

Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands

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Abstract

Biological effects of climate change are expected to vary geographically, with a strong signature of latitude. For ectothermic animals, there is systematic latitudinal variation in the relationship between climate and thermal performance curves, which describe the relationship between temperature and an organism's fitness. Here, we ask whether these documented latitudinal patterns can be generalized to predict arthropod responses to warming across mid- and high temperate latitudes, for taxa whose thermal physiology has not been measured. To address this question, we used a novel natural experiment consisting of a series of urban warming gradients at different latitudes. Specifically, we sampled arthropods from a single common street tree species across temperature gradients in four US cities, located from 35.8 to 42.4° latitude. We captured 6746 arthropods in 34 families from 111 sites that varied in summer average temperature by 1.7–3.4 °C within each city. Arthropod responses to warming within each city were characterized as Poisson regression coefficients describing change in abundance per °C for each family. Family responses in the two midlatitude cities were heterogeneous, including significantly negative and positive effects, while those in high-latitude cities varied no more than expected by chance within each city. We expected high-latitude taxa to increase in abundance with warming, and they did so in one of the two high-latitude cities; in the other, Queens (New York City), most taxa declined with warming, perhaps due to habitat loss that was correlated with warming in this city. With the exception of Queens, patterns of family responses to warming were consistent with predictions based on known latitudinal patterns in arthropod physiology relative to regional climate. Heterogeneous responses in midlatitudes may be ecologically disruptive if interacting taxa respond oppositely to warming.

Keywords: arthropods, climate change, ectotherms, global warming, latitude, thermal tolerance, urban heat island, urbanization

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Introduction

Understanding and predicting biological responses to climate change is an ongoing research challenge, and a large literature documents shifts in phenology, range limits, and population abundance of organisms over the past 50 years [e.g., reviewed by Chen *et al.* (2011) and Parmesan (2006)]. These responses are highly variable, however, and it is still unclear whether species responses will remain idiosyncratic or whether consistent patterns will emerge across space, time, and taxa (Pelini *et al.*, 2009; Doak & Morris, 2010; Andrew *et al.*, 2013).

Although species' behaviors, interactions, and life histories all shape their responses to global change (Tylianakis *et al.*, 2008; Diamond *et al.*, 2011; Sunday *et al.*, 2014), physiology has emerged as an important

predictor. Several studies have convincingly used physiological thermal limits of terrestrial ectotherms to explain their sensitivity to climate change or experimental warming (Buckley, 2008; Sinervo *et al.*, 2010; Diamond *et al.*, 2012a; Sunday *et al.*, 2012). For example, results from a forest warming experiment in North Carolina, USA, showed that ant species with higher critical thermal maxima (CT_{max}) became more abundant in warmed plots than did species with lower CT_{max}, suggesting that such species will also be most robust to future climate change (Diamond *et al.*, 2012a; Stuble *et al.*, 2013).

Practically speaking, however, the utility of species-specific physiological predictors is limited because the thermal tolerances of most populations of organisms are not known (Crozier & Dwyer, 2006; Higgins *et al.*, 2012). Taking insects as an example, published data on thermal tolerances are available for fewer than 300 of the millions of extant species (e.g., Addo-Bediako *et al.*, 2000; Finlay *et al.*, 2006; Sunday *et al.*, 2014). This

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limitation may be partly overcome by generalizing from documented relationships between latitude and thermal tolerance in ectotherms (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011). Global-scale studies demonstrate that, while climate does vary with latitude, ectotherms' physiological heat tolerance (measured as the temperature that causes loss of mobility or death) varies much less (Sunday *et al.*, 2011; Diamond *et al.*, 2012b). Thus, ectotherms at cold, high latitudes should

be able to tolerate, or benefit from, more degrees of warming than can ectotherms at already-warm, low latitudes. More specifically, tropical ectotherms tend to be thermal specialists adapted to environmental temperatures that are relatively stable throughout the year (Addo-Bediako *et al.*, 2000; Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Sunday *et al.*, 2011). Their thermal performance curves, which describe fitness relative to temperature (e.g., Fig. 1), reach an optimum near

