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Current Opinion in Insect Science

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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Current Opinion in Insect Science 2015, **11**:71–77

This review comes from a themed issue on **Global change biology**

Edited by **Steven L Chown**

For a complete overview see the Issue and the Editorial

Available online 30th October 2015

http://dx.doi.org/10.1016/j.cois.2015.10.001

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.

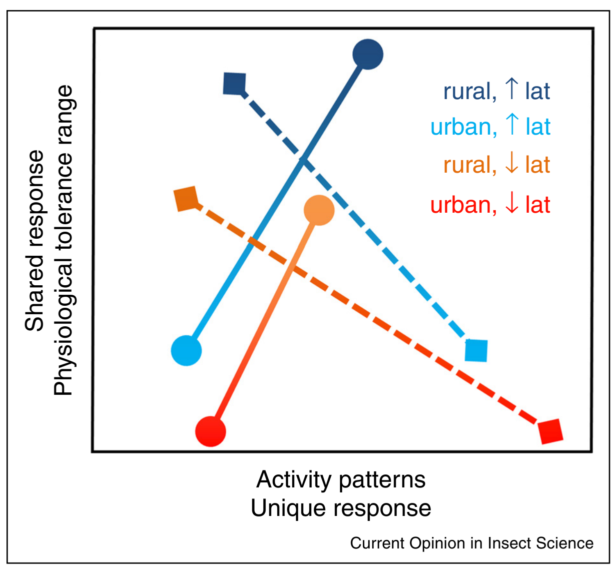
Shared and unique phenotypic responses to urbanization

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].