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SYMPOSIUM

Physiology Evolves Convergently but Lags Behind Warming in Cities

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Synopsis Cities, through the generation of urban heat islands, provide a venue for exploring contemporary convergent evolution to climatic warming. We quantified how repeatable the evolution of heat tolerance, cold tolerance, and body size was among diverse lineages in response to urban heat islands. Our study revealed significant shifts toward higher heat tolerance and diminished cold tolerance among urban populations. We further found that the magnitude of trait divergence was significantly and positively associated with the magnitude of the urban heat island, suggesting that temperature played a major role in the observed divergence in thermal tolerance. Despite these trends, the magnitude of trait responses lagged behind environmental warming. Heat tolerance responses exhibited a deficit of 0.84°C for every 1°C increase in warming, suggesting limits on adaptive evolution and consequent adaptational lags. Other moderators were predictive of greater divergence in heat tolerance, including lower baseline tolerance and greater divergence in body size. Although terrestrial species did not exhibit systematic shifts toward larger or smaller body size, aquatic species exhibited significant shifts toward smaller body size in urban habitats. Our study demonstrates how cities can be used to address long-standing questions in evolutionary biology regarding the repeatability of evolution. Importantly, this work also shows how cities can be used as forecasting tools by quantifying adaptational lags and by developing trait-based associations with responses to contemporary warming.

Introduction

Whether shared selection pressures lead to the same evolutionary response among different lineages is a long-standing question in evolutionary biology (Losos 2011). This question has taken on new relevance under recent climate change, with evidence in support of repeatable, rapid evolution of climate-relevant traits among a number of species, but also in support of limits on evolutionary change (Martin et al. 2023). Yet, our inferences remain fairly limited, despite the importance of understanding the forces that shape and constrain rapid evolution of climate-relevant traits for making conservation and land-management decisions (Thompson et al. 2023). In particular, while there is now widespread evidence of contemporary evolution, the majority of these studies focus on nonclimatic agents of selection such as antibiotics or pesticides (Reznick et al. 2019). Similarly, there are abundant data on climatic niche evolution; however, most studies on this topic focus on changes over historical, geological time scales (Bennett et al. 2021), rather than contemporary time scales. What is needed is a body of work focused on contemporary evolution of climate-relevant traits. Cities, through the rapid spatio-temporal generation of urban heat islands, provide an ecologically relevant venue for exploring contemporary evolution to climatic warming (Diamond and Martin 2021a).

Already, there is evidence of repeatability in evolutionary responses to urbanization. An informal vote-counting meta-analysis revealed evidence of parallel evolution in cities (Santangelo et al. 2020). Here, parallel evolution describes the evolution of similar phenotypes or genotypes among multiple independent populations in response to urbanization from similar initial conditions (sensu Bolnick et al. 2018). For example, this would involve evolutionary responses to different

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urbanization gradients within the same species. When focusing specifically on adaptive evolution, 9 out of 9 species exhibited some degree of parallelism, ranging from 67 to 100% similar responses across multiple urbanization gradients for a given species. These patterns were taxonomically widespread, as this analysis included arthropods (Diamond et al. 2018; Saavedra-Rodriguez et al. 2018; Theodorou et al. 2018), birds (Mueller et al. 2013), fresh and saltwater fishes (Reid et al. 2016; Kern and Langerhans 2018), lizards (Winchell et al. 2016), and plants (Thompson et al. 2016; Yakub and Tiffin 2017). Work published since this synthesis has lent further support for parallelism in adaptive evolution across cities, for example, in the timing of the induction of seasonal diapause in butterflies and moths (Merckx et al. 2021).

These studies of parallel evolution across cities comprise a range of different organismal traits and agents of selection, including tolerance of pollution, morphological alterations to cope with habitat structural modifications, and changes in body shape to cope with altered hydrology. Yet, few of these studies are focused on the evolution of climate-relevant traits. In fact, the majority of studies on the evolution of climate-relevant traits in cities involve responses of one or more species within a single city rather than the responses of a single species across multiple cities (Diamond and Martin 2020). These studies can be harnessed to address the repeatability of evolution of climate-relevant traits in cities using a different approach that explores the potential for convergent evolution among different species. Here, convergent evolution describes the evolution of similar phenotypes or genotypes among multiple independent populations in response to urbanization from different initial conditions (Bolnick et al. 2018). For example, this would involve evolutionary responses to urbanization among different species across one or more urban gradients. In support of contemporary convergent evolution of climate-relevant traits in cities, a recent formal meta-analysis of the evolution of heat and cold tolerance traits in response to urbanization detected significant gains in heat tolerance and losses in cold tolerance among a diverse group of ectothermic species (Diamond and Martin 2021b). Since this meta-analysis, several additional studies with comparable types of data have been published (Pagliaro and Knouft 2020; Campbell-Staton et al. 2021; Nelson et al. 2021; Brans et al. 2022; Sato and Takahashi 2022; Yilmaz et al. 2022; Diamond et al. 2022a; Lenard 2023; Harris et al. 2024), allowing for a larger-scale synthesis of convergent evolution of thermal tolerance in cities.