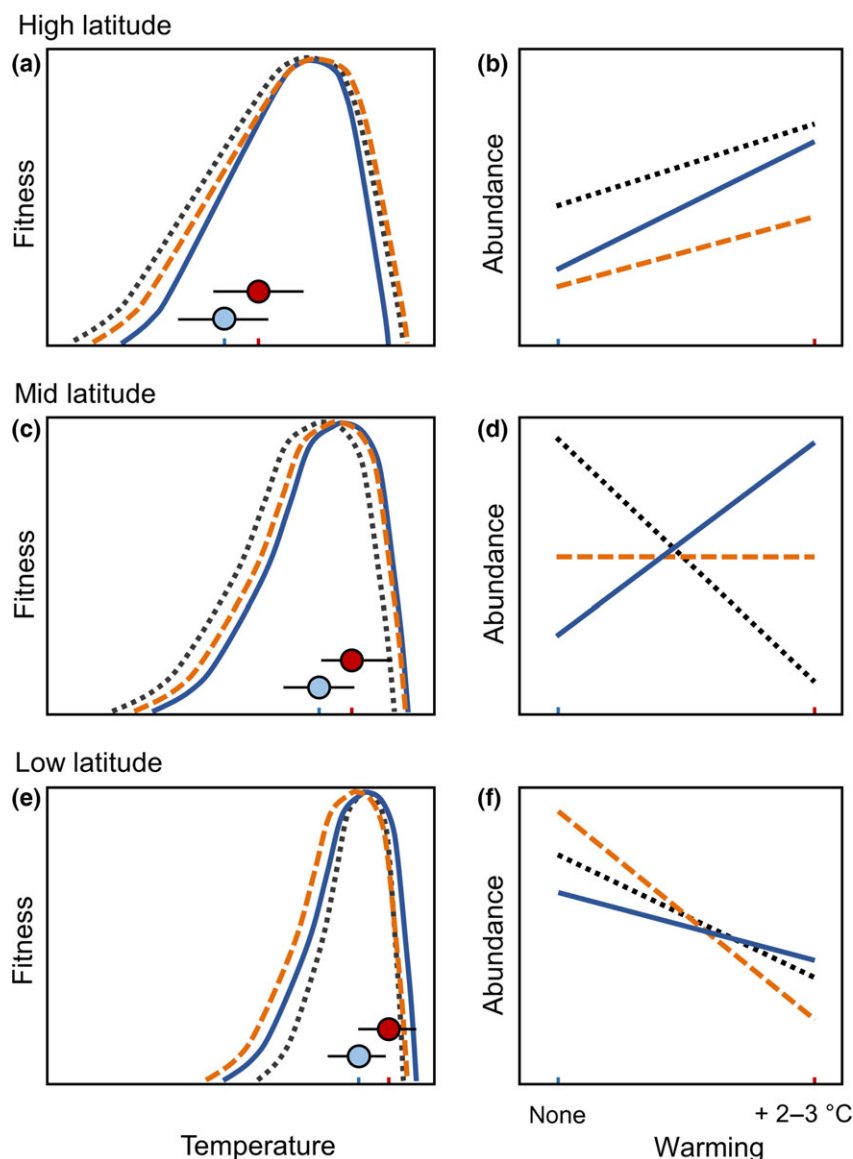


Fig. 1 Conceptual sketch of predicted responses to warming among ectotherms at high latitudes (top), midlatitudes (middle), and low latitudes (bottom). Panels a, c, and e represent thermal performance curves; at lower latitudes, they are narrower and optimized closer to current ambient temperatures. Variability among taxa is represented by the three response curves shown at each latitude. As the environment warms from current/cool urban temperatures (blue dots, blue ticks) to future/hot urban temperatures (red dots, red ticks), fitness will change, leading to altered abundance of the affected taxa (b, d, and f). X-axes in panels b, d, and f represent the temperature difference between red and blue dots in a, c, and e, respectively. Due to the shape and location of the fitness curves relative to regional climate, responses should be generally smaller and more positive at high latitudes (b), larger and more variable at midlatitudes (d), and generally negative at low latitudes (f).

prevailing ambient temperatures, with narrow safety margins of a few °C or less before the onset of heat stress and fitness decline (Deutsch *et al.*, 2008; Fig. 1e). At temperate latitudes, ectotherms are thermal generalists adapted to tolerate a wide range of temperature variation across seasons and years. Their heat tolerance is similar to that of tropical animals, but their cold tolerance is lower and their thermal performance curves broader (Addo-Bediako *et al.*, 2000; Sunday *et al.*, 2011) (Fig. 1a). For these species, ambient temperatures are frequently cooler than optimal, such that modest warming should increase fitness.

Although this temperate-tropical contrast is well supported, particularly for latitudes below 20° and above 40° (Kingsolver *et al.*, 2013), expected response patterns within the temperate zone are less well developed (Pelini *et al.*, 2014). Two recent studies have predicted, on the basis of measured physiological tolerances, that midlatitudes (between 20° and 40°) will encompass strong variability among taxa in fitness effects of urban warming and climate change (Kingsolver *et al.*, 2013; Chown & Duffy, 2015). Here, we develop several predictions for patterns of arthropod response to warming across midlatitude to high temperate latitude, using abundance as a proxy for fitness. Specifically, on average, midlatitude ectotherms have narrower, steeper thermal performance curves and smaller safety margins than do those at high latitudes (Fig. 1a, c) (Deutsch *et al.*, 2008; Sunday *et al.*, 2011), implying a greater relative change in abundance per °C warming at midlatitudes than at high latitudes (Fig. 1b, d). Further, whereas abundance of tropical ectotherms should generally decline with warming, and that of high-latitude ectotherms should generally increase, average response across species at midlatitudes should approach zero. Interspecific variation that averages to zero, however, will encompass both strong negative and strong positive responses (Fig. 1d). Finally, we predict that, as a result of these effects, warming of a few °C should lead to unchanged or declining diversity at midlatitudes (where warming will cause some species to decline and others to increase) but increasing diversity at high latitudes (where most taxa will become more abundant and detectable, and some cold-intolerant taxa from lower latitudes may also join the assemblage). In summary, our specific predictions are that arthropod response to warming – defined here as change in abundance per °C – will be variable and centered near zero at midlatitudes but uniform and positive at high latitudes; be smaller in magnitude at high latitudes; and will lead to unchanged or declining diversity at midlatitudes but increasing diversity at high latitudes.

