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Shared and unique responses of insects to the interaction of urbanization and background climate

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Urbanization profoundly alters biological systems; yet the predictability of responses to urbanization based on key biological traits, the repeatability of these patterns among cities, and how the impact of urbanization on biological systems varies as a function of background climatic conditions remain unknown. We use insects as a focal system to review the major patterns of responses to urbanization, and develop a framework for exploring the shared and unique features that characterize insect responses to urbanization and how responses to urbanization might systematically vary along background environmental gradients in climate. We then illustrate this framework using established patterns in insect macrophysiology.

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Introduction: insects and urban land-use change

Urbanization is transforming the global landscape. Three percent of the global land mass, excluding Greenland and Antarctica, is urbanized, and nearly half a percent is now covered in surfaces impervious to water such as roads, sidewalks and buildings [1•]. These pockets of urban development are scattered across much of the global landmass, such that gradients of rural to urbanized land occur across the full suite of global temperature and precipitation regimes [2••]. The field of urban ecology has burgeoned under increasing global urbanization [3,4]; yet, much of this work has focused on responses of more complex levels of ecological organization, for example, efforts to quantify changes in richness of communities along individual urbanization gradients.

In this review, we target two areas for further development in urban ecology. First, we consider the mechanisms that underlie biological responses to urbanization. We outline predictive associations between environmental variables and biological responses, and we assess the degree to which biological responses to urbanization may be repeatable among cities. Second, we consider urbanization in a broader biogeographic context, exploring the impacts of urbanization against different background climates. We focus on insect responses to urbanization, as insects are widespread and can be found across the entire range of urbanization gradients and background climates. Insects also play important functional roles in ecosystems as pollinators, biological controls, scavengers, decomposers, and resources for other organisms [5].

Patterns of insect responses to urbanization

One of the hallmarks of biological responses to urbanization is altered community composition [6]. Although there has been a strong focus on replacement of native communities by non-native and/or invasive species in urban environments, recent meta-analyses have indicated that while urban exotics are certainly present, many native species are retained in urban environments, albeit as a subset of the rural or undeveloped area species pool (e.g., [7,8••,9••]). Specifically in insects, exotic bee species are overrepresented in urban parks in New York [10], as is the invasive Argentine ant in urbanized areas of California [11]; yet, two species of native scale insects (tree pests) are overrepresented in urbanized areas of North Carolina [12••,13,14], and native ant communities along this same gradient are remarkably similar [15].

Thus, for many insects, but not all, the same species occur in rural and urban habitats ([16,17], but see [18]). Insects therefore allow us to examine both ecological filtering for species unique to urban and rural environments, and the morphological, physiological, and demographic consequences of urbanization for species shared among rural and urban environments. Importantly, to be able to forecast insect responses to urbanization, uncovering the nature and relative contribution of such mechanisms underlying the observed shifts in community composition and structure is crucial.

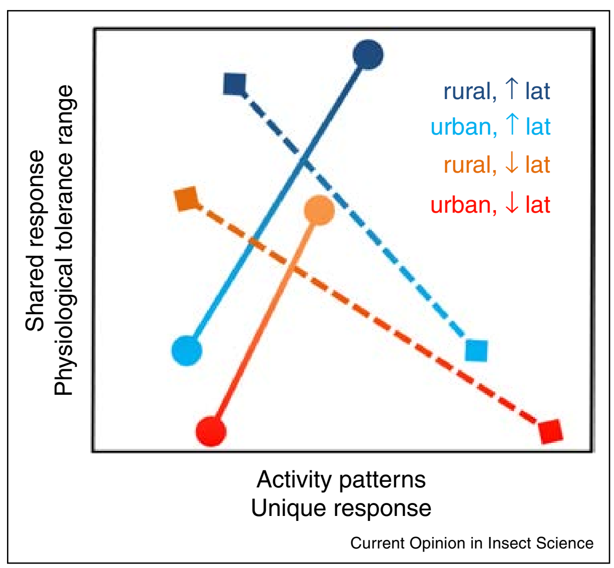
Shared and unique phenotypic responses to urbanization

