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Community ecology

Physiological thermal limits predict differential responses of bees to urban heat-island effects

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Changes in community composition are an important, but hard to predict, effect of climate change. Here, we use a wild-bee study system to test the ability of critical thermal maxima (CT_{max}, a measure of heat tolerance) to predict community responses to urban heat-island effects in Raleigh, NC, USA. Among 15 focal species, CT_{max} ranged from 44.6 to 51.3°C, and was strongly predictive of population responses to urban warming across 18 study sites ($r^2 = 0.44$). Species with low CT_{max} declined the most. After phylogenetic correction, solitary species and cavity-nesting species (bumblebees) had the lowest CT_{max}, suggesting that these groups may be most sensitive to climate change. Community responses to urban and global warming will likely retain strong physiological signal, even after decades of warming during which time lags and interspecific interactions could modulate direct effects of temperature.

1. Introduction

Abundance and geographical ranges of many species have already responded to recent climate change, and these shifts are thought to arise in part from mismatches between environmental temperatures and organisms' physiological tolerances [1,2]. Accordingly, physiological traits such as CT_{max}, a measure of heat tolerance, are promising predictors of species' sensitivity to environmental warming, particularly for ectotherms [3–5]. *In situ* changes in community composition are a common effect of warming (e.g. [6,7]), but physiological traits are generally used to explain the distribution and ecology of individual species, or of many species at coarse, global scales [4,5]. Physiological traits have rarely been used to predict community-wide changes, and only in response to short-term warming [3]. In the longer term, direct responses to warming may be complicated by time lags and biotic interactions [8,9], and it remains unclear whether to expect a strong physiological signal in species' relative responses to warming within a given locality.

Here, we address this question using a wild-bee study system. As pollinators, bees provide an essential ecosystem service whose magnitude depends on community composition [10]. Historical data indicate that bee community composition and species distributions are shifting with climate change [11,12], making bees a timely subject for studies of thermal tolerance. We present phylogenetic and ecological correlates of bee thermal tolerance, and a field study using variation in urban heat-island intensity to test the prediction that species with lower CT_{max} are those whose populations decline the most with warming.

Table 1. Parameter estimates and statistical tests for best-fitting models describing the relationship between CT_{max} and life-history traits, and between CT_{max} and population response to warming. (Social and cavity-nesting are the baseline conditions to which others are compared; *p*-values <0.05 are bold.)

model	term	coefficient	s.e.	*t*	*p*-value
$CT_{max} \sim$ body size + sociality + nesting	intercept	45.37	1.02	44.5	**0.000**
	body size	−0.14	0.25	−0.6	0.574
	nest (ground)	2.43	0.59	4.1	**0.002**
	nest (stem)	2.20	0.77	2.9	**0.017**
	sociality (solitary)	−3.13	0.35	−8.9	**0.000**
response to warming $\sim CT_{max}$	intercept	−5.98	1.68	−3.6	**0.004**
	CT_{max}	0.11	0.036	3.2	**0.007**

2. Material and methods

For additional details of all methods and analyses, see the electronic supplementary material.

(a) Physiological tolerance

We measured CT_{max} for 15 common bee species (*Agapostemon virescens; Lasioglossum bruneri; Bombus bimaculatus; Megachile campanulae; Bombus griseocollis; Lasioglossum imitatum; Bombus impatiens; Megachile exilis; Halictus ligatus/poeyi; Megachile mendica; Ptilothrix bombiformis; Ceratina calcarata; Megachile rotundata; Xylocopa virginica; Ceratina strenua*) collected in urban habitats near our laboratory in Raleigh, NC, USA (35.8° N, 78.68° W). We placed bees individually in 45 ml glass vials, which we heated 0.5°C min^{-1} in a water bath. We monitored bees every minute and recorded CT_{max} as the point when postural control was lost [13,14]. All assays were performed from May through August 2014–2015. We pinned and identified tested bees and measured intertegular distance (a proxy for body size) [15]. We categorized each species by social behaviour (social, solitary) and nesting habitat (ground, cavity, stem/wood) using the literature and expert opinion.