We test these predictions using a novel natural experiment consisting of a series of urban warming gradients

distributed across 6.6° latitude in the eastern United States. Because of the urban heat island effect, cities average 2–3 °C warmer than surrounding landscapes, similar to the extent of warming projected for the eastern United States over the next 50–100 years (George *et al.*, 2007; Gaffin *et al.*, 2008; Alder & Hostetler, 2013; Kunkel *et al.*, 2013). In addition, urban heat island intensity varies within a city such that some areas remain nearly as cool as surrounding rural environments. As a result, cities provide a mosaic of temperatures that, if mapped onto temporal predictions, correspond to conditions experienced in both current and future forests. Previous work has demonstrated that urban arthropod populations respond to such within-city temperature differences in ways that parallel their responses to long-term historical warming outside the city (Meineke *et al.*, 2013; Dale & Frank, 2014; Youngsteadt *et al.*, 2015). Thus, we tested our predictions by sampling arthropods – the most abundant ectotherms – across urban warming gradients in two midlatitude cities (below 40° latitude) and two high-latitude cities (above 40°). We sampled arthropods from street trees growing at hotter and cooler sites within each city and asked how their abundance varied with urban warming at each latitude.

Materials and methods

Study sites

We sampled arthropods in Raleigh, NC (latitude 35.78, longitude –78.64), Baltimore, MD (39.28, –76.62), Queens, New York City, NY (40.75, –73.87), and Boston, MA (42.36, –71.06) (City size, population, and climate are summarized in Table 1). These cities span 6.6° latitude and much of the extent of temperate hardwood forest in the eastern United States. In each city, we selected 32 red maple (*Acer rubrum*) street trees as study sites. *Acer* is the most commonly planted genus of street tree throughout the region (Raupp *et al.*, 2006), and *A. rubrum* is one of the most common representatives of the genus, providing a consistent arthropod habitat across our sampled environmental gradients.

To identify study trees within each city, we used ARCMAP 10.0 (ESRI, Redlands, CA, USA) to overlay a street map, zoning map, grid of 2 km squares, Landsat thermal image (Chander *et al.*, 2009; Meineke *et al.*, 2013) and, where available, a municipal street-tree inventory (Fig. S1). We considered sites only within city limits (municipal administrative boundaries) of each city. To reduce variation in land use among sampling sites, we used zoning maps to exclude nonresidential areas (e.g., commercial, office, and industrial zones). In Raleigh, we further excluded the low-density ‘rural residential’ zone that occurs within city limits. Finally, we divided each city into quadrants, randomly selected four 2 km grid squares per quadrant, and used a combination of GIS and on-site searching to identify the hottest and coldest sites that contained

Table 1 Characteristics of sampled cities

	Latitude	Area (km ²)*	Population†	Metropolitan area (km ²)‡	Summer average (°C)§	Summer average max (°C)¶	Warming by 2100 (°C)**
Boston	42.4	125	645 966	9033	21.7	26.1	2.9–5.4
Queens	40.8	280	2 296 175	21 482	23.2	27.3	2.9–5.3
Baltimore	39.3	210	622 104	6738	23.8	29.5	3.1–5.8
Raleigh	35.8	369	431 746	5486	25.8	31.4	2.9–5.3

*Land area within city limits;

†human population within city limits in 2013 (U.S. Census Bureau 2013 estimates);

‡extent of metropolitan area (U.S. Census Bureau 2013 data);

§seasonal (June, July, August) air temperature normal, 1981–2010, at BOS, JFK, BWI, and RDU airport weather stations (Arguez *et al.*, 2010);

¶seasonal maximum temperature normals at the same weather stations;

**extent of warming in the summer (June, July, August) average temperature predicted by 2100 for the county containing each city; the range of values derives from RCP 4.5 and 8.5 emissions scenarios and the mean model predictions available at the USGS National Climate Change Viewer (Alder & Hostetler, 2013).

A. rubrum street trees in residential zones in each selected grid square. This design was intended to ensure that we sampled from hotter and cooler sites throughout each city's thermal mosaic, while reducing potential covariation between temperature and other habitat characteristics that could influence insect populations.

We monitored air temperature in the selected tree canopies using DS1923 iButton data loggers (Maxim Integrated, San Jose, CA, USA) to record temperature synchronously every 3 h. In summer 2012, iButtons were installed and shielded as described by Meineke *et al.* (2013) and downloaded in spring and fall 2013. Here, we present summer temperatures, as our predictions are based on latitudinal variation in thermal safety margins. For each site, the temperature used in analysis is the mean of 583 temperatures recorded from June 15 to August 26, 2013; these dates encompass the hottest time of year, and the period when the maximum number of iButtons was recording concurrently in all cities. The extent of summer urban warming at each site was simply that site's summer average temperature minus the summer average temperature of the coolest site in the same city; this value represents the intensity of each city's urban heat island at each sampling site. Note that although iButtons were installed at the time of arthropod sampling in 2012, the complete summer temperature data are for the following summer; thus, our temperature data are a good representation of the intensity of urban warming (which is consistent property of a site across summers, Fig. S2), but they do not represent the specific weather experienced by the arthropods sampled (Fig. S3). Although we used 2013 temperature data in our analyses, we explored how the use of these measurements may have affected our results by back-predicting 2012 summer temperatures at each site. To do this, we developed site-specific linear regression equations that related iButton temperatures to weather station temperatures in 2013 and then used those relationships to estimate 2012 site temperatures from 2012 weather station data (Text S1, Figs S4 and S5).

Finally, to determine whether our sampling design separated urban warming from other habitat features at the scale

of the focal tree, we used a vegetation complexity index (VCI) to measure the amount and three-dimensional structure of vegetation at each site by adapting the methods of Shrewsbury & Raupp (2000) and Dale & Frank (2014). We established two transects of 9.1 m (30 ft), each centered on the focal tree, with one parallel to the street and one perpendicular. We divided each transect into 10 equal segments (0.9 m each), and assessed each segment for the presence or absence of vegetation in five vertical strata: turf; herbaceous vegetation and forbs; shrubs; understory trees; and overstory trees (excluding the focal tree). We computed the VCI as the total number of occupied segments, with a maximum value of 100 (2 transects × 10 segments each × 5 strata per segment). Within each city, we used simple linear regression to determine whether temperature was independent of VCI.

