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Urban insect bioarks of the 21st century

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Insects exhibit divergent biodiversity responses to cities. Many urban populations are not at equilibrium: biodiversity declines or biodiversity recovery from environmental perturbation is often still in progress. Substantial variation in urban biodiversity patterns suggests the need to understand its mechanistic basis. In addition, current urban infrastructure decisions might profoundly influence future biodiversity trends. Although many nature-based solutions to urban climate problems also support urban insect biodiversity, trade-offs are possible and should be avoided to maximize biodiversity–climate cobenefits. Because insects are coping with the dual threats of urbanization and climate change, there is an urgent need to design cities that facilitate persistence within the city footprint or facilitate compensatory responses to global climate change as species transit through the city footprint.

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Urban insect biodiversity

Unsurprisingly, cities with their attendant novel biophysical landscapes can lead to declines in insect species richness and the abundance of individual species [1,2], but not exclusively. In some cases, enhanced urban insect richness can be driven by the concentration of exotic insects in highly urbanized landscapes [3]. While in other cases, urban insect richness has been shown to be the same or higher than insect richness at nearby undeveloped locations based solely on trends among native species [4,5].

Because each of the possible biodiversity gradients — declines, increases, or the maintenance of biodiversity — have been documented for insects living across urbanization gradients, this variation likely reflects the fact that a combination of different mechanisms underlies these patterns. Such variation could arise from methodological issues in quantifying biodiversity or from biologically meaningful factors [6]. These include the taxonomic identity of the insects under consideration, the regional species pool and species-specific capacity to colonize and persist in or around cities, and aspects of the development and geographic position of the particular urban landscape. Below, we unpack these different potential contributions to insect biodiversity trends across urbanization gradients, and consider how ongoing and future changes in cities could either serve to enhance or dampen urban insect biodiversity.

Challenges and opportunities in quantifying insect biodiversity in cities

Before considering how to quantify urban insect biodiversity, it is important to clarify what is meant by 'urban'. We adopt a broad definition encompassing human-modified landscapes for settlement and associated functions (e.g. commercial and industrial development), though we acknowledge the large heterogeneity of such environments [7]. Throughout, we refer to comparisons of urban versus rural habitats (or gradients between the habitats) as a heuristic to distinguish urban habitats from habitats with little-to-no human modification. This definition excludes human-modified habitats for agricultural use from consideration as 'rural'.

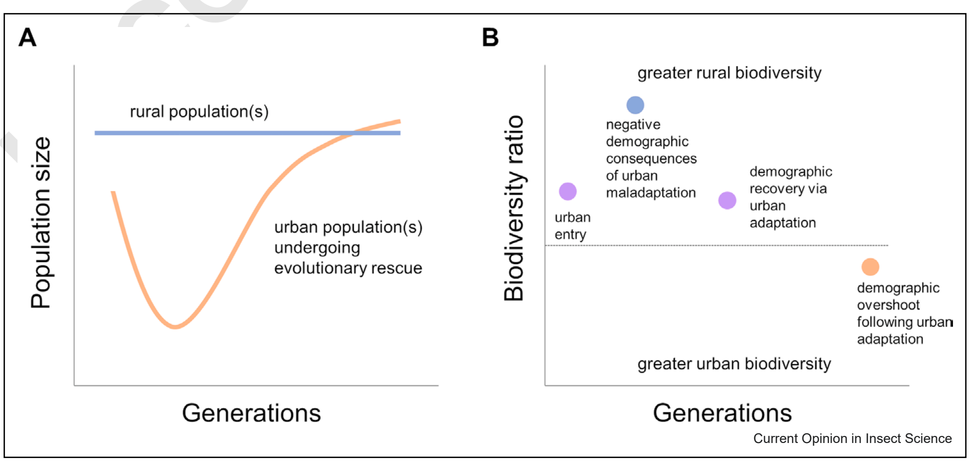
On the surface, the quantification of urban biodiversity is simple enough: standard survey methods such as visual observations, pitfall traps, bait traps, and light traps can be used to quantify the number of species and their individual abundances at sampling points from beyond the urban footprint to the city core. However, in practice, both universal and urban-specific factors make this task complex [8]. As one example, site-selection biases can yield misleading estimates of biodiversity gradients [9], and such considerations can be magnified in cities with rapid landscape changes over compressed spatial scales [10]. As another example, urban changes themselves might interfere with the ability to sample particular groups of insects, for example, light pollution that interferes with light trapping, or air pollution that interferes with bait trapping [11].

