

ECOLOGY OF ORGANISMS IN URBAN ENVIRONMENTS

Thermal physiology and urbanization: perspectives on exit, entry and transformation rules

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Summary

1. More than 50% of the global human population lives in urban settings, which, for urban agglomerations with > 1 million inhabitants, span a 30 °C range in mean annual temperature and 4000 mm annual precipitation range.
2. Although the biodiversity impacts of urbanization are most commonly investigated at the assemblage level, these impacts are mediated through organismal physiology and behaviour.
3. At the individual level, mechanistic models, which provide an explicit means to understand how organisms meet the requirements of heat, water and nutrient balance, offer a useful way to assess physiological and behavioural responses to urban environments and their consequences for population dynamics.
4. Physiological determinants of assemblage variation can usefully be investigated by examining entry, exit and transformation rules. These are biases in the processes that determine which individuals join or leave a population or assemblage, and processes that act on individuals, which remain part thereof.
5. Direct evidence for physiological adaptation (broadly construed as phenotypic plasticity, genotypic change or some interaction between them) to urban environments is remarkably limited, owing largely to low numbers of investigations, given that most studies that have been conducted reveal some form of adaptation.
6. A warming tolerance approach, applied to insects globally, demonstrates that transposing sampled populations to the nearest urban area reduces warming tolerance by several degrees, though this effect is on average more marked for the Southern than the Northern Hemisphere. The lowest warming tolerance is found between 30 and 35°N or S, suggesting that in the absence of mitigation, the urban heat island effect of cities here will have the most pronounced impacts on insect populations.
7. Physiological approaches offer a useful means for understanding the urban–rural gradient across a wide range of climatically variable settings during a period of background environmental change.

Key-words: adaptation, phenotypic plasticity, thermal tolerance, urban heat island, urbanization gradient, warming tolerance

Introduction

Most humans now live in cities. The urban population shift also shows little sign of abating (Grimm *et al.* 2008; Faeth, Saari & Bang 2012). Urban areas are now found across a wide range of climates and elevations and are therefore overlaid on considerable natural variation. Intrinsic factors, such as human cultural norms and the density and form of urban development, further contribute

to variability among different urban areas (Tratalos *et al.* 2007; Alberti 2010), with considerable influence on the ecological consequences of urbanization.

Ecological effects of urbanization are initially realized through substantial changes to the physical environment (Gaston, Davies & Edmondson 2010; Somers *et al.* 2013), resulting in a marked urban–rural gradient. They include impacts on the atmosphere (e.g. particulate and light pollution), water bodies (e.g. chemical pollutants) and the land surface (e.g. change in land cover type and pattern).

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In turn, these substantial changes in the environment have impacts on urban ecosystems and their members at the individual, population and community levels. The most common approach to investigating the ecological consequences of urbanization involves quantitative analysis of species by site matrices (e.g. McGeoch & Chown 1997; McIntyre 2000; McKinney 2008; Raupp, Shrewsbury & Herms 2010). Such analyses are regularly accompanied by assessment of environmental variables that might explain the change in assemblage properties, and the identification of indicator taxa (McGeoch 1998; Cuffney *et al.* 2011; Luck & Smallbone 2011). However, the effects of the environment on individuals are necessarily mediated proximally through behavioural and physiological responses (Huey 1991; Porter *et al.* 2000; Davis, Malas & Minor 2014).

Over the short term, impacts of urbanization may be mediated by phenotypic plasticity, while long-term responses may involve changes in genotype frequency, with some interaction between the two being almost inevitable (Ghalambor *et al.* 2007). Key to understanding the biodiversity impacts of urbanization is therefore determining how organismal physiologies mediate responses to urbanization, either through some form of macrophysiological, species-sorting or environmental filter process (Keddy 1992; Gaston *et al.* 2009), or via phenotypic plasticity and/or genotypic change (Marzluff 2012).

Here, we explore these physiological consequences of urbanization for biodiversity. Because the urban heat island effect is such a pronounced abiotic environmental consequence of urbanization (Gaston, Davies & Edmondson 2010; Somers *et al.* 2013), it forms our primary exemplar. Nonetheless, we recognize that other environmental changes have impacts too, such as the influence of water availability (e.g. Shochat, Warren & Faeth 2006; Cavia, Cueto & Suárez 2009), nutrient regimes (Tene Fossog *et al.* 2013) and changing light environments (Gaston *et al.* 2013) and soundscapes (Gil & Brumm 2014). We also recognize that despite their importance, physiological approaches of the kind we discuss are rarely applied to understanding the biodiversity consequences of the urban-rural gradient. For example, in a recent overview of urban impacts on bird reproductive physiology, temperature-related effects on physiology were all assessed by analogy with other situations, such as elevational differences (Deviche & Davies 2014). Likewise, Marzluff's (2012) review of urban evolutionary ecology, mostly in birds, considered no examples of physiological traits associated with thermal tolerance or water balance. In consequence, we focus on approaches that can inform the field and those that have already done so.