Arthropod sampling and identification

To sample arthropods, we placed a 7.6 × 12.7 cm yellow sticky card (Olson Products, OH, USA) in each tree. Yellow sticky cards capture a variety of herbivorous, predatory, and parasitic arthropods and provide a snapshot of arthropod diversity at a site. In each city, cards were installed over the course of 2–3 days and left in place for 6 days in Raleigh and 5 days in all other cities. To select comparable summer sampling dates across the latitudinal gradient, we identified a logistically feasible start date at the lowest latitude and used data from two weather stations per city to predict when each would reach the same number of degree-days in the summer of 2012, using the degree-day calculator at <http://uspest.org/wea/> with single-sine model and base temperature of 10 °C. We planned our sampling trips accordingly, and Raleigh was sampled July 16–24; Baltimore July 29–August 5; Queens August 25–September 1; and Boston September 8–14, such that each had experienced ~2500 degree-days at the time of sampling. This approach ensured that arthropod populations experienced similar thermal accumulation for growth and development prior to sampling in each city.

All arthropods were identified to family according to Goulet & Huber (1993) and Triplehorn & Johnson (2004); parasitoid wasps were identified to morphospecies. Previous studies have shown that the largest share of variation in insect thermal tolerance (critical thermal maximum and minimum; upper and lower lethal temperatures) partitions at the level genus or family, but not species (Addo-Bediako *et al.*, 2000; Chown *et al.*, 2002). Thus, families are reasonable sampling units for our questions; see also Text S2 and Table S1.

Data analysis

To test our prediction that families would have heterogeneous responses to warming in midlatitude cities but consistent responses in high-latitude cities, we adapted the bootstrap method of Gotelli *et al.* (2010) to detect thermal trends in community composition, as described by Pelini *et al.* (2014). We analyzed each city separately. Briefly, in the R 3.0.0 computing environment for Windows (R Core Team, 2013), we $\ln(x + 1)$ transformed the family counts and fit a separate simple linear trendline to each family's abundance relative to the extent of urban warming across sites, then calculated the variance in slopes of these trendlines among families. We used a bootstrap test with 1000 randomizations of the data to determine whether this variance was greater than expected due to random sampling of the entire assemblage pooled across sites, given the observed number of individuals per sample. This method can also account for bias due to incomplete sampling by incorporating undetected taxa into the analysis. This alternate version of the test is also described by Gotelli *et al.* (2010). Briefly, we used the Chao2 richness estimator (Chao, 1984) to determine the number of undetected families in each city's assemblage, assigned each undetected family a total abundance half that of the least common detected family in the same city, and included these additional taxa in the pooled community that was used to generate the null distribution of slopes.

While the bootstrap test explicitly tests heterogeneity among families – that is, whether families' responses to warming vary more than expected by chance – we used a complementary method to simultaneously estimate trends in abundance relative to urban warming for each family and for the entire arthropod assemblage. To compute these estimates and determine which responses were significantly different from zero, we adapted the hierarchical model of Gotelli *et al.* (2010) and analyzed each city separately. In this model, the relation between arthropod counts and warming is modeled with Poisson error, and each family's response to warming (comparable to a Poisson regression coefficient) is modeled as a member of a normally distributed population of such responses. As described by Gotelli *et al.* (2010), we fit this model using a Bayesian analysis with Markov chain Monte Carlo algorithms in WINBUGS v. 1.4.3 software (Lunn *et al.*, 2000). We excluded taxa that occurred at fewer than five sites (this includes all the undetected taxa), assumed uninformative prior distributions, and fit the model using five Markov chain simulations, each independently initialized and computed for 21 000 draws. After discarding the first 1000 draws from each

chain as burn-in, we checked for convergence by inspecting, for each parameter, time series plots of the Gelman–Rubin statistic (values <1.1 indicate convergence) and of the five chains themselves (Kéry, 2010). We thinned the sample by keeping every fifth draw for a final sample of 20 000 draws, which we used to compute estimates and 95% credible intervals for the family and whole-assemblage responses to warming. 'Responses' are comparable to Poisson regression coefficients and represent change in abundance per °C of warming.

To explicitly test our prediction that the magnitude of family responses would be greater in midlatitude cities than high-latitude cities, we took the absolute values of the responses estimated above and tested whether response magnitude was independent of city using a permutation test, with asymptotically estimated null distribution, in the R package 'coin' (Hothorn *et al.*, 2006; R Core Team, 2013). For post hoc, pairwise comparisons between cities, we used a pairwise permutation test function (available at rcompanion.org) within coin and corrected *P*-values for false discovery rate according to Benjamini & Hochberg (1995).

Finally, to determine whether the changes in abundance of each family led to overall changes in diversity across each warming gradient, we computed three diversity measures for each site: family density [number of families observed per sample (Gotelli & Colwell, 2001)]; family richness [number of families per sample after rarefaction or extrapolation (at 18 sites) to a shared sample size of 25 individuals, computed in ESTIMATES v. 9.1.0 (Colwell *et al.*, 2012; Colwell, 2013)]; and PIE [probability of interfamily encounter, calculated according to Hurlbert (1971)]. We used simple linear regressions to test for changes in arthropod diversity with warming, and performed separate analyses for each measure in each city using JMP Pro v. 10.0.0 (SAS Institute, Cary, NC, USA).

