

Review

Adaptive Evolution in Cities: Progress and Misconceptions

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Current narratives suggest that urban adaptation – the adaptive evolution of organisms to cities – is pervasive across taxa and cities. However, in reviewing hundreds of studies, we find only six comprehensive examples of species adaptively evolving to urbanization. We discuss the utility and shortcomings of methods for studying urban adaptation. We then review diverse systems offering preliminary evidence for urban adaptation and outline a research program for advancing its study. Urban environments constitute diverse, interacting selective agents that test the limits of adaptation. Understanding urban adaptation therefore offers unique opportunities for addressing fundamental questions in evolutionary biology and for better conserving biodiversity in cities. However, capitalizing on these opportunities requires appropriate research methods and dissemination of accurate narratives.

Adaptive Evolution in Cities

Urbanization reshapes ecosystems and restructures biodiversity [1]. Although ecologists have addressed ecological questions in urbanized landscapes for decades [2], urban (see Glossary) contexts have only recently captivated evolutionary biologists [3,4]. Most urban evolution research has focused on non-adaptive processes [5]. However, there are iconic instances of urban adaptive evolution. The classic example of peppered moths (*Biston betularia*) evolving a darker coloration in response to pollution coating of trees was one of the first examples of both rapid adaptive evolution and adaptation in response to urbanization [6–9]. Despite limited work during the ensuing half-century, the past decade has witnessed an explosive interest in urban adaptation (Table 1 and supplemental information online) and in using urban adaptation to address fundamental biological questions such as convergence (Box 1).

Collectively, the literature suggests a large role for urban local adaptation. Given that biologists often overemphasize adaptive evolutionary responses to anthropogenic pressures such as climate change [69], researchers should thus be cautious in using adaptation as a default explanation for phenotypic divergence between urban and nonurban populations [3], especially without robust tests of this assumption. Urban-driven phenotypic shifts may result from processes that are neither adaptive (e.g., because of neutral evolution) [5,63] nor evolutionary (e.g., owing to phenotypic plasticity; Box 2) [71]. Despite multiple discussions of evolution in cities [3,72–76], no study has systematically critiqued the evidence for urban adaptive evolution. We review evidence for urban adaptation, highlight successful approaches, and describe challenges and misconceptions.

We identified >1380 studies (supplemental information online) using an ISI Web of Science search (accessed 21 August 2020) and studies citing recent urban evolution perspectives [3,72–76], supplemented by additional studies of which we were aware. Of these, we reviewed 270 that were relevant to urban biological adaptation (supplemental information online). From this subset, we identified six systems (encompassing >20 studies) that conclusively demonstrate urban

Highlights

There has been a recent, explosive interest in studying adaptive evolution in cities. However, many responses to urbanization may be misattributed as adaptation because sufficient evidence is lacking.

We identified only six systems that offer strong evidence for urban–nonurban divergence that is both genetically based and adaptive.

Common issues for inferring urban adaptation include assessing phenotypic or genetic divergence as the only criterion, using inappropriate developmental stages, and inadequately assessing fitness.

More robust tests of adaptive urban evolution, particularly employing adequate experimental approaches and in more diverse taxa and locations, are urgently needed.

Appropriately attributing adaptive urban evolution will maximize the use of cities in exploring fundamental evolutionary, ecological, and eco-evolutionary hypotheses.

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adaptation. These systems provide strong evidence for urban–nonurban differences that are both genetically based and confer a fitness advantage (Atlantic killifish, *Fundulus heteroclitus*; peppered moths, *Biston betularia*; acorn ants, *Temnothorax curvispinosus*; water fleas, *Daphnia magna*; ragweed, *Ambrosia artemisiifolia*; and holy hawksbeard, *Crepis sancta*; Table 1). Twenty-three additional systems demonstrate some degree of potentially adaptive, heritable urban–nonurban differences, but have limitations that necessitate additional work (Table 1).

