$  million inhabitants), but no relationship in cities under 700 thousand inhabitants. Like Kozlov et al. (2017), we found that the effect of urbanization on an herbivory metric was independent of latitude, however, we found that herbivore abundance increased as urbanization increased. Moreover, the urbanization metrics used by Kozlov et al. and us (human population size and impervious surface, respectively) are not correlated within our study area nor did we observe significant relationships between human population and herbivore abundance or tree condition (Supplementary material Appendix A, Table A4, Fig A3). Unlike human population metrics, impervious surface has direct, measurable effects on temperature and drought (Lahr et al. 2018). The differences between these studies again illustrate the need to evaluate latitude-herbivory patterns for additional taxa and systems. This work adds to a small literature (e.g., Andrew and Hughes 2005a, Kozlov et al. 2015) that specifically examines latitudinal patterns of sap-feeding insect herbivory.

Latitude-herbivory patterns are among the most studied in ecology and, while still an area of debate, strong patterns have been identified across study locations and systems (e.g., Andrew and Hughes 2005b, Salazar and Marquis 2012); the relevance of these and other patterns to human-dominated systems is largely unknown (e.g., Dale and Frank 2018). Our predictions sourced from patterns found in natural areas were unable to predict the herbivore abundance patterns for these sap-feeding insects on *A. rubrum* across the latitudes occupied by our eight study cities. Yet, urbanization and latitudinal temperature can affect tree health and tree-provided ecosystem services (Way

and Oren 2010, Mullaney et al. 2015, Rahman et al. 2015, Meineke et al. 2016). Understanding the response of urban trees to these factors and their interactions is necessary not only to effectively manage these trees, but also to make predictions about the response of natural forests to future warming. Thus, cities may provide glimpses of the conditions that rural, peri-urban, or higher-latitude urban trees may experience with increased temperatures from land-use change and the urban heat island effect or global change (Lahr et al. 2018). For example, we found that scale insect abundance was greatest in midlatitude study cities, indicating that the abundance of these scale insects may be limited by intolerance to cold in the north and to heat in the south (e.g., McClure 1983). To the extent that urban and global warming extend the northern range of these insects, their southern range may contract. The effects of global change are predicted to vary in intensity and magnitude geographically, and biological responses to changes in latitudinal temperature may be more pronounced in some locations (e.g., due to physiological thermal tolerances). Therefore, background temperatures in some locations may reach values where the interactions of impervious surface and latitudinal temperature become important, even as impervious surface currently bests the effect of latitude for this urban tree system.