A framework is needed that we can apply broadly to describe the responses of species to urban development gradients. Ideally, the framework would allow us to partition variation in a suite of phenotypic traits among responses to urbanization that are shared (i.e., that have similar magnitude and direction) and responses to urbanization that are unique to particular species. Langerhans and DeWitt [19] developed a general framework to investigate shared and unique features of evolutionary diversification along environmental gradients that we can apply here to understand insect phenotypic responses to urbanization gradients. Here we consider the shared and unique responses of insects to changes in environmental temperature across a rural to urban gradient. Although there is substantial variation in how urban development alters bioclimatic variables, cities generally exhibit an increase in mean daily surface and air temperature compared with nearby rural areas, a pattern often referred to as the 'urban heat island' effect [20]. The magnitude of urban warming relative to background temperature is typically greater at night than during the day. Indeed this unique signature of warming can have profoundly different effects on insects than their responses to constant temperature or symmetrical warming. Zhao and colleagues [21•] explored this idea in grain aphids and found substantial reductions in survival and adult performance leading to an overall reduction in the intrinsic rate of population increase under a nighttime-biased warming regime. Clearly there are important sources of variation to consider when quantifying urban climates and their impacts on insects. In our development of a framework for exploring the shared and unique features of insect responses to urbanization, the influence of such variation will be most pronounced when making comparisons among cities; by contrast, our framework should be more robust to this variation when making comparisons along rural to urban gradients for a given city.

The first step in building this framework requires that researchers measure a common suite of phenotypic traits of organisms across an environmental gradient. Such a requirement may appear superficially obvious, however, the measurement of traits in a comparable manner is often not trivial. For example, in insects, thermal tolerance traits are highly sensitive to pre-trial acclimation temperature regimes and the rate of temperature increase ([22–24], see also [25] for a consideration 'tolerance landscapes' rather than single tolerance estimates). Assuming our traits of interest are measured in a comparable manner, we can formalize our treatment of the traits, urbanization gradient, and species identity into a statistical model.

How should we build our model to reveal shared and unique features of responses to urbanization? As an example, we consider two traits: thermal tolerance range (the difference between upper and lower temperature tolerances) and activity pattern (e.g., the timing of peak foraging), which we measure for two species in both rural and urban habitats. We can now construct a multivariate analysis of variance in which canonical axes, representing linear combinations of the response variables (thermal tolerance range and activity pattern), are generated for each term (urban versus rural habitat, species identity, and their interaction). The resulting canonical axes describe trait responses that are shared by each species across rural and urban environments (shared response); differences in traits based on species identity (specific history effect); and trait responses across rural and urban environments that differ based on species identity (unique response) (Figure 1). Using this approach we may learn that insect thermal tolerance ranges become more narrow for both species in urban environments — that is, thermal tolerance range is shared among species, as indicated by a significant urbanization term; but that activity patterns are idiosyncratic among species — that is, activity pattern such as the timing of peak foraging is unpredictably earlier or later among urban populations of species compared with rural populations, as indicated by a significant urbanization–species interaction term. A major goal of this approach is to identify which traits respond *predictably* to urbanization, that is which traits are shared among species, to begin to uncover the mechanisms underlying responses to urban development.

Figure 1



Shared and unique features of species responses to urbanization and background environment. Lines and symbols represent different species (though they could also represent different genotypes for intra-specific comparisons). The dark blue to light blue transition represents the urbanization gradient at high latitudes; the orange to red transition represents the urbanization gradient at low latitudes.Adapted from [19].

A priori we would predict that morphological, physiological and performance traits are the most likely to exhibit shared responses across urbanization gradients, whereas behavioral traits are the most likely to exhibit unique responses as these traits are generally more variable and exhibit low phylogenetic signal, that is, there is less evidence of genetic or developmental constraints on behavioral traits [26]. Much of the current body of literature considers the impacts of temperature on morphology and physiology. For example, morphology responds strongly to urbanization in carabid beetles: body size of individuals has been shown to decrease with increasing levels of urbanization ([27]; see also [28] which finds that size structure of beetle communities changes under urbanization, favoring small and medium beetles over large). This is perhaps unsurprising as insects are ectothermic species, the majority of which follow the temperature-size rule, a widespread pattern of phenotypic plasticity in which organisms achieve smaller final body sizes with increasing temperature. Yet there are exceptions to the rule; for example, scale insects inhabiting warmer urban environments were found to be larger and more fecund [14]. Some have linked the reversal of the temperature-size rule to low-resource quality conditions [29]. As urbanized areas are often highly heterogeneous with respect to resource quality and quantity (for example [30]), we may instead see a mosaic of insect species some of which follow and some of which break the temperature size rule along urbanization gradients, potentially owing to the added effects of variation in resource quality.

