nature climate change

Perspective

https://doi.org/10.1038/s41558-024-01996-2

# Interactions between climate change and urbanization will shape the future of biodiversity

Received: 13 March 2023

Accepted: 22 March 2024

Published online: 26 April 2024

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Climate change and urbanization are two of the most prominent global drivers of biodiversity and ecosystem change. Fully understanding, predicting and mitigating the biological impacts of climate change and urbanization are not possible in isolation, especially given their growing importance in shaping human society. Here we develop an integrated framework for understanding and predicting the joint effects of climate change and urbanization on ecology, evolution and their eco-evolutionary interactions. We review five examples of interactions and then present five hypotheses that offer opportunities for predicting biodiversity and its interaction with human social and cultural systems under future scenarios. We also discuss research opportunities and ways to design resilient landscapes that address both biological and societal concerns.

Climate change and urbanization are two of the most important human impacts on the planet[1,2]. The global climate has warmed 1.2 °C during the past 120 years and could warm another 4 °C by 2100[1]. Besides warming, climate change is also altering precipitation, surface hydrology and sea levels[1]. Concurrently, people increasingly live in cities[3], with 68% expected to be urban dwellers by 2050[2]. Urbanization, defined here as encompassing both demographic and associated physical changes[4], is rapidly altering natural landscapes. Developing

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sustainable cities will therefore be necessary to maintain links between people and biodiversity[5–7].

Both climate change and urbanization threaten global biodiversity and ecosystems[5,8,9]. Climate change is expected to increase extinction rates, alter biodiversity patterns, degrade natural ecosystem processes and reduce their benefits to humans[8,10]. Some organisms have responded to climate change by shifting their ranges[8] or modifying their traits via phenotypic plasticity[11]. Concurrently, some populations have genetically adapted to warmer temperatures[12], altered precipitation[13], storms[14] and ocean acidification[15]. Although cities occupy a small proportion of the global land surface, most people experience biodiversity there[9], and biodiversity's effects extend far beyond the city[16–21]. Urbanization affects population connectivity, community diversity and composition, and ecosystem properties[9,19,22]. Urbanization also can elicit both adaptive and non-adaptive evolutionary processes[5,17], which can alter ecological interactions, ecosystem properties and ecological resilience[16,23], ultimately reshaping the links between nature and society[9].

Despite the coincident challenges that climate change and urbanization pose, their biological effects are usually considered separately[24–27]. Research on the biological impacts of climate change often ignores how cities affect climate change responses[10,28], and research on the biological impacts of urbanization often ignores the effects of changing climates[9,17]. Yet the joint effects of climate change and urbanization might often depend on their reciprocal interactions. Moreover, the socioeconomic factors driving climate change also shape urbanization patterns, including the people most vulnerable to their outcomes, and their joint escalation often depends on the same policies and technological changes. We plot five possible socioeconomic pathways that assume different levels of urbanization and climate change[29,30] in Fig. 1. Urbanization and climate change usually coincide, but urbanization can also occur without substantial climate change in a sustainability scenario assuming rapid technological innovation.

Here we develop a framework for understanding the interactive effects of climate change and urbanization on the ecology and evolution of species living in and near cities. We review five examples of these interactions and identify five general testable hypotheses. We then suggest several ways to improve the understanding of these joint disturbances and how to design landscapes that address both natural and societal concerns in a warmer and more urbanized world. We acknowledge the complex human elements of urbanization, including the role of cities in shaping economic and social inequality, which contribute to how climate change, urbanization and biodiversity interact. However, we focus on the biological impacts of urbanization and climate change on non-humans, as socioeconomic responses to urban expansion and climate change have been dealt with elsewhere[31].

## Integrating joint effects of climate change and urbanization

Throughout, we refer to climate change and urbanization as anthropogenic drivers that modify environments. Climate change and urbanization sometimes alter the same environmental conditions (hereafter, shared impacts), such as by jointly increasing temperatures. The joint effects of climate change and urbanization might be additive or interact synergistically or antagonistically. Alternatively, these impacts might be unique to each driver rather than being shared. Even when impacts are unique, biological responses might still interact non-additively, such as when adaptation to urban pollution constrains adaptation to climate change[32].

Although urbanization affects climates at more local scales than global climate change[24,33], their joint impacts often extend well beyond the immediate cityscape[16–21], including interactions with species and ecosystems in surrounding regions and the long-distance tele-coupling of socioeconomic impacts[34]. Particularly relevant to understanding their interaction is whether urban development patterns align with climatic gradients. Cities are often connected by transportation networks into linear, interconnected nodes, which can run parallel (for example, north-to-south coastal North American cities) or orthogonal (for example, west-to-east Mediterranean cities) to climate gradients. This alignment can determine whether cities facilitate or impede dispersal or gene flow along latitudinal or elevational clines[35].

Interactions between climate change and multiple urban stressors can often explain variable responses in cities. For example, the phenology of plants in cities depends on both climate-induced warming and light pollution[36]. Also, cities are highly heterogeneous and vary along multiple human dimensions, including population density, history, socioeconomics, and racial and cultural composition. These differences can affect the distribution of organisms, responses to urbanization and impacts on people. For instance, past discriminatory lending policies in the United States known as redlining deterred home ownership and investment in minority neighbourhoods[37]. These practices led to fewer parks, shade-providing trees and other natural amenities[31] that affect not just local ecosystems but also people's vulnerability to climate change.

The growing evidence that ecology and evolution meaningfully interact across similar temporal and spatial scales[23,38] necessitates integrating their joint and potentially non-additive (hereafter, interactive) responses[9,16,27]. Moreover, we recognize the need to incorporate humans into this framework because social dynamics reflect a rapidly changing reality, driving unexplored socioeco-evolutionary dynamics and affecting human well-being in tangible ways[9,31].