Results

We captured and identified a total of 6746 individual arthropods in 34 families from 111 street trees, with 10–296 individuals and 4–19 families collected per tree (Table 2). Rarefaction curves indicated that family-level richness was greatest in the lowest latitude city (Raleigh) and similar in the other three cities (Fig. S6). Seventeen of the original 128 sites were excluded due to loss or failure of iButtons or sticky cards or due to anomalous temperature readings (e.g., Fig. S2). Site temperatures recorded by iButtons demonstrate dampened seasonal temperature fluctuations in midlatitude sites relative to high-latitude sites (Fig. 2, Fig. S4). With the exception of summer 2013, temperatures also tended to be warmer at lower latitudes, consistent with the long-term climate patterns recorded at weather stations near each city (Table 1, Fig. S3). Within each city, our sampling captured within-city summer warming gradients of 1.7–3.4 °C (Table 2), and these within-city temperature differences are comparable to the

Table 2 Summary of arthropod samples collected

City	Sites excluded	Sites used	Total arthropods	Total families	Warming gradient (°C)
Boston	2	30	1274	27	2.3
Queens	3	29	2214	25	2.1
Baltimore	7	25	1507	25	3.4
Raleigh	5	27	1751	32	1.7
Total	17	111	6746	34	

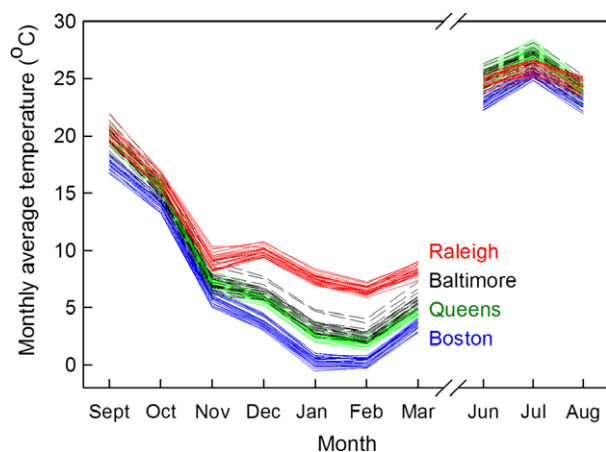


Fig. 2 Mean monthly temperatures recorded in 111 red maple street tree canopies from September 2012 to August 2013. Each line represents one site. Results demonstrate the latitudinal difference in seasonal temperature variation between cities, and the extent of urban warming within cities. Note the break in the X-axis when iButtons were not recording in all cities in April–May 2013.

magnitude of global warming expected to affect each city before the end of the century (Tables 1 and 2). In three of the four cities, temperature was independent of local vegetation complexity; in Queens, however, hotter sites were also less vegetated (Table 3).

We predicted that response to warming would vary more among taxa at midlatitudes than high latitudes (Fig. 1), and the bootstrap test for heterogeneity supported this component of our predictions. Family responses to warming were more heterogeneous than expected by chance in the two midlatitude cities (bootstrap test, Raleigh $P < 0.001$;

Table 3 Summary of regressions testing independence of vegetation complexity and temperature in each city

City	β	r^2	F	P
Boston	-0.01	0.02	0.53	0.47
Queens	-0.06	0.51	27.82	<0.0001
Baltimore	-0.04	0.13	3.39	0.08
Raleigh	0.00	0.01	0.21	0.65

Baltimore $P < 0.001$). In contrast, family assemblages in the two high-latitude cities demonstrated relatively coherent responses, with nonsignificant tests for heterogeneity indicating that the relative abundance of families did not change across the warming gradient (Queens $P = 0.945$, Boston $P = 0.122$). The Chao2 richness estimator suggested that we failed to detect one family in Raleigh and five families in Queens, but inclusion of undetected families in the null model did not alter the results of the heterogeneity test (Raleigh, $P < 0.001$, and Queens, $P = 0.915$). Mid-latitude heterogeneity was also apparent in the family response estimates obtained using the hierarchical model (Fig. 3a, Table 4, Table S2).

In three of the four cities, the hierarchical models were consistent with the prediction that the assemblage-wide average response to warming would be more positive with increasing latitude. In the two midlatitude cities, the assemblage-wide mean response to warming was not statistically different from zero, with a slight negative trend in Raleigh and a slight positive trend in Baltimore (Fig. 3b). Queens interrupted this pattern with an overall negative response to warming; in Boston, the highest latitude city, overall response to warming was positive (Fig. 3b). In each city, the number of significantly responding taxa made up 31–47% of the families analyzed (Table 4). The midlatitude responses centered near zero reflected similar numbers of increasing and decreasing families: In Raleigh, we identified seven families whose abundance declined significantly with warming, and five that increased. In Baltimore, four declined and four increased. In Queens, five declined and none increased. In Boston, five increased and none declined (Fig 3a, Table 4). This effect was not simply due to the disappearance of strongly or negatively responding families at the highest latitude; rather, families with divergent responses at midlatitudes converged on similar responses at high latitudes (Fig. 4). Further, increasing and declining taxa included multiple arthropod trophic groups, with herbivores, predators, and parasitoids each represented by some increasing and some declining taxa (Table 4).