Similar to morphology, while there are relatively few examples of insect physiological tolerances assessed in rural and urban environments [31], we can make general predictions based on widespread patterns in insect tolerances. Macrophysiological work in insects generally supports increases in the range of temperatures insects can tolerate with increasing latitude and with increasing temperature variability [32]. Much of this response is on the low end of the thermal performance curve, a continuous function that describes phenotypic plasticity in performance traits in response to temperature. Broader thermal tolerance ranges are therefore largely achieved with improved tolerance of cooler temperatures, rather than shifts in tolerance of high temperatures [33–35].

Latitudinal gradients in environmental temperature parallel the temperature profile in rural to urban gradients; low latitude areas exhibit more narrow environmental temperature profiles with increases in mean temperature compared with high latitude areas. Similarly, urban areas exhibit more narrow environmental temperature profiles with increases in mean temperature compared with nearby rural areas [36–38]. We may then expect that, similar to macrophysiological patterns of insect thermal tolerances as a function of latitude, insects in urban environments, compared with rural environments, will exhibit narrower ranges of thermal tolerance driven by a reduction in the ability to tolerate low temperatures and a more modest increase in the ability to tolerate high temperatures. Although the data to address this hypothesis are few, tolerances of high temperatures have been shown to increase in urban ants compared with rural ants [31].

Of course documenting how physiological traits vary along urbanization gradients is a first step on the way to understanding urban ecology as a predictive science. The increase in thermal tolerance of urban ants could be a result of a phenotypically plastic response wherein exposure to increased urban environmental temperature affords greater tolerance of higher temperatures [39]. Though a non-mutually exclusive competing hypothesis is also possible: insects may achieve greater thermal tolerance in urban areas through adaptive evolutionary change [40]. Dissecting the mechanisms underlying systematic variation in physiological tolerance and other traits as a function of urbanization, which operate over different time scales and potentially under different constraints, will be crucial for developing forecasts of insect responses to urban development (for related papers addressing this issue under climate change see [41,42]).

The interaction of urbanization and background climate

Insects must respond to urban development in the context of the background climates of different biogeographic regions. Therefore, although we might use macrophysiology to generate predictions for insect responses to urbanization, insect responses to urbanization occur over regional to global scales, and we should account for contingencies introduced by background climatic conditions. Indeed, in tropical areas, where macrophysiological studies suggest insect and other ectothermic species to be at the greatest risk from climate change [43], urban development is accelerating at greater rates than other locations [4], making the exploration of insect responses to urbanization and both current and future background climate all the more urgent.