Biodiversity patterns emerge from the population dynamics of individual species [6]. Understanding population-level responses to urbanization can both link biodiversity patterns with their mechanistic underpinnings and identify methodological issues in quantifying urban biodiversity. To wit, urban boundaries are often porous with respect to movement of individuals, and transient use of urban habitats could complicate biodiversity assessments. At the most extreme, strong gene flow across the urbanization gradient, for example, driven by high dispersal capability, could blur the distinction between urban and nonurban populations of some species [12]. Alternatively, meta-population dynamics within or across the urbanization gradient [13] could enhance or diminish apparent biodiversity depending on the time point at which the populations are sampled. For example, some butterflies are resident outside the city footprint, but transiently use urban spaces for resource supplementation [14]. Relatedly, urban-associated changes in phenology driven by urban heat island effects or artificial light at night [15,16] could similarly bias estimates of biodiversity when there are limited sampling intervals across the activity season of a particular species. As a consequence, single or limited time point measurements of biodiversity across an urbanized-to-undeveloped gradient might fail to capture relevant urban biodiversity.

Indeed, the importance of sampling frequency within the activity season of an organism also extends to issues surrounding sampling intervals over longer, cross-generation timescales. For example, evolutionary rescue of insect populations in cities is expected to be preceded by demographic loss followed by recovery [17], so biodiversity estimates could be biased depending on when populations are sampled in the rescue process (Figure 1). These initial demographic losses could be severe given the effects of urban fragmentation on effective population sizes [18], and thus measurement of increasing or decreasing population trends could be more relevant than comparisons of absolute biodiversity estimates across urbanization gradients at a given time point. Relatedly, species with long generation times, such as periodical cicadas, necessarily incur limits on evolutionary rescue under rapidly changing environments [19] such as those found in cities. This could subject them to extirpation lags that would be missed in biodiversity measurements without decadal-scale sampling.

Further supporting the need for long-interval sampling, widespread geographic range shifts under contemporary climate change are likely to influence urban biodiversity. There is relatively high variation in the magnitude (and sometimes direction) of the shift among species, with some species able to perfectly track their historical climatic niches, while other species imperfectly track climate and experience 'climate debt' [20]. Although the nature of the shift response is likely to modulate whether species encounter and are able enter the urban environment (e.g. species experiencing large climate debt might be excluded from already-warm cities), range-shifting species could influence urban biodiversity in a number of ways. For example, in the case of leading-edge expansions, climate-driven range shifts could add new species to the urban landscape, bolster numerical representation of a species already occurring within the

Figure 1



A hypothetical example of temporal changes in urban versus rural biodiversity patterns assuming evolutionary rescue (demographic loss and recovery) of the urban populations. **(a)** Population size over time (expressed as number of generations) for unperturbed rural populations and urban populations undergoing evolutionary rescue characterized by a demographic decline followed by recovery in conjunction with adaptive evolution to altered urban environments. **(b)** Biodiversity-level consequences of urban evolutionary rescue that initially results in greater rural biodiversity owing to negative effects of urban entry and negative demographic consequences of urban maladaptation followed by narrowing of the urban–rural biodiversity gap, leading to maintenance of biodiversity across the gradient or potential overshoot of the urban population through the urban adaptation process.

urban environment, bring new alleles into extant urban populations that influence evolutionary trajectories and population demography [21], and impact the abundance of other current urban-dwelling species [22]. The effects of different climatic forces on pushing-and-pulling species ranges and distributions under global climate change are currently under intense study [23], as are the effects of the human footprint on contemporary range shifts, mostly from the perspective of dampening range shifts [20]. However, the mechanistic linkages between these two research areas, that is, how urban areas act as repellers, or potentially even attractors, as species shift their geographic ranges under climate change, are not well established. While datasets exist that are relevant for addressing this question, including those on climate-driven range shifts [20] and urban biodiversity [1,2], the degree of overlap of comparable species in comparable geographic locations might be limited.