## Joint climate change and urbanization effects

We highlight five well-understood examples of how climate change and urbanization jointly influence ecological and evolutionary processes. Although these examples do not represent all ways in which climate change and urbanization interact, they collectively demonstrate that such interactions influence a diversity of organisms and eco-evolutionary processes. An emerging conclusion from these examples is that although both climate change and urbanization often act in parallel on environments, ecology and evolution, their effects are not purely additive but often act antagonistically.

### Temperature

The greenhouse gas accumulation that underlies climate change has warmed the world by 1.2 °C in the past century, while the heat island effect from urban land cover change has warmed cities by 2 °C, on average[39]. These heat island effects are experienced globally, with different patterns depending on latitude, climate and biome as well as city-specific characteristics such as population density, impervious surface and canopy cover[39,40] (Fig. 2). However, the rising temperatures from climate change and urban heat islands are non-additive. Due to differences in evapotranspiration, rural regions are warming more quickly than cities, thereby reducing future heat island effects by 24%[24,41]. Irrigation in urban environments in arid regions also can reduce temperatures relative to rural regions, thus countering the local effects of climate-induced warming[42].

Where climate change and urbanization jointly increase temperatures in cities, their aggregate effects can alter the biology of urban organisms[24,43], which can in turn modify urban microclimates. For instance, climate change increases urban tree growth and survival in cool climates but decreases tree survival in warm climates[44,45]. Hence, climate change might promote tree shading in cooler climates while reducing shading in hotter climates, with impacts on both wildlife and people.

Joint warming might also induce phenotypic changes in urban organisms[46,47]. Both climate change and urbanization induce later cessation of flowering in summer-blooming woody plants[48]. However, an observed slowing of temperature-driven responses in urban plants might eventually reduce phenological responses to extreme