(b) Response to warming in the field

We sampled bees at 18 sites (15 residential yards, three parks) that varied in urban heat-island intensity in and around Raleigh. Urban warming generates a temporally stable mosaic of hotter and cooler locations that typically differ by 1–3°C in air temperature [16]. To document heat-island intensity at each site, we installed iButton data loggers (DS1921, Maxim Integrated, San Jose, CA, USA) that recorded temperature hourly from 9 May to 19 July 2015. For analysis, we used mean early-evening temperatures (19.00–21.00) because solar radiation affected daytime air-temperature measurements [17]. We sampled bee communities at each site 11 times over two summers (May–August 2014–2015) using pan traps, vane traps and aerial netting. Hereafter, 'bee abundance' refers to the total number of bees collected per species per site.

(c) Data analysis

We characterized each species' response to urban warming as a Poisson regression coefficient describing a loglinear relationship between bee abundance and site temperature. To estimate coefficients for all species jointly, thereby stabilizing estimates for rare species, we fit a hierarchical model in WinBUGS v. 1.4 [18] (see the electronic supplementary material).

Because related species may not be statistically independent, we conducted analyses in a phylogenetic framework. We constructed a maximum-likelihood tree of the 15 species using 10 genes. We then constructed a series of phylogenetic generalized least-squares models to test two hypotheses: (i) CT_{max} depends on body size, sociality and nesting habitat, and (ii) species' response to urban warming depends on CT_{max}. For each hypothesis, we constructed four models that differed only in their phylogenetic covariance structures: none, Brownian motion, Pagel's λ and Ornstein–Uhlenbeck. We present the results of the best-fitting models, as determined by Akaike information criterion adjusted for small sample size (AICc). We also examined phylogenetic signal within CT_{max} by comparing four models of evolution to a phylogenetically independent (white noise) model. Analyses required R (v. 3.1.1) packages ape v. 4.1, geiger v. 2.0.6, nlme v. 3.1 and MuMIn v. 1.15.6 [19–23].

3. Results

Species' critical thermal maxima (CT_{max}) ranged from 44.6 to 51.3°C ($n = 3$–32 per species). We did not detect strong phylogenetic signal in CT_{max} (see the electronic supplementary material). CT_{max} covaried with life-history traits but not with body size (table 1). Cavity-nesting species had low heat tolerance, with fitted mean CT_{max} about 2°C lower than that of stem/wood-nesting or ground-nesting bees after controlling for body size and sociality (figure 1*a*). For solitary bees, fitted mean CT_{max} was about 3°C lower than for social species (figure 1*b*). The best-fitting model incorporated phylogenetic signal using Pagel's λ correction, with $\lambda = -6.35$ (95% CI: −6.58, −6.12), indicating negative phylogenetic correlation in model residuals.

CT_{max}, in turn, was a strong predictor of population response to urban warming: species with the lowest CT_{max} were those whose populations declined the most (table 1 and figure 2). The best-fitting model did not incorporate the phylogeny. We refit it with ordinary least squares to determine that $r^2 = 0.44$. The result that species declined at different rates implies that community composition also shifted with warming; see the electronic supplementary material for an explicit test of compositional change.

4. Discussion

We show that interspecific variation in CT_{max}, a measure of physiological heat tolerance, corresponds to community change across steep, local temperature gradients imposed by urban warming. Although urban warming is an imperfect proxy for climate change, it provides a unique opportunity to test predictions about biological effects of long-term warming

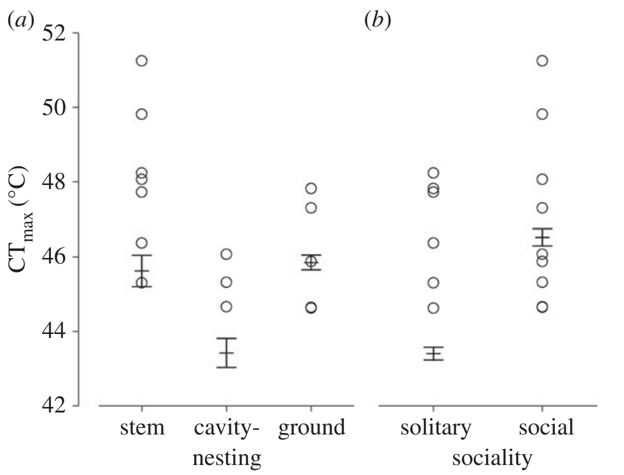

Figure 1. Bee CT_{max} as it relates to (*a*) nesting habitat and (*b*) sociality. Circles are data (one point per species); whiskers are fitted means ± s.e. from the phylogenetic model, with body size held constant.

