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 (CTmax, a measure of heat tolerance) to predict community responses to urban heat-island effects in Raleigh, NC, USA. Among 15 focal species, CTmax 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 CTmax declined the most. After phylogenetic correction, solitary species and cavity-nesting species (bumblebees) had the lowest CTmax, 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 CTmax, 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 CTmax are those whose populations decline the most with warming.
We placed bees individually in 45 ml glass vials, which we near our laboratory in Raleigh, NC, USA (35.8 Xylocopa virginica; Ceratina strenua; impatiens; Megachile exilis; Halictus ligatus/poeyi; Megachile mendica; campanulae; Bombus griseocollis; Lasioglossum imitatum; Bombus virides; Lasioglossum bruneri; Bombus bimaculatus; Megachile

categorized each species by social behaviour (social, solitary) measured intertegular distance (a proxy for body size) \[15\]. We conducted analyses in a phylogenetic framework. We constructed a maximum-likelihood tree of the 15 species using 10

test predictions about biological effects of long-term warming

We measured \(C_{\text{max}}\) for 15 common bee species (Agapostemon virescens; Lasiglossum bruneri; Bombus trimaculatus; Megachile campanulae; Bombus griseocollis; Lasiglossum immaculatus; Bombus impatiens; Megachile exilis; Halictus ligatus/poeyi; Megachile mendica; Pilobombix bombiformis; Ceratina calcara; Megachile rotundata; Xylocopa virginica; Ceratina strenua) collected in urban habitats near our laboratory in Raleigh, NC, USA (35.8° N, 78.68° W).

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).

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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) \(C_{\text{max}}\) depends on body size, sociality and nesting habitat, and (ii) species’ response to urban warming depends on \(C_{\text{max}}\). For each hypothesis, we constructed four models that differed only in their phylogenetic covariance structures: none, Brownian motion, Pagel’s \(\lambda\) 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 \(C_{\text{max}}\) 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].
at temperatures that correspond to those predicted regionally by the end of the century [24,25]. The relationship between CTmax 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 CTmax to species’ relative responses to warming within local communities.

CTmax 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]), CTmax 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 home owners.

Data accessibility. Files for bee abundance, site temperatures, CTmax and 10-gene alignment are available from Dryad: http://dx.doi.org/10.5061/dryad.34d4k0 [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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