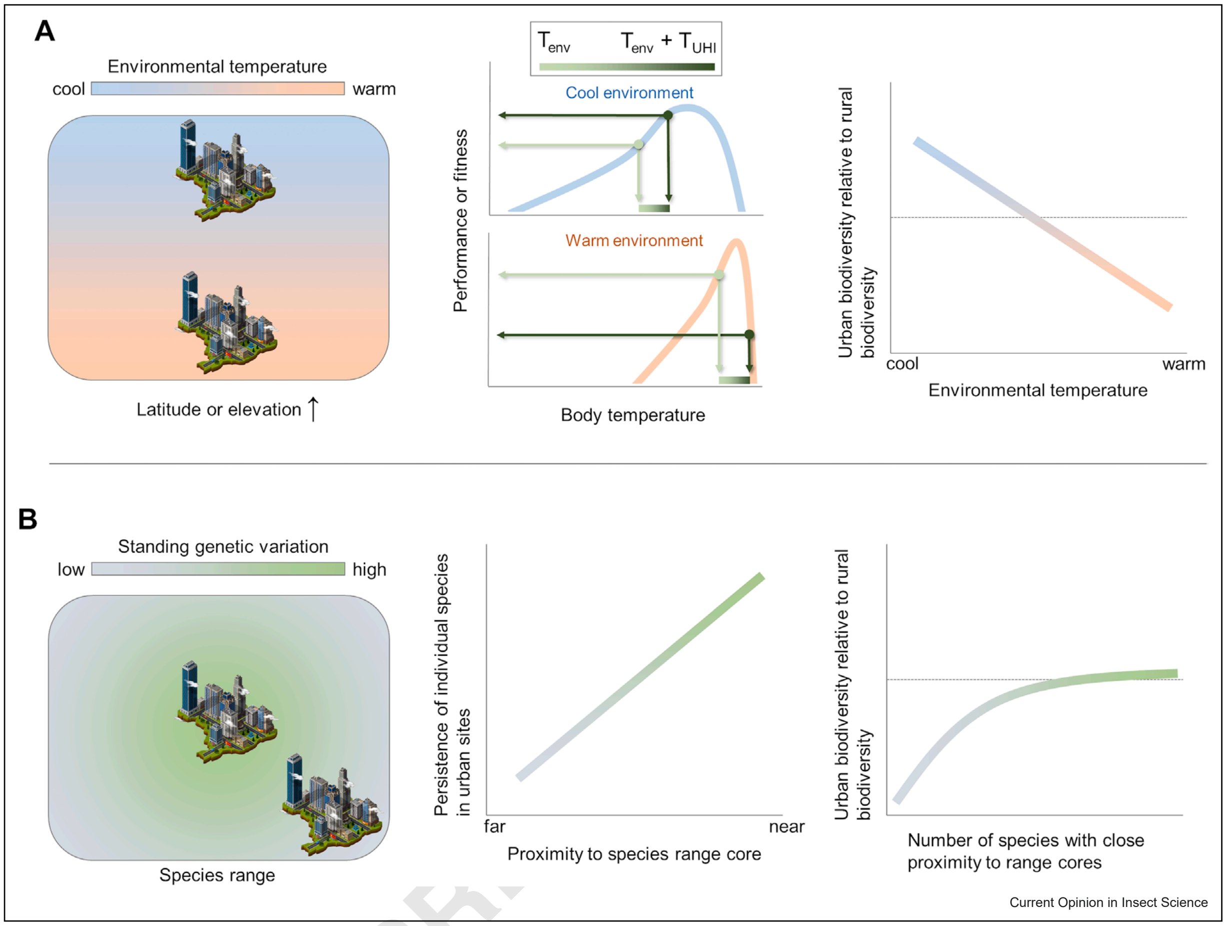
As one tangible way to begin to tackle this question of the interactive effects of climate change and urbanization, we can consider how the background climate throughout a species' range and its effects on thermal physiology might mediate local population responses to urbanization. Biogeographic studies of the effects of background climate on physiological traits of insects show that thermal tolerance breadth tends to increase with latitude [24]. This pattern largely arises from gains in the ability of high-latitude species to tolerate low temperatures coupled with minimal changes across latitude in the ability of species to tolerate high temperatures. Global climate change is anticipated to relax constraints on populations limited by low-temperature physiology at high latitudes, potentially leading to increased population growth [25]. Cities, through the generation of urban heat islands, might have similar effects at high latitude. Specifically, insect populations at high-latitude cities could thrive in these environments and be 'pulled' into urban habitats (Figure 2a). By contrast, low-latitude cities could negatively impact insect population growth, as these populations tend to already be close to their thermal optimum and upper thermal limits, leaving them vulnerable to additional warming and 'pushing' them out of urban habitats [26]. Indeed, recent work in ants is suggestive of this process [27]. Yet, the evidence from Lepidoptera is more mixed. While there are data showing large declines in urban moth diversity at low latitude (e.g. in southern Ecuador, Ref. [28]), there are also data showing evidence of declines in urban moth and butterfly diversity at high latitude (e.g. in Belgium, Ref. [11]). Thus, refinement of expectations might be in order. Specifically, while urbanization might consistently diminish biodiversity for some taxa, the magnitude of species loss might be relatively lower for high-latitude cities. This pattern is borne out by comparing urban biodiversity loss of the Lepidopteran exemplar studies described above. Urban moths in Ecuador exhibited a 65% loss in diversity compared with rural moths (based on the Shannon index of biodiversity) [28], whereas moths in Belgium exhibited a 43% loss in diversity (also using the Shannon index) [11]. Whether this pattern holds more broadly is unclear, and is an area ripe for formal synthetic analysis. As a final update to our expectations, it is necessary to point out that the strength of the urban heat island effect relative to the background climate can diminish in magnitude or even change direction in already-warm habitats at the lowest latitudes [29]. In this case, very low-latitude urban environments might not act as repellers, or might even become attractors.