Here, we used these new data to update our estimates of contemporary convergent evolution to climatic warming in cities and explore how moderators might influence the magnitude and direction of trait responses. We began by examining the repeatability of trait differences in heat tolerance, cold tolerance, and body size between urban and rural populations across different species. We considered data from common garden studies where the genetic basis of evolutionary divergence can be established and data from comparisons among wild-caught organisms where only phenotypic divergence can be established. In the latter instance, differences between urban and rural populations could arise from genetic divergence, phenotypic plasticity, or a combination of both mechanisms. We next examined how moderators might influence trait responses. We expected the magnitude of trait divergence between urban and rural populations to be positively related to the magnitude of climatic change across the urbanization gradient, i.e., the urban heat island (Diamond and Martin 2021b). Further, such variation in the magnitude of the urban heat island allowed us to explore potential lags in the ability to keep pace with increasing climatic warming. Recognizing that many factors might contribute to the ability of populations to keep pace with climatic warming (Martin et al. 2023), we nonetheless asked whether the lag, or the difference between divergence in tolerance and the urban heat island, was nonzero overall, and whether the lag changed with increasing amounts of warming. In addition to variation in the magnitude of the urban heat island, our synthesis generated substantial variation in baseline tolerance, allowing us to explore whether species with lower baseline tolerance were more labile in their ability to shift in response to urban warming (Diamond et al. 2015; and see arguments in Heerwaarden and Kellermann 2020).

In drawing comparisons among the different trait types, we expected that population divergence in body size would be less repeatable compared with thermal tolerance given that size is a component of many other traits, including thermal tolerance (Leiva et al. 2019). Thus, indirect selection on these other traits could diminish the consistency of evolutionary responses of body size to urbanization among different species (Yilmaz et al. 2019; Diamond and Martin 2020). Finally, we examined the association between divergence patterns in heat tolerance and body size. In aquatic systems, we expected that warmer waters would cause oxygen demand to outpace supply, and that evolution of greater heat tolerance in urban environments would be facilitated by the evolution of smaller size to reduce oxygen demand (Leiva et al. 2019). In terrestrial systems, we expected either no relationship or a positive relationship between size and tolerance. In the first case, a more variable role for oxygen limitation in terrestrial habitats coupled with the many indirect factors that potentially shape size could lead to a lack of consistent trend in size divergence between urban and rural populations. Alternatively, large size could lead to greater thermal tolerance via thermal inertia, or slower rates of increases in body temperature in warm environments (Stevenson 1985; Chown and Nicolson 2004).

Methods

Trait database

In this study, we expanded on a dataset of evolutionary and phenotypic divergence of heat and cold tolerance traits. We used the same approaches and search criteria as those used to construct the original dataset (see Diamond and Martin 2021b for details; last search date was 25 February 2024). Here, however, one of our main questions was to assess the ability of populations to keep pace with climatic warming. Because this involved direct comparisons of the magnitude of divergence in thermal tolerance with the magnitude of the urban heat island, we excluded studies from the original dataset that reported time-based metrics such as heat knockdown time and chill coma recovery time. Further, we only considered studies that reported trait values at the species level. Specifically, we excluded studies of community weighted means. In cases where studies contained multiple treatment groups (e.g., temperature acclimation regimes) or subpopulations (e.g., sexes), we reported the urban-rural trait difference for each group.

We attempted to find data on divergence in body size between urban and rural populations for each species in the tolerance dataset. Most studies co-reported tolerance and size information. In other cases, data on divergence in size between urban and rural populations were only available from a different study than the study containing data on divergence in tolerance. In these cases, we ensured congruence between species identity and the urbanization gradient under study. We did not mix genetic and phenotypic data types. Ultimately, six species (out of 22) from four studies (out of 22) in the tolerance dataset lacked corresponding size divergence data.

In most cases, authors provided either relevant summary statistics and their associated SEs or access to their raw data, allowing us to fit models of trait change across the urbanization gradients of interest, and extract estimates of mean trait values and their associated SEs for urban and rural populations. We followed the model specification in each original study, including random effects for sites and other grouping structures. In a subset of cases, we needed to use other data extraction and estimation approaches. Here, we used a combination of: (1) reported test statistics and sample sizes to calculate standardized mean difference values (i.e., using the *fes* function from the *compute.es* package; Del Re 2013); (2) raw data points extracted from figures with the aid of WebPlotDigitizer (Rohatgi 2022) and subsequent linear modeling to estimate means and errors of traits in urban and rural populations; or 3) means and errors extracted from figures with the aid of WebPlotDigitizer (see Supplementary Table S1 for a summary of studies included in the size and tolerance divergence datasets, and details of data extraction). We followed the authors of a given study in the formation of sub-groups for analysis, for example, based on developmental acclimation temperature, sex, or based on different types of measurements on the same organism such as body mass and length. Together, the data comprised urban-rural differences for heat tolerance among 22 species (86 observations from 22 studies), cold tolerance among 7 species (39 observations from 10 studies), and body size among 16 species (69 observations from 13 studies). At the study level, data published since the Diamond and Martin (2021b) meta-analysis, comprise 41% of the 22 studies used in the current analyses.

In general, we were able to extract estimates of the magnitude of the urban heat island directly from most studies, either as reported in the text or quantified from raw environmental data provided by the authors. We used the most consistently reported metric of the urban heat island, the difference in average growing season temperature between urban and rural habitats. In two cases (Sato and Takahashi 2022; Harris et al. 2024), we used reported impervious surface area values and estimated the urban heat island based on conversion factors between impervious surface and land surface temperature reported in the literature (Yang et al. 2021) (see Supplementary Table S1 for urban heat island data sources).