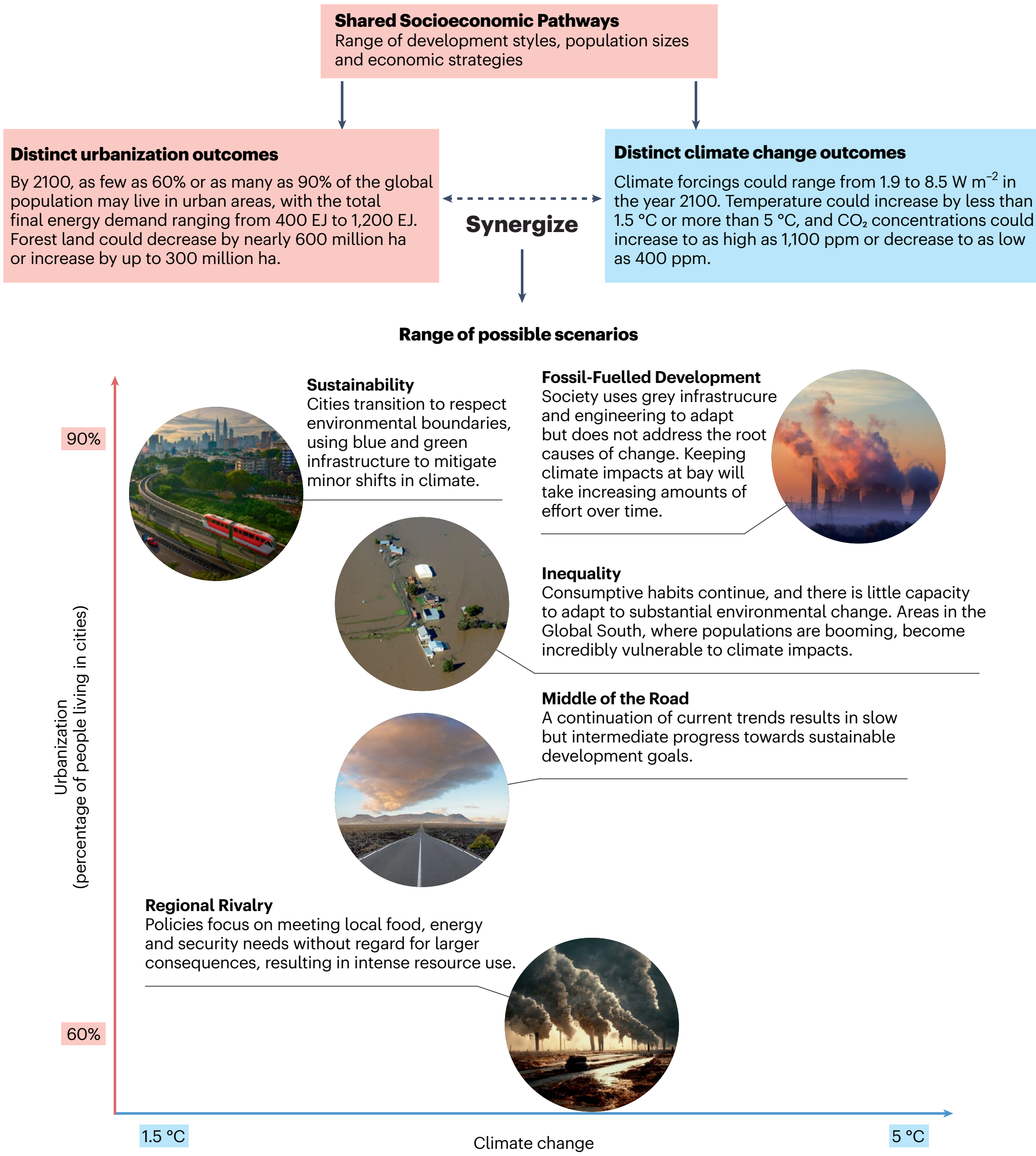


**Fig. 1 | Future scenarios for global urbanization and climate change.** Different future scenarios for global urbanization and climate change as envisioned by the Shared Socioeconomic Pathways developed by the global climate change research community[29,30]. The five scenarios depict the world in 2100, when 60–90% of the global population could live in cities and global temperatures could rise by 1.5 °C to 5 °C. These developmental and economic strategies often influence (and are influenced by) the land use and greenhouse gas emissions policies that jointly drive urbanization and climate change. However, alternative futures are possible. Although urbanization and climate change might occur jointly as depicted in the Fossil-Fuelled Development scenario, a highly urbanized world with limited climate change is also possible assuming sufficient technological innovation as depicted in the Sustainability scenario. The difference between the two scenarios is that technology is applied in the Sustainability scenario to address the root causes of climate change. In addition, the Sustainability scenario assumes that the environmental effects of future cities are mediated by green design, and their compact design reduces impacts on surrounding natural areas. Note that these scenarios represent the main narratives that have been accepted by the global climate change research community to indicate divergent climate change projections, but many other scenarios are possible.

temperatures, with greater reductions expected in cities in cold climates[47]. Moreover, such responses might differ among species or between urban and rural populations, potentially creating phenological mismatches that affect trophic interactions, pollination and mating[49–51]. These phenotypic changes are also sometimes attributed to genetic adaptations to warming from urbanization and climate change[12,52,53]. In such cases, adaptive responses to heat extremes from one driver might be co-opted for the other, assuming shared impacts. Alternatively, the extreme heat from both drivers might reduce population sizes, cause extirpations or decrease genetic variation for upper thermal limits[54], thus reducing overall adaptive capacity.

## Water availability

In many dry climates, climate change is causing precipitation to decrease or become more variable[1]. Climate change threatens many species that rely on predictable rainfall[55], but supplemental watering and irrigation of vegetation could help them. As climates dry, people in cities might water more to maintain desirable species, ecosystems and human benefits. To illustrate, annual primary productivity is usually higher in Phoenix, United States, than in the surrounding desert due to watering[56]. City dwellers also create artificial ponds and lakes: water bodies increased 33-fold over 70 years in Phoenix and subsequently affected regional nitrogen cycling[57]. Hence, cities might provide oases

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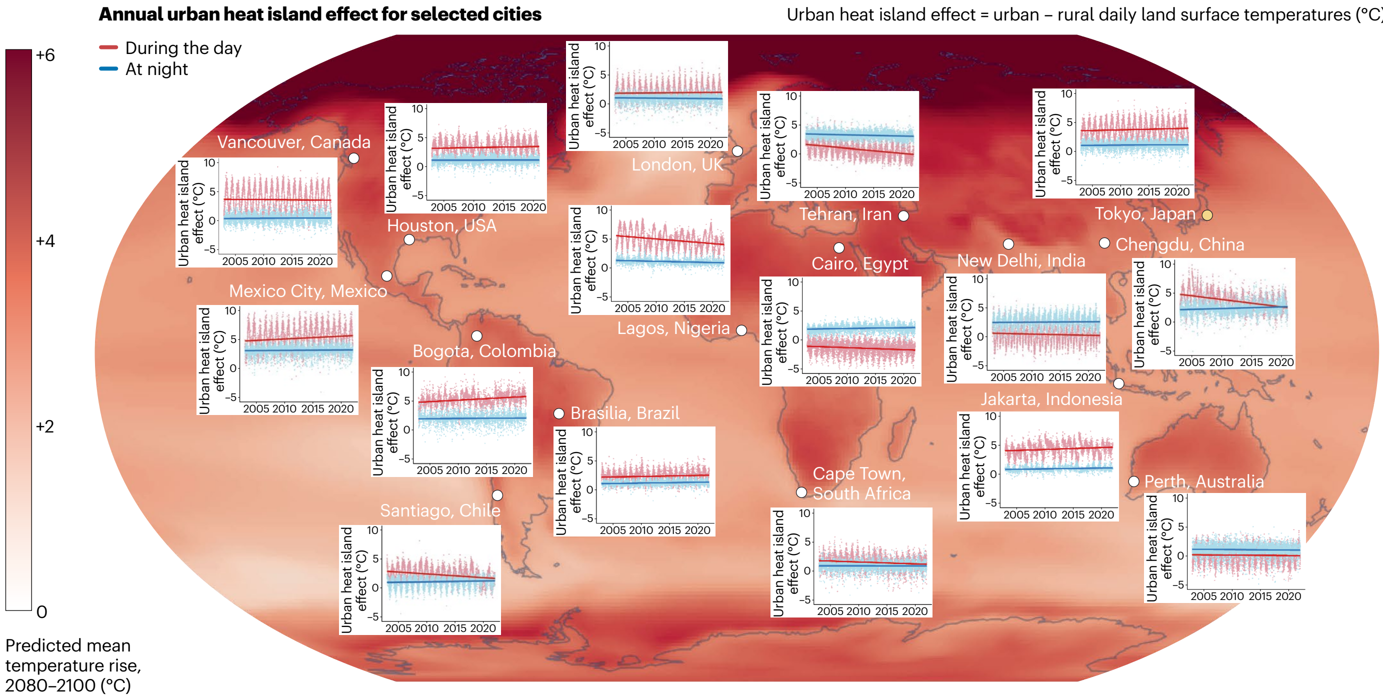


