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Getting ahead of the curve: cities as surrogates for global change

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Urbanization represents an unintentional global experiment that can provide insights into how species will respond and interact under future global change scenarios. Cities produce many conditions that are predicted to occur widely in the future, such as warmer temperatures, higher carbon dioxide (CO_2) concentrations and exacerbated droughts. In using cities as surrogates for global change, it is challenging to disentangle climate variables—such as temperature—from co-occurring or confounding urban variables—such as impervious surface—and then to understand the interactive effects of multiple climate variables on both individual species and species interactions. However, such interactions are also difficult to replicate experimentally, and thus the challenges of cities are also their unique advantage. Here, we review insights gained from cities, with a focus on plants and arthropods, and how urban findings agree or disagree with experimental predictions and historical data. We discuss the types of hypotheses that can be best tested in cities, caveats to urban research and how to further validate cities as surrogates for global change. Lastly, we summarize how to achieve the goal of using urban species responses to predict broader regional- and ecosystem-level patterns in the future.

1. Species interactions in cities: getting ahead of the curve

Cities are the future. Urban populations are expected to increase by 2.5 billion in the next 30 years [1] and urbanization will affect the physical environment, responses and interactions of all organisms that live in cities. Already, cities have warmer temperatures, higher carbon dioxide (CO_2) levels and exacerbated 'droughts' due to less infiltration and greater runoff of precipitation [2–6]. In relation to global change, species in cities—in particular, plant and arthropod taxa that have underscored research North America and Europe—have responded to urban and climate variables with phenological shifts, physiological changes and adaptive evolution (e.g. [7–9]). Relationships between species have been altered by abiotic and biotic interactions, ecological niches have shifted and new communities have developed (e.g. [10–12]). Similar climate conditions and impacts may occur outside of cities in future global change scenarios [5,13] (figure 1). Cities have thus been recognized for their potential importance as surrogates for global changes happening at larger scales, such as global warming, and for their potential use in observing and predicting broader ecological and evolutionary processes [9,14–20].

A critical question in moving forward with the use of cities as surrogates for global change is whether and, perhaps more usefully, when results from any one city or study organism are generalizable. To date, research has been performed disproportionately in North America and Europe, in fields ranging from atmospheric and earth sciences (e.g. [21,22]) to evolutionary biology (e.g. [23])—disciplines that are not traditionally well integrated—and has focused on the responses of plants and arthropods [24]. Even within the spectrum of ecological research, which is itself broad, separating the effects of global warming and urban warming, by, for example, comparing cities across latitudes [9,25], or comparing functional groups among cities [26,27], are relatively
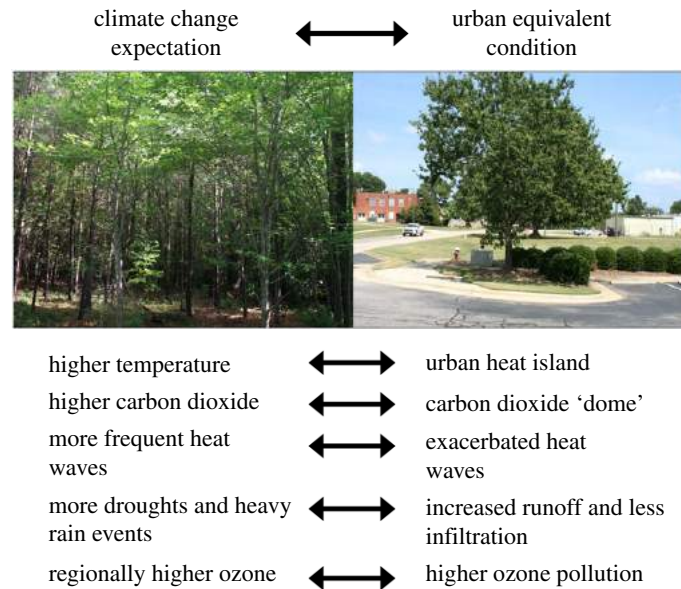
Figure 1. Climate change expectations and urban equivalent conditions. Pictured are a suburban forest (left) and an urban street tree (right) in the southeastern USA, located 5 km apart. (Online version in colour.)

