Do cities simulate climate change? A comparison of herbivore response to urban and global warming

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Abstract

Cities experience elevated temperature, CO_2, and nitrogen deposition decades ahead of the global average, such that biological response to urbanization may predict response to future climate change. This hypothesis remains untested due to a lack of complementary urban and long-term observations. Here, we examine the response of an herbivore, the scale insect *Melanaspis tenebricosa*, to temperature in the context of an urban heat island, a series of historical temperature fluctuations, and recent climate warming. We survey *M. tenebricosa* on 55 urban street trees in Raleigh, NC, 342 herbarium specimens collected in the rural southeastern United States from 1895 to 2011, and at 20 rural forest sites represented by both modern (2013) and historical samples. We relate scale insect abundance to August temperatures and find that *M. tenebricosa* is most common in the hottest parts of the city, on historical specimens collected during warm time periods, and in present-day rural forests compared to the same sites when they were cooler. Scale insects reached their highest densities in the city, but abundance peaked at similar temperatures in urban and historical datasets and tracked temperature on a decadal scale. Although urban habitats are highly modified, species response to a key abiotic factor, temperature, was consistent across urban and rural-forest ecosystems. Cities may be an appropriate but underused system for developing and testing hypotheses about biological effects of climate change. Future work should test the applicability of this model to other groups of organisms.

Keywords: Acer rubrum, climate change, global warming, herbivory, historical comparison, *Melanaspis tenebricosa*, urban ecosystem, urban warming

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Introduction

Understanding how global climate change will alter biodiversity and ecosystem services is a necessary foundation for conservation and adaptation strategies (Sala *et al.*, 2000; Huey *et al.*, 2012). But the ecological effects of climate and other global-change drivers, such as CO_2 and N deposition, remain difficult to predict or test (Tylianakis *et al.*, 2008; van der Putten *et al.*, 2010; Schweiger *et al.*, 2010). Current experimental approaches are limited in their ability to manipulate these drivers over ecologically relevant spatial and temporal scales (Leuzinger *et al.*, 2011). Several authors have therefore proposed that urban ecosystems could provide novel insights into the effects of future global change (Carreiro & Tripler, 2005; George *et al.*, 2007; Grimm *et al.*, 2008). Because of their physical properties and pollutant emissions, cities experience elevated

temperature, CO_2, and N deposition decades ahead of the global average (e.g., Howarth *et al.*, 2002; Dentener *et al.*, 2006; Friedlingstein *et al.*, 2006; George *et al.*, 2007; Gaffin *et al.*, 2008; Carreiro *et al.*, 2009; Briber *et al.*, 2013; Kunkel *et al.*, 2013). These long-term changes may have altered the ecology or evolution of urban organisms in ways that will occur outside the city in the future. However, urbanization also generates unique habitat structures, disturbance regimes, and species assemblages in which ecological interactions are poorly understood (Shochat *et al.*, 2006; Martin *et al.*, 2012). It is unclear whether urban results provide valid predictions for other habitats.

A few studies have shown that plants and insects respond similarly–in terms of growth, pollen production, or abundance–to increasing urbanization and to elevated temperature (Searle *et al.*, 2012; Meineke *et al.*, 2013) or CO_2 (Ziska & Caulfield, 2000; Ziska *et al.*, 2003) in growth cabinets. These studies suggest that temperature and CO_2 do explain some biological effects of urbanization, but they provide no comparison to

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natural areas, where ecological interactions may differ. We know of only one study that examined species response to a global-change driver in both urban and rural settings. In this example, birch flowering advanced with warming along an urbanization gradient and during 19 years of rural observations (Jochner *et al.*, 2013). It is not known whether such congruence extends to other organisms, trophic levels, or interactions. In this study, we present the first explicit comparison of responses to urbanization and global warming in an animal, using an insect herbivore as a study organism.