**Fig. 2 | Global variation in urban heat island effects through time for selected global cities.** The urban heat island effect is calculated as the annual land surface temperature in urban areas minus that in surrounding rural areas during the day (red) and night (blue) for 2003–2020 (for detailed methods, see Supplementary Information). Urban heat island effects range from −1 °C to 6 °C, and their relative magnitudes and temporal trends depend on regional climate and the interaction between temperature and humidity in urban and rural areas. Note that land surface temperatures provide a different view than analyses based on air temperatures, by generally indicating a stronger urban heat island effect (larger temperature differences) at night than during the day[40]. The base map depicts the mean annual surface temperature change (in °C) in 2081–2100 for the SSP2-4.5 scenario based on 34 models from the IPCC WGI Interactive Atlas[131]. Data from refs. 132,133. Figure reproduced with permission from ref. 131 under a Creative Commons license CC BY 4.0.

for species as climate change dries surrounding areas. However, supplying that water often means denying water to other people or organisms, and therefore irrigation in cities might stop abruptly during water shortages, threatening water-dependent species.

Globally, variable precipitation often drives spatial patterns of selection and adaptation[58]. Plants have adapted to irrigated agricultural areas[59] and to climate-induced drought[13], suggesting the potential for fitness trade-offs to shape how urban and rural species differentially persist through drought. Adaptations to irrigated cityscapes could thus increase or decrease fitness, depending on how regional precipitation changes. These adaptations could provide services (for example, shade) or disservices (for example, vector-borne diseases) to humans[60].

## Stream hydrology

Climate change and urbanization can also jointly alter streamflow, with the magnitude and direction of effects depending on regional climate and urban infrastructure[25,61,62]. Climate change can cause extreme precipitation events in and downwind of cities[63], which produce larger stormflows[61,64]. Impervious surfaces, reduced interception by vegetation, channelization and microclimatic alterations in the city can increase stormflow variability and magnitude and trigger flooding[62,65]. In other regions, climate change reduces precipitation and river flows. High evaporative potential in urban environments can exacerbate drying effects on streams, whereas urban channelization can increase base and storm-related streamflow[57,66].

These joint impacts on streamflow can affect species through divergent interactive effects. For example, urbanization and the greater flow intermittency expected with climate change synergistically decreased stream macroinvertebrate richness by 80% in one study[67]. However, the joint predicted responses of fish communities to urbanization and climate change were mostly antagonistic in another study[25].

Urbanization- and climate-driven changes in precipitation also can shape adaptive evolution. For example, climate-induced reductions in streamflow and saltwater exchange in Californian estuaries produced lotic habitats, which drove the evolution of reduced bony plates in stickleback fish[66]. However, estuarine channelization, dredging and ocean breaching selected for more bony plates, highlighting how human modifications can act antagonistically on phenotypic evolution[66]. More generally, a review of multiple stressors on aquatic biodiversity[68] suggests that they often act antagonistically, such that populations are resilient to multiple stressors due to existing co-adaptations to environmental heterogeneity.

## Habitat connectivity

Many species must disperse to track their climatic niches as they shift across the landscape[69]. Dispersal-limited species that cannot track shifting climates might undergo range retraction and experience increasing fragmentation[70]. Urbanization also fragments habitats and therefore can enhance climate-mediated extinction risks by preventing species from tracking their moving climatic niche[71]. For example, expanding Californian cities have isolated mountain lion populations, threatening them with extirpation[72]. Species that would normally track climate change now face an increasingly inhospitable matrix due to urbanization[35,73], creating potential negative synergies between the two drivers.

Environments fragmented by urbanization can also select for species with different dispersal abilities relative to natural environments. For instance, insect assemblages in cities included better-dispersing species than those in rural areas[74,75]. These changes in dispersal ability could also affect gene flow, adaptations to new disturbances, and recovery from inbreeding and genetic drift[76]. For example, gene flow among poorly dispersing mice was limited in the city, whereas gene flow in free-flying bats remained high[77]. Although urbanization reduces

 https://doi.org/10.1038/s41558-024-01996-2

gene flow for many species[77,78], it can also enhance connectivity relative to rural areas for others[79], such as black widow spiders and pepperweed[80,81]. Improved urban connectivity for these species could thus counteract encroaching fragmentation from climate change.

Fragmentation from climate change and urbanization could also select for the evolution of either reduced or enhanced dispersal ability, depending on the mode and relative benefits of dispersal. Urban fragmentation selected for 5% fewer dispersing seeds of holy hawksbeard plants[82] but was associated with 12% longer flights in urban damselflies[83]. Climate-tracking species also might evolve increased dispersal at their range edge to colonize newly suitable, low-competition habitats[69,84]. Hence, the evolution of dispersal in response to fragmentation from one driver could constrain or enhance the effects of fragmentation from the other driver.

### Aquatic pollution

Urban water bodies are often polluted with excess nutrients[85], and climate-induced changes in precipitation can increase nutrient run-off in temperate regions and concentrate nutrients in arid regions[86]. Increasing phosphorus, in particular, facilitates opportunistic phytoplankton such as cyanobacteria, which can produce a positive feedback that shades other species, promoting more cyanobacteria growth under warmer conditions[87]. Simultaneously, climate change and urbanization raise water-body temperatures, jointly facilitating cyanobacteria growth[87].

Cyanobacteria can decrease lake species diversity, alter trophic dynamics, kill fish, degrade freshwater supplies and sicken people[86,88]. Urbanization and climate change can synergistically shift water bodies towards dominance by toxic cyanobacteria, which threatens water quality and human health. Some grazers such as the water flea, however, adapt to consume toxic cyanobacteria, which reduces cyanobacteria and improves water quality[89,90]. Adaptive shifts of consumer communities or populations towards resistant species or genotypes could therefore mediate these effects.