recent initiatives. In this review, we will (i) examine insights that have been gained specifically from cities, regarding phenological, physiological, population, community and latitudinal responses by and interactions among species (electronic supplementary material, table S1). Where possible, we will discuss how urban results do or do not agree with experimental predictions or historical data, and how combinations of climate and urban variables, current and historical data or other approaches may be used to isolate effects of interest from confounding urban variables in cities. Then, we will (ii) consider the types of hypotheses that can be best addressed in cities, caveats to urban research and what can be done to further validate cities as surrogates for global change. Lastly, we will (iii) summarize the potential for urban species responses to inform broader predictions. Owing to a much greater amount of research on plants and arthropods, our review will focus on these taxa and their responses to warming; however, we emphasize that cities may ultimately present the only globally accessible and cost-effective means to observe the interactions of other taxa—from microbes to vertebrates—in response to multiple interactive climate variables, in different regions of the world. With their potential as 'space for time' substitutions, species responses in cities have occurred over a time scale and geographical scope that will complement our understanding of global change gained from historical, experimental and modelling data.

2. Global change insights gained from cities

(a) Phenological responses

Within cities, along urban–rural gradients and among cities at different latitudes (figure 2), studies have demonstrated phenological adjustments by urban species, sometimes in response to measured changes in urban temperature and sometimes in response to urban variables (such as impervious surfaces) that correlate with temperature. For example, long-term records show that the phenology of multiple flowering plants has advanced in 10 central European cities relative to

rural areas, with stronger trends in recent years [7]. Earlier plant phenology and urbanization are similarly correlated in remote sensing studies [30–33]. The combined effects of climate variables—specifically temperature—and urban variables on phenology have been observed via long-term records or on-the-ground observations for other flowering plants [34,35], urban insects [27,36] and urban birds [37,38]. Phenological advances in response to warming in cities are generally supported by experimental studies (e.g. reviews in [39,40]) and historical datasets from herbarium or museum collections [41–44].

Interactions between urban species are also affected by changes in phenology. In Raleigh, NC, USA, a herbivorous scale insect was not only more abundant on oak trees in warmer relative to cooler areas [45], but the phenology of the herbivore became decoupled from the phenology of the parasitoid wasps that previously formed a natural biocontrol, leading to decreased parasitism at a critical stage of herbivore development and increased herbivory on trees in warmer parts of the city [11] (electronic supplementary material, figure S3). Similarly, reduced parasitism of cereal leaf beetles, a herbivore pest of grain crops, was observed during multiple warmer springs in an agricultural setting [46]. However, field warming experiments may have context-dependent effects on plant and insect phenology [47]. For example, warming advanced the phenology of host trees more than the phenology of a herbivorous caterpillar [48], but in another study, warmed caterpillar eggs had high survival on host trees despite the lag period between egg hatch and bud burst [49]. Overall, there are increasing trends towards phenological asynchrony between plants and herbivores or pollinators [50,51], and asynchrony in multi-trophic interactions [24,52,53].