We begin with a brief overview of the urban heat island effect. Next, we consider biophysical models as a means for understanding how local-scale environmental variation might be mediated through organismal physiology to affect key population parameters. Then, we consider species sorting as a consequence of a physiological filter associated

with urbanization. In particular, we examine the way in which the urban heat island effect may affect thermal safety margins (or warming tolerances), which are already thought to be narrow for tropical species, thus posing considerable threats to populations (Deutsch *et al.* 2008; Hoffmann, Chown & Clusella-Trullas 2013; Sunday *et al.* 2014). Finally, we consider the evidence for both phenotypic plasticity and genotypic change in physiological traits in response to urbanization.

The form of urban heat island effects

Urban heat islands (UHIs) involve a significant increase in average ambient temperature and decline in thermal variability in urban relative to surrounding, climatically similar areas (Oke 1982; Gaston, Davies & Edmondson 2010). UHIs are primarily the result of indirect solar warming (Rizwan, Dennis & Liu 2008), changes in wind speed, and thermal dynamic alterations, brought about by urbanization. In colder climates, UHIs may also be directly generated through domestic and industrial heating (Oke *et al.* 1991), even in relatively small settlements (Hinkel *et al.* 2003).

Urban heat islands have been well documented for long-established cities, such as London (Jones & Lister 2009) and Paris (Sarrat *et al.* 2006), and in developed countries where extended time-series data are available from local weather monitoring stations. While there has been some recent expansion of these cities and their respective UHIs, the core heat anomaly at the city centre is often established and stabilized (Jones & Lister 2009). Moreover, much urban development of older cities consists of redevelopment of existing urban areas, which could reduce the respective UHI with careful planning and building practices (Hamilton *et al.* 2014). By contrast, relatively recent and rapid urban growth in developing regions of the world is leading to spatial expansion of urban heat islands (e.g. Tran *et al.* 2006; Parés-Ramos, Álvarez-Berríos & Aide 2013; Yi *et al.* 2014).

For assessing UHIs, an important consideration is the substantial natural environmental variation on which cities are overlaid. Urban agglomerations of >1 million people span a 30 °C range of mean annual temperature and a 4000 mm range in total annual precipitation (Fig. 1). Such variation has a considerable influence on the environmental impacts of urbanization, including UHIs, and in consequence on the effects of urbanization on biodiversity. Quantifying such abiotic environmental variation is important because ultimately it influences organismal temperature, water balance and energy state (Kearney *et al.* 2013), and therefore, the probability of survival and reproduction. Global-scale climatic data combined with weather forecasting models can provide fine-scale spatially and temporally explicit data (Kearney, Matzelle & Helmuth 2012) from which biologically relevant microclimate information can be derived (Kearney *et al.* 2014). Many cities have also deployed or are deploying sensor networks,

which enable continuous monitoring of environmental conditions (Muller *et al.* 2013). When coupled with appropriate biophysical models, such environmental data can be used to provide both real-time situational reports and forecasts for changes in the abiotic and biotic environments.

Biophysical approaches to impacts and responses

Physiology and behaviour mediate abiotic environmental influences on population dynamics and larger scale ecological patterns in a variety of ways (Porter *et al.* 2000; Helmut, Kingsolver & Carrington 2005). Although organisms respond to many intrinsic and extrinsic demands simultaneously, activity, abundance and distribution can readily be modelled by explicitly considering the

influence of temperature, water balance and nutritional availability on physiological state, survival and/or reproduction (Andrewartha & Birch 1954). Several approaches are available for doing so, such as biophysical models, matrix population models and integral projection models (Kearney & Porter 2009; Lončarić & Hackenberger 2013; Rees, Childs & Ellner 2014).

Building on existing biophysical models, which link individual energetics with population dynamics (Porter *et al.* 2000), the thermodynamic niche approach (Fig. 2) provides an integrated assessment of how habitat, weather and food availability interact with heat, water and energy budgets to determine animal activity, fitness and abundance (Kearney *et al.* 2013; Tingley *et al.* 2014). The thermodynamic niche approach and other mechanistic modelling approaches have been made spatially explicit through the application of geographic information systems