The most extensive evidence pertains to urban adaptation to heat islands and chemical pollution. Fewer studies have explored adaptation in response to infrastructure, sound or light pollution, and human behavior. Others explore general pan-urban adaptation (i.e., no specific selective agent was tested). We encountered several urban studies that assert adaptation without thoroughly exploring other possible mechanisms (phenotypic plasticity or neutral evolution) that might underlie urban–nonurban differences. Further, many studies implied fitness benefits in urban contexts without explicitly testing for differential survival or reproduction. Although all studies contribute to our knowledge of urban biology, we call for researchers to be transparent about whether their results are 'consistent with' rather than 'evidence for' urban adaptation (Table 1).

Why Study Adaptation in Urban Contexts?

Urban areas encompass tremendous heterogeneity across spatial and temporal scales. They also expose organisms to myriad novel, often interacting, conditions that can act as strong selective agents. Urban environments are therefore unique macrocosms for studying a suite of fundamental and applied biological questions, such as the roles of microsite variation and adaptive gradients across space (e.g., at an center vs the edge of an urban park), temporal variation in exposure to different agents of selection, and human intervention (e.g., infrastructure conversion, pollution mitigation, urban restoration) in shaping adaptive outcomes (see Outstanding Questions). Urbanized landscapes can help to answer the limits of adaptive evolution because they constitute multifarious selective agents that are intensified and condensed across small temporal and spatial scales. These multiple urban stressors constitute unprecedented challenges to life and can rapidly lead to species extinction, **maladaptation**, or adaptation – all of which have substantial consequences at community and ecosystem levels. Nevertheless, work in urban environments can only address these questions if we are critical of the evidence for urban adaptation.

Detecting Urban Adaptation – Approaches, Strengths, and Limitations

As with demonstrating adaptation in any system, researchers must show that distinct urban phenotypes are genetically heritable (i.e., evolved) rather than environmentally induced (i.e., plastic) (Box 2) and that they confer fitness advantages (i.e., are adaptive). Specifically, populations are urban-adapted when their genetically heritable traits confer higher fitness in urban than in nonurban habitats [84]. However, researchers can still accurately identify urban populations as being locally adapted without knowledge of which specific traits are involved. Both manipulative and non-manipulative studies are essential for assessing urban adaptation (Figure 1). Although researchers typically document observations of urban–nonurban phenotypic and genotypic divergence first, manipulations can also be useful when urban–nonurban divergence is not apparent *in situ* (e.g., internal phenotypic changes and/or **countergradient variation**) [34–36,41–44,51–53]. We outline below a suite of manipulative and non-manipulative approaches, including their strengths and limitations, that are used to study urban adaptation.

Manipulative approaches – **common gardens**, **reciprocal transplants**, and introduction experiments – are staples of evolutionary ecology and generally offer the most direct evidence

Glossary

Adaptation: evolved, genetically based phenotypes that confer a fitness advantage in a particular context.

Adaptive: when a phenotype confers a fitness advantage in a particular habitat. Both genetically based trait differences (i.e., adaptations) and plastic trait changes can be adaptive.

Adaptive evolution: the change in the frequency of beneficial genetically based phenotypes in response to natural selection.

Common garden: an experimental design wherein individuals are reared in identical environmental conditions from an early life stage (e.g., embryo) to disentangle the effects of genetics and phenotypic plasticity on phenotypes.

Common gardening experiment: an extension of common-garden, transplant, or introduction experiments in which the differential impacts of local adaptation between different source populations on community dynamics and ecosystem functions are assessed.

Countergradient variation: environmentally plastic components of a phenotype occur in a contrasting direction to the genetic components of a phenotype. This often produces a similar phenotype in divergent environments, meaning that genetic differences in phenotypes can only be observed via manipulative experiments.

Exaptation: a trait is used by an organism in a situation other than what natural selection originally shaped it for. Exaptation was introduced into the biologist's lexicon to deal with the inaccuracies that the phrase 'preadaptation' (below) implies [107].

Genetic assimilation: when natural selection eventually leads to genetic control of a phenotype that previously manifested via environmental plasticity.

Genetic accommodation: when natural selection acts on a plastic phenotype, influencing the genetic regulation underlying plasticity and leading to heritable variation in the extent to which a phenotype is plastically expressed.