Statistical analyses

All analyses were performed in R, version 4.2.1 (R Core Team 2022). We constructed formal, random effects meta-analyses using the *rma.mv* function in the *metafor* package (Viechtbauer 2010). Population divergence in heat tolerance, cold tolerance, and body size were modeled separately. For models of heat and cold tolerance, we considered the following moderators of divergence: data type, the magnitude of the urban heat island, and baseline tolerance. We also considered habitat type as a two-level categorical moderator comprising organisms from aquatic and terrestrial environments, but only for models of heat tolerance, as the data for cold tolerance came exclusively from terrestrial habitats. Data type was treated as a two-level categorical variable comprising genetic and phenotypic data. This variable aligns with the study design, as genetic data came from laboratory common garden studies with assessment of traits on organisms that underwent a generation of developmental acclimation to standardized conditions (F_1 or later generations). Phenotypic data came from wild-caught organisms that did not undergo a generation of developmental acclimation to standardized conditions (F_0 generation). The magnitude of the urban heat island was treated as a continuous variable. Baseline tolerance was estimated as the tolerance of the rural population and was treated as a continuous moderator. Owing to a priori expectations that phenotypic data types might upwardly bias estimates from the combined effects of plasticity and evolution to trait divergence, we initially considered interactions between data type and the other moderators for models of heat tolerance. In the case of nonsignificant interactions, these terms were dropped from the final model. The data for cold tolerance were too sparse to consider interactions between moderators.

For heat tolerance, the trait difference was expressed as urban CT_{max}—rural CT_{max}. For cold tolerance, the trait difference was expressed as (urban CT_{min}—rural CT_{min}) × −1 to be interpretable as higher values indicating better cold tolerance, since higher CT_{min} values indicate worse cold tolerance. Models of heat and cold tolerance incorporated measurement error based on the squared, pooled SEs and included a random intercept for species. Visualization of the relationship between moderators and trait divergence was accomplished using the *regplot* function from the *metafor* package. We used the *emmprep* function from the *metafor* package, followed by the *emmeans* function from the *emmeans* package (Lenth 2021) to obtain estimated marginal means for factor levels when appropriate.

For models of potential lag in the response of heat and cold tolerance traits, we quantified the expected trait shift as the 1:1 relationship between the magnitude of the urban heat island and the tolerance trait difference between urban and rural populations, assuming increases in heat tolerance and losses in cold tolerance among urban populations (sensu Diamond and Martin 2021b). In practice, for heat tolerance, we subtracted the divergence in heat tolerance (urban CT_{max}—rural CT_{max}) from the urban heat island to estimate the lag. For cold tolerance, we summed the divergence in cold tolerance (urban $CT_{min—}$rural CT_{min}) × −1 and the urban heat island to estimate the lag. Thus, if populations increased their heat tolerance and lost their cold tolerance by the same magnitude as the urban heat island, the lag would be zero for both heat and cold tolerance. We performed two sets of models, one where we estimated the mean lag for heat and cold tolerance (an intercept-only model) and examined whether the intercept was significantly different from zero and a second where we modeled the lag as a function of the urban heat island and examined whether the slope was significantly different from zero.

We modeled body size in a broadly similar fashion as the tolerance trait responses. Owing to the magnitude of urban–rural differentiation in body size having no direct interpretation for keeping pace with urban climatic warming, we calculated body size responses as standardized mean differences using the *escalc* function with the SMDH method argument from the *metafor* package. The model included measurement error variances as computed by the *escalc* function when co-estimating the standardized mean differences. We included the moderators of data type, habitat type, body size metric (length versus mass), and magnitude of the urban heat island. We considered interactions between data type and the other moderators. We further considered the interaction between habitat type and the magnitude of the urban heat island, since the size divergence might be expected to trend more negative for aquatic organisms in response to warmer temperatures, but either trend flat or positive for terrestrial organisms. Interaction terms were excluded from the final model in the case of nonsignificance.

For each of the focal response variables, divergence in heat tolerance, cold tolerance, and body size, we also ran intercept-only meta-analytical models with the same structure for measurement error variance and random effects as the moderator-based models for each response described above. These models allowed us to estimate the overall urban-rural divergence for each trait.

For the moderator of baseline tolerance, when this term was statistically significant in models of divergence in tolerance, we performed a complementary analysis to assess the potential effect of regression to the mean (following Deery et al. 2021). Specifically, we aimed to determine whether repeated sampling within species artificially produced the negative relationship between divergence and baseline tolerance. We generated a null distribution by randomly sampling baseline tolerance with replacement, and separately, randomly sampling urban tolerance with replacement. As our original meta-analysis contained a random intercept for species, we performed the random sampling within each species. We performed two versions of the resampling, one where the original number of samples per species was preserved, and another where each species was sampled one time (corresponding to the lowest within-species replication present in our dataset). We then