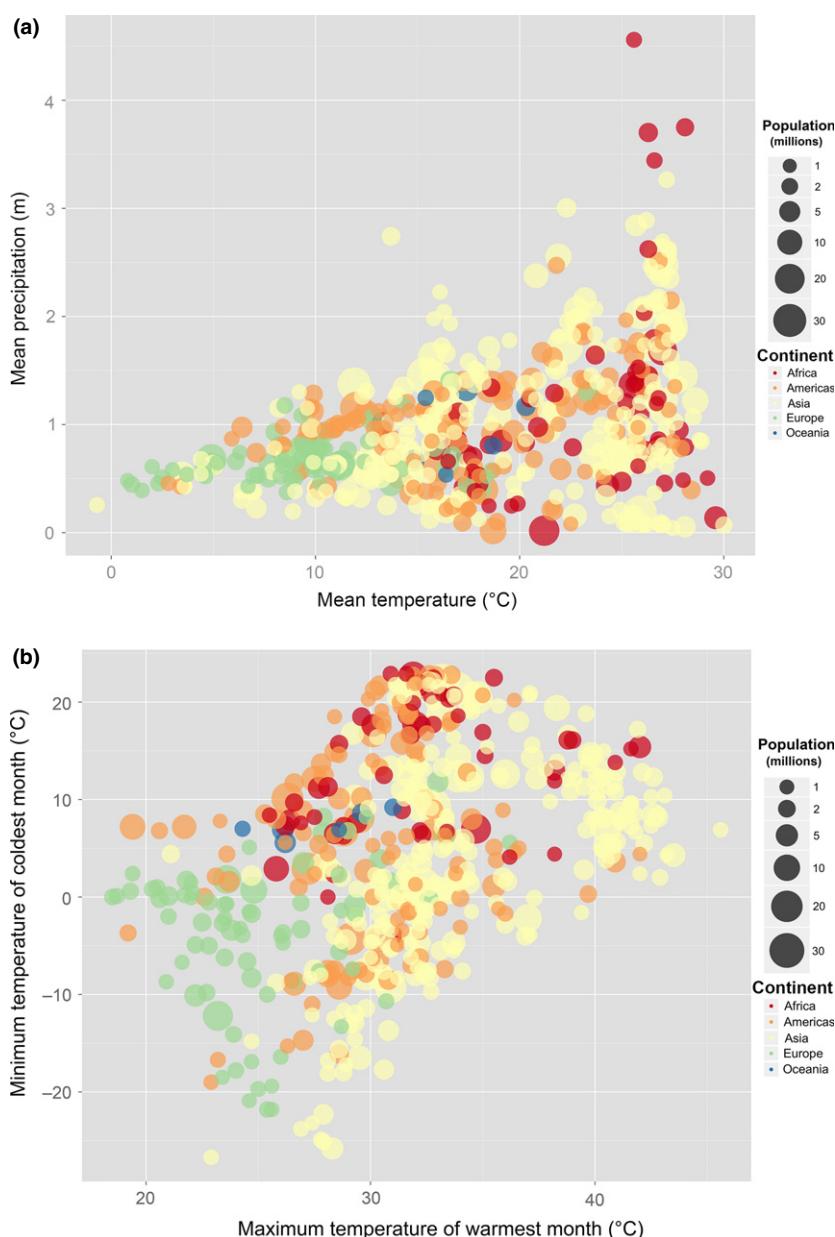
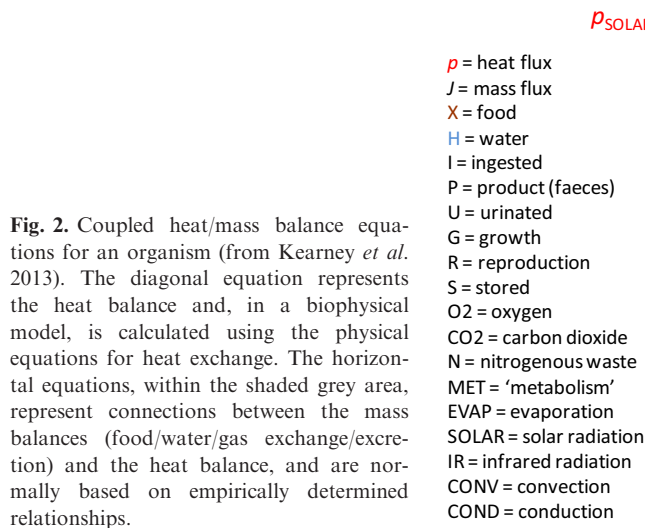


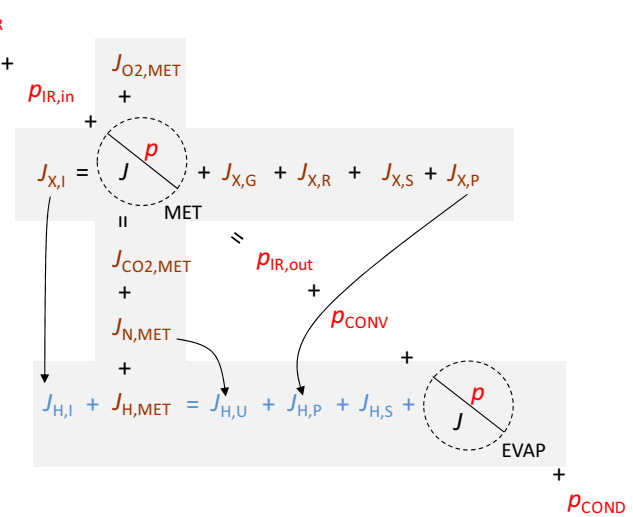
Fig. 1. Climatic data for major urban agglomerations of the world (≥ 1 million inhabitants; www.citypopulation.de) extracted from the WorldClim data set (30 arc-sec resolution; Hijmans *et al.* 2005). (a) Mean annual temperature (BIO1) against mean annual precipitation (BIO12). (b) Maximum temperature of the warmest month (BIO5) against minimum temperature of the coldest month (BIO6).