## Joint hypotheses about climate change and urbanization

Given that the interaction of climate change and urbanization remains understudied, we next provide five testable hypotheses for how climate change and urbanization might interact to influence eco-evolutionary processes to spur research and fruitful debate (Fig. 3). These hypotheses are arranged to highlight potential advantages of city organisms over rural organisms, then potential advantages of rural organisms over city organisms, followed by changes in phenotypic synchrony and movement.

### Out-of-the-city hypothesis

We predict that species and genotypes that thrive in cities, which are often characterized by broad, generalist niches[19], will already possess traits that enable higher fitness under climate change, thus facilitating invasions into surrounding, less-developed regions[26,53,91,92]. Species adapted to both urbanization and climate change can spread through multi-city networks, especially if urbanization and climate change gradients align and cities have similar characteristics. For example, urban ant communities are dominated by species better adapted to warmer and drier regions than nearby forest communities[93]. These species might dominate further through human facilitation, including many introduced or cultivated species. As an example of this, many garden plants are already tracking climate change through cultivation and assisted migration by humans[94]. If climate change has similar, city-like effects on environments in nearby undeveloped areas, these species might expand into the countryside and replace native species. For example, species that thrive in urban heat islands might readily colonize nearby rural areas that are warming through climate change.

Urban-adapted genotypes might also dominate during climate change. Urban acorn ants, water fleas and lizards have adapted to urban heat islands[52,95,96] and thus might eventually spread into surrounding regions that are warming, promoting evolutionary rescue of those populations from climate change[97]. If urban fragmentation causes or selects for better dispersal[98], these urban genotypes might spread even faster. Such dynamics can ultimately produce a race between migration from lower-latitude or lower-elevation rural populations as they track climate change and the expansion of local species or genotypes with traits adapted to cities that also match changing climate conditions[70,99]. Given the geographic distance required for rural organisms to track climate change relative to urban genotypes, the adjacent urban organisms might win out. For instance, New York City daily temperatures are 2 °C warmer, on average, than those in nearby regions, which matches the same average temperatures in rural climates 220 km to the south.

These expanding urban species and genotypes might enhance the resilience of rural ecosystems by maintaining functional traits, but they could also threaten rare or threatened native species and spread human-aided species or genotypes. These urban species might disrupt ecosystems and human well-being if cities facilitate invasive species or disease agents that then spread outwards[80,91,100]. Such joint dynamics could lead to the 'urbanization' of regional communities and population genetics, an analogue of 'community thermophilization,' whereby communities become dominated by warm-adapted species during climate change[74].

Urban organisms might also adapt to city-specific conditions that, through trade-offs, maladapt them to unique rural features. For instance, the water flea's adaptations to pesticides also increase their susceptibility to natural parasites[101]. Thus, even if urban organisms adapt to shared conditions from urbanization and climate change, their adaptations to unique local conditions might limit their expansion into surrounding rural regions. Alternatively, impacts from urban organisms might be restricted to a small zone around cities, leaving larger-scale range shifts unaffected. Transplant experiments between cities and surrounding areas and experimental manipulations simulating future climate conditions provide important ways to test predictions from this hypothesis and each of the subsequent ones (Box 1 and Fig. 3)

### City-to-city transfer hypothesis

We predict that cities arranged along climate gradients and linked via transportation corridors will promote the colonization of cities by urban-adapted species and genotypes, including under changed climates, thereby enhancing overall biotic homogenization across urban environments along climate gradients[19,92]. Invasive species are often moved along urban transportation networks or intentionally introduced[102], and plants cultivated beyond their normal range support more rapid range expansions in response to climate change[94]. By maintaining native and exotic plants, urban green space can also supplement resources that facilitate climate tracking[103].

Urban corridors might also facilitate gene flow along climate gradients. One third of studies indicate that urbanization facilitates gene flow[79], and therefore cities already promote the movement of human-associated species, which can help them track climate change. Evidence for convergent adaptations across cities suggests that strong gene flow can homogenize urban genotypes and phenotypes[80,81,104]. During climate change, this extensive gene flow could facilitate the expansion of genotypes already adapted to warming conditions into historically cooler regions, thus adapting populations to changing climates[94]. Urban biodiversity could therefore be maintained regionally despite warming in a manner similar to that proposed for well-connected natural systems. Although such dynamics could maintain some species facing urbanization and climate change, they might also spread pests, human pathogens and invasive species across human-dominated landscapes as climates warm[105].