Intriguingly, historical collections have demonstrated that the phenology of multiple wild bee species advanced in parallel with that of bee-pollinated plants [42]. The use of historical data in combination with urban sampling is potentially a very powerful approach in understanding phenological responses. For example, Primack et al. [41] observed current flowering times of arboretum plants in Boston, MA, USA,
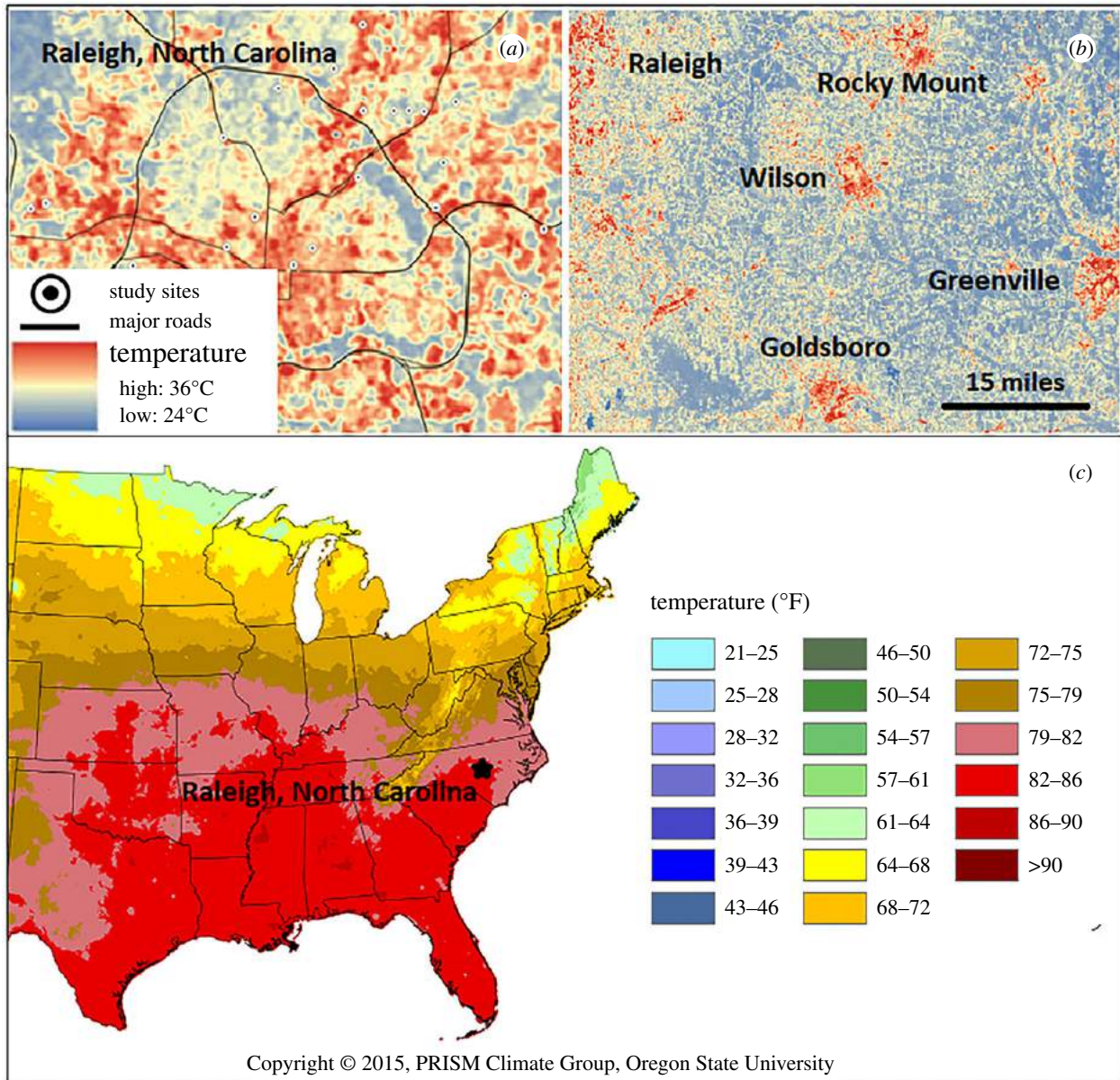
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Figure 2. Examples of how within-city, urban – rural and latitudinal comparisons can be used to study species responses to differences in temperature. (*a*) Within-city differences in temperature in Raleigh, NC, USA (adapted with permission from Dale & Frank [28,29]). (*b*) Urban – rural differences in temperature in eastern North Carolina (image provided by Elsa Youngsteadt). The Landsat thermal images in (*a*,*b*) are from 18 August 2007. (*c*) Average monthly temperature for August 2007 and latitudinal differences in temperature across the eastern USA, with Raleigh, NC indicated for reference (image from the PRISM Climate Group; www.prism.oregonstate.edu; data accessed 15 January 2017).

relative to flowering times of historical specimens of the same plants. Natural history collections or long-term records of invertebrate and vertebrate sightings could be used to complement herbarium studies and shed light on how phenological shifts have influenced species inter-actions over longer periods of time than are feasible to measure experimentally. Understanding how urban species have responded to gradual changes in climate variables over time will improve our ability to validate cities as surrogates for global change.