(Kearney & Porter 2009; Chown 2012). Thus, spatial variation in abundance (such as between cities and adjacent landscapes) can be modelled. In addition, because the thermodynamic niche model is trait based, organismal responses as a consequence of plasticity, evolutionary change, or some combination of the two can be readily assessed (Kearney *et al.* 2009).

The most notable disadvantages of mechanistic models are the absence of trait values for many species (Higgins *et al.* 2012), the variation in trait values among closely related species (though this depends on the trait in question – see e.g. Araújo *et al.* 2013; Clusella-Trullas & Chown 2014), and the time, effort and resources required to collect trait value information (Kearney & Porter 2009). Several developments suggest that these concerns are dwindling. First, new approaches are being developed which estimate physiological parameters from data on species distributions. They use a model structure that defines and constrains, in a biologically realistic way, how environmental factors influence performance (Higgins *et al.* 2012). In doing so, they represent a substantive departure from simple assumptions about physiological traits based on distributional data (e.g. Bonier, Martin & Wingfield 2007), which have been shown to be flawed for several reasons (e.g. Boucher *et al.* 2014). Secondly, the development of trait-based approaches to understanding assemblage structure and dynamics has improved substantially both the availability of trait data (e.g. Jones *et al.* 2009; Kattge *et al.* 2011; Wilman *et al.* 2014) and the theoretical framework for applying it (e.g. Petchey & Gaston 2006; Shipley, Vile & Garnier 2006; Cavender-Bares *et al.* 2009). Finally, assessment of multiple phenotypic traits for many individuals and species (i.e. phenotyping or phenomics) is not only being more commonly used in gathering plant trait data (Houle, Govindaraju & Omholt 2010; Furbank & Tester 2011), but is also being deployed for collecting trait information on animals (e.g. Jumbo-Lucioni *et al.* 2010; Kellermann *et al.* 2012).

To date, mechanistic models for understanding the distribution, abundance, behaviour and likely stresses on



organisms in cities have not been broadly applied. Some work on vertebrates, and on insect disease vector distribution in cities, has been undertaken, though most often correlative or matrix population models are used (e.g. Chaves *et al.* 2011; Cailly *et al.* 2012; Uriá, Mahiques & Gras 2013; Sol *et al.* 2014). Likewise, several models have been applied to understand likely physiological stress experienced by humans (e.g. Blazejczyk *et al.* 2012). Nonetheless, the availability of fine-scale climatic data and growing trait databases suggest that such approaches could provide considerable insight into the mechanisms underlying the distribution of urban diversity and the likely future of that diversity as climates continue to change in response to anthropogenic forcing. We illustrate the potential for such an approach in the next section using a broad-scale assessment of thermal tolerances in the context of a macrophysiological 'exit' rule. The approach is informed by the close fit between upper thermal tolerance limits and geographic ranges found in some Australian *Drosophila* (Overgaard, Kearney & Hoffmann 2014).

Entry and exit rules: the urbanization filter

A general framework for understanding the way in which the impacts of urbanization are mediated through organismal thermal physiology (or other aspects of the physiological phenotype) is provided by considering the mechanistic basis of three sets of processes that determine assemblage membership: entry rules, exit rules and transformations (Gaston *et al.* 2009). Entry rules are biases in the processes that determine which individuals join a population or assemblage, exit rules are biases in the processes that determine which individuals leave a population, and transformations concern processes that act on individuals which remain part of an assemblage or population (Fig. 3).