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**Literature Cited**

- Abrams, M. D. 1998. The Red Maple Paradox: what explains the widespread expansion of red maple in eastern forests? - *Bioscience* 48: 355–364.
- Addo-Bediako, A. et al. 2000. Thermal tolerance, climatic variability and latitude. - *Proc. R. Soc. B Biol. Sci.* 267: 739–745.
- Allen, C. D. et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. - *For. Ecol. Manage.* 259: 660–684.
- Andrew, N. R. and Hughes, L. 2005a. Diversity and assemblage structure of phytophagous Hemiptera along a latitudinal gradient: predicting the potential impacts of climate change. - *Glob. Ecol. Biogeogr.* 14: 249–262.
- Andrew, N. R. and Hughes, L. 2005b. Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds. - *Oikos* 108: 176–182.
- Anstett, D. N. et al. 2016. Sources of controversy surrounding latitudinal patterns in herbivory and defense. - *Trends Ecol. Evol.* 31: 789–802.
- Bale, J. S. et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. - *Glob. Chang. Biol.* 8: 1–16.
- Baskett, C. A. and Schemske, D. W. 2018. Latitudinal patterns of herbivore pressure in a temperate herb support the biotic interactions hypothesis. - *Ecol. Lett.* 21: 578–587.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. - *J. Stat. Softw.* 67: 1–48.
- Bolund, P. and Hunhammar, S. 1999. Ecosystem services in urban areas. - *Ecol. Econ.* 29: 293–301.
- Bowman, D. M. J. S. et al. 2014. A warmer world will reduce tree growth in evergreen broadleaf forests: evidence from Australian temperate and subtropical eucalypt forests. - *Glob. Ecol. Biogeogr.* 23: 925–934.
- Burns, R. and Honkala, B. 1990. *Silvics of North America: 2. Hardwoods*. United States Department of Agriculture, Forest Service. Agriculture Handbook 654. Washington, DC.
- Coley, P. D. and Barone, J. A. 1996. Herbivory and plant defenses in tropical forests. - *Annu. Rev. Ecol. Syst.* 27: 305–335.
- Crumpacker, D. W. et al. 2010. Implications of climatic warming for conservation of native trees and shrubs in Florida. - *Conserv. Biol.* 15: 1008–1020.
- Dale, A. G. and Frank, S. D. 2014a. Urban warming trumps natural enemy regulation of herbivorous pests. - *Ecol. Appl.* 24: 1596–1607.
- Dale, A. G. and Frank, S. D. 2014b. The effects of urban warming on herbivore abundance and street tree condition. - *PLoS One* 9: e102996.
- Dale, A. G. and Frank, S. D. 2017. Warming and drought combine to increase pest insect fitness on urban trees. - *PLoS One* 12: e0173844.
- Dale, A. G. and Frank, S. D. 2018. Urban plants and climate drive unique arthropod interactions with unpredictable consequences. - *Curr. Opin. Insect Sci.* 29: 1–7.
- Dale, A. G. et al. 2016. Forecasting the effects of heat and pests on urban trees: Impervious surface thresholds and the “pace-to-plant” technique. - *Arboric. Urban For.* 42: 181–191.
- Dallimer, M. et al. 2016. The extent of shifts in vegetation phenology between rural and urban areas within a human-dominated region. - *Ecol. Evol.* 6: 1942–1953.
- DeLong, E. et al. 1988. Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparametric approach. - *Biometrics* 44: 837–845.
- Demler, O. V. et al. 2012. Misuse of DeLong test to compare AUCs for nested models. - *Stat. Med.* 31: 2577–2587.