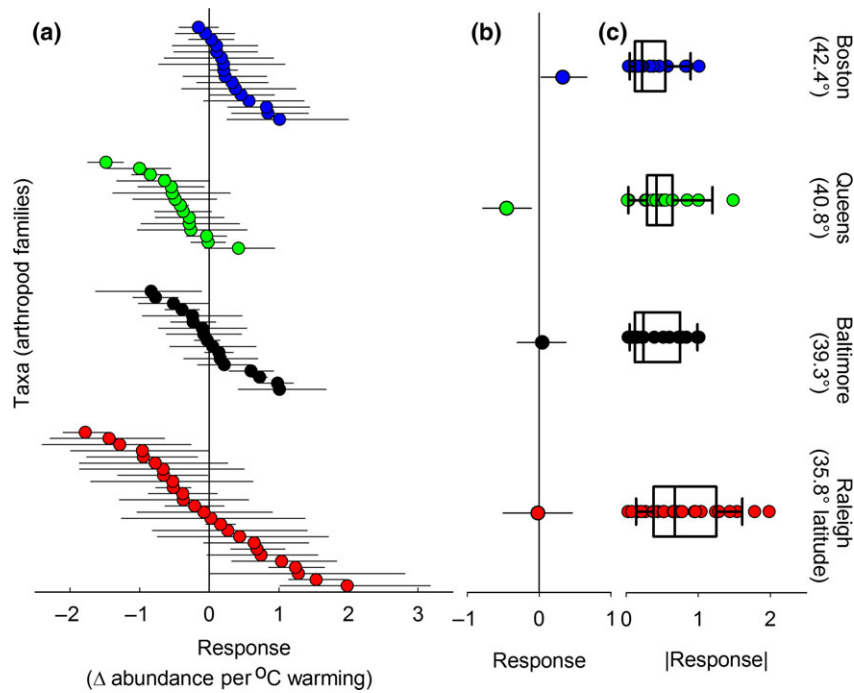


Fig. 3 Arthropod responses to urban warming in cities in the eastern U.S. Panels show (a) responses of individual families in each city, illustrating greater heterogeneity at midlatitudes compared to high latitudes; (b) assemblage-wide average responses, illustrating zero-centered responses at midlatitudes, and (c) absolute magnitudes of family responses, with the largest responses at the lowest latitude. See Table 4 for identities of taxa with nonzero responses. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 4 Summary of taxa whose abundance declined or increased significantly with warming in each city, corresponding to Fig. 3, read top to bottom; within each column, taxa are ordered from most negative to most positive response, and each family's trophic group* is coded in parentheses

	Boston	Queens	Baltimore	Raleigh
Declined		Coccidae (h) Ichneumonidae (pt) Ceraphronidae (pt) Mymaridae (pt) Aleyrodidae (h)	Eulophidae (pt) Aphididae (h) Ceraphronidae (pt) Ichneumonidae (pt)	Thripidae (h) Ceraphronidae (pt) Diapriidae (pt) Entomobryidae (d) Bethyidae (pt) Coccinellidae (p) Signiphoridae (pt)
Increased	Ceraphronidae (pt) Coccinellidae (p) Encyrtidae (pt) Aphididae (h) Dolichopodidae (p)		Scelionidae (pt) Aleyrodidae (h) Encyrtidae (pt) Formicidae (v)	Aphelinidae (pt) Formicidae (v) Cicadellidae (h) Scelionidae (pt) Eulophidae (pt)
% of families responding†	31% (5 of 16)	33% (5 of 15)	47% (8 of 17)	46% (12 of 26)

*Trophic groups include detritivores (d), herbivores (h), parasitoids (pt), predators (p), and taxa too variable to assign (v).

†Of all the families for which responses were estimated, this is the percentage with significantly nonzero responses to warming.

Although we did not measure summer 2012 site temperatures directly, estimated site temperatures (Text S1, Fig. S4) suggest that the three lowest latitude cities experienced broadly overlapping summer temperatures, while the highest latitude city, Boston, was much

cooler. These estimates contrast with the weather station data themselves, which arrayed in order of decreasing temperature with increasing latitude (Fig. 4). Despite the differences in 2012 and 2013 summer temperatures, fitting the hierarchical model to

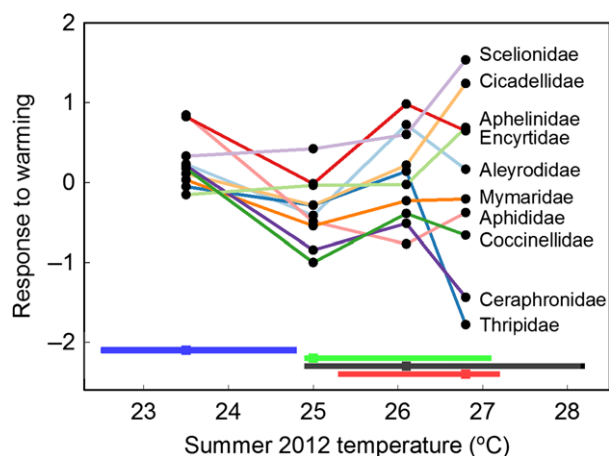


Fig. 4 Family responses converged as latitude increased and temperature decreased. This alternate visualization of the results in Fig. 3a highlights changes across cities in the response to urban warming in the 10 most common families (families that had the highest average abundance across all cities, and occurred in at least 5 sites per city). Here, family responses in each city are plotted relative to average summer 2012 temperature at the nearest airport weather station, such that cities are arrayed from lowest latitude on the left to highest latitude on the right. The horizontal bars along the X-axis indicate the range of estimated 2012 site temperatures in each city; from top to bottom the bars represent Boston (blue), Queens (green), Baltimore (black), and Raleigh (red). The tick in each bar indicates the temperature of the corresponding weather station during the same time period.

estimated 2012 warming extents did not qualitatively alter the results (Fig. S7).