Arthropod herbivores are sensitive to changes in temperature, CO_2, and N deposition, making them likely to respond to both urbanization and global change (Bale *et al.*, 2002; Currano *et al.*, 2008; Massad & Dyer, 2010; Netherer & Schopf, 2010). Within species-specific thermal limits, warming accelerates arthropod development and reproduction and improves winter survival (Kingsolver, 2009; Robinet & Roques, 2010), often benefiting herbivores more than higher trophic levels (Kaya & Tanada, 1969; Voigt *et al.*, 2003; de Sassi & Tylianakis, 2012). Furthermore, CO_2 and N deposition are expected to alter host-plant quality in ways that tend to favor increased herbivory (Massad & Dyer, 2010). A recent review and meta-analysis revealed great variability in herbivore responses, but provided modest empirical support for these predictions (Tylianakis *et al.*, 2008; Massad & Dyer, 2010). Consistent with the expected direct effects of warming on arthropods, two species of scale-insect herbivores benefit from urbanization by becoming more abundant on trees in the hottest parts of a city (Meineke *et al.*, 2013; Dale & Frank, in press b).

If urbanization is an appropriate model for global change, species that benefit from urban warming should respond similarly to historical and recent climate warming in rural forests. Here, we test this prediction using urban, rural, and historical abundance data for the gloomy scale insect, *Melanaspis tenebricosa* (Hemiptera: Diaspididae). This species reaches extraordinary densities in cities in its native range in the southeastern United States, where it severely damages red maple (*Acer rubrum*) and other host trees by feeding on vascular tissue (Fig. 1a) (Metcalf, 1922; Deitz & Davidson, 1986; Frank *et al.*, 2013; Dale & Frank, in press a). Within a city, more intense urban warming is associated with increased *M. tenebricosa* body size, fecundity, and population growth (Dale & Frank, in press b).

Although historical records of insect abundance are rare, we overcame this limitation for *M. tenebricosa* by examining herbarium specimens of host plants, which retain evidence of scale insects. *Melanaspis tenebricosa* secretes a waxy cover that adheres to branches even
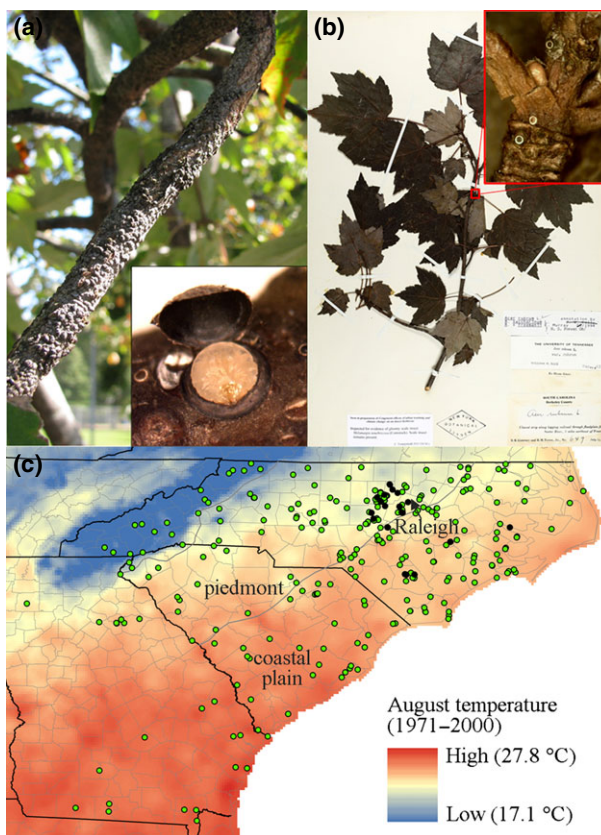

Fig. 1 Description of the study system. (a) *M. tenebricosa* scale insects reach damaging densities on *A. rubrum* street trees. Each bump on the branch is a scale-insect cover, which adheres to the tree even after the soft-bodied insect (inset) dies. (b) *M. tenebricosa* covers remain intact on herbarium specimens more than a century old. The pictured specimen was collected in 1939. Three *M. tenebricosa* covers appear on the highlighted portion of the branch (inset). (c) Locations of 306 sites in the southeastern United States where *A. rubrum* herbarium specimens were collected between 1895 and 2011 (green points); 20 of these sites were resampled in 2013 (black points). Samples were associated with historical temperatures for the year and location of collection; here, map background represents average August temperatures during an example reference period, 1971 – 2000 (ranging from 17.1 °C, blue, to 27.8 °C, red).