Although some evidence exists for a global suite of urban exploiters, such as feral pigeon, rats and mice, pest insects and several species of plant (La Sorte, McKinney & Pyšek 2007; La Sorte *et al.* 2008), which contribute to

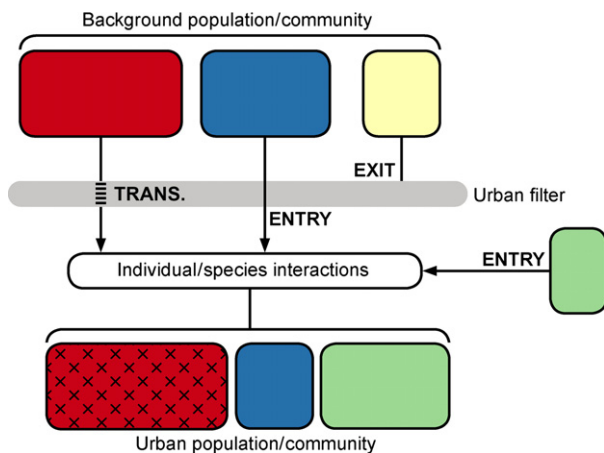


Fig. 3. Schematic of the urban physiological filter. Entry rules determine which species or individuals from the original assemblage can survive the urban transition (blue boxes). In addition, they describe which species may further enter the urban assemblage, such as those introduced purposefully or accidentally by humans (green boxes). Exit rules determine which species will not survive the urban transition (yellow box). Transformations are indicated by which individuals and species will change in response to the changing environmental conditions through phenotypic plasticity or genotypic change (for populations) or some interaction of the two (red and hatched red boxes). Interactions among species, which may also be mediated by abiotic environmental conditions (such as through variation in rate-temperature responses among predators and prey), are important and are indicated.

homogenization of diversity (McKinney 2006), investigations typically show that urban diversity comprises a subset of species derived from more local assemblages (Raupp, Shrewsbury & Herms 2010; Menke *et al.* 2011; Ślipiński, Żmihorski & Czechowski 2012; Martinson & Raupp 2013; Aronson *et al.* 2014). Moreover, a growing number of investigations demonstrates systematic changes leading to substantial transformations in the traits of urban populations (e.g. Searle *et al.* 2012; Meineke *et al.* 2013). In consequence, all three processes clearly contribute to assemblage modification, with exit rules dominating, given substantial initial disturbance associated with habitat alteration and fragmentation.

Humans are a major contributor to entry rules through the deliberate introduction of a wide range of plant species to the urban environment. Such introductions are one of the most significant drivers of change, with diversity in other terrestrial groups, and particularly insects, being determined by them (Faeth, Saari & Bang 2012). Although the physiological form of this entry rule might not be immediately obvious, performance and behaviour are influenced in several ways. These include the manner in which animals seek to realize their nutritional intake targets (e.g. flying foxes in Melbourne Australia, Williams *et al.* 2006), responses to changes to abiotic environmental conditions, including the thermal environment, as a consequence of alterations in plant structure, and through interactions between these factors (Cregg & Dix 2001). In New York City, for example, floral abundance and the

availability of sunlight both have positive effects on butterfly and bee species richness, and together with garden area in the case of bees account for approximately 60% of its variation among sites (Matteson & Langelotto 2010). One mechanistic explanation for this finding is the well-established importance of solar radiation for the thermal physiology and activity of day-flying insect pollinators (Chown & Nicolson 2004; Barton, Porter & Kearney 2014).

Broad environmental tolerances, tolerance of disturbance (associated with fast growth rates and high reproductive output), and the ability to exploit areas with high nutrient loading are also important contributors to population success in cityscapes (Pyšek *et al.* 2009, 2010; Sol *et al.* 2014). For example, in the Seattle metropolitan area, urban insect diversity is only weakly related to temperature, suggesting that broad thermal tolerances are an important component of the urban environmental filter (Van Nuland & Whitlow 2014). If thermal specialists were an important component of insect diversity, stronger relationships of diversity with temperature would be expected because of turnover or richness variation. The urban heat island effect may also benefit groups directly in temperate regions by increasing survival and performance. Thus, elevated temperatures are likely to mean less chance that species encounter their lower lethal temperatures or limits to activity, especially if they are able to overwinter in warm sites. Because of positive relationships between temperature and performance (such as fecundity or growth rate), at least until the optimum temperature is reached (Angilletta 2009), elevated ambient temperatures may also promote enhanced performance. Examples of enhanced survival in urban environments include the Argentine ant in New Zealand and North American cities (Gordon *et al.* 2001; Hartley & Lester 2003), survival of monk parakeets in North American urban areas located in cold regional environments, where both the urban heat island effect and high food abundance may account for their success (Davis, Malas & Minor 2014), and expansion of the range of the rufous-backed robin in Mexico (Martínez-Morales *et al.* 2010). Enhanced performance, associated with the UHI, has been found for scale insects in Raleigh, North Carolina (Meineke *et al.* 2013). Downstream outcomes of entry rules, such as phenological shifts (e.g. Townroe & Callaghan 2014), may be complicated by interactions among simultaneous environmental change drivers (such as climate change). They may also be complicated by dispersal from rural sources to urban sinks in mobile groups such as insects (Altermatt 2012), but perhaps not in less mobile ones such as plants (e.g. Zhang *et al.* 2004; Neil & Wu 2006; Yang, Tian & Chen 2013).