The relative biogeographic position of a city within a species' range could have similar effects to the position of a city across latitude. Cities at cold-range edges could relax constraints on low-temperature physiology, whereas cities at warm-range edges might exert additional pressure on high-temperature physiology to be able to persist in that location [30]. Though, these effects might be opposed by other forces. For example, the location of the city within the species geographic range can also determine the standing genetic variance and thus influence the response to selection (Figure 2b). The ability to colonize and persist in cities might be more difficult at range edges due to low genetic diversity and high genetic load (accumulation of deleterious mutations) compared with range cores [31]. Thus, at leading-range edges, while relaxation of constraints on low-temperature physiology might allow entry to the urban environment, the rate of genetic adaptation might be slowed. At trailing-range edges, the negative effects of high urban temperatures on organismal physiology combined with limited evolutionary potential might hasten extirpations. Although the effects of the latitudinal position of cities and their position within a species' geographic range are largely unknown, empirical tests of and support for these hypotheses could enable broad-scale forecasting of urbanization effects on insect biodiversity. That is, readily obtained biogeographic variables such as the latitudinal position of a particular city and its relative position within species ranges might usefully approximate harder-won data such as thermal physiological traits or genetic diversity.

Using data on urban insect biodiversity patterns and the underlying mechanisms

The data collected to understand urban insect biodiversity patterns and their underlying mechanisms can be used to address a spectrum of basic-to-applied research goals. We have demonstrated this idea with our exploration of the effects of latitude and geographic position within a species' range on whether urban habitats will serve as repellers or attractors of insect biodiversity based on thermal physiology and evolutionary potential.

Figure 2



Hypotheses for the influence of geographic position (high or low latitude; equivalently, high or low elevation) and geographic position within a species range (edge or core) for the effects of urbanization on insect populations with potential consequences for biodiversity estimation across urban-to-rural gradients. **(a)** Persistence of individual species is expected to be greater owing to higher standing genetic variation at the range core. For cities positioned near the range cores of increasing numbers of species, overall biodiversity in urban environments is expected to approach that of undeveloped rural areas. **(b)** Biodiversity in cities in cool-background climates (high latitude or elevation) could be enhanced relative to rural habitats, whereas urban biodiversity could be dampened in warm-background climates. Thermal physiology could mediate these responses with cities and their urban heat island effects pushing populations toward their thermal optimum in cool environments, leading to performance and fitness benefits, or causing populations to exceed their thermal optimum in warm environments, leading to performance and fitness declines.

Yet, there are many more questions that can be addressed with data on responses to urbanization. For basic research goals, cities can be used as sandboxes to interrogate core ecological and evolutionary questions [10,32]. As specific, but by no means comprehensive examples, cities can be used to explore colonization and extinction dynamics in the context of island biogeography. Urban-driven habitat fragmentation generates urban islands and differences in proximity of those islands to the rural mainland locations that can be used to test expectations for biodiversity responses [32]. Likewise, cities can be used to explore coexistence mechanisms, as cities modify many aspects of the niche (e.g. patch size and connectivity, and spatiotemporal variation) with consequences for altered species interactions [33]. Because different aspects of the urban niche can be characterized by either greater homogeneity of spatiotemporal habitat variation or greater heterogeneity compared with nearby undeveloped areas [7], cities provide unique opportunities to disentangle the drivers of species coexistence. Further, given the now-widespread support for contemporary evolution, cities can be used to examine rapid evolutionary responses to altered urban landscapes [10]. For example, cities can be used to explore understudied topics such as plasticity-led evolution [34,35], or classic questions such as the repeatability and pace of contemporary evolution [36], and the prevalence and strength of contemporary local adaptation [37,38]. Cities can also be used to better understand hypotheses with mixed empirical support such as the potential trade-off between basal physiological tolerance and trait plasticity [39].

While these types of inquiries can help to address fundamental questions in ecology and evolution, critically, a better understanding of the mechanisms that underlie urban success or failure can also improve urban land management and conservation plans [40]. Indeed, a greater understanding of mechanism appears crucial as the data so far suggest highly taxon-specific responses to cities. For example, even within the same urbanization gradient, biodiversity losses were documented in Lepidoptera and Diptera, whereas biodiversity gains were found in Hymenoptera (with a particular focus on bees) [41]. Yet, whether this enhanced urban biodiversity is driven by resource supplementation in cities or the remarkably high physiological tolerances of this taxon relative to others that might allow them to persist at high abundance in urban environments [42] is unclear. The mechanistic distinction is important because different mechanisms suggest pursuing different management and conservation strategies, for example, in this case, whether supplemental resources need to be maintained for bees, and whether other intervention strategies are needed for butterflies and flies such as increasing thermal refuges in urban habitats or assisted evolution [43].

In the context of land management and conservation, it is important to bear in mind that the effects of urbanization extend beyond the city footprint. In the most simplistic sense, this occurs through spillover of both environmental effects and individuals between urbanized and natural areas. Thus, the influence of urban changes on populations can have direct influences on the broader regional fauna [44]. But the relevance of cities can also extend beyond their footprint in more abstract ways. In particular, as cities are mesocosms of broader global changes to the environment and climate — that is, climatic warming and aridification, habitat loss, degradation and fragmentation, and general reshuffling of species in time and space — they can be used as space-for-time substitutions to gain insights into future changes beyond the city footprint [32,36]. For example, beneficial thermal acclimation and evolutionary responses to urban heat island effects can be used to uncover population capacities for responding to climatic warming more broadly [36]. Beyond their use as proxies for global climate change effects, cities also directly interact with global climate change. For example, as many species, including insects, are shifting their geographic ranges to track historical climatic niches, they are encountering new habitats, including urbanized landscapes. Urban design elements such as dispersal corridors, linear parks, or greenways can facilitate transit through urbanized landscapes, enabling compensatory responses to climate change [45].