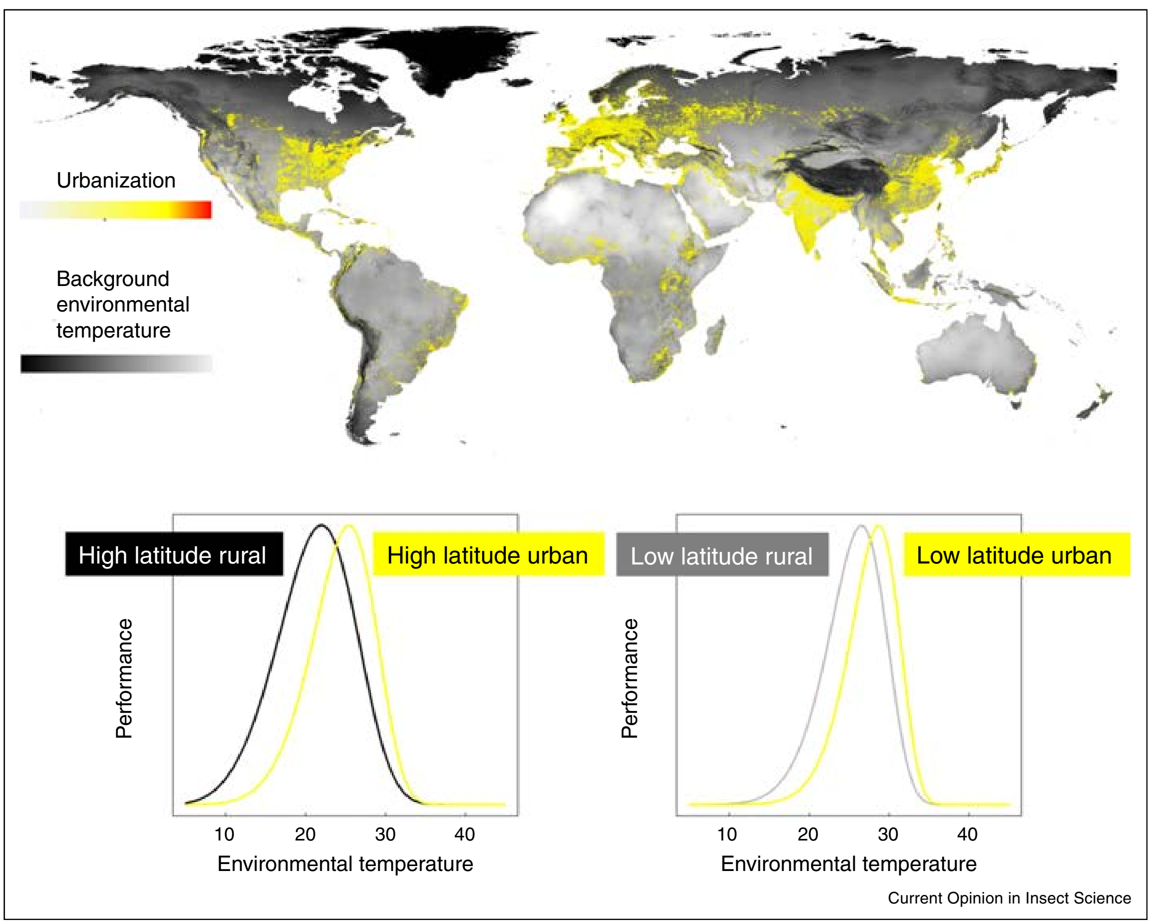
Even at higher latitudes, insects may be strongly impacted by the combined effects of urbanization and background climate. Recent work on butterflies has found empirical support for the importance of background climate in responses to urbanization: nearly half of an assemblage of twenty Ohio, USA butterfly species exhibited atypical delays in first and peak appearance phenology (the timing of life cycle events) in response to urbanization in a geographically warm region of the state, whereas more typical advancements were seen in response to urbanization in a geographically cool region of the state [44••]. Although phenology is a complex trait, temperature is a major driver for many ectothermic species [45]. If we extend this idea that the impacts of urbanization, particularly urban warming, are contingent upon background climate to our above discussion of thermal tolerance traits, we can develop a new set of predictions for how tolerance traits might respond to urbanization in geographically cool and warm locations.

We can predict that macrophysiological trends will be replicated within geographic locations along urbanization gradients, that is, we expect the broad thermal tolerance of insects in geographically cool locations (e.g., high latitude) to narrow along urbanization gradients, and the already-narrow thermal tolerance of insects in geographically warm locations (e.g., low latitude) to narrow even further with urban development (Figure 2). One important exception to this expectation is urban development in desert and xeric shrubland ecoregions, where rural environmental temperatures are remarkably similar to urban temperatures, and can even exceed urban temperatures in daytime summer temperature profiles [20].

Interestingly, a recent meta-analysis that included arthropod species acclimation potentials in metabolic traits along a latitudinal gradient found evidence for the opposite pattern to the previously established thermal tolerance-based macrophysiological pattern, that is, that plasticity was greater at lower latitudes [46]. This discrepancy points to the need for more data on plasticity and evolutionary potential in physiological traits across environmental gradients, particularly as low latitude environments and urban environments tend to speed organismal development and lengthen the growing season which may facilitate adaptive evolutionary change [47]. Yet, some traits can exhibit reduced evolutionary potential at higher temperatures [48–50].

Returning to the framework for shared and unique features of insect responses to urbanization gradients we set out earlier, we can now update this framework to consider the additional environmental gradient of background climate. To formalize this treatment, we simply need to modify the terms of our multivariate analysis of variance, such that we have the original terms of urbanization gradient, species identity, the urbanization–species interaction, and the new terms of background climate, background climate–species interaction, background climate–urbanization interaction, and the three-way background

Figure 2



The extent of global urbanization overlaid on background environmental temperature [36,37]. Hypothetical thermal performance curves for the impact of urban warming on insects at high and low latitudes, with lower and higher background environmental temperatures, respectively.