- Deutsch, C. A. et al. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. - *Proc. Natl. Acad. Sci.* 105: 6668–6672.
- Di Luzio, M. et al. 2008. Constructing retrospective gridded daily precipitation and temperature datasets for the conterminous United States. - *J. Appl. Meteorol. Climatol.* 47: 475–497.
- Diamond, S. E. et al. 2017. Heat tolerance predicts the importance of species interaction effects as the climate changes. - *Integr. Comp. Biol.* 57: 112–120.
- Dobbertin, M. 2005. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. - *Eur. J. For. Res.* 124: 319–333.
- Dobzhansky, T. 1950. Evolution in the tropics. - *Am. Sci.* 38: 209–221.
- Doughty, C. E. and Goulden, M. L. 2009. Are tropical forests near a high temperature threshold? - *J. Geophys. Res. Biogeosciences* 114: 1–12.
- Fox, J. and Weisberg, S. 2011. *An R companion to applied regression.* - Sage Publications, Inc.
- Frank, S. D. et al. 2013. Biology, injury, and management of maple tree pests in nurseries and urban landscapes. - *J. Integr. Pest Manag.* 4: 1–14.
- Giri, C. et al. 2013. Next generation of global land cover characterization, mapping, and monitoring. - *Int. J. Appl. Earth Obs. Geoinf.* 25: 30–37.
- Hermis, D. A. and Mattson, W. 1992. The dilemma of plants: to grow or defend. - *Q. Rev. Biol.* 67: 283–335.
- Ibanez, I. et al. 2010. Forecasting phenology under global warming. - *Philos. Trans. R. Soc. B Biol. Sci.* 365: 3247–3260.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. - *Am. Nat.* 101: 233–249.
- Just, M. G. et al. 2018. Impervious surface thresholds for urban tree site selection. - *Urban For. Urban Green.* 34: 141–146.
- Khaliq, I. et al. 2014. Global variation in thermal tolerances and vulnerability of endotherms to climate change. - *Proc. R. Soc. B Biol. Sci.* 281: 20141097.
- Knight, C. A. and Ackerly, D. D. 2002. An ecological and evolutionary analysis of photosynthetic thermotolerance using the temperature-dependent increase in fluorescence. - *Oecologia* 130: 505–514.
- Kozlov, M. V. and Klemola, T. 2017. Hemispheric asymmetries in herbivory: do they exist? - *J. Ecol.* 105: 1571–1574.
- Kozlov, M. V. et al. 2015. Sap-feeding insects on forest trees along latitudinal gradients in northern Europe: a climate-driven patterns. - *Glob. Chang. Biol.* 21: 106–116.
- Kozlov, M. V. et al. 2017. Decreased losses of woody plant foliage to insects in large urban areas are explained by bird predation. - *Glob. Chang. Biol.*: 1–11.
- Kunkel, K. E. et al. 2013. *Regional Climate Trends and Scenarios for the U.S. National Climate Assessment. Part 2: Climate of the Southeast U.S.* US Dept. of Commerce, National Oceanic and Atmospheric Administration. NOAA Technical Report NESDIS 142-2. Washington, DC.
- Lahr, E. C. et al. 2018. Getting ahead of the curve: cities as surrogates for global change. - *Proc. R. Soc. B Biol. Sci.* 285: 20180643.
- Levin, D. A. 1976. Alkaloid-bearing plants: an ecogeographic perspective. - *Am. Nat.* 110: 261–284.
- Lim, J. Y. et al. 2015. Assessing the latitudinal gradient in herbivory. - *Glob. Ecol. Biogeogr.* 24: 1106–1112.
- Mattson, W. J. and Haack, R. A. 1987. The role of drought in outbreaks of plant-eating insects influence on insect populations. - *Bioscience* 37: 110–118.
- McClure, M. S. 1983. Temperature and host availability affect the distribution of *Matsucoccus matsumurae* (Kuwana) (Homoptera: Margarodidae) in Asia and North America. - *Ann. Entomol. Soc. Am.* 76: 761–765.