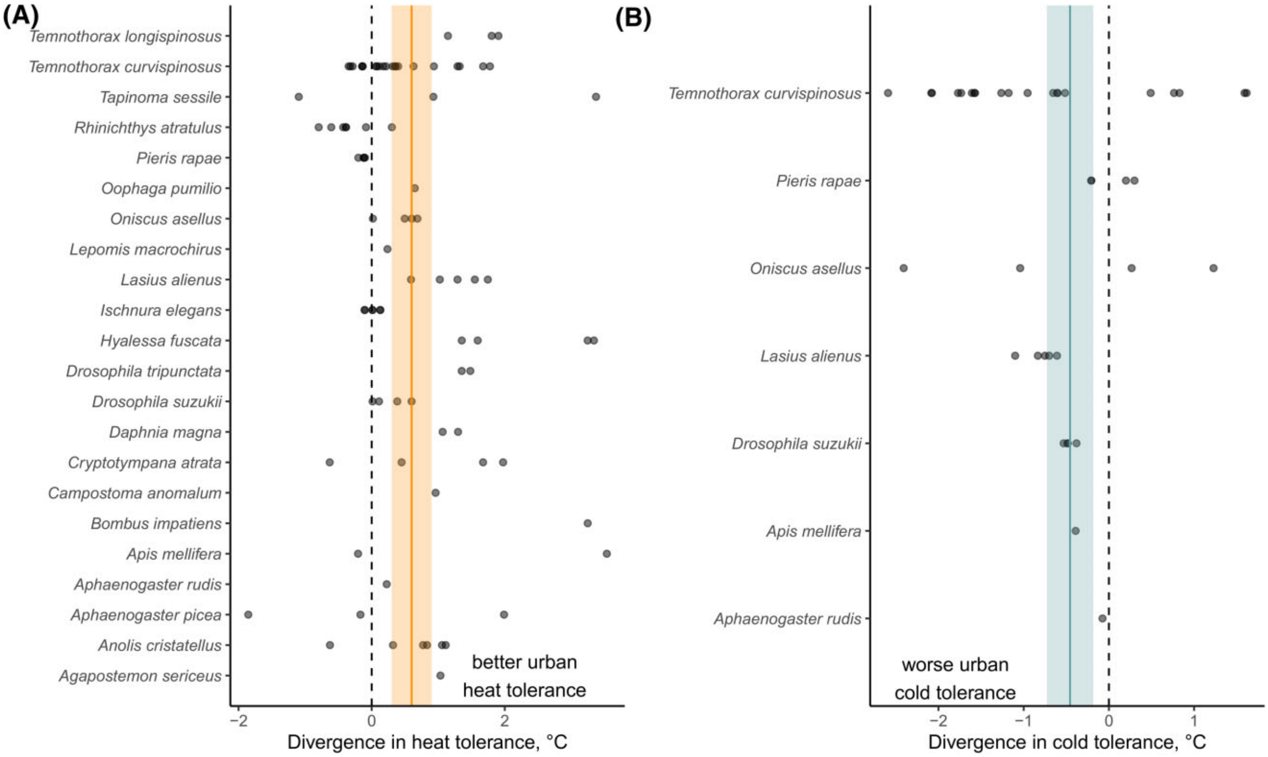

Fig. 1 Divergence in heat and cold tolerance, grouped by species. Points represent observation-level differences. The difference for heat tolerance was defined as urban CT_{max}—rural CT_{max}. The difference for cold tolerance was defined as (urban CT_{min}—rural CT_{min}) × −1 because higher CT_{min} value indicate worse cold tolerance. The vertical dashed line at zero indicates no change in trait values between urban and rural populations. Solid vertical lines and ribbons indicate the meta-analytic means and 95% confidence intervals for divergence in each trait.

refit our meta-analytic model of divergence in tolerance as a function of baseline tolerance, calculating a new pooled SE for the response based on the resampled data and including the original moderator variables. We performed 1000 permutations of the data, and then assessed how frequently we obtained a result with an estimated coefficient for the effect of baseline tolerance on divergence in tolerance that was as or more extreme than the estimate from our original meta-analytic model.

Finally, we more explicitly examined the potential role of changes in body size and their consequences for changes in tolerance across the urbanization gradient. We focused exclusively on heat tolerance, as there were insufficient data to explore this relationship for cold tolerance. We constructed a meta-analytic model of divergence in heat tolerance as a function of divergence in body size, habitat type, and their interaction to allow for differential association between size and heat tolerance across aquatic versus terrestrial habitats. We pooled across the other moderators of divergence in heat tolerance considered above to avoid oversaturating the model. We again dropped the interaction from the final model in the case of nonsignificance.

Results

Our results provide support for convergent evolution of thermal physiological traits in response to urban heat islands. We detected a significant, ecologically meaningful increase in heat tolerance among populations in urban environments compared with rural environments (estimated meta-analytic mean for the change in CT_{max}: 0.600°C, 95% CI [0.300, 0.901]; Fig. 1A, Supplementary Table S2). We also detected a significant decrease in cold tolerance among populations in urban environments compared with rural environments (estimated meta-analytic mean for the change in CT_{min}: −0.456°C, 95% CI [−0.729, −0.184], note here the directionality is such that negative values indicate losses in cold tolerance, or, equivalently, increases in CT_{min} values, from rural to urban populations; Fig. 1B, Supplementary Table S2).