Finally, we tested the prediction that the magnitude of family responses would be greater in midlatitude cities. The permutation test indicated that response magnitude did vary among cities ($P < 0.01$). Magnitudes were largest in the lowest latitude city, Raleigh; in order from lowest to highest latitude, median response magnitudes were 0.68, 0.24, 0.42, and 0.22. In other words, at the lowest latitude, families experienced greater changes in abundance per °C than in Baltimore (adjusted $P < 0.05$) or Boston (adjusted $P < 0.05$), but were nonsignificantly greater than in Queens (adjusted $P = 0.15$). No other pairs of cities differed in magnitude of family responses (Fig. 3c).

The observed changes in family-level abundances and response magnitudes did not lead to strong overall patterns in diversity. Extent of warming was, in general, a poor predictor of total arthropod abundance or family-level density, richness, or PIE, with universally low r^2 values and few statistically significant relationships (Table 5). Specifically, significant relationships were evident only in Baltimore and Queens. In Baltimore, family richness (but not family density or PIE)

Table 5 Results of regressions testing for effects of warming on arthropod diversity measures in each city

City	β	r^2	F	P
<i>Family density</i>				
Boston	1.50	0.08	2.37	0.14
Queens	-2.16	0.15	4.85	0.04
Baltimore	-0.52	0.03	0.65	0.65
Raleigh	0.53	0.01	0.22	0.64
<i>Family richness, rarefied to 25 individuals</i>				
Boston	0.78	0.03	0.88	0.36
Queens	0.14	0.00	0.04	0.84
Baltimore	-0.90	0.17	4.79	0.04
Raleigh	-0.44	0.01	0.27	0.61
<i>Probability of interfamily encounter</i>				
Boston	0.00	0.00	0.00	0.94
Queens	0.13	0.13	3.98	0.06
Baltimore	-0.05	0.11	3.06	0.09
Raleigh	-0.03	0.02	0.51	0.48

Uncorrected P -values < 0.05 are bold.

declined with warming, indicating that more individuals had to be (and were) sampled at hotter sites to observe as many families. In Queens, family density (but not richness or PIE) declined with warming, indicating that the decline in number of observed families was due to sampling fewer individuals at hot sites. These isolated effects, however, did not lead to a latitudinal pattern in the effects of warming on diversity.

Discussion

Our results demonstrate that arthropod responses to warming vary geographically, and in three of the four cities we sampled, were largely consistent with known latitudinal patterns of ectotherm physiology relative to regional climate. We measured 'response to warming' as change in abundance per °C urban warming at each of four latitudes. Without knowledge of the taxon-specific thermal physiology of the arthropods we sampled, we correctly predicted assemblage-wide response patterns in three of four temperate cities, based on latitude alone (Deutsch *et al.*, 2008; Kingsolver *et al.*, 2013). Departure from predictions in the fourth and largest city, Queens, may be linked to habitat loss that is correlated with warming in that city, as discussed below.

We expected that arthropods in midlatitude cities would have assemblage-wide responses centered near zero, but would encompass large positive and negative responses; in high-latitude cities, we expected arthropod responses to be small, positive, and more consistent throughout the assemblage (Kingsolver *et al.*, 2013; Chown & Duffy, 2015) (Fig. 1). As predicted, the family responses in midlatitude cities were centered near zero

(reflecting similar numbers of increasing and decreasing families), and in the highest latitude city, responses were overall positive (Fig. 3b). The results from these three cities are consistent with our prediction that mid-latitudes should represent a transition zone between the largely negative responses expected in the tropics and the largely positive or neutral responses predicted at higher latitudes. The heterogeneous, zero-centered effects at midlatitudes may be no less ecologically damaging than universal decline. When interacting species respond oppositely to warming, interactions such as mutualism and biological control will be disrupted (Tylianakis *et al.*, 2008; Meineke *et al.*, 2014). Such trophic effects could be in part responsible for our observed data; once direct physiological effects of warming alter the abundance of some species, those effects could propagate through a community via trophic cascades (Walther, 2010). Indeed, our sampled taxa included multiple trophic groups, most commonly herbivores, and parasitoids. Among the herbivores were potential tree pests such as thrips (Thripidae), whiteflies (Aleyrodidae), and aphids (Aphididae); the parasitoid wasps we sampled are potential biological control agents that regulate populations of other arthropods, including herbivores. Each of these trophic groups (herbivores and parasitoids) included taxa that increased and taxa that declined with warming in the two low-latitude cities. Future work should further investigate the causes and consequences of strong, divergent responses to warming among interacting taxa. The most chaotic transition zones, currently located at midlatitudes in the eastern USA, should move poleward in the future, as continued warming brings arthropods closer to their thermal optima and maxima, even at higher latitudes.

In contrast to the variable responses in the two mid-latitude cities, responses within each of the two high-latitude cities were more consistent. Arthropods in one of these cities (Boston) followed our prediction of widespread, small, positive responses to warming; those in Queens, New York City, did not. In Queens, five arthropod families declined, the assemblage-wide response was significantly negative, and responses were only marginally less steep than those in the lowest latitude city (Fig. 3). This pattern is unlikely to derive directly from heat stress in the warmest sites in Queens, which appears to have experienced summer 2012 temperatures similar to those in the two lower latitude cities, where some taxa did increase with warming (Fig. 4, Fig. S7). Given the premise that arthropod heat tolerance is broadly conserved across latitudes, temperatures in Queens should not have been more devastating than those in the other cities. Instead, aspects of urbanization other than warming – such as habitat loss and

isolation – are more extreme in Queens than in the other three cities and could have contributed to arthropod declines (McKinney, 2008). For example, our vegetation measurements show that the hottest sites in Queens are also the least vegetated, indicating that street trees in these sites are relatively isolated from other trees or from complementary resources (such as nectar or water), potentially negating or modulating the direct effects of warming. Thus, our results in Queens represent the combined effects of warming and habitat loss.