Local adaptation: a local population is locally adapted when it has higher fitness in its local environment relative to foreign individuals of the same species as a result of different selection pressures in these different environments.

Maladaptation: a local population is maladapted when it has lower fitness in its local environment relative to foreign

of urban adaptation. These approaches are not restricted to measuring the potential evolution of organismal traits, and can also be used to test the impacts of local adaptation on communities and ecosystems (e.g., using **common gardening experiments**) [84]. To our knowledge, such experiments have not yet been used to study the impacts of urban adaptation on community or ecosystem processes.

Common-garden Experiments

In common-garden experiments, researchers rear individuals from multiple populations from early life stages under the same experimental conditions to disentangle genetically based effects from plastic environmental effects on urban phenotypes (Figure 1A and Box 2). For example, researchers grew pepperweed (*Lepidium virginicum*) in shared conditions in the laboratory from seeds harvested from five regions in the northern USA, demonstrating that urban pepperweed evolved different life-history characteristics, including producing more seeds [59].

Researchers can vary common conditions to reflect environmental variation along urbanization gradients. For instance, urban killifish studies employ multiple pollutant concentrations, and urban water flea and acorn ant studies use multiple temperature regimes (Table 1). Because conditions are controlled, these studies can approximate both genetic and plastic contributions to urban–nonurban variation. Common gardens also allow researchers to assess local adaptation if they measure fitness tradeoffs across environments – although alone this is insufficient evidence unless conducted under realistic urban field conditions. For instance, common gardens with damselflies (*Coenagrion puella*) offer mixed evidence of fitness benefits (e.g., on growth, flight endurance, lifetime mating success) and therefore of urban adaptation [35,85].

Transplant Experiments

Reciprocal

The gold standard for detecting local adaptation is the reciprocal transplant [86] where researchers rear individuals from different populations (e.g., urban and nonurban) in both their local source environment and reciprocally in an alternative environment(s) in the field (Figure 1B). Whereas multi-treatment common gardens show evidence of local adaptation to manipulated controlled drivers, reciprocal transplants provide the most direct and biologically relevant evidence of urban adaptation, and can simultaneously capture multiple urban selective agents. At present, only two urban reciprocal transplant studies have been performed. One study demonstrated urban adaptation through flowering trait divergence in ragweed in Minneapolis–St. Paul, Minnesota, USA [55]. The other study did not detect local adaptation in urban blue tits (*Cyanistes caeruleus*), but did find that urban habitats lowered fledgling success [87].

Unidirectional

During unidirectional transplant experiments, researchers rear individuals from divergent environments in a single destination environment. One unidirectional transplant study showed that urban holy hawksbeard plants had a fitness advantage in urban sites compared to nonurban plants, but did not also transplant into nonurban sites [57]. Another study showed conflicting patterns of selection for a genetic antiherbivory and cold-tolerance trait in urban white clover (*Trifolium repens*) transplanted in Toronto, Ontario, Canada [61]. The agent of selection, and even the evolutionary mechanism underlying this trait, remain unclear, and recent models suggest that parallel patterns across urban gradients could arise via neutral rather than adaptive processes (Table 1) [63].

Introduction Experiments

In introductions, researchers release organisms and monitor potential evolutionary change in individuals of known provenance in areas (such as cities) where they are currently absent.

individuals of the same species.

Alternatively, when the local mean fitness of a population is lower than its replacement rate.

Natural selection: the evolutionary process by which particular phenotypes have higher survival and/or reproductive success in a given ecological context.

Nonurban: environmental contexts other than urban environments. A common contrast with urban habitats is with 'rural' environments, which can include both natural and agricultural environments.

Phenotypic plasticity: non-genetically based phenotypic variation resulting from environmental effects. Plastic phenotypes can occur in response to developmental environments, and can be either irreversible or can change throughout the lifetime of an individual.

Polyphenism: a type of environmentally induced plasticity that produces two or more distinct and discrete phenotypes from the same genotype.