after the insect dies (Fig. 1b), and the abundance of these covers on herbarium specimens can be associated with historical temperatures for the year and location the specimen was collected (Fig. 1c). We used these features of *M. tenebricosa* biology to test our overall hypothesis by (i) modeling urban and historical scale-insect abundance relative to site temperatures, (ii) determining the time scale over which *M. tenebricosa* populations responded to historical temperature fluctuations, and (iii) revisiting rural forest sites represented by historical specimens to test the prediction that

scale-insect abundance would increase with recent, historically unprecedented climate warming.

Materials and methods

Study organism

Melanaspis tenebricosa is an armored scale insect herbivore of soft-wood maples (principally *Acer rubrum* and *Acer saccharinum*) in the southeastern United States (Metcalf, 1922; Deitz & Davidson, 1986). It damages trees by extracting fluids from woody tissue, causing branch dieback and occasionally tree death (Metcalf, 1922; Frank *et al.*, 2013). The life cycle includes one generation per year: *M. tenebricosa* overwinters as mated adult females. In spring (April–May) these females grow rapidly and develop eggs, from which crawlers emerge throughout the summer (Metcalf, 1922). Crawler emergence peaks in July and August; the young develop rapidly and mate from late August into September, after which males die and fertilized females overwinter (Metcalf, 1922).

Urban sampling

We sampled *M. tenebricosa* populations on 32 street trees in the city of Raleigh, North Carolina, USA, a growing urban area with a population of about 423 000. To select study sites, we used ArcMap 10.0 to overlay a Raleigh street map, zoning map, street-tree inventory, a grid of 2-km squares, and a Landsat thermal image. The thermal image was acquired on August 18, 2007, and prepared as described in (Chander *et al.*, 2009; Meineke *et al.*, 2013). We divided the city into quadrants, randomly selected four grid squares per quadrant, and located the hottest and coldest sites that contained *A. rubrum* (red maple) street trees in low-density residential zones in each selected grid square. On July 9 – 12, 2012, we used a 3.6-m pole pruner to remove four branches per tree, one from each cardinal direction. We examined 15 or 30 cm of each branch under a dissecting microscope and counted the number of living scale insects. We also installed a DS1923 hygrochron iButton data logger (Maxim Integrated, San Jose, CA, USA) in each tree as described in (Meineke *et al.*, 2013; Dale & Frank, in press b). iButtons recorded temperature every 3 h. August average temperature in 2012 was calculated for each site as the mean of all 248 August temperature readings; two sites were excluded due to iButton failure. These temperature and scale-insect abundance data were pooled with those of a similar scale-insect sample collected from 25 additional *A. rubrum* street trees in Raleigh on May 18, 2012, described in (Dale & Frank, in press b). Although these sampling efforts were separated by 52 days, total scale-insect abundance did not differ between dates (Wilcoxon test, $S = 836$, $Z = 1.56$, $P = 0.120$) and data were pooled.

Because scale-insect abundance was an overdispersed count variable, we used a generalized linear model with a negative binomial error distribution and log link function to model scale-insect count as a function of August 2012 temperature at each site, with branch length as a covariate. The analysis was performed in the GENMOD procedure of SAS 9.3 for Windows.

Although we analyzed count data, Fig. 2 shows the same data and model predictions in insects per cm for ease of comparison among sites and historical samples.

We note that, although arthropod development is driven by thermal accumulation rather than average temperature, developmental thresholds for *M. tenebricosa* are unknown. We therefore use August average temperature to characterize differences in summer temperature between sites, since (i) August is one of the hottest months in the region (ii) *M. tenebricosa* has only 1 generation per year, and (iii) August temperatures capture variation between sites that is consistent throughout the summer. Specifically, at a subset of 26 sites where iButtons were deployed in April 2012 (Dale & Frank, in press b), August average temperature was highly correlated with monthly average in each of the other spring–summer months during which the sampled insects developed (April $r = 0.53$, $P = 0.0068$; May $r = 0.92$, $P < 0.0001$, June $r = 0.90$, $P < 0.0001$, and July $r = 0.86$, $P < 0.0001$).