For heat tolerance, we found that the magnitude of the urban heat island was a significant moderator of divergence, such that warmer urban environments contributed to greater magnitude of trait divergence (Fig. 2A; Supplementary Table S3). However, we also found evidence of a lag, defined as the difference between the urban heat island and divergence in heat

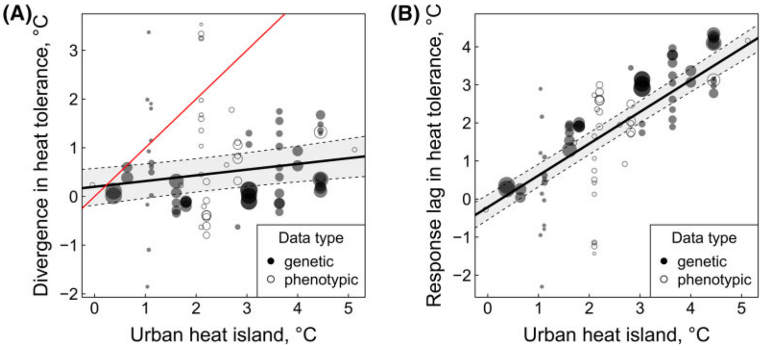

Fig. 2 Effect of the urban heat island on: (A) divergence in heat tolerance (CT_{max}) and (B) lag in the response of heat tolerance. Divergence in heat tolerance is expressed as urban CT_{max}—rural CT_{max}. Data type is distinguished by filled circles for genetic data, and open circles for phenotypic data. Symbol size indicates relative differences in model weight, with larger circles corresponding to greater weight. Predicted values from the meta-analytic model are indicated with a solid line within the 95% confidence interval (gray ribbon, dashed lines). The 1:1 line is indicated in panel A, such that for every 1°C increase in the magnitude of the urban heat island, there is a concomitant 1°C increase in CT_{max} of the urban population relative to the rural population.

tolerance (test of whether the intercept-only model was significantly different from zero: $\beta = 1.62$, SE $= 0.276$, $z = 5.87$, $P < 0.0001$). In addition, the lag increased with greater amounts of warming (test of whether the slope of the lag was significantly different from zero: $\beta = 0.835$, SE $= 0.0361$, $z = 23.1$, $P < 0.0001$) (Fig. 2B).

Also for heat tolerance, we found that baseline tolerance was a significant moderator of divergence, but that its effect was dependent on whether the data were genetic or phenotypic (Fig. 3; Supplementary Table S3). Although there was no relationship for phenotypic data ($\beta = 0.0145$, SE $= 0.0277$, $z = 0.523$, $P = 0.601$), we found that for genetic data, populations with lower baseline heat tolerance exhibited greater increases in heat tolerance in response to urban warming ($\beta = -0.134$, SE $= 0.0332$, $z = -4.03$, $P < 0.0001$; the result was robust to the test of regression to the mean, Supplementary Table S4). Given the strong dependence of heat tolerance responses on data type, we ran separate meta-analytic models for genetic data and for phenotypic data to estimate the overall magnitude and direction of divergence in heat tolerance for each data type. Although phenotypic data tended to show greater divergence in heat tolerance compared with genetic data (Fig. 3), both showed increases in heat tolerance that were significantly different from zero (phenotypic: $\beta = 0.700$, SE $= 0.250$, $z = 2.80$, $P = 0.00514$; genetic: $\beta = 0.522$, SE $= 0.185$, $z = 2.82$, $P = 0.00479$).

For cold tolerance, we found greater divergence under larger magnitude urban heat islands. Specifically, populations in warmer urban environments had greater increases in CT_{min} and thus losses in cold tolerance (Fig. 4A, Supplementary Table S3). We did not find significant effects of data type or baseline tolerance on divergence in cold tolerance (Supplementary Table S3). The loss of cold tolerance lagged behind the amount of warming (test of whether the intercept-only model was significantly different from zero: $\beta = 1.74$, SE $= 0.412$, $z = 3.21$, $P < 0.0001$), and the magnitude of the lag increased under higher amounts of warming (test of whether the slope of the lag was significantly different from zero: $\beta = 0.248$, SE $= 0.0780$, $z = 3.17$, $P = 0.00151$). Effectively, the rate at which urban populations lost their cold tolerance was lower in warmer environments.

Although we found that overall size differentiation was not significantly different from zero (Supplementary Table S2), we did find evidence of significant moderators of size divergence. Divergence was more negative for mass compared with length-based measurements (Supplementary Table S3). We also found that divergence was dependent upon habitat type (Supplementary Table S3). The contrast of aquatic versus terrestrial habitat was negative and significant (aquatic—terrestrial: $\beta = -0.519$, SE $= 0.222$, $z = -2.34$, $P = 0.0192$). The estimated marginal means and significance tests for each habitat type indicated that while size divergence in terrestrial habitats was not different from zero ($\beta = 0.0716$, SE $= 0.115$, $z = 0.623$, $P = 0.533$), body size of urban populations decreased significantly in aquatic habitats ($\beta = -0.448$, SE $= 0.188$, $z = -2.38$, $P = 0.0175$) (Fig. 5A). We did not detect significant effects of data type or the urban heat island in models of size divergence (Supplementary Table S3).

Finally, when considering body size divergence as a predictor of divergence in heat tolerance, we found that greater divergence in size was associated with greater divergence in heat tolerance ($\beta = 0.224$, SE $= 0.0856$, $z = 2.61$, $P = 0.00904$; Fig. 5B). The relationship between heat tolerance and size divergence did not appear to be driven by opposite trends for habitat types