Preadaptation: when a trait is used by an organism for a situation other than what natural selection shaped it for. The term 'exaptation' was introduced to revise the ambiguity associated with this phrase because it suggests that adaptation occurs in anticipation of future natural selection.

Reciprocal transplant: an experimental design wherein individuals are reared in both their local environment and reciprocally in a foreign environment from an early life stage (e.g., embryo) to test for local adaptation by assessing differences in survival and reproductive success in the two environments.

Transgenerational plasticity: heritable but non-genetic phenotypic effects that are passed on from parents to offspring. These can manifest through a variety of mechanisms ranging from hormones or nutrients provisioned into embryonic yolk to epigenetic chemical modification of DNA transcription through histone modifications and methylation. These effects are also called 'parental effects' and are difficult to distinguish from adaptation without studying F1 or F2 offspring reared in common gardens.

Urban: environments built by and for humans to live and work in. Urban environments are diverse and include city centers, residential (periurban and exurban suburbs) areas, commercial centers, and industrial spaces.

Introductions are important opportunities for tracking urban adaptation in real time, and can decipher why particular species are absent from urban areas, and also identify urban selective agents to which species are unable to adapt [77]. For ethical reasons, native species that have become locally extirpated from urbanization are particularly amenable for urban 'rewilding' and introduction experiments [77]. Assessing genomic changes and selection gradients before and after introductions can offer valuable insight into how **natural selection** operates in cities. Furthermore, urban introductions may be the only way to examine traits, such as dispersal, that are difficult to assess with transplants or common gardens. The only urban introduction example we are aware of are the seminal, but limited, introductions of peppered moths that aimed to understand selection imposed by industrial pollution. In these experiments, marked melanic and light moths were released into industrial and non-industrial areas, and demonstrated adaptive urban crypsis [6,8,30].

Non-Manipulative Approaches

These methods, including observational studies, identify urban–nonurban phenotypic or genotypic variation, and provide the groundwork for exploring potential urban adaptation. Although these approaches alone are insufficient for determining adaptation, they are a typical starting point for many studies. We note that countergradient variation is an important consideration wherein a lack of, or unexpected, phenotypic variation in the field can only be exposed when individuals are reared in common gardens. Urban countergradient variation has been demonstrated in damselflies and ragweed [35,55], and should be explored further when alternative urban phenotypes are expected but not observed.

Longitudinal Studies

Phenotypic changes tracked through time can reflect evolution, but only if phenotypes have a known genetic basis (discussed in the section on Heritable Trait Surveys). For example, longitudinal studies showed evolutionary change in threespine stickleback (*Gasterosteus aculeatus*) armor (a Mendelian trait) in the progressively ameliorated urban Lake Washington, Seattle, Washington, USA (Table 1) [21]. By contrast, anatomical shifts in urban brown rats (*Rattus norvegicus*), common bats (*Pipistrellus kuhlii*), and Guadalupe bass (*Micropterus treculii*) may suggest urban adaptation [88–90], but cannot disentangle plasticity from evolution and do not link phenotypes to fitness. To support urban adaptation, these primarily observational studies will require subsequent experimentation.

Selection Gradient Studies

These studies quantify the magnitude and form of selection by assessing relationships between traits and fitness (or fitness proxies). However, natural selection does not lead to adaptation if it acts on completely plastic traits. As such, manipulative approaches are still necessary to demonstrate evolutionary responses to selection. Selection gradients have revealed natural selection in urban birds [13,91–95] and plants [55–57,96,97]. For instance, urban selection gradients have linked trait variation to observed reproductive output in great tits (*Parus major*) in Montpellier, France, and in yellow jessamine vines (*Gelsemium sempervirens*) in North Carolina, USA [94,96]. However, without additional experiments to determine trait heritability, it is unclear whether selection actually leads to evolution in these cases.

Heritable Trait Surveys

Many phenotypes have both complex genetic and plastic components; thus, observations alone are typically insufficient for identifying adaptation. For phenotypes with a well-known genetic basis, however, surveys of urban–nonurban trait differences can be directly linked to allele-frequency shifts and thus evolution (Figure 1C). For instance, surveys of peppered moth

Urban adapter: a loosely used term originally intended to describe species that inhabit and have acclimated or habituated to residential areas, but is now often confused with species that have adaptively evolved to urbanized landscapes.