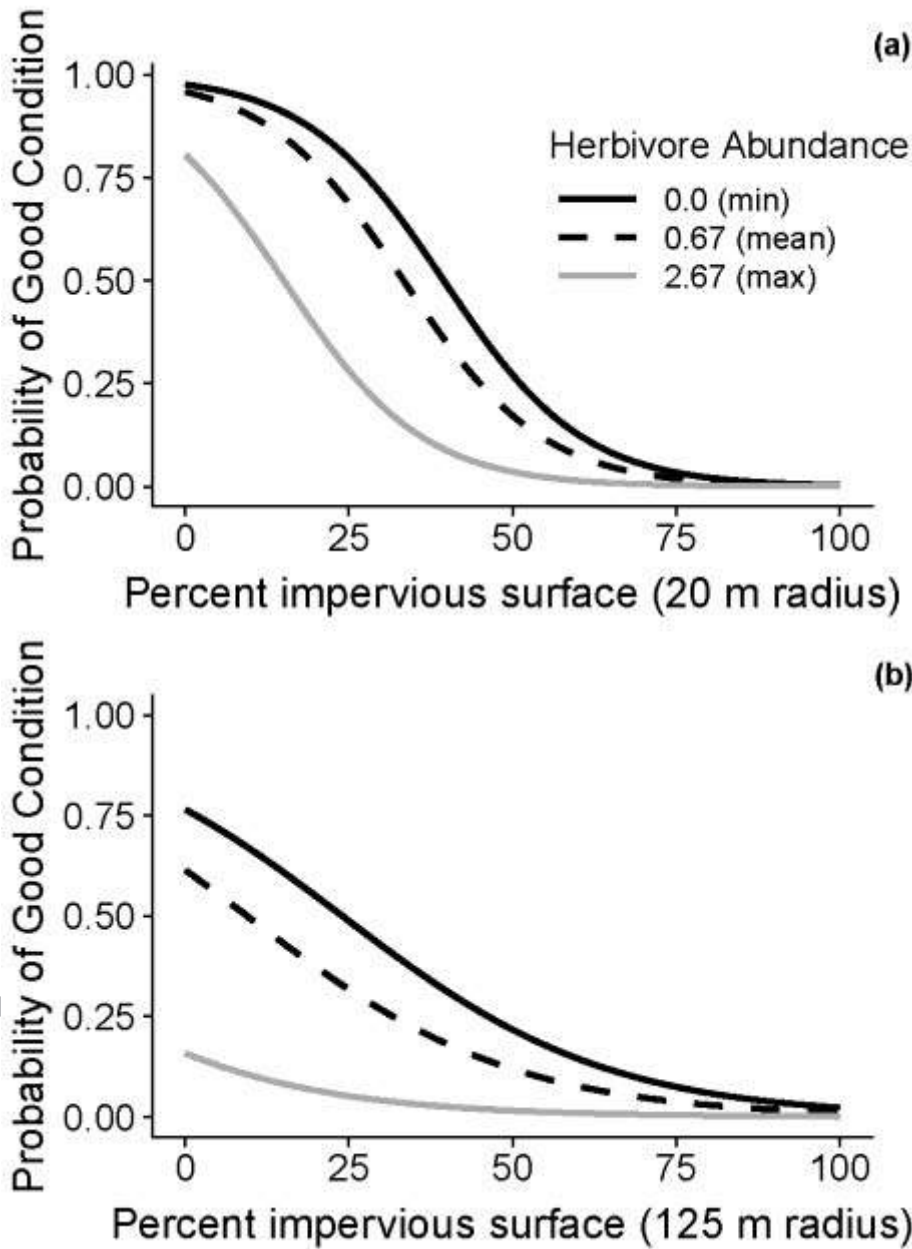
- Meineke, E. K. and Frank, S. D. 2018. Water availability drives urban tree growth responses to herbivory and warming. - *J. Appl. Ecol.* 55: 1701–1713.
- Meineke, E. K. et al. 2013. Urban warming drives insect pest abundance on street trees. - *PLoS One* 8: 2–8.
- Meineke, E. K. et al. 2016. Urban warming reduces aboveground carbon storage. - *Proc. R. Soc. B Biol. Sci.* 283: 20161574.
- Metcalf, Z. 1912. The gloomy scale, an important enemy of shade trees in North Carolina. - *J. Elisha Mitchell Sci. Soc.* 28: 88–91.
- Mody, K. et al. 2009. Stress magnitude matters: different intensities of pulsed water stress produce non-monotonic resistance responses of host plants to insect herbivores. - *Ecol. Entomol.* 34: 133–143.
- Moles, A. T. et al. 2011. Assessing the evidence for latitudinal gradients in plant defence and herbivory. - *Funct. Ecol.* 25: 380–388.
- Moreira, X. et al. 2015. Latitudinal variation in herbivory: Influences of climatic drivers, herbivore identity and natural enemies. - *Oikos* 124: 1444–1452.
- Mullaney, J. et al. 2015. A review of benefits and challenges in growing street trees in paved urban environments. - *Landsc. Urban Plan.* 134: 157–166.
- Nakagawa, S. and Schielzeth, H. 2013. A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. - *Methods Ecol. Evol.* 4: 133–142.
- Nekola, J. and White, P. 1999. The distance decay of similarity in biogeography and ecology. - *J. Biogeogr.* 26: 867–878.
- Nunes, K. A. et al. 2016. Variation in herbivory along a latitudinal gradient for native and exotic Asteraceae. - *Plant Ecol.* 217: 481–493.
- O’Sullivan, O. S. et al. 2017. Thermal limits of leaf metabolism across biomes. - *Glob. Chang. Biol.* 23: 209–223.
- Oke, T. R. 1988. The urban energy balance. - *Prog. Phys. Geogr.* 12: 471–508.
- Peñuelas, J. et al. 2011. Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. - *Glob. Ecol. Biogeogr.* 20: 597–608.
- Putnam, J. 1880. Biological and other notes on Coccidae. - *Proc. from Davenport Acad. Nat. Sci.* 2: 293–347.
- Rahman, M. A. et al. 2014. Effect of urbanization and climate change in the rooting zone on the growth and physiology of *Pyrus calleryana*. - *Urban For. Urban Green.* 13: 325–335.
- Rahman, M. A. et al. 2015. A comparison of the growth and cooling effectiveness of five commonly planted urban tree species. - *Urban Ecosyst.* 18: 371–389.
- Raupp, M. J. et al. 2006. Street tree diversity in eastern North America and its potential for tree loss to exotic borers. - *Arboric. Urban For.* 32: 297–304.
- Robin, X. et al. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. - *BMC Bioinformatics* 12: 77.
- Roman, L. A. et al. 2013. Identifying common practices and challenges for local urban tree monitoring programs across the United States. - *Arboric. Urban For.* 39: 292–299.
- Salazar, D. and Marquis, R. J. 2012. Herbivore pressure increases toward the equator. - *Proc. Natl. Acad. Sci.* 109: 12616–12620.
- Schymanski, S. J. et al. 2013. Stomatal control and leaf thermal and hydraulic capacitances under rapid environmental fluctuations. - *PLoS One* 8: e54231.
- Sunday, J. M. et al. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. - *Proc. Natl. Acad. Sci. U. S. A.* 111: 5610–5615.
- Tonidandel, S. and LeBreton, J. M. 2011. Relative importance analysis: a useful supplement to regression analysis. - *J. Bus. Psychol.* 26: 1–9.
- Watson, W. T. 2005. Influence of tree size on transplant establishment and growth. -