Historical samples

We examined *A. rubrum* specimens collected in North Carolina, South Carolina, and Georgia, USA (Fig. 1c), between 1895 and 2011, preserved in four US herbaria (Duke University, New York Botanical Garden, North Carolina State University, University of North Carolina at Chapel Hill). We examined specimens under a dissecting microscope and recorded the number of *M. tenebricosa* covers, length of visible branch, and date and locality of collection. Specimens collected in urban areas were excluded. We used online Google Maps (accessed October 2012 – September 2013) and modern and historical topographic, county, and highway maps to assign coordinates to localities described on specimen labels.
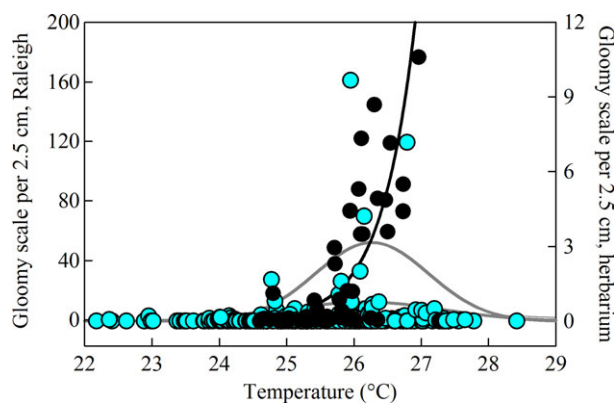

Fig. 2 Scale-insect abundance vs. August average temperature in the year of collection in the urban (black) and historical (blue) datasets. Urban data were fit with a generalized linear model (black line, Table 1). Historical data encompassed greater temperature variation and were fit with a Gaussian peak model using a quantile regression (Table 2); predictions for the upper 90th, 95th, and 98th percentiles of *M. tenebricosa* response are shown here (gray lines). The x-axis is truncated at 22 °C, below which no scale insects were observed; see also Figure S1.

Table 1 Generalized linear model tests of factors that predict *M. tenebricosa* abundance on urban trees. (Temperature refers to 2012 August average, length to branch length examined)

Parameter	df	Estimate ± SE	Wald X^2	P
Intercept	1	−43.59 ± 12.93	11.37	<0.001
Temperature (°C)	1	2.01 ± 0.49	16.77	<0.001
Length (in)	1	−0.08 ± 0.02	11.36	<0.001
Dispersion	1	3.11 ± 0.54		

Table 2 Parameter estimates, significance tests, and local fit statistics for Gaussian quantile regression models describing historical gloomy-scale abundance as a function of August temperature in the year of collection. (Parameter a describes peak height; b, peak value; c, peak shape)

Quantile	Parameter	Estimate ± SE	t	P	AIC
0.75	a	0.04 ± 0.01	4.39	<0.001	−646.37
	b	26.29 ± 0.70	37.40	<0.001	
	c	1.83 ± 0.68	2.70	0.007	
0.90	a	0.12 ± 0.04	3.17	0.002	−257.76
	b	26.70 ± 1.12	23.79	<0.001	
	c	2.67 ± 1.07	2.50	0.013	
0.95	a	0.25 ± 0.07	3.34	<0.001	−27.49
	b	26.14 ± 0.77	34.14	<0.001	
	c	1.78 ± 0.60	2.99	0.003	
0.98	a	0.68 ± 0.23	2.92	0.004	249.30
	b	26.30 ± 0.57	46.50	<0.001	
	c	1.49 ± 0.41	3.66	<0.001	

Analyses presented in Data S1 indicate that examination of mounted plant specimens reveals patterns of scale-insect abundance that are highly correlated to those observed on fresh, unmounted branches.