Urban adaptation: adaptive evolution taking place in organisms living in an urban environment. The term also refers to a phenotype that evolves in response to natural selection in an urban environment. This biological meaning contrasts with other uses of the term to denote how cities are designed and managed for future social and environmental change.

Table 1. Study Systems Conclusively Demonstrating, or Providing Evidence Consistent with, Urban Adaptation

CLADE	SPECIES	URBAN DRIVER ^a	FOCAL TRAIT(S)	ELEMENT 1: IS PHENOTYPIC DIVERGENCE GENETICALLY BASED? ^{b,c}	ELEMENT 2: IS THE GENETICALLY-BASED DIVERGENCE ADAPTIVE? ^{b,d}	REFERENCES
Amphibians	Tungara frog (<i>Physalaemus pustulosus</i>)	Noise pollution	Male calling	Suggestive evidence: Reciprocal transplant study with wild-caught adults	Suggestive evidence: Urban shifts in male calls were associated with greater mating success and survival	[10]
Birds	Dark-eyed Junco (<i>Junco hyemalis</i>)	Pan-urban effects	Stress physiology, behavior	Suggestive evidence: Common garden study with wild-caught juveniles		[11,12]
	Great tit (<i>Parus major</i>)	Pan-urban effects	"Tie" size (coloration)	Strong evidence: Field observations of shifts in the frequency of a strongly genetically determined trait	Suggestive evidence: Selection analysis parallels the phenotypic divergence: urban birds with smaller ties had higher survival in urban environments	[13]
	European blackbird (<i>Turdus merula</i>)	Pan-urban effects	Migratory and boldness behaviors	Suggestive evidence: Common garden study with wild-caught nestlings		[14,15]
Fish	Atlantic killifish (<i>Fundulus heteroclitus</i>) ^e	Water pollution	Chemical tolerance, aryl hydrocarbon receptor signaling pathway	Strong evidence: Multi-treatment laboratory common garden experiments with multi-generation lab-reared organisms tested at the embryo and larval stages Transcriptomic and genomic analyses	Strong evidence: Urban population fish exhibited higher survival in polluted environments compared with rural population fish within a laboratory common garden study Repeated evolution of whole-organism chemical tolerance and sub-cellular aryl hydrocarbon receptor pathways important for chemical tolerance across multiple urban replicates	[16–20]
	Stickleback (<i>Gasterosteus aculeatus</i>)	Amelioration of urban water pollution	Armor plating	Strong evidence: Field observations of temporal shifts in the frequency of a strongly genetically determined	Suggestive evidence: Armor plating in response to predators is adaptive in similar studies. Increased plating corresponds with ameliorated water quality, possibly enhancing predation pressure	[21]
	Creek chub (<i>Semotilus atromaculatus</i>)	Water flow	Morphology, locomotor performance	Strong evidence: Longitudinal study of fish morphology as water flow changed Common garden study with wild-caught juveniles on morphology and locomotor performance		[22,23]
Fungi	Chitinolytic fungi (<i>Chrysosporium pannorum</i> , <i>Trichoderma koningii</i>)	Heat island	Growth rate	Strong evidence: Multi-temperature laboratory common garden study	Suggestive evidence: Growth rate was the focal trait, but its role as a fitness proxy is unclear given difficulty of measuring fitness in many fungi Somewhat repeated (two out of four species tested) evolution of specialist-generalist tradeoffs, which are expected from theory, provides some evidence for adaptive evolution	[24]

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Table 1. (continued)