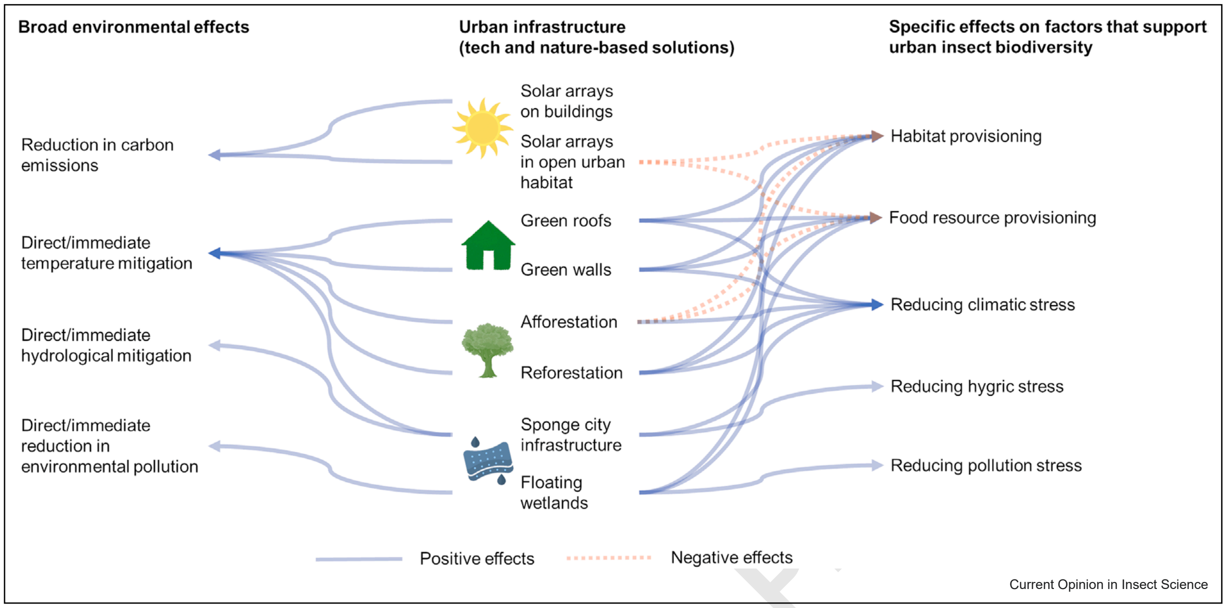
Urban insect conservation and management

From these studies of the capacity of urban insects to cope with environmental change through trait plasticity and rapid evolutionary change, it is clear that compensatory mechanisms, while nonzero, are often insufficient to completely buffer insects against these changes [38,46,47]. In effect, these mechanisms might buy time for insect populations. This is true not only in the biological sense of plasticity buying time for evolution to occur [34], but also in the policy-focused sense of buying time until mitigation measures can be enacted to ameliorate the negative aspects of urban land-use change. In the meantime, it is worthwhile to consider the extent to which cities can be a refuge or 'bioark' [48] for insect biodiversity, now and into the future. We view such considerations for building urban insect bioarks through the lens of the mechanistic, population-level thinking we developed earlier.