- Horttechnology 15: 118–122.
- Way, D. A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. - *Tree Physiol.* 30: 669–688.
- Williams, A. P. et al. 2012. Temperature as a potent driver of regional forest drought stress and tree mortality. - *Nat. Clim. Chang.* 3: 292–297.
- Xiam, G. et al. 2011. National land cover database 2006: percent impervious product. - *Pe&Rs* 77: 754–762.
- Youngsteadt, E. et al. 2014. Do cities simulate climate change? A comparison of herbivore response to urban and global warming. - *Glob. Chang. Biol.* 21: 97–105.
- Youngsteadt, E. et al. 2017. Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands. - *Glob. Chang. Biol.* 23: 1436–1437.
- Zhang, S. et al. 2016. Latitudinal variation in herbivory: hemispheric asymmetries and the role of climatic drivers. - *J. Ecol.* 104: 1089–1095.
- Zhang, S. et al. 2017. A re-evaluation of hemispheric asymmetries in herbivory: a response to Kozlov & Klemola 2017. - *J. Ecol.* 105: 1575–1579.
- Zhou, W. et al. 2017. Shifting concepts of urban spatial heterogeneity and their implications for sustainability. - *Landsc. Ecol.* 32: 15–30.
- Zuckerberg, B. et al. 2012. Overlapping landscapes: a persistent, but misdirected concern when collecting and analyzing ecological data. - *J. Wildl. Manage.* 76: 1072–1080.