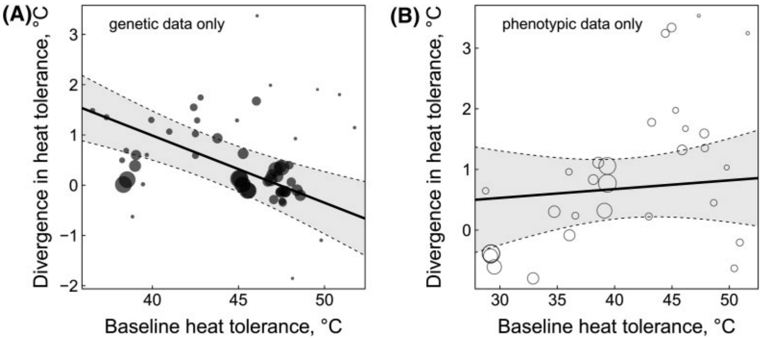

Fig. 3 Divergence in heat tolerance (CT_{max}) as a function of baseline heat tolerance (rural CT_{max}): (A) for genetic data only; (B) for phenotypic data only. Divergence in heat tolerance is expressed as urban CT_{max}—rural CT_{max}. Data type is distinguished by filled circles for genetic data, and open circles for phenotypic data. Symbol size indicates relative differences in model weight, with larger circles corresponding to greater weight. Predicted values from the meta-analytic model are indicated with a solid line within the 95% confidence interval (gray ribbon, dashed lines).

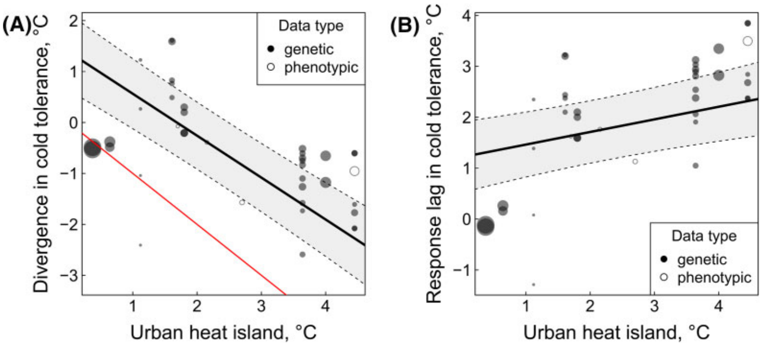

Fig. 4 Effect of the urban heat island on: (A) divergence in cold tolerance (CT_{min}); and (B) lag in the response of cold tolerance. Divergence in cold tolerance is expressed as (urban CT_{min}—rural CT_{min}) × −1, and the lag is expressed as the sum of the urban heat island and divergence in cold tolerance. Data type is distinguished by filled circles for genetic data, and open circles for phenotypic data. Symbol size indicates relative differences in model weight, with larger circles corresponding to greater weight. Predicted values from the meta-analytic model are indicated with a solid line within the 95% confidence interval (gray ribbon, dashed lines). The 1:1 line is indicated in panel A, such that for every 1°C increase in the urban heat island, there is a concomitant 1°C increase in CT_{min} (loss of cold tolerance) of the urban population relative to the rural population.

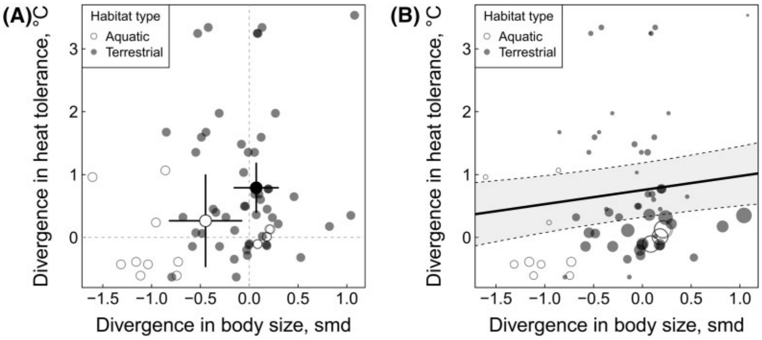

Fig. 5 Relationship between divergence in heat tolerance and body size across aquatic and terrestrial habitats. In both panels, divergence in heat tolerance (urban CT_{max}—rural CT_{max}) is plotted as a function of divergence in body size (standardized mean difference, urban—rural). Points are observation-level comparisons, shaded according to their habitat of origin, either aquatic (open symbols) or terrestrial (filled symbols). (A) Bivariate point estimates and 95% confidence intervals for divergence in heat tolerance and size are shown (based on the estimated marginal means from the respective meta-analytic models, Supplementary Table S3, for aquatic and terrestrial habitats). Vertical and horizontal dashed lines at zero indicate no divergence in size and heat tolerance, respectively. (B) Predicted values from the meta-analytic model of heat tolerance divergence as a function of size divergence are indicated with a solid line within the 95% confidence interval (gray ribbon, dashed lines). Symbol size indicates relative differences in model weight, with larger circles corresponding to greater weight.

(e.g., smaller size being associated with greater heat tolerance in aquatic environments, but lower heat tolerance in terrestrial environments), as this relationship was qualitatively similar just among the well-replicated terrestrial data subset ($\beta = 0.229$, SE $= 0.0882$, $z = 2.59$, $P = 0.00956$). Furthermore, the interaction of size divergence and habitat type was not significant and was dropped from the final model; the main effect of habitat type was also not significant ($\beta = 0.325$, SE $= 0.446$, $z = 0.727$, $P = 0.467$) as we found in our focal model of heat tolerance (Supplementary Table S3).