Analysis of historical data

To associate each specimen with historical temperatures, we downloaded temperature grids (4 km resolution) from the PRISM Climate Group (Daly *et al.*, 2008). We used ArcMap to extract August high and low temperatures from the grids for each site in each year from 1895 to 2013. We then computed mean August temperatures for each site for the year of collection and for up to 20 years leading up to collection. (For example, the 2-year August average was the mean of the August temperature in the year of collection and the August temperature in the year prior; the 3-year August average included the August of the year of collection and the Augusts of two previous years, and so on.) We assumed that insects collected in winter and early spring (January – April) were most influenced by the previous summer (in the calendar year prior to collection), while those collected from May through December were associated with the August of the calendar year of collection. Henceforth, 'year of collection' refers to the growing-season year, not calendar year.

Because a scatterplot of scale-insect density vs. August temperature in the year of collection indicated peak scale-insect abundance at intermediate temperatures, we analyzed the data using a Gaussian peak model. Because the error distribution deviated from assumptions of least-squares regression, and because minimum insect abundance appeared unaffected by temperature while the maximum appeared to respond, we used quantile regression to examine the rate of change of scale-insect abundance relative to temperature throughout its distribution (Cade & Noon, 2003). Because more than half the data points were zeros, we examined response in quantiles 0.75, 0.9, 0.95, and 0.98. Analysis was performed using the base and quantreg 5.05 packages of R 3.0.0 computing environment for Windows (Koenker, 2013; R Core Team, 2013). Scale-insect density was log transformed for analysis; for ease of comparison to urban data, Fig. 2 shows untransformed data and back-transformed model predictions.

In addition to analyses of historical scale-insect abundance above, we also asked whether scale-insect *presence* was related to average August site temperature in the year of collection or over the previous years, up to 20 years. We excluded from this analysis 10 specimens collected before 1914, the end of the first 20-year period. We used the 'glm' function in the base package of R to construct 20 non-nested logistic regression models in which probability of scale-insect presence was a function of one of the August averages (1 August through 20 Augusts) and branch length examined (R Core Team, 2013). We used Akaike Information Criterion (AIC) to evaluate results.

When the 8-year August average was found to be the best predictor of scale-insect presence (Figure S2, Table S1), we hypothesized that historical fluctuations in this variable should have caused widespread increases and decreases in scale-insect populations across the region. To test this hypothesis, we focused on North and South Carolina piedmont and coastal plain, where we had the best coverage of historical samples (Fig. 1c). To define hot and cold years in this region, we took the grand mean of the 8-year August averages at all sampled sites in all years throughout the time period represented by historical samples in the region (1905–2010). This value was 25.4 °C; 'hot' years, then, were those in which the 8-year August average for all sites was greater than 25.4 °C, and 'cold' years were those with lower temperatures. The mid-20th century was characterized by a series of striking decadal-scale temperature fluctuations (Fig. 3) and a peak in regional plant collecting such that each hot or cold period was represented by at least 15 herbarium samples. We counted the number of specimens with and without scale insects collected during these hot and cold periods and used the LOGISTIC procedure of SAS 9.3 to test the null hypothesis that the odds of finding a scale insect did not differ between hot periods and cold periods; specimen length, latitude, and region (piedmont or coastal plain) were included as covariates.

Resampling herbarium sites

To examine scale-insect response to recent warming, we revisited 20 sites where herbarium samples were collected between 1970 and 1997 during years with cool 8-year August averages (Fig. 1c, Table S1). From each of 2 – 3 trees per site, we used a 3.6-m pruner to collect two branches equal in length to the

original historical specimen from the same site. Samples were collected in August and September 2013. We processed these samples as if they were herbarium specimens, placing them in a plant press in a drying room (46 °C, 6% RH) for 5–9 days. Samples were then taped to a 28 × 46 cm paperboard and examined under a dissecting microscope. We recorded the number of *M. tenebricosa* covers on each specimen and calculated a modern site median of scale insects per sample; we rounded this value down to conservatively avoid detecting increases of less than one whole insect per sample. Had the single historical specimen from each site been drawn from a population equal in density to the modern population, the historical specimen should have equal probability of hosting more or fewer insects than modern samples from the same site. We tested this null hypothesis using a Wilcoxon signed rank test in JMP 10.0.0.