(b) Physiological responses

Physiological responses by species in cities include changes in rates of photosynthesis and growth of plants and changes in abundance and thermal tolerance of insects. Urban red maples had higher rates of photosynthesis [54] and growth in warmer relative to cooler sites within a city [28,55], and

red maple seedlings in a warming experiment were also able to acclimate photosynthetically [56]. However, while temperate forest trees generally respond positively to increases in temperature in warming experiments [57–60] (but see [61,62]), urban trees are more variable and have demonstrated lower rates of photosynthesis with warming [21,63] or no difference in rates of photosynthesis [64]. Expla-nations for these inconsistent physiological responses by trees could relate to the interactive effects of multiple climate variables in cities (such as relative humidity, CO_2 or soil moisture), urban variables (such as impervious surface, soil compaction or building architecture), choice of focal species and/or biotic interactions (with herbivores and pathogens, pollinators or natural enemies). Gregg *et al.* [65] found that increased growth of poplar seedlings in New York City was not due to warming, soil alteration or other urban variables, but, instead, was related to the negative effect of higher rural ozone concentrations on rural trees. Where urban species

responses agree with warming experiments and/or historical data, we can be more confident in the robustness of cities as surrogates for warming. The challenge, in moving forward, is determining why responses diverge. For example, the likelihood that air pollutants produced in cities may ultimately have a greater impact on trees in rural environments [65,66], or the possibility that warmer nighttime temperatures have greater effect than more commonly modelled daytime temperatures [64,67], may explain divergence between urban and experimental results.

Physiological changes may include acclimation or adaptive evolution in response to climate or urban variables in cities. Plasticity allows a genotype to acclimate or express a different phenotype under altered environmental conditions, while adaptive evolution is a change in the frequency of a genetically based trait, due to selective pressure, that results in higher reproductive success [18,68]. In an example of adaptation, Cheptou et al. [8] observed selection in favour of non-dispersing seeds in an annual plant in Montpellier, France, which improved urban fitness. Selection on functional traits also occurred in the city; urban plants retained physiological changes in size, rates of photosynthesis and concentrations of leaf nitrogen when grown together in a greenhouse with plants from rural sites [69].

The ability to cope with a broader range of temperatures and also acclimate to warmer overall temperatures may result in trade-offs between traits. For example, colder winter temperatures at ground level, due to snow removal in cities, selected against cyanogenesis in urban clover [23]. This otherwise beneficial anti-herbivory trait was selected against because of the greater potential for freezing to damage plant cells, and subsequent auto-toxicity, without an insulating cover of snow in cities [23]. The effects of warmer temperatures are more commonly studied in the context of global change, and while the frequency of cold days and cold nights are expected to decrease in the future, occasional cold winter extremes will continue to occur [70]. It is important to understand physiological responses of species to hot and cold temperatures, because more limited exposure to cold temperatures could result in more negative impacts when such temperatures do occur. Historical records may provide additional insights into how species balance general thermal tolerance with an ability to respond to cold and hot temperature extremes.

Plasticity in physiological responses to urban warming has also been demonstrated for insects, other invertebrates and fungi. Urban leaf cutter ants had higher thermal tolerance relative to rural ants in São Paolo, Brazil [71], as did urban chitinolytic fungi [72], and the abundance, survival or fecundity of multiple species of scale insects increased with temperature in Raleigh, NC, USA [11,28,29,45,55,73]. However, hatching success of land snail (*Arianta arbustorum*) eggs decreased in warmer urban areas [74], and recent studies have shown that solitary bees and bumble bees are more sensitive to warming [75,76], and that a more impervious surface, which is generally correlated with temperature, may increase the susceptibility of honey bee (*Apis mellifera*) colonies to disease [77]. The direct effects of warming on arthropods and other ectotherms are frequently mediated by habitat architecture and geometry, which may be more heterogeneous in cities but also more predictable, as buildings remain the same shape and size throughout the year [78]. Thus, for modelling the effects of climate variables that depend, to an extent, on arthropod behaviour in relationship to habitat, physiological responses of arthropods may potentially be more predictable in cities relative to warming experiments.

(c) Population and community-level responses

Plant and arthropod populations and community structure and function respond to both climate and urban variables in cities. Higher urban temperatures and CO_2 concentrations in Baltimore, MD, USA, relative to a rural site, closely matched short-term (approx. 50 year) climate predictions [5] and affected the structure of plant communities that were germinated from the same soil and seed bank. Urban plant productivity was higher after 1 year in Baltimore [14], relative to rural plant productivity, and urban plant succession reflected a greater ratio of perennials to annuals after 5 years [10], which could have multiple impacts on plant community function by affecting pollinator resources, habitat for beneficial or pest insects and multi-trophic interactions.