For exit rules it is clear that, in addition to the major landscape change and direct species extinction precipitated by humans (Shochat, Warren & Faeth 2006; Buczkowski & Richmond 2012), selective loss of particular species or groups is also important. Thermal tolerance and the relationship between performance and temperature in many groups (notably plants and ectothermic animals) can be

key mediators of population loss from urban environments. In the case of ants in the city of Raleigh, North Carolina, species that are typical of cooler and moister natural environments do not persist, likely reflecting physiological influences of the UHI (Menke *et al.* 2011). A similar situation appears to be true for lichens, where rather than the impacts of pollution, differences in temperature and water availability also appear to be driving assemblage structure in an urban setting in Portugal (Munzi *et al.* 2014).

Given that temperature has such a significant impact on ectotherm function, one way to assess the potential general impact of cityscapes on ectotherms globally is to determine the role cities might play in altering warming tolerance (WT – the difference between a population's critical thermal maximum and habitat temperature) or thermal safety margins (TSM – the difference between a population's optimum performance temperature and habitat temperature) (Deutsch *et al.* 2008). Although estimates of both WT and TSM are substantially affected by microclimate and behavioural regulation in terrestrial species (Sunday *et al.* 2014; Pincebourde & Casas 2015; Woods, Dillon & Pincebourde 2015), they provide a useful first, global-scale approximation of the potential influence of urban heat islands on ectotherm extinction risk. Analogous measures are the thermal buffer (difference between critical thermal maximum and maximum temperature) (Kingsolver, Diamond & Buckley 2013) and tolerance of extremes (difference between critical thermal maximum and maximum habitat temperature) (Faulkner *et al.* 2014).

Using data from Hoffmann, Chown & Clusella-Trullas (2013) and Sunday *et al.* (2014), we estimated insect warming tolerance (as the difference between upper thermal physiological limits and maximum monthly land surface temperature, i.e. more akin to the tolerance of extremes of Faulkner *et al.* 2014; see Supporting Information) both for the locations from which the populations used in the thermal tolerance assessments were collected, and from the nearest urban agglomeration (median distance = 113.3 km; see Supporting Information). Transposing sampled populations to the nearest urban area clearly reduces warming tolerance by several degrees, though this effect is on average relatively stronger for the Southern than the Northern Hemisphere (Fig. 4). The smallest warming tolerances, both outside and within urban areas, are found between about 30 and 35° in latitude, reflecting their high ambient maximum temperatures (see also Hoffmann, Chown & Clusella-Trullas 2013). These areas will also experience substantial ongoing global warming (IPCC 2014), meaning elevated risk for insect populations. Nonetheless, the extent to which this extinction risk will be realized for various populations will depend considerably on how cities seek to manage the UHI, if they do so at all (Alberti 2010). For example, the City of Melbourne, Australia has recognized the threat posed by urban heating and climate change. It has therefore implemented an urban forest strategy to reduce these impacts (<http://participate.melbourne.vic.gov.au/projects/>

urban-forest-precinct-plan/), which, in turn, will have substantial effects on resident animal populations (see Sunday *et al.* 2014; Woods, Dillon & Pincebourde 2015 for discussion of the underlying reasons).

Declines in predators or parasites (especially in insect assemblages) are also frequently recorded in urban areas. While a variety of mechanisms for the declines has been proposed (Raupp, Shrewsbury & Herms 2010), one relatively understudied impact is related to differences in the slope of rate–temperature relationships among trophic levels. The relationship between temperature and various rates (e.g. activity, resource acquisition, physiological rates) is often steeper in predators than in their prey (Dell, Pawar & Savage 2011). Increased temperatures associated with UHIs are therefore likely to mean greater costs to predators, which in the long-term may in consequence suffer population declines owing to resource limitation (Martinson & Raupp 2013). This mechanism is similar to the one proposed for increases in metabolic costs generally in ectotherms as global temperatures rise (Dillon, Wang & Huey 2010). Indeed, such increases in costs may be realized especially where organisms typically rely on low-temperature environments for reduced metabolism during dormancy or diapause, but which may be less available in warmer cityscapes (for an analogous discussion see Williams, Shorthouse & Lee 2003; Williams, Henry & Sinclair 2015).

How exit rules play out may differ substantially among cityscapes because of their substantial abiotic variation (Fig. 1). For example, across the U.S.A. in aquatic invertebrate assemblages, the extent of urban impact depends on background temperature and precipitation conditions. In areas of higher temperature and lower precipitation, urbanization impacts tend to be less marked than in moister, cooler areas (Cuffney *et al.* 2011). Such context dependence of the impact of urbanization (and other land-use change) seems typical for many ecological systems and assemblages (e.g. Lake *et al.* 2010; Bang, Faeth & Sabo 2012).