Results

Urban street trees in Raleigh, NC, experienced a range of thermal environments spanning 2.3 °C in August average temperature in 2012. Living *M. tenebricosa* were found on 84% of the 55 trees examined, and their density increased with temperature, reaching a maximum
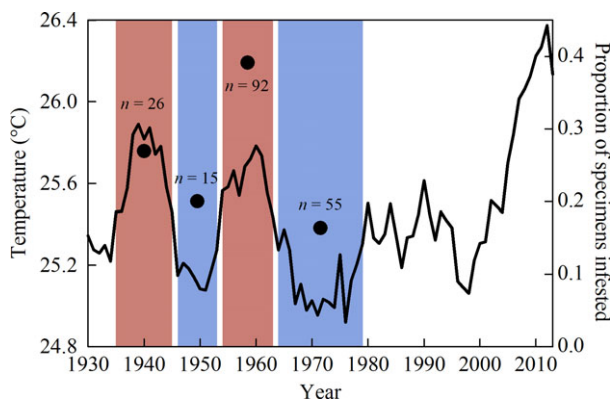

Fig. 3 Proportion of herbarium specimens on which *M. tenebricosa* was detected (black circles) during relatively warm (red) and cool (blue) years. The black line represents the 8-August average across all sampled sites in NC and SC. *Melanaspis tenebricosa* was significantly more common during warm periods (Table 3).

of 177 insects per 2.5 linear cm of twig at the hottest site (Table 1, Fig. 2).

To assess the relationship between *M. tenebricosa* abundance and historical and regional temperature variation, we examined 342 herbarium specimens representing 306 unique site-year combinations sampled in the rural southeastern United States between 1895 and 2011 (Fig. 1c). Median twig length preserved per site was 38 cm (range 2.5 – 358 cm). *Melanaspis tenebricosa* covers were visible on herbarium specimens from 29% of sites, reaching a maximum density of 9.7 covers per 2.5 linear cm. Had we been able to examine this branch on all sides, as we did in the urban sampling, we would have seen about 30 scale-insect covers per 2.5 linear cm (Data S1), sixfold less than the peak density in the city. Scale-insect density on herbarium specimens was related to temperature in the year of collection with a Gaussian quantile regression model (Table 2, Fig. 2, Figure S1). For all quantiles analyzed, abundance peaked in the model at temperatures between 26.1 and 26.7 °C, a range that also encompassed the steepest increase in urban scale-insect density (Fig. 2).

In a separate analysis of scale insect presence-absence on historical samples, the odds of finding a scale insect on a herbarium specimen increased with temperature, with the best logistic regression fit provided by the average of 8 Augusts up to and including the year of collection (Table S1, Figure S2). This variable further predicted scale-insect occurrence through time: *M. tenebricosa* was found on significantly more herbarium specimens collected during periods with above-average 8-year August average temperatures than during cooler periods, while controlling for geographic variation (Fig. 3, Table 3).

Finally, we revisited 20 sites represented by historical samples and found a widespread increase in gloomy-scale abundance from past to present (Figure S3), coincident with a 1.06 ± 0.08 °C (mean ± SE) increase in the 8-year August average across sites. *Melanaspis tenebricosa* covers were detected on modern samples from 17 of these sites, compared to only eight historical samples. Overall, scale-insect density increased at 16 sites,

Table 3 During a series of mid-century temperature fluctuations, *M. tenebricosa* was more likely to occur on herbarium specimens collected during warm years. (Temperature refers to hot or cold time period; region, piedmont or coastal plain; length, branch length observed; *P* values < 0.05 are bold)

Parameter	Estimate ± SE	Wald X^2	P	AIC	pseudo-r^2
Whole model		23.16	**<0.001**	207.52	0.21
Intercept	−3.79 ± 7.41	0.26	0.609		
Temperature (°C)	−0.58 ± 0.20	7.88	**0.005**		
Region	0.20 ± 0.20	1.00	0.317		
Latitude	0.05 ± 0.21	0.05	0.829		
Length (in)	0.04 ± 0.010	18.48	**<0.001**		

stayed the same at 2, and decreased at 2 (Wilcoxon signed rank test, $S = 62.5$, $P = 0.004$). Across sites, the median increase in *M. tenebricosa* density was 1 additional insect per 25 cm of branch per 1 °C increase in the 8-year August average. Even the most heavily infested rural samples did not approach insect densities observed in the city; rather, they were consistent with densities observed at other rural sites in the historical record. The maximum insect density on a modern rural sample was 0.9 live scale insects per 2.5 linear cm, corresponding to 5.1 covers per 2.5 linear cm.