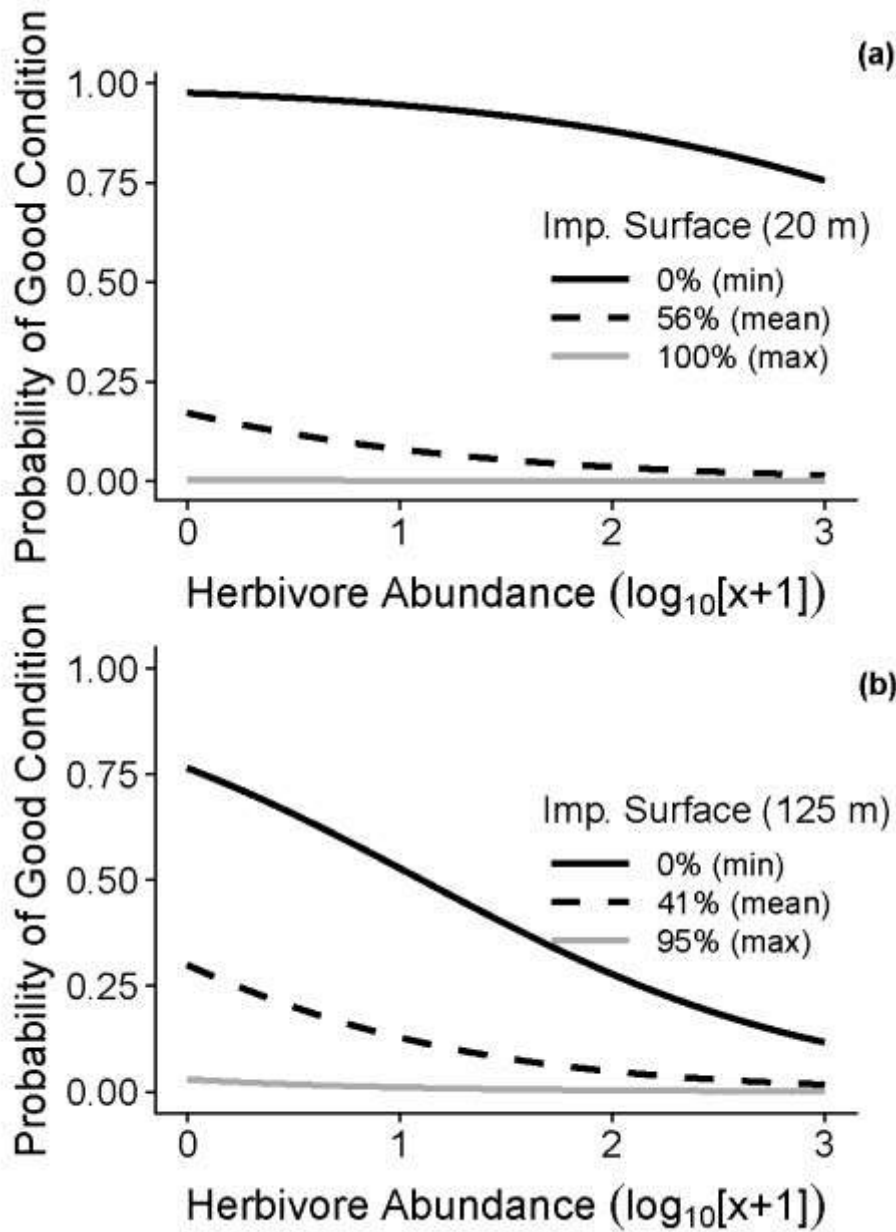
Supplementary material (Appendix oik.XXXXXX at [www.oikosjournal.org/readers/appendix](http://www.oikosjournal.org/readers/appendix)). Appendix A.

## Figure legends

**Fig 1** Lines are predicted probabilities of Good tree condition using a logistic model with impervious surface ((a) Imp20; (b) Imp125) and herbivore abundance as predictor terms. For each line, herbivore abundance ( $\log_{10}[x+1]$ ) was held at a constant value (solid black = minimum, dashed black = mean, solid gray = maximum) while impervious surface varied



**Fig 2** Lines are predicted probabilities of Good tree condition using a logistic model with impervious surface and herbivore abundance as predictor terms. For each line, impervious surface ((a) Imp20; (b): Imp125) was held at a constant value (solid black = minimum, dashed black = mean, solid gray = maximum) while herbivore abundance ( $\log_{10}[x+1]$ ) varied