Transformations: phenotypic plasticity and genotypic change

Transformations of physiological characteristics or responses mediated by physiological traits in cityscapes are readily distinguished (Isaksson 2015). One way to think about the influence of urban environments on phenotypes is the way in which phenotypic variance is typically realized through genotype effects (V_G), a systematic environmental effect (V_E) and genotype by environment interactions ($V_{G \times E}$) (Via & Lande 1985). Thus, different genotypes might either be selected for in urban contexts, or urban environments might simply have an effect on all genotypes, or there may be genotype by environment interactions (Marzluff 2012; Donihue & Lambert 2015). An important component of the phenotypic variation is ‘...the environmentally sensitive production of alternative

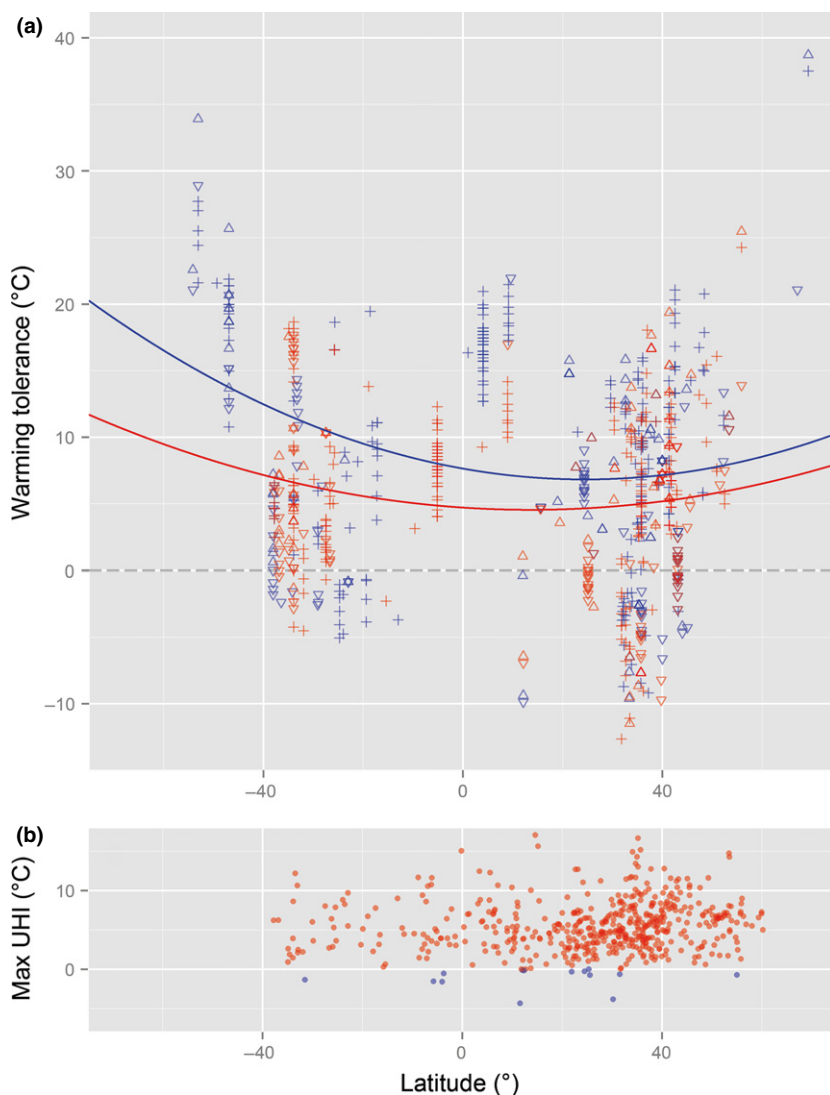


Fig. 4. Original and urban-adjusted warming tolerance of insects to assess the potential effects of urban heat island warming. Warming tolerance (a) was calculated as either the difference between critical thermal maximum (+), upper lethal temperature 50 (▽) or upper lethal temperature 100 (Δ) (data from Hoffmann, Chown & Clusella-Trullas 2013; Sunday *et al.* 2014) and the maximum environmental temperature. Original warming tolerance (blue) was calculated using the maximum environmental temperature of the original sampling location, and urban-adjusted tolerance (red) was calculated using the maximum environmental of the nearest urban agglomeration. Low values indicate small margins between the environmental temperature and upper thermal tolerances, while negative values are indicative of thermal tolerances being exceeded. Second-order iterative least-squares regression shown for all original (blue) and urban-adjusted (red) warming tolerances. Estimates of maximum urban heat island temperature increase for urban agglomerations (b) were calculated as the difference between the highest urban temperature and the background average. Blue dots indicate values less than zero. Detailed methods can be found in Supporting Information.

phenotypes by given genotypes’, or phenotypic plasticity (DeWitt & Scheiner 2004).