Discussion

Comparison of urban and rural patterns

We found that the insect herbivore *M. tenebricosa* was most common during periods of historical and recent warming in the southeastern United States and in the hottest parts of Raleigh, NC. Maximum insect abundance in historical and urban datasets occurred at similar temperatures, supporting the hypothesis that biological responses to urbanization and global change are comparable.

In the historical dataset, scale-insect abundance peaked in an optimal temperature range from 26.1 to 26.7 °C August average, with lower abundance at hotter and cooler sites (Fig. 2, Table 2). It is striking that Raleigh urban temperature variation fell within the range of the steepest increase in the historical response curve (Fig. 2). In some parts of the study region, where rural temperatures are already at or above the optimal values shown in Fig. 2, we predict that *M. tenebricosa* populations would decline due to further warming from climate change or urbanization.

Despite the qualitative similarity in insect response to urban and historical warming, *M. tenebricosa* response to temperature was stronger and more consistent in the city than in historical rural samples (Fig. 2, Table 2). This relationship implies that rural *M. tenebricosa* populations, even when released from temperature limitation, were often suppressed by other factors such as host-plant nutrition or defense or natural enemies (Hanks & Denno, 1993; Cade & Noon, 2003; Massad & Dyer, 2010). An alternative interpretation is that variability in the response to temperature is an artifact of under-sampling, a limitation inherent to using herbarium samples for an insect sample. However, in our modern data from rural forests, abundance estimates based on multiple branches, individual branches, and herbarium-like samples were well-correlated (Data S1). These patterns suggest that, even if each historical site had been sampled more intensively, we would still see some very low insect densities at ideal temperatures. A

more pronounced biological response to urban than historical warming was also observed in a study of birch flowering phenology, which advanced 4.4 days per 1 °C warming in cities, compared to 1.9 days in rural areas (Jochner *et al.*, 2013).

Key questions, then, are what urban conditions account for the greater magnitude of biological response to warming in the city, and whether rural forests will experience comparable conditions in the future. Both this study and the Jochner *et al.* (2013) study in birch focused on temperature, but CO_2 and N deposition were certainly greater in urban areas than in most historical rural forests with shared temperatures (Groffman *et al.*, 2004; George *et al.*, 2007; Carreiro *et al.*, 2009; Briber *et al.*, 2013). We hypothesize that the combined effects of elevated temperature, CO_2, and N in cities may account for quantitative differences between urban and historical datasets. For example, elevated N deposition is a feature of both present-day cities and future rural forests that, by altering host–plant nutrition and defense, could release herbivore populations from nutrient limitation and maximize the direct effects of temperature (Tylianakis *et al.*, 2008; Massad & Dyer, 2010; Raupp *et al.*, 2010; Searle *et al.*, 2012). Alternatively, uniquely urban features that lack global-change analogues could produce similar effects on herbivores. For example, extreme urban habitat fragmentation and extensive impervious surface might reduce natural enemy abundance or efficacy, (Hanks & Denno, 1993; Shrewsbury & Raupp, 2006; Peralta *et al.*, 2011), while other urban factors such as reduced wind speed may enhance plant growth (Gregg *et al.*, 2003; Bang *et al.*, 2010). Such urban effects could release *M. tenebricosa* populations from top-down or bottom-up controls, facilitating response to temperature in cities. Testing these alternative hypotheses should be a subject of future experimental studies to determine whether *M. tenebricosa* could become as common in future rural forests as it is in Raleigh today and, by extension, the degree to which urban areas provide reasonable simulations of future global change.