## Table Legends

**Table 1** Summary information for study cities.

City, State	<i>Acer rubrum</i> (n)	Latitude (°N)	Summer (°C)	Winter (°C)	Imp125 (%)	Imp20 (%)	Herbivore abundance (log <sub>10</sub> scale insects/15 cm)	DBH (cm)				
Newark, DE	35	39.68	29.43	-3.30	42.24 (25.3)	b	55.06 (24.8)	bc	0.47 (0.1)	b	21.54 (1.9)	d
Asheville, NC	34	35.60	28.24	-2.51	46.12 (22.2)	b	54.79 (26.8)	bc	0.28 (0.1)	b	30.81 (2.0)	ab
Knoxville, TN	36	35.96	30.44	-1.03	38.99 (21.6)	bcd	55.17 (26.9)	bc	0.63 (0.1)	b	32.84 (2.1)	a
Raleigh, NC	32	35.78	30.91	-0.34	28.23 (18.2)	d	53.59 (21.9)	cd	1.14 (0.1)	a	24.28 (1.5)	cd
Charlotte, NC	30	35.23	30.97	0.35	40.43 (23.7)	bc	57.5 (23.2)	bc	1.09 (0.1)	a	33.78 (2.1)	a
Atlanta, GA	31	33.75	30.60	0.93	69.05 (21.0)	a	69.51 (26.9)	a	1.08 (0.1)	a	30.13 (2.7)	abc
Savannah, GA	30	32.08	32.27	4.75	37.06 (18.2)	bcd	66.23 (20.7)	ab	0.48 (0.1)	b	31.37 (2.5)	ab
Gainesville, FL	35	29.65	32.48	6.83	29.37 (18.7)	cd	40.97 (27.4)	d	0.30 (0.1)	b	26.86 (2.1)	bcd

Latitude, summer, and winter mean temperature values are reported for each city center. Mean values presented for impervious surface estimates (Imp125, Imp20), Herbivore abundance, and DBH with standard error of the mean within parentheses. Different letters indicate differences between cities using Benjamini–Hochberg (BH) post hoc comparisons ( $\alpha = 0.05$ ) with Kruskal–Wallis analysis. Cities are listed in ascending order of mean winter temperature.

**Table 2** Binomial logistic regression model results for predicting Poor tree condition for both spatial extents and impervious surface estimation methods (20 m field-estimated; 125 m, remotely-sensed).

model	n	overall model				term	estimate (SE)	z	P	RIW
		$\chi^2$	P	AUC	AIC					
20 m extent	263	137.9	<0.001	0.917	170.8	Intercept	-3.72 (0.61)	-6.08	<0.001	
						Imp20	0.09 (0.01)	7.13	<0.001	0.82*
						Herbivory	0.86 (0.35)	2.50	0.012	0.18*
125 m extent	263	64.6	<0.001	0.801	244.1	Intercept	-1.18 (0.34)	-3.46	<0.001	
						Imp125	0.05 (0.01)	5.43	<0.001	0.62*
						Herbivory	1.07 (0.30)	3.58	<0.001	0.38*

Relative importance weight (RIW)

\*denotes significant RIW (Tonidandel and LeBreton 2011)



**Table 3:** Linear mixed-effects regression model results for predicting herbivore abundance for both spatial extents and impervious surface estimation methods (20 m field-estimated; 125 m, remotely-sensed).

model	n	overall model		group	term	estimate (SE)	<i>t</i>	<i>P</i>
		AIC	marginal R <sup>2</sup>					
20 m extent	263	582.9	0.200	fixed	Intercept	-98.88 (35.89)	-2.76	0.031
					Imp20	0.01 (0.00)	5.56	<0.001
					Summer	6.47 (2.36)	2.75	0.032
					Summer <sup>2</sup>	-0.11 (0.04)	-2.73	0.033
				random	variance (SD)		City	0.04 (0.21)
							Residual	0.45 (0.68)
125 m extent	263	588.99	0.175	fixed	Intercept	-91.29 (38.31)	-2.38	0.055
					Imp125	0.01 (0.00)	4.90	<0.001
					Summer	5.95 (2.52)	2.36	0.056
					Summer <sup>2</sup>	-0.10 (0.04)	-2.34	0.058
				random	variance (SD)		City	0.23
							Residual	0.68