Insects, through their generally high capacity to respond to environmental change (e.g. large population sizes and fast generation times) and their small body size [46], are likely more amenable to reaping the benefits of urban refugia compared with other taxa, such as large mammals. However, insects are still subject to important constraints, such as their complex life cycles, that need to be accounted for in conservation plans [49]. For example, in phytophagous insects, cities need to support both larval host plants and adult food resources [50]. Other insects, such as Odonates, require both freshwater and terrestrial habitat for development [51]. And many insects, including beetles and butterflies, pupate belowground, yet cities can be limited in availability of leaf litter and appropriate soil substrate, especially with leaf removal and widespread soil compaction in urban landscapes [1]. Recognizing the needs of urban insects, a number of direct and indirect support initiatives have already been enacted. Direct support for particular species or taxa is evidenced by milkweed planting for monarch butterflies, pollinator gardens more generally for Lepidopterans, and installation of bee hotels [50]. However, care must be taken with these approaches, as they can all too easily provide little-to-no support for insects, or worse, become ecological traps [52]. Indirect support could come from altered mowing regimes such as 'no-mow May' that can provide larval and adult resources for insects in cities. Related research in remediated agricultural systems demonstrates an association between the timing of mowing and insect abundance [53]. Similarly, 'leave the leaves' initiatives could provide habitat structure for ground-dwelling, metamorphosing, or dormant insects, as the availability of litter is positively associated with biodiversity in some urban insect communities [54]. Such interventions carry minimal-to-no risk of inadvertent harm to insects.

Although it is useful to consider practices that better support insects in cities, it is equally important to consider interventions that avoid harm to urban insects. In particular, cities can generate ecological and evolutionary

Figure 3



A depiction of how interventions to mitigate urban hazards might not always benefit urban insects. The relationships between urban infrastructure and both its broad environmental effects (left-pointing arrows) and its specific effects on factors that support urban insect biodiversity (right-pointing arrows) are shown. Positive effects are indicated with blue-shaded solid arrows. Negative effects in orange-shaded dashed arrows. Neutral effects are indicated by the absence of an arrow. These relationships are intended to be used as a general heuristic, as the positive, neutral, or negative nature of the effects could change depending on the particularities of implementation (e.g. afforestation with a monoculture versus diverse plantings) and of timescale (e.g. solar arrays that reduce carbon emissions and eventually lead to reducing climatic stress in cities).

traps for insects. The traps arise through insect responses to cues that are typically adaptive in the rural environment, but lead to low fitness in urbanized landscapes [55]. For example, Odonates use polarized light to determine oviposition sites for their eggs. However, in cities, they interpret polarized light from vehicle windshields as an oviposition cue, depositing eggs in an environment that will not support their development [51]. Artificial light at night in cities can likewise trap insects [56]. For example, glow-worms preferred to remain under simulated street light rather than disperse to find mates in more poorly lit areas [57]. Such traps can be avoided through interventions, for example, by reducing urban light pollution.

As a further related consideration, there can be challenges associated with the specificity of interventions, that is, aiding benign insects while curtailing the spread of harmful insect species (e.g. disease vectors and crop pests) in cities [49]. Indeed, cities can directly increase the number of harmful insects through the activation of so-called 'sleeper' species, that is, unproblematic insect species that become harmful, such as through release from natural enemies in urban landscapes [58]. In response to harmful urban insect species, much effort has been devoted to interventions to mitigate their spread and their effects. However, interventions to halt the spread of harmful insects such as mosquito disease vectors can have negative effects on nontarget insect species [59]. Human commensal insects in cities, for example, bedbugs and cockroaches, are an especially acute form of this problem, as interventions such as habitat elimination are difficult or impossible and interventions such as insecticides can harm nonpest insects [60]. Urban food production is an interesting example of this issue: from a production standpoint, the goal is to maximize insect services such as pollination while minimizing disservices such as herbivory. However, from a biodiversity perspective, discouraging herbivory could be less than ideal, since many nonpest insects use crops as a resource while providing ecosystem services in other capacities (e.g. as pollinators or food for other species) [61]. Relatedly, direct farming of insects (e.g. honeybee apiculture) can have negative consequences for native pollinators [62]. These considerations suggest a multifaceted view of urban biodiversity that incorporates functional diversity and the multiple roles that many species play in ecosystems might be warranted [49,63].