Change over time

Temperature variation in the historical dataset encompassed change across space (latitude and elevation) and time (periods of warming and cooling). Although spatial climatic gradients are widely studied as a proxy for climate change, our historical samples allowed us to examine change over time directly. We found that *M. tenebricosa* was more prevalent on herbarium specimens collected during warm periods than during

cool periods (Fig. 3, Table 3), suggesting that this species has tracked historical climate variability and is likely to also track future changes.

As an additional test of this possibility, we resampled 20 localities described on herbarium specimen labels. We found more *M. tenebricosa* at these sites in 2013 than on the corresponding historical specimens collected during cooler periods (Figure S3). We took precautions to make fair comparisons between fresh samples and historical samples by comparing twigs of equal length, processing fresh samples as if they were herbarium specimens, and by making conservative estimates of scale-insect abundance on modern samples (i.e., by rounding modern median abundance values down to the nearest whole insect). We therefore believe that the results represent a real increase in *M. tenebricosa* abundance from past to present.

These analyses of change over time, together with the result that August temperature averaged over 8 years was the best predictor of *M. tenebricosa* abundance, suggest that *M. tenebricosa* responds to temperature trends on a roughly decadal time scale. Because *M. tenebricosa* has one generation per year and poor dispersal ability (Metcalf, 1922; Logan *et al.*, 2003; Frank *et al.*, 2013), population expansion may be best detected after multiple warm years.

Summer temperatures in the southeastern United States are expected to increase by about 1–3 °C over the next 50 years, depending on future greenhouse gas emissions (Alder & Hostetler, 2013; Kunkel *et al.*, 2013). Our urban and historical data show that *M. tenebricosa* populations increase measurably in response to temperature changes of similar magnitude and speed. If the magnitude of scale-insect response to temperature remains within historical limits, impacts on forests may be minor, but if the thermal response is amplified to urban magnitudes by interaction with other global-change drivers, *M. tenebricosa* could threaten tree health in rural forests. Sucking insect herbivores such as *M. tenebricosa* deplete host resources, slowing plant photosynthesis, growth, and reproduction more than do defoliating insects (Classen *et al.*, 2005; Zvereva *et al.*, 2010). Even incremental increases in herbivory by sucking insects could alter forest dynamics (Wolf *et al.*, 2008).

Implications

We provide the first comparison of animal response to urbanization and climate change. Although urban habitats are unique, our results show that an herbivore's response to urban warming correctly predicts its functional response to global warming in surrounding natural habitats. One implication of this result is that cities may serve as regional sentinels: Monitoring urban insect abundance could indicate which species will emerge as pests in surrounding rural forests in the next several decades. More broadly, the congruence in our results suggests that urban areas may represent a valid but underutilized source of insight into how species dynamics and interactions will be altered by the net, long-term effects of multiple global-change drivers. Future work should determine how broadly this parallel extends. For example, the urban abundance of large vertebrates may be so severely limited by habitat patch size that urban atmospheric and temperature effects are undetectable. Future work should also determine whether elevated urban CO_2 and N deposition account for amplified biological response to urban warming over historical rural warming–a pattern now evident in both a plant and an herbivore. Using urban habitats around the globe to develop and test hypotheses about biological effects of climate change will complement existing experimental and modeling approaches and improve understanding of how ecosystems will be altered in this century.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Validation of historical abundance data.
Figure S1. Complete historical dataset showing log-transformed *M. tenebricosa* abundance with Gaussian quantile regression model fits.
Figure S2. AICs for models relating probability of *M. tenebricosa* presence on 296 historical samples to August average temperatures for 1 to 20 years up to and including the year of collection.
Figure S3. Scale insect density increased from past to present at 16 of 20 sites, while prevailing temperatures also increased.
Table S1. The likelihood of detecting *M. tenebricosa* on an herbarium specimen increased with the average temperature of 8 Augusts at the specimen locality.
Table S2. Historical locality descriptions, 2013 coordinates, and 2013 *M. tenebricosa* abundance for historically sampled sites revisited in 2013