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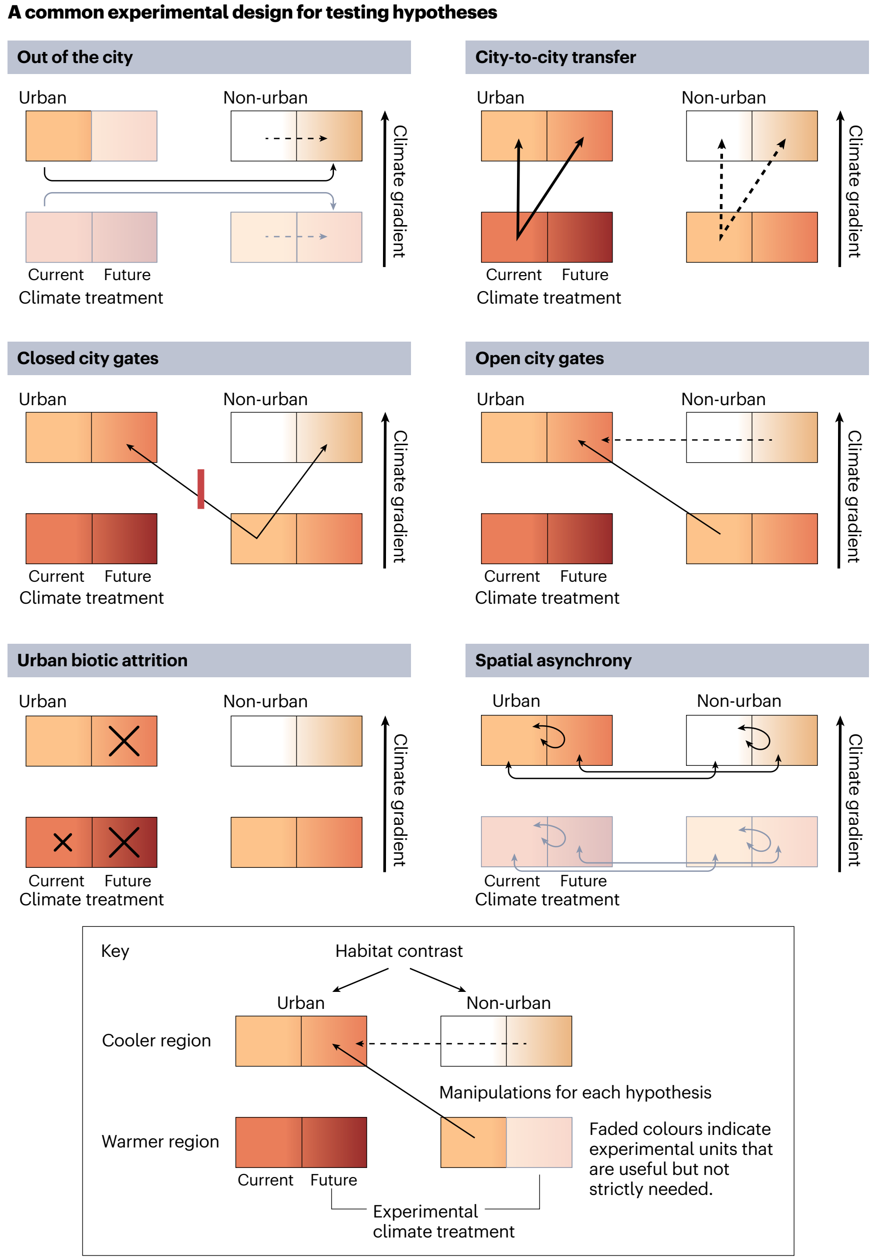


**Fig. 3 | A common experimental design for testing hypotheses.** Each row represents a different region aligned along a climate gradient, and the columns indicate urban and rural habitats. Within each region/habitat cell, there is a current, ambient climate condition (left) and a future, altered climate (right). The arrows and symbols indicate the types of manipulations necessary to test the hypotheses. Dashed arrows indicate treatments predicted to be weaker than those indicated by solid arrows. Some predictions do not strictly require the full design and therefore are faded to simplify the design.

The city-to-city transfer hypothesis will be more likely for species associated with humans. This hypothesis also assumes that cities are similar enough that adaptations to one city are adaptive in other cities. Nearby cities connected by transportation corridors might be relatively similar but could still differ substantially in important characteristics such as socioeconomics, infrastructure and development patterns.

## City gates hypotheses

We predict that urban organisms could exclude genotypes and species from rural areas expanding their ranges to track climate change if the spatial configuration of cities blocks their passage (closed city gates hypothesis). Urban species might possess traits that suit them to both urban and climate change conditions, thereby producing an ecological priority effect over other species tracking climatic changes[26]. Such priority effects might occur through both more fit species and better adapted genotypes, with the latter signalling an eco-evolutionary priority effect, whereby resident species adapt to local conditions and decrease the establishment of late-colonizing species or genotypes[99]. Such dynamics have been observed in experiments[106] and across natural islands[107] but remain untested in cities. Furthermore, adaptation to the urban environment and potential expansion to nearby regions during climate change (see 'Out-of-the-city hypothesis') could prevent other species and genotypes from tracking climate change across regional landscapes, thereby increasing extinction risks and promoting adapted urban species over native species.

The city gate hypothesis depends on how well city genotypes and communities resist invasions, which, in turn, will depend on the species or genotypic characteristics that confer fitness advantages to both shared and unique conditions in cities and to climate change. Although scientists usually envision invasion dynamics as being dominated by

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**BOX 1**

## Designing experiments to test hypotheses

We developed a common transplant experiment design to test hypotheses (Fig. 3). We envision setting up experiments in paired urban and rural habitats along climate gradients (for example, latitude/altitude) with an ambient and a future climate manipulation (for example, raised temperature). Reciprocal transplants of populations would be especially useful to test local adaptation to urban/rural habitats and to regional climate, which would inform whether species, genotypes or both are manipulated in future experiments. If natural transplants are not possible because of ethical or practical concerns, then common garden experiments that manipulate key environmental factors can be implemented instead. Testing individual hypotheses will also require treatments with and without interactions between transplanted populations/species or that allow colonization of species from nearby habitats. The predicted outcomes of each hypothesis are:

Out-of-the-city hypothesis: Species or genotypes from the city outcompete rural species or genotypes in the rural climate change treatment.

City-to-city transfer hypothesis: Species or genotypes will easily establish in transplants in cities up the climate gradient and in the climate change treatment. This prediction also requires a monitoring programme to assess whether movements are greater between cities than between rural areas.

City gates hypotheses: Species or genotypes from rural areas will establish less (closed gate) or more (open gate) in cities than in rural areas along the climate gradient and in the climate change treatment.