Arthropods may be affected directly by climate and urban variables in cities, and also via indirect effects on their predators and host plants [79]. Meineke et al. [80] found that spider abundance in urban trees in a mid-latitude city in the USA did not increase with warming, even though herbivore (prey) abundance did, and Turrini et al. [81] observed limited top-down control of aphids on urban relative to rural plants in Switzerland, but also found that plant biomass mitigated the benefit of aphid predators. Experimental warming affected plant community composition in China due to competitive interactions between plant species, but only in the presence of a beetle herbivore [82]. In other experiments, the combined effects of elevated warming, CO_2 and drought on an insect herbivore were mediated by changes in plant secondary compounds and nitrogen content [83], and elevated warming, CO_2 and nitrogen deposition affected floral attractiveness and nectar chemistry for bees [84]. In a herbarium collection, the abundance of scale insects preserved on red maples tracked historical temperature fluctuations [12], representing direct responses of scale insects to temperature but also indirect responses to changes in the condition of their host trees [28,55,73]. Thus, insect responses to the direct effects of temperature (or CO_2) are often difficult to separate from indirect effects on herbivores via the responses of their plant hosts [79,85].

Overall, studies of interactions among species or trophic levels are still outweighed by individual studies of plants or arthropods [24,47], and there is a general consensus that long-term and larger-scale experimental studies are needed to understand how interactive climate variables will affect population-level responses and community- and ecosystem-level processes [51,53,85,86]. Using cities as surrogates for some effects of global change is an opportunity to add to our understanding of the effects of multiple climate variables and the responses and interactions of understudied taxa like vertebrates, worldwide, at potentially lower cost in terms of time, money and infrastructure relative to traditional experimental manipulation of climate variables.

(d) Latitudinal responses

Species responses to urban temperature may vary with respect to differences in background temperature due to

latitude [17]. More positive effects of global change are generally predicted for species at higher latitudes [87,88]. Indeed, over a latitudinal range from 35.8° to 42.4°, arthropod abundance was positively correlated with increased within-city temperature in a high-latitude city in the eastern USA [25]. However, responses were of a greater magnitude and were more variable from positive to negative in lower latitude cities. Heterogeneous responses may ultimately cause greater disruptions of ecological dynamics than consistent directional responses—whether positive or negative—because species that currently interact with each other may respond differently to future warming [25] (electronic supplementary material, figure S3).

Latitude and urbanization may also have non-additive effects on species. Although shifts towards earlier phenology are common in response to latitude or urbanization alone, the interaction of these two factors led to delays in emergence and changes in the abundance of multiple species of butterflies in OH, USA, suggesting that butterflies responded to multiple environmental (climate and/or urban) variables [36], or that butterflies had a nonlinear response to temperature [89,90]. Long-term phenologies of flowering trees across the UK have been shown to be influenced by latitude and urbanization, with more pronounced advances occurring in northern areas [35] (but see [90]), and similarly over a large latitudinal gradient, urbanization and temperature had increasing effects on phenology for more than half of China's 32 major cities [33]. Recurrent adaptive evolution of cyanogenesis in clover was also strongly associated with both urbanization and latitude [23,91], while reflecting different selective pressures in different world regions [92].

3. Future directions in cities

(a) Hypothesis testing and study species in cities

Observing the effects of multiple climate variables over long periods of time and at a large spatial scale is a unique advantage in the use of cities as surrogates for global change. Cities are ideal for observing the effects of gradual changes in temperature and CO_2 on long-lived plants and animals that may be difficult to grow and manipulate experimentally. The responses of mature trees to global change are critical to ecosystem health and services, and long-lived arthropods or those with an overwinter diapause—which is often regulated by temperature—may also be ideally studied in cities, rather than in short-term experiments, to fully capture multi-trophic interactions over a species' entire lifespan. Cities can likewise be used to observe and test responses of insects that are difficult to confine experimentally, such as wild bees, which require a large amount of space and a variety of habitat and floral resources, or temperature-dependent outbreaks of insects such as defoliating caterpillars (e.g. [93,94]). Lastly, there are intriguing examples of vertebrate responses to urban variables, such as anoles with longer limbs that better suit their city habitat [95], and understanding these responses alongside corresponding climate variables and trophic interactions in cities would provide valuable insights into future regional and ecosystem-level patterns.