Table 1

Multivariate analysis of variance for the shared and unique features of insect responses to environmental gradients of urbanization and background climate.

Phenotype = Urbanization + Background climate + Species + Urbanization × Background + Urbanization × Species + Background × Species + Urbanization × Background × Species

Term	Interpretation
Urbanization	Species have shared responses to urbanization
Background climate	Species have shared responses to background climate
Species	Species have unique responses
Urbanization × Background climate	Species have shared responses to the relationship between urbanization and background climate
Urbanization × Species	Species have unique responses to urbanization
Background climate × Species	Species have unique responses to background climate
Urbanization × Background climate × Species	Species have unique responses to the relationship between urbanization and background climate

climate–urbanization–species interaction. Similar to the interpretation for the single (urbanization) gradient case discussed earlier, species exhibit unique responses to urbanization, background climate, or the relationship between urbanization and background climate if their respective interaction effects with species are significant. Species exhibit shared responses to urbanization, background climate, or the relationship between urbanization and background climate if their respective interaction effects are non-significant (Table 1). Here we are not only interested in which traits respond *predictably* to urbanization, but also the degree to which these shared-unique patterns are *repeatable* among cities, and critically, the degree to which deviations from repeatability in the strict sense can be explained by background climate.

Limitations and areas for development

Although we were able to develop predictions for insect responses, particularly thermal tolerance traits, to urbanization and background climate, we acknowledge that there are important sources of variation in the urbanization process, its impacts on relevant bioclimatic variables, and how insects are using altered urban environments that are likely to introduce uncertainty into our global-scale predictions. Already there is a large amount of variation in the composition and configuration of city landscapes (e.g., compact highrise versus open lowrise layouts, albedo of building materials, and vegetation cover) which in turn impacts bioclimatic variables including temperature and precipitation [51]. Moving forward, there is a similarly high level of uncertainty in models of the amount and nature of future urban expansion [4]. Further, this between-city variation in the urbanization process and its impact on urban climates is paralleled by within-city variation in microclimates. As an example of urban environmental heterogeneity, urban scale insects in Raleigh, North Carolina inhabiting trees on opposite sides of a street can experience temperature differences of over 3 °C, depending on the proximity of their host trees to buildings and vegetation [12••]. And while scale insects might have relatively limited mobility, many insects can behaviorally modulate their exposure to environmental heterogeneity, for example, taking advantage of warm areas in cases of insufficient thermal accumulation, and avoiding warm areas when temperatures exceed thermal optima [52]. Finally, as with macrophysiological and niche modeling approaches considered broadly, the potential for species interactions to limit species occupying areas that they could otherwise tolerate physiologically [53], could introduce uncertainty into our predictions for insect tolerance responses to urbanization and background climate. Thus we have identified three areas for future development: systematic examinations of variation in the urbanization process and consequences for bioclimatic variables; quantification of urban microclimates on scales comparable to those experienced by insects, and how insects are behaviorally modulating their exposure to these environments; and the role of species interactions in insect responses to urbanization and background climate.

Synthesis and future directions

We reviewed the major patterns of insect community responses to urbanization, focusing on the subset of native species and additional exotics represented in urban environments. We then developed a conceptual and statistical framework to explore the shared and unique features that characterize insect responses to urbanization and how responses to urbanization might systematically vary along background environmental gradients in climate (Figure 1; Table 1). To illustrate use of the framework, we explored how insect thermal tolerance — one of the most likely traits to be shared among species as they respond to urbanization — might be expected to respond to increases in environmental temperature from urbanization and background climate (Figure 2). Although we largely focused on environmental temperature and species-level thermal tolerances, we emphasize that our framework can be extended to other environmental variables, such as precipitation which vary across large biogeographic scales and which vary (at least with respect to reduced water availability) along urbanization gradients

[54], other response traits such as desiccation tolerance [55,56], and community-level responses by considering richness of different trophic levels or functional groups. Identifying the traits that are predictable under urbanization and background climate will get us closer to understanding their mechanistic basis, such as the roles of phenotypic plasticity and adaptive evolutionary change we considered here. Owing to rapid changes in urban land use change and background climates under global climate change, uncovering the mechanisms underlying insect shared and unique responses to urbanization against different background climates will be crucial for forecasting insect diversity under environmental change.

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- •• of outstanding interest

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