In red oak seedlings, for example, the New York urban environment promotes a larger biomass relative to rural sites primarily as a consequence of changes in growth allocation, with greater allocation to leaves and a reduction in below-ground carbon costs in the urban-grown seedlings (Searle *et al.* 2012). The difference seems to be largely a systematic environmental effect. Similar effects have also been found for plant phenology and growing season length in a variety of urban settings compared with more rural areas, with clear indications of the impacts of the UHI (Zhang *et al.* 2004; Neil & Wu 2006; Gazal *et al.* 2008; Jochner *et al.* 2012). In urban settings in western Poland, a systematic environmental effect, attributed to UHIs, appears to be driving stronger changes in migrant arrival dates than is taking place in more rural settings (Tryjanowski *et al.* 2013).

In four species of chitinolytic fungi compared among urban and rural sites close to Louisville, Kentucky, two of the species show similar genotypic effects over a range of

environments. The urban isolates grow faster than the rural ones across a range of temperatures. Two other species show genotype \times environment interactions, with the urban isolates growing faster than the rural ones at high temperatures (26 °C) and the converse being the case at lower temperatures (18 °C) (McLean, Angilletta & Williams 2005). In the lizard *Anolis cristatellus*, introduced from the warmer Puerto Rico to the cooler Miami, Florida, critical thermal minima declined by 3 °C over 35 generations, likely reflecting an evolutionary response to the cooler Miami environment (Leal & Gunderson 2012).

Less clear cut is change in the scale insect *Parthenolecanium quercifex*, which is more abundant on willows in warmer than cooler parts of Raleigh, North Carolina. Individuals from the warmer environments show a much greater increase in abundance in controlled greenhouse environments than those from the cooler environments. Whether plasticity or adaptation is responsible for the difference is not clear (Meineke *et al.* 2013). Systematic differences in upper thermal tolerance (on average a 20% increase in ability to remain mobile at 42 °C in urban over

rural individuals) have also been found among populations of urban and more rural leafcutter ants (Angilletta *et al.* 2007), though whether the difference is a consequence of genotypic change or phenotypic plasticity has not been determined.

Conclusion and prospects

The impacts of urbanization are not only substantial, but are also overlaid on a range of other changing environmental circumstances, of which global climate change is one of the most significant. Interactions among these different change drivers may have unexpected effects. For example, both global change and urbanization cause changes in phenology (shifting events earlier) of butterflies in Ohio, but their interaction can delay first appearances and influence peak abundance phenology (Diamond *et al.* 2014). The ways in which such interactions are likely to play out will vary substantially across the large environmental gradient spanned by cities (Fig. 1), especially given northern higher latitude declines in temperature variability owing to changes in lower temperature extremes (Screen 2014). Such changes can be both beneficial and detrimental to organisms depending on their life cycles and the stage and physiological basis of their overwintering strategies (e.g. Williams, Henry & Sinclair 2015).

With urban areas spanning such a wide range of environmental conditions, and environmental change proceeding in different ways in different settings, generalizations about biodiversity impacts of the urban–rural gradient may be much enhanced by adopting a physiological perspective. Doing so will require a range of approaches, of which we consider the following the most significant. (i) The integrated scheme (Fig. 3) we propose for understanding the role of thermal physiology in structuring urban assemblages relative to their rural counterparts should form a template for development of understanding in this area. Clearly, alterations in behaviour, physiological regulation and physiology are among the first responses organisms have at their disposal to deal with changing environments (Isaksson 2015). The scheme we have proposed provides an integrated means for understanding these responses and simultaneously provides direct links to ecology and macrophysiology (Gaston *et al.* 2009). (ii) Investigations of urban assemblages could readily be further developed using a mechanistic approach (e.g. Kearney *et al.* 2013) by recognizing that modern phenotyping and biophysical frameworks enable the approach to be deployed quite straightforwardly. (iii) Explicit investigations of physiological responses to cityscapes are required across a range of groups. Despite the fact that it seems obvious that such responses should occur, and evolve through time, investigations of thermal tolerance, water balance, performance and nutrient regulation in populations or assemblages living in urban areas compared with those in the surrounding rural landscape are surprisingly uncommon.

Should these and related approaches be adopted, the physiological perspective that has been applied so widely and successfully to understand the impacts of other forms of environmental change (e.g. Chown & Gaston 2008; Cooke *et al.* 2013) can be used further to mitigate and manage the impacts of urbanization. Doing so will, in our view, improve the prospects for biodiversity in the urban environments, which now constitute such a significant part of the global, terrestrial landscape.

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Data accessibility

Data in this paper are from published articles (Hoffmann, Chown & Clusella-Trullas 2013; Sunday *et al.* 2014) or are available online from the NASA Land Processes Distributed Active Archive Center (LP DAAC 2015) or from www.citypopulation.de. All other data are present in the manuscript and its supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Data S1. Methods for Figure 4.