Urban biotic attrition hypothesis: Species or genotypes from the city will decline in the climate change treatment and will not be invaded by other species or genotypes from the surrounding habitat relative to rural habitats.

Spatial asynchrony in species interactions hypothesis: Species with access to both urban and rural climate change experiments might have higher or lower fitness, depending on the specific interaction type, than those without because of the divergent phenologies of the species with which they interact.

competition, trophic or mutualistic interactions might also play important roles[99]. Climate-expanding, generalist and superior competitors might overcome the 'city gates', while specialists and poor competitors might face higher thresholds, further homogenizing species assemblages and population genetics. However, if cities decrease population sizes and lower species and genetic diversity, then the opposite effect might occur by creating niches for climate-expanding species to invade, thus opening the city gates (open city gates hypothesis).

### Urban biotic attrition hypothesis

We predict that cities could undergo 'urban biotic attrition', whereby cities lose species faster than surrounding regions, as adapted from the lowland biotic attrition hypothesis postulated for lowland tropical regions[108]. Applying the same idea to cities, we propose that urban species diversity will decline during climate change because no species exist in the surrounding region that can survive novel urban climates and therefore colonize and replace the declining resident species. This effect would be more likely when cities are isolated and differ strongly from each other. For instance, cities might become the hottest places in a region, and if interconnections with other cities are limited or those cities differ in attributes, then species extirpations might occur without replacement[71]. This lost diversity might reduce ecosystem stability and function and increasingly affect people, such as by increasing vector-borne disease[105] and exacerbating climate extremes by reducing urban trees and their cooling effect.

Urban biotic attrition might also affect genetic diversity by decreasing population sizes, increasing drift and eliminating adaptive variation. Similar to species, genotypes adapted to these no-analogue climates are unlikely to exist in neighbouring regions and provide a source of adaptive gene flow. In situ adaptation to no-analogue conditions might therefore be the only mechanism that maintains populations in these regions[109], but the loss of genetic diversity and maladaptive gene flow could reduce this potential for evolutionary rescue[97].

### Spatial asynchrony in species interactions hypothesis

Both climate change and urbanization can affect the timing of life history events (phenology) such as green-up, migration and offspring production[47,110,111]. When interacting species modify their phenologies at different rates in altered environments, the resulting phenological mismatch can alter interaction strengths and fitness[51]. As urbanization proceeds, phenological responses might diverge between urban and rural regions, which can exaggerate or diminish climate change effects[110]. Given these joint effects, we predict altered interactions for highly dispersive species that forage across urban-to-rural gradients. To illustrate, if a predator forages in both the city and the countryside, they might compensate for mismatches with their resources in one habitat by foraging more in the other habitat. For instance, fruit bats near Tel Aviv roost in rural areas but preferentially forage in the city, where they have adopted more exploratory and diverse diets[112]. In addition, phenological delays between the two regions might provide a more continuous supply of resources for species that can track asynchronous peaks in resources through movement. For instance, urban regions often provide longer and more continuous floral resources for pollinators[113,114]. Concurrently, climate change is expected to create phenological mismatches between plants and pollinators[115], potentially allowing urban plantings to rescue some pollinators and their benefits to humans. Urbanization thus might buffer the effects of climate change on dispersive consumers and pollinators, assuming strong interactions and generalist species that span the urban-to-rural gradient through extensive movement patterns.

Climate change could lessen these asynchronies by reducing differences between cities and nearby regions. Climate change reduces phenological differences via antagonistic effects on conditions (for example, temperature and precipitation), biological constraints and the local counter-gradient adaptation of phenology. Evidence from plant green-up indicates a slowing down of phenological responses at high urban temperatures, suggesting that surrounding plant phenologies will catch up to cities as climate change progresses[47]. Also, local adaptation of traits or plasticity could reduce asynchronies between urban and rural areas, as exemplified by the evolution of locally adapted flowering times in common ragweed[116].

## Future directions

We conclude by suggesting future directions that test the above hypotheses, develop additional ones and apply insights to create better cities for people and biodiversity.

### Modelling joint interactions and impacts

An important next step is to develop better-coupled models of the joint impacts of climate change and urbanization that allow interactions between the drivers, their environmental impacts and eco-evolutionary feedbacks. Such coupled models often reveal unanticipated interactive effects[117]. These interactive effects will depend on climatic, social, economic and ecological contexts; therefore, exploring how climate–urban interactions differ in strength or direction across realistic gradients will be critical to gain broader understanding.

### Urban observation networks

Long-term, paired monitoring of urban and nearby rural ecosystems will play an important role in testing hypotheses (for example, ref. 118). Optimally, multiple monitoring sites would also be arranged along relevant axes of city characteristics such as age, history and socioeconomics. For example, the age of city infrastructure could influence existing genetic variation and whether organisms can adapt to novel selection[119]. Furthermore, researchers should scale from individual cities to multi-city networks given the hypothesized importance of city networks and connections with surrounding areas. This monitoring network could also test whether current urban responses can predict future climate responses. Monitoring should include not just species abundances but also traits attributed to plasticity and adaptations via experiments and adaptive and neutral genetics, with the latter indicating population sizes, connectivity and inbreeding. Inclusive community science, when combined with sufficient controls to facilitate accuracy, provides one way to collect these data in the places where people live, while involving local people in the scientific process. Long-term monitoring takes time to set up and bear results, and therefore it should be an immediate priority.