The complexity of interventions to promote insect biodiversity in cities is further evidenced at the level of major urban infrastructure changes. Urban infrastructure developed to mitigate urban hazards such as elevated temperature, extreme hydrological events, and environmental pollution, can have both positive and negative effects on factors that shape insect biodiversity in cities. Many solutions to urban hazards could benefit insects in cities (Figure 3). For example, green roofs and walls,

Box 1 Ways forward in building the urban insect bioark.

1. *Test key hypotheses with currently available data*. Given the broad availability of insect biodiversity datasets and gridded climatological and land-use datasets, questions such as whether cities are predictable repellers or attractors of insect biodiversity based on factors such as geographic position and local climate — among many others — can already be addressed.
2. *Understand the mechanisms driving urban insect biodiversity patterns*. Although support for various mechanisms can be developed from correlational studies, more experiments are needed to understand the causal mechanisms driving insect entry, exit, and transformation in cities [70]. These data can be used to better tailor conservation and management plans for urban insects.
3. *Quantify spatiotemporal dynamics of urban insect biodiversity*. This question could be answered through improved monitoring, making full use of community science [6], tech-based monitoring (e.g. drones) [71], and eDNA [72]. However, with the growing number of resources available on temporal dynamics of insect populations, such as the InsectChange database [73], EntoGem [74], and long-term ecological research (LTER and ILTER), including sites specifically in urbanized settings, such questions might begin to be tackled immediately. Importantly though, the standard issues with inferring changes over time apply to such datasets (see exchange between Ref. [75] and Ref. [76]).
4. *Understand the relationship between urbanization and climate change.* Doing so can take several forms, from using cities as proxies for expectations under future climate change, to understanding the interaction between urbanization and climate. In the latter case, this could involve urban design elements that achieve climate-biodiversity cobenefits within the city footprint or elements that support insects as they respond to global climate change, for example, dispersal corridors for range-shifting, climate-tracking species [45]. Likewise, forecasting future climate where a city is located and developing appropriate infrastructure for those changes (e.g. cities that are in locations becoming more arid versus more mesic under climate change) could help benefit urban insect biodiversity in the future [77].
5. *Achieve biodiversity–climate goals in cities*. Because of the often-substantial linkages and feedbacks between the climate system and biodiversity [78], recognition and implementation of the urban climate interventions that lead to climate and biodiversity cobenefits, rather than strong trade-offs, can simultaneously benefit future climate and insect biodiversity goals [77].

reforestation, sponge city infrastructure, and floating wetlands are designed to ameliorate urban warming, aridity, and pollution, with downstream benefits that provision insects with habitat, food resources, and mitigation of abiotic urban stressors [45,49,64,65]. However, some urban solutions could have negative effects, such as the development of renewable energy infrastructure within urban insect habitats [66] (but see Ref. [67]). Likewise, afforestation that radically changes community structure and ecosystem function could harm open-habitat insect species or facilitate the invasion of insect pest species that displace others [68].

Given these considerations, there are several clear recommendations for building and assessing the efficacy of urban insect bioarks (Box 1). We argue that an understanding of the ecological and evolutionary mechanisms shaping urban insect spatiotemporal population dynamics might enable improved forecasting of urban insect biodiversity. Such mechanistically informed forecasts would ideally aid conservation practitioners, land managers, and urban planners to maximize cobenefits for people and nature, including insects, in cities while minimizing trade-offs. In the context of building urban insect bioarks, we re-emphasize our broad definition of what is considered ‘urban’. Although megacities certainly impact insect biodiversity, the effects are still apparent at much lower levels of urbanization such as within suburban locations or informal settlements [69]. Therefore, low-to-moderate levels of urbanization cannot be ignored in policy and management decisions to conserve urban insects.

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Declaration of Competing Interest

None.

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Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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