Cities are also an ideal location to study the formation and function of novel no-analogue communities. Intentional and unintentional species introductions in cities, habitat fragmentation and more challenging abiotic conditions have resulted in urban communities with no current rural analogues. Overall changes in biodiversity and species interactions are a major prediction of global change scenarios (e.g. [13,96,97]); however, changes in community assemblages do not necessarily mean a loss of biodiversity [98]. Thus, unique relationships between species in cities may predict future community interactions in rural environments. For example, urban corridors may facilitate the movement and persistence of heat-tolerant species of ants [99], butterflies [36,100] and spiders [101], as well as the establishment of non-native anoles [102] and the migration of birds [103]. Street trees and other amenity plants are often established outside of their native range, so comparisons can be made on the same species in hotter or cooler regions where they may exist naturally in the future [104]. Herbarium, entomological and natural history collections of other taxa can shed light on when new species were introduced in cities and how species have responded and interacted since their introductions. Such collections are frequently made at urban and rural locations and can be compared across space and time [41,43,44,105–107].

(b) Validating climate variables and evolutionary potential of species in cities

In the context of using cities as surrogates for the effects of global change, the measurement of multiple terrestrial climate variables such as temperature, relative humidity, precipitation and soil moisture, and atmospheric climate variables such as CO_2 and ozone ('essential climate variables' as defined by the NOAA Global Observing Systems Information Center, https://www.ncdc.noaa.gov/gosicas; accessed 30 January 2018) will contribute greatly to understanding species responses in cities and their relevance at the regional and ecosystem level. For example, increased evapotranspiration, such as in Madison, WI, USA [22], is influenced by soil moisture and urban warming, and may play a significant role in tree physiology [108–110], condition and herbivory [55,73]. Simultaneous measurement of climate variables and urban variables such as land cover, population density and impervious surface is crucial in addressing confounding factors associated with urban environments, such as air quality [65,66], water or soil pollution [111–114], soil compaction and invasive species [115–117].

Understanding the potential for acclimation or adaptive evolution by urban species (and the potential for non-adaptive genetic drift and gene flow) is also important in validating cities as surrogates for global change. Given concerns that many organisms will be unable to keep pace with environmental change via migration or adaptation [68,118–120], the responses of urban species that are unable to move beyond city limits or that experience delayed reproductive maturity—such as trees—may inform our understanding of the potential for natural populations to cope with global change and/or to experience non-adaptive processes [20,120]. Plastic and evolved responses to climate and urban variables have been demonstrated for individual species in cities (e.g. reviews in [18,20,68,121]), but the repeatability of such patterns among cities remains relatively untested (but see [23]), as does the degree to which plasticity facilitates or constrains evolution in cities, or whether genetic drift of gene flow may explain divergence in cities [121]. In addition to their direct effects on species responses to

climate variables, trait changes at the organism level may have cascading effects on multi-trophic interactions and on critical ecosystem services. Identifying drivers of urban adaptation and understanding the short- relative to long-term role of plasticity in urban species responses are important steps in making generalizable predictions based on urban species responses and interactions.

4. Conclusion: making predictions from cities

In this review, we summarize insights gained from cities into how climate and urban variables influence species responses and interactions. We discuss phenological and physiological responses at population, community and latitudinal scales of interaction, we examine how insights gained from cities compare with experimental studies and historical data, and we consider future directions for urban research in terms of hypothesis testing and validating cities as effective surrogates for effects of global change. The overall goal of this review is to determine how and when urban species responses can be used to predict broader regional- and eco-system-level patterns in the future, and to demonstrate that using cities as surrogates for global change can improve our geographic and taxonomic understanding of species responses and interactions.

Overall, the ability to study mature organisms that are ahead of the curve, experiencing the effects of multiple climate variables, and undergoing biotic and abiotic interactions *in situ* are significant advantages of urban research. These advantages will complement the understanding we have gained from field experiments, growth chamber studies and modelling efforts. While care must be taken to disentangle multiple driving variables and confounding effects in cities,

difficulties also exist in experimental manipulation of climate variables, in the cost of manipulating multiple variables or species over long periods and in the geographic restriction of many experimental systems to temperate latitudes [122,123]. Addressing these caveats in cities will produce results that are more generalizable between individual study systems, cities and ecosystems. Thus, while studies using cities as surrogates for the effects of global change have been primarily limited to the effects of warming on plants or arthropods, cities potentially represent an accessible and cost-effective means to observe the interactions of diverse taxa in response to multiple interactive climate variables and to make use of complementary experimental and historical data to define testable hypotheses. Species responses and interactions in cities are currently an underused resource in making broader ecological predictions.

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7

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