Our predictions took into account the expected broadening of arthropod thermal performance curves at higher latitudes, where stronger seasonal differences favor thermal generalists. At higher latitudes, the rate of fitness (or abundance) change per degree of warming should be slower than at lower latitudes, even over a shared temperature range. This pattern is supported in a comparison of Baltimore and Raleigh. In these two cities, arthropods experienced overlapping summer temperatures, yet the magnitude of arthropod response to warming was smaller in Baltimore than in Raleigh. Where temperatures do not overlap, however, it is impossible to separate the contribution of curve breadth from that of local temperatures, as cooler temperatures map onto shallower tails of thermal performance curves (including those that are otherwise steep; Fig. 1). This situation is exemplified in a comparison of Boston and Raleigh. In Boston, response magnitudes were smaller than in Raleigh, and temperatures were also always cooler. The smaller observed responses to warming in Boston could have resulted from the putatively broader response curves at this high latitude, from cooler temperatures, or both.

Despite the remarkable family and assemblage-wide responses to warming in each city, we did not observe striking shifts in arthropod diversity with urban warming at any latitude (Table 5). Although family richness declined slightly with warming in Baltimore, and family density declined slightly with warming in Queens, warming generally explained small and mostly non-significant amounts of variation in all diversity metrics. It is nevertheless worth noting that the parameter estimates for rarefied species richness and PIE both followed the expected trends among cities – namely, decline with warming at midlatitudes and increase at high latitudes. These effects were not statistically significant in our sample, perhaps because family declines rarely represented complete losses, and because diversity metrics were buffered by the numerous taxa that did not respond significantly to warming. We detected significant responses to warming in 31–47% of the taxa tested, leaving more than half the families in each city potentially stable across the warming gradients

(Table 4). Our results suggest that changes in community composition, rather than diversity or richness per se, may be the main effects of warming on arthropod communities in temperate latitudes in the next several decades.

Few other studies have examined the simultaneous effects of warming on entire animal communities across latitudes. One exception is a long-term forest warming experiment at two sites located near the endpoints of the latitudinal transect we sampled (Pelini *et al.*, 2011b). Work in this system has focused on ants and has consistently found striking and heterogeneous effects of warming on community composition and species abundances at the midlatitude site, and weaker effects at the high-latitude site (Pelini *et al.*, 2011a, 2014; Diamond *et al.*, 2012a; Stuble *et al.*, 2013). These results are similar to ours and support the pattern of midlatitude heterogeneity. In the experimental forest system, species-specific thermal tolerances are also known, and appear to be good predictors of positive and negative responses to warming at the midlatitude site (Diamond *et al.*, 2012a; Stuble *et al.*, 2013) [at least in some years, but see (Pelini *et al.*, 2014)]. Our results extend the findings of this experimental work by demonstrating that similar patterns occur across more diverse arthropod assemblages whose thermal tolerances are not explicitly known.

Inevitably, the cities in this study vary in more attributes than their latitude. Land area, population density, canopy cover, urban growth rates, and other characteristics all vary between cities (e.g., Table 1). By assessing effects of warming within each urban area separately, we effectively 'factor out' the effects of each city's unique qualities on its baseline arthropod populations and ask how those populations respond to warming within each city. But as our results in Queens suggest, other aspects of the urban environment may override or modulate the effects of warming, such that further tests in additional cities would be desirable. Extending urban latitudinal gradients into the tropics is likely to be particularly fruitful in testing the full range of predictions outlined in Fig. 1. Few studies have yet taken advantage of urban study systems for such questions, with a pair of notable exceptions that have documented increased thermal tolerance among urban ants (Angilletta *et al.*, 2007) and have developed predictions for the effects of urban warming on insect species (Chown & Duffy, 2015).

Although thermal tolerance is one factor among many – including behavioral changes and species interactions – that shape species' responses to warming, our results are largely consistent with the patterns expected if physiology is one of the underlying factors. Exceptions to the expected patterns, as in Queens, are

themselves potentially informative in developing hypotheses about how other environmental factors interact with the physiological effects of warming to shape arthropod populations. To the extent that future warming is coupled with habitat loss, more species may decline than predicted by physiology alone. Nonetheless, we show that a remarkably simple model, based on previously documented geographic variation in ectotherms' thermal safety margins, captures broad patterns of arthropod responses to urban warming.

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Supporting Information

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

Figure S1. Landsat thermal images of each city.

Figure S2. Extents of warming in 2012 and 2013.

Figure S3. Latitudinal variation in summer climate in the sampled cities.

Text S1. Details of predicted 2012 site temperatures.

Figure S4. Mean monthly site temperatures, including predicted temperatures.

Figure S5. Comparison of iButton-measured and predicted site temperatures.

Text S2. Phylogenetic signal in response to warming.

Table S1. Phylogenetic signal in response to warming.

Figure S6. Sample-based rarefaction curves for each city.

Table S2. Family responses to warming in each city.

Figure S7. Hierarchical model results based on predicted 2012 site temperatures.