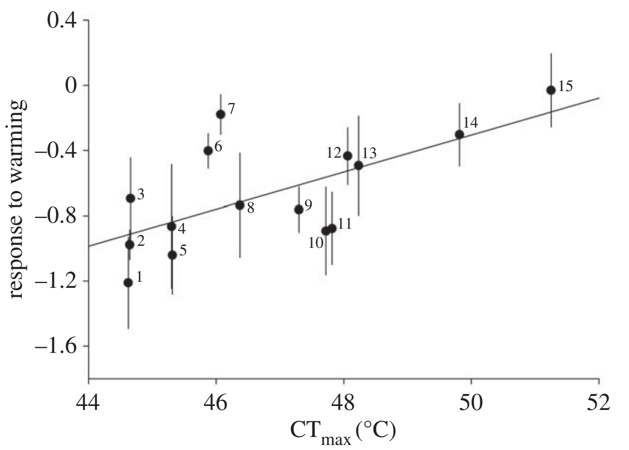

Figure 2. CT_{max} predicts species' responses to warming in the field. Points are species; 'response to warming' is a Poisson coefficient (± s.e.) describing change in species' abundance per degree Celsius urban warming. Species are: 1, *Agapostemon virescens*; 2, *Lasioglossum bruneri*; 3, *Bombus bimaculatus*; 4, *Megachile campanulae*; 5, *Bombus griseocollis*; 6, *Lasioglossum imitatum*; 7, *Bombus impatiens*; 8, *Megachile exilis*; 9, *Halictus ligatus/poeyi*; 10, *Megachile mendica*; 11, *Ptilothrix bombiformis*; 12, *Ceratina calcarata*; 13, *Megachile rotundata*; 14, *Xylocopa virginica*; 15, *Ceratina strenua*.

at temperatures that correspond to those predicted regionally by the end of the century [24,25]. The relationship between CT_{max} and response to urban warming also suggests a process for community assembly in urban ecosystems. While previous studies have suggested global, latitudinal patterns in ectotherm tolerance to urban warming [26], our results extend the predictive power of CT_{max} to species' relative responses to warming within local communities.

CT_{max} may predict which species are at greatest risk from future warming. We show that bees that nest in pre-existing cavities, such as rodent burrows, had the lowest thermal tolerance. All cavity-nesters in our dataset were bumblebees, a group known to be experiencing climate-related range contractions [11]. We thus corroborate the global pattern of bumblebee heat sensitivity at local and organismal scales. Despite bumblebees' membership in the 'social' category, social bees were overall more heat tolerant than solitary bees, suggesting that solitary life history may predict climate sensitivity.

Our results strongly suggest that species' physiology shapes community composition, even after decades of warming during which time lags and interspecific interactions could modulate direct effects of temperature. Although major reviews have compiled heat tolerance data for hundreds of ectotherms (e.g. [4]), CT_{max} has rarely been measured for bees (but see [27]), and most ecological communities remain poorly represented. Filling this data gap will be an important step towards improved predictions of species composition in urban and future climates.

Ethics. We used standard protocols for field collection and thermal tolerance assays, and minimized handling time and stress of individuals. Ethics committee approval was not required. Permissions to conduct fieldwork were granted by NC State University, City of Raleigh Department of Parks, Recreation and Cultural Resources and volunteer homeowners.

Data accessibility. Files for bee abundance, site temperatures, CT_{max} and 10-gene alignment are available from Dryad: http://dx.doi.org/10.5061/dryad.34dk0 [28].

Authors' contributions. A.L.H. and S.D.F. designed the study, A.L.H. collected data, M.M.L.-U. and E.Y. analysed data, E.Y. drafted the manuscript, all authors revised and approved the manuscript and are accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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