### Realistically unnatural experiments

We advocate for experiments, as realistic in size, diversity and complexity as possible, that simulate interacting joint effects of climate change and urbanization and estimate the direction, strength and interactions of biological responses. Cities are already manipulated systems and are commonly touted as analogues of certain climatic changes[120]. They therefore provide opportunities to leverage or design divergent urban management actions to facilitate whole-ecosystem experiments not normally possible in natural systems[120]. For example, a herbivore's response to urban heat islands in one study predicted its response to global warming in natural habitats[121]. Towards this end, researchers could alter temperature, native vegetation, species compositions or genetics in experiments in both urban and rural environments to simulate impacts on climate change and its disparate effects across the urbanization gradient to test five hypotheses (Box 1). One could imagine introducing non-invasive species expanding their range with climate change (the city gates hypotheses) into some urban parks or constructed green habitats, but not others, and then evaluating whether and why they can survive and their overall impacts on ecosystems and people. Such introductions would first need to prove their safety and gain permission from local communities and authorities through an ethical and inclusive process.

### Socio-ecological dynamics

Current research suggests that social, cultural and economic factors are embedded within urban policymaking, built environments and ecosystems and their benefits to humans, including important consequences for equality[122,123]. For instance, research has demonstrated that poor neighbourhoods often have lower canopy cover and access to green infrastructure, which exacerbates human health risks from heat waves[124]. As scientists test and develop hypotheses about interactions between climate change and urbanization, they should explicitly incorporate the socio-ecological dynamics that drive eco-evolutionary outcomes. Including social conditions in hypotheses will improve predictions for urban–eco-evolutionary dynamics and create more effective and equitable climate solutions for all people, especially historically excluded groups.

More systematic attention should be focused on how technology transforms the relationship between people and the natural world in cities[27]. For example, the emergence of autonomous systems poses both challenges and opportunities to minimize impacts from climate change and urbanization[125]. Another aspect relates to how political and belief systems affect urban and climate change resilience. One prediction is that cities with strong environmental policies will be more resilient to climate change. However, this link might be weakened if climate change is not a specific environmental priority or if interactions between urbanization and climate change are not considered. Moreover, research should consider which socioeconomic elements of a given city are 'resilient' in different scenarios and policies. For example, research should consider the major beneficiaries and leaders of political and economic systems and the large extensions of slums or poor neighbourhoods that comprise substantial portions of many emerging mega-cities in different parts of the world.

### Building climate-resilient cities

Studying the interactive effects of climate change and urbanization could also improve the ability to design, renovate and rebuild cities damaged by extreme weather, war or other disasters in a way that makes them more resilient to climate change[126]. For example, the design of older cities often exacerbates climate change effects, such as by concentrating flooding and heat island effects and excluding natural corridors or parks. As society envisions cities of the future, nature-based solutions can mitigate the joint effects of climate change and urbanization[127]. Adding natural vegetation and aquatic infrastructure can dampen climate change extremes in cities, which could reduce out-of-the-city dispersal and urban attrition (two of our hypotheses) while also providing benefits to people, ranging from pollination to improved mental well-being. Society can also make better decisions about green infrastructure by supporting larger natural areas in cities and creating corridors between these areas to promote genetic variability[128]. Creating climate-resilient cities can also begin to address social inequalities in access to nature and its benefits. Low-income, marginalized communities often bear the brunt of both climate change and intense urban development[9,31]. Situating nature-based solutions preferentially in these neighbourhoods could address these historical legacies.

Arranging green infrastructure within and between cities into strips parallel to climatic gradients would create corridors to allow species to track climate change and thus facilitate, rather than impede, movement through cities[35]. These green-striped cities could spread ecosystem benefits throughout more of the city than large, isolated parks, which also tend to occur in wealthier, less diverse neighbourhoods. Designing this infrastructure will need to account for biological and engineering contexts and regulatory constraints, and incorporate local and diverse voices to be effective and fair[124].

Lastly, cities might be designed to act as refugia for some native species because people buffer the impacts of climate change on their own habitats, such as by creating irrigated landscapes and artificial ponds and planting diverse native vegetation in drying landscapes[57,129]. So-called reconciliation ecology seeks to design habitats that benefit both humans and native wildlife[130].

## Conclusions

Climate change and urbanization interact through their socio-economic drivers, impacts on environmental conditions and effects on ecology and evolution. Organisms mediate the effects of these impacts through demographic, plastic and evolutionary responses. Many responses interact in ways that minimize the summed impacts of climate change and urbanization. This compensatory effect might originate from recent or long-term adaptations to environmental heterogeneity and multiple disturbances, which extend resilience from one driver to another. We propose five hypotheses about possible interactive effects and suggest how they can be tested through long-term observations and experiments. As climate change and urbanization increasingly dominate the world, society must consider their joint impacts to mitigate their interactive effects on biodiversity, ecosystems and people.

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## Acknowledgements

This study is a collaborative effort of the National Science Foundation Research Coordination Network: Eco-Evolutionary Dynamics in an Urban Planet: Underlying Mechanisms and Ecosystem Feedbacks (DEB 1840663). We acknowledge the many participants in this working group that directly and indirectly contributed to our development of the five presented hypotheses. M.C.U. was supported by NSF award no. DEB-1119877, National Science Foundation NRT grant no. 2022036, NASA awards no. 80NSSC22K0883 and no. 80NSSC19K0476, the Arden Chair in Ecology and Evolutionary Biology, and a Leverhulme visiting professorship. P.R. thanks the Max Planck Society for funding.

## Author contributions

M.C.U., M.A., L.D.M. and K.I.B. conceived of the overall idea. All authors wrote the paper. Y.Z. provided data used in the heat island calculations. A.N.M. developed Fig. 1. M.A. led the research coordination network that brought these authors together.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41558-024-01996-2.

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**Peer review information** *Nature Climate Change* thanks Jie Liang, Robert McDonald and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.