Discussion

We tested whether the shared selection pressure of the urban heat island led to convergent evolutionary responses in thermal tolerance and body size (Diamond and Martin 2020). We used a cross-species meta-analytic approach to assess the degree of convergent evolution in these traits among distinct lineages. In general, while we found high repeatability of evolutionary responses to urbanization in heat tolerance and cold tolerance, we found low repeatability in body size. Despite evidence of significant shifts toward greater heat tolerance in cities, the rate of trait change lagged behind changes in environmental temperature, especially under strong urban heat islands. Our study demonstrates how cities can be used to understand fundamental questions in evolutionary biology regarding the repeatability of evolution, and more applied questions regarding the ability of populations to keep pace with contemporary climatic warming.

Contemporary convergent evolution of thermal tolerance

The results of our study bridge a critical gap between historical evolution in response to climatic variation (Bennett et al. 2021) and contemporary convergent evolution studies not necessarily focused on climate (Reznick et al. 2019). We find strong support for contemporary convergent evolution in thermal tolerance, with significant gains in heat tolerance and losses in cold tolerance in response to climatic warming in cities (Fig. 1). These patterns are paralleled with global biogeographic latitudinal and elevational clines (Sunday et al. 2019). However, in the current study, we were able to ascribe, at least partially, a genetic basis to those changes, as we detected these patterns among both genetic and phenotypic data. Though, as an important side note, the estimated divergence in heat tolerance was significantly greater for phenotypic compared with genetic data (Fig. 2A, Supplementary Table S3), reinforcing the value of using common garden designs to disentangle genetic from environmental contributions to trait variation. Further, our study suggests that temperature is a major driver of divergence in tolerance as we found that the magnitude of divergence was related to the magnitude of the urban heat island (Figs 2A and 4A). Specifically, we found evidence of larger gains in heat tolerance and losses in cold tolerance where the urban heat island was stronger (Supplementary Table S3).

Although it is perhaps more straightforward to consider divergence in heat tolerance in response to urban warming given the likely adaptive nature of such changes, the patterns of divergence in cold tolerance are still worthy of consideration. It is possible that genetic correlations between heat and cold tolerance traits drive the observed pattern of diminished cold tolerance in cities, though there is mixed support for this idea (e.g., Baer and Travis 2000; Freda et al. 2019; Schou et al. 2022). Alternatively, there could be an adaptive basis for this response as selection could drive the loss of cold tolerance via jettisoning of costly machinery to maintain performance at low temperatures in warmer conditions (Dierks et al. 2012).

Lags in thermal tolerance responses

Assessing the ability of evolution to keep pace with climatic change is an increasingly vital component of forecasting efforts, yet one that remains notoriously difficult to estimate (Martin et al. 2023). Often, laboratory experimental evolution studies, estimates of additive genetic variation in climate-relevant traits, or modeling efforts are used to assess the ability to keep pace with warming, and each carries its own set of benefits and limitations (e.g., Radchuk et al. 2019; Feiner et al. 2021; Santos et al. 2021). Although our approach to quantify contemporary evolution (and phenotypic change) among climate-relevant traits in response to urban heat islands is not without its own set of limitations (Diamond and Martin 2021a), our study nonetheless demonstrates the use of cities as a viable forecasting tool. Indeed, our study joins other approaches finding support for the presence of adaptational lags in response to climatic warming (reviewed in Martin et al. 2023) and urban land-use change (Diamond et al. 2022b). The mean lag in heat tolerance estimated in our study was substantial at 1.6°C and suggests that while there is evidence of adaptive evolution to warming in cities, urban populations might remain vulnerable to extreme high temperatures. Further, the increase in lag of 0.84°C for every degree of urban warming suggests that urban populations might be exhausting additive genetic variation in heat tolerance as they respond to urban conditions or that urban populations need more generations for trait responses to catch up to the rapid warming associated with relatively recent (e.g., since the industrial revolution) and ongoing urban development. Here again, it is a bit more challenging to interpret the response lags in cold tolerance as an adaptational lag (though they could be if cold tolerance is costly). Although the mean lag in cold tolerance equaled that of heat tolerance, the rate of change in lag across the urban heat island was lower at 0.25°C and indicated that urban populations proportionally retained greater cold tolerance under higher amounts of warming. Indeed, recent work in acorn ants showed that winter-acclimated colonies exhibited no difference in chill coma recovery time between urban and rural populations suggesting the potential importance of retaining some aspects of low-temperature performance in warmer urban environments (Prileson et al. 2023). How cities impact seasonal variation in temperature and the consequences of these changes for thermal physiology remains an important open question.

There are of course several caveats to point out in the interpretation of response lags. First, there is the question of whether the expectation of a degree Celsius change in tolerance trait value for every degree Celsius change in urban temperature is ecologically relevant. This is because changes in the frequency of sublethal temperatures could have as much or greater impact than changes in extreme temperatures, for example, through increases in hours of restriction for activities such as foraging or mating that can be more temperature-sensitive than survival (Sinervo et al. 2010). Directly related to this issue is the fact that we are comparing differences in tolerance of temperature extremes by using divergence in CT_{max} with differences in urban warming based on mean growing season temperatures, as these were the most consistently available thermal index. It is possible that use of indices of temperature extremes to be more directly comparable to tolerance traits could show reduced (or potentially greater) lag.

Second, there is the question of whether we are accurately quantifying climate exposure. In most cases (but not all, see Supplementary Table S1), we had access to environmental temperature data at the microclimatic scale. To illustrate the importance of this consideration, even for a single urbanization gradient with sampling areas that broadly overlapped, estimation of the urban heat island differed substantially (i.e., from less than 2°C to over 4°C) among butterflies, ants, and isopods (Diamond et al. 2018; Yilmaz et al. 2021; Lenard 2023), contingent upon their specific urban microclimatic needs and niches. For studies where we could only approximate temperature differences, for example, based on impervious surface area, estimates of the lag and related quantities could be over- or underestimated. The ability of species to use such microclimatic variation through behavioral plasticity could likewise influence climate exposure and subsequent evolutionary responses (e.g., the Bogert effect wherein behavioral plasticity limits adaptive evolution; Muñoz 2022).

Third, there is the question of what adaptational lags in one trait mean for keeping pace with climatic change more broadly. Specifically, organisms can use other compensatory mechanisms beyond adaptive evolution of heat tolerance including behavioral plasticity (e.g., selection of microclimates, diurnal or seasonal changes in the timing of activity) and physiological plasticity (e.g., beneficial thermal acclimation) (Huey et al. 2012). In consequence, just because populations are not keeping pace with urban warming via evolutionary increases in heat tolerance does not mean they are not keeping pace through other mechanisms. However, in the long term, evolutionary change is the only mechanism that will allow populations to keep pace with the extreme climatic changes forecasted over the next century (Martin et al. 2023).

The role of baseline tolerance in divergence

In the context of adaptational lags, there has been further discussion regarding associations between baseline tolerance and the magnitude of evolutionary responses (reviewed in Logan and Cox 2020). Our study found that baseline tolerance was predictive of divergence in heat tolerance, with populations farther from their upper limit exhibiting a greater magnitude of shift (Figs 2B and 3B). It is unclear from our meta-analysis what mechanistic underpinnings drive this association. One possibility is that there is simply stronger selection at lower baseline tolerance trait values (Logan et al. 2014). Another possibility is that there is diminished capacity to shift physiological trait values as they approach high and low extremes.

Phylogenetic comparative analyses suggest the presence of some genetic or developmental constraints on physiological trait evolution, especially on heat tolerance (Kellermann et al. 2012; Bennett et al. 2021). However, intraspecific variation in heat tolerance is remarkably high (Sasaki et al. 2022), and heritability is nonzero (Diamond 2017). Indeed, studies of contemporary evolution find evidence of ecologically relevant magnitudes of trait responses across diverse taxa (Martin et al. 2023). Furthermore, related explorations of baseline tolerance-plasticity tradeoffs that likewise rely on the concept of evolutionary limits, suggest mixed to little support for such constraints (Heerwaarden and Kellermann 2020; Gunderson 2023).

(Non)divergence in body size

Unlike the consistency of thermal tolerance to climatic warming over contemporary and historical timescales, body size exhibits more mixed responses. For example, studies provide evidence of shrinking (e.g., Zimova et al. 2023) and increasing (e.g., Solokas et al. 2023) body size with contemporary climatic warming over time. Shrinking body size with climatic warming is consistent with a widespread form of phenotypic plasticity for ectotherms (that comprise the entirety of our meta-analysis study organisms) known as the temperature-size rule (Angilletta and Dunham 2003), though other mechanisms can drive these patterns (Ozgul et al. 2009). Indeed, among the temporal longitudinal studies described above, it is also possible that these patterns are driven by evolutionary changes. Here, the expectations become a bit murkier, in part owing to the many other traits that body size innervates (Angilletta et al. 2004). The general response from our study was of high variation in size divergence, but little systematic trend toward higher or lower sizes (Fig. 5A). Similar results were found in a study of community weighted mean body size in response to urbanization, with different magnitude and direction of responses among different taxa (Merckx et al. 2018). In this case, highly dispersive taxonomic groups had higher community weighted mean body size in the city, potentially as a mechanism to counteract urban fragmentation via enhanced size and dispersal capability.

The one exception we found to the pattern of nonsystematic variation in size divergence was in the trend across aquatic and terrestrial habitats. Aquatic organisms exhibited reduced body size in urban environments, potentially owing to constraints imposed by oxygen limitation in aquatic habitats (Leiva et al. 2019). While these results suggest some predictability in size trends for specific urban habitats, more data are needed to understand how broadly these patterns hold, as urban aquatic environments remain desperately understudied (Langerhans and Kern 2020). The patterns for terrestrial organisms were somewhat more complex. Although divergence in size was not significantly different from zero, when considered as a predictor, greater divergence in size was associated with greater divergence in heat tolerance (Fig. 5B). Thus, while there are likely many forces that shape the responses of body size to urbanization, it is possible size could be under selection through its effects on heat tolerance, for example, with larger size contributing to greater thermal inertia (Chown and Nicolson 2004).

Future directions

As next steps in exploring contemporary (non)convergent evolution in urban environments, there should be sustained investment in building out the empirical data on trait responses to urbanization, including common garden studies to uncover a genetic basis for changes. This will allow other moderators of rates of evolutionary change such as generation time, background climatic conditions, capacity for thermal buffering (e.g., via behavioral or physiological plasticity), dispersal capacity (e.g., as a factor influencing gene flow), and location within the geographic range (e.g., as a factor influencing genetic diversity) to be examined. Such trait-based associations, in addition to better estimates of the ability of populations to keep pace with climatic warming, could provide a novel, complementary set of forecasts and forecasting tools to those already employed.

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Supplementary data

Supplementary data available at *ICB* online.

Conflict of interest

The authors declare no conflict of interest.

Data availability

Data are available via the Open Science Framework, https://osf.io/kajgm/, DOI 10.17605/OSF.IO/KAJGM.

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