CLADE	SPECIES	URBAN DRIVER ^a	FOCAL TRAIT(S)	ELEMENT 1: IS PHENOTYPIC DIVERGENCE GENETICALLY BASED? ^{b,c}	ELEMENT 2: IS THE GENETICALLY-BASED DIVERGENCE ADAPTIVE? ^{b,d}	REFERENCES
Insects	Mosquito (<i>Anopheles gambiae</i>)	Chemical pollution	Nitrate and pesticide tolerance	Suggestive evidence: Field-caught larval comparisons of chemical pollution tolerance Candidate gene and genomic studies identifying the kdr locus as putatively underlying tolerance		[25–29]
	Peppered moth (<i>Biston betularia</i>) ^e	Air pollution	Wing coloration	Strong evidence: Field observations of temporal shifts in the frequency of a strongly genetically determined trait in congruence with environmental change	Strong evidence: Expected tradeoffs in survival: release experiments demonstrated moths tended to match their colors to substrate and that bird predators disproportionately ate lighter moths in polluted urban areas and darker moths in unpolluted nonurban areas Reversible evolution after environmental amelioration	[6–9,30,31]
	Blowfly (<i>Calliphora vicina</i>)	Heat island	Life history	Strong evidence: Common garden study with larvae from wild-collected females		[32]
	Grasshopper (<i>Chorthippus brunneus</i>)	Heat island	Life history	Strong evidence: Common garden study with F1 offspring		[33]
	Damselfly (<i>Coenagrion puella</i>)	Heat island, heat wave, chemical pollution	Growth rate, behavioral responses to pesticides, energy budgets	Strong evidence: Multi-treatment common garden experiments with larvae collected from wild-caught females	Suggestive evidence: Urban populations had higher survival than rural populations across all temperature treatments Nonurban damselfly adults had higher lifetime reproductive success. The genetically-based divergence towards slower urban growth rate was potentially an adaptation to longer urban growing seasons	[34–37]
	Wormlion flies (Diptera: Vermilionidae)	Pan-urban effects	Behavioral traits	Suggestive evidence: Common garden study using field-caught larvae		[38]
	Speckled wood butterfly (<i>Pararge aegeria</i>)	Pan-urban effects	Behavioral traits	Strong evidence: Common garden study using F1 larvae from wild-collected females		[39,40]
	Acorn ant (<i>Temnothorax curvispinosus</i>) ^e	Heat island	Heat tolerance, cold tolerance, reproductive phenology	Strong evidence: Multi-temperature laboratory common garden experiments with F1 and F2 generation lab-reared adult organisms	Strong evidence: Expected tradeoffs in fecundity among urban and nonurban populations across a multi-temperature laboratory common garden study: urban-origin fecundity greatest in warm environments and nonurban-origin fecundity greatest in cool environments	[41–45]

Table 1. (continued)

CLADE	SPECIES	URBAN DRIVER ^a	FOCAL TRAIT(S)	ELEMENT 1: IS PHENOTYPIC DIVERGENCE GENETICALLY BASED? ^{b,c}	ELEMENT 2: IS THE GENETICALLY-BASED DIVERGENCE ADAPTIVE? ^{b,d}	REFERENCES
					Positive directional selection for greater heat tolerance in urban environments and for greater cold tolerance in rural environments that match genetically-based trait divergence	
	Small ermine moth (<i>Yponomeuta cagnagella</i>)	Light pollution	Light avoidance behavior	Suggestive evidence: Common garden study using wild-caught larvae		[46]
Mammals	Gray squirrel (<i>Sciurus carolinensis</i>)	Pan-urban effects	Coat melanism (coloration)	Strong evidence: Field observations of shifts in the frequency of a strongly genetically determined trait	Suggestive evidence: Crypsis and roadkill surveys suggest relaxed pressure from human hunting and lower roadkill rates contributed to melanistic squirrels in urban environments	[47]
Non-insect invertebrates	Grove snail (<i>Cepaea nemoralis</i>)	Heat island	Shell color	Strong evidence: Citizen science field observations of shifts in the frequency of a strongly genetically determined trait	Suggestive evidence: Other studies show shell color linked with thermal performance Repeated evolution of shell color across multiple urbanization gradients	[48]
	Isopod (<i>Oniscus asellus</i>)	Heat island	Heat tolerance	Strong evidence: Two-temperature laboratory common garden experiments with F1 lab-reared offspring		[49]
	Water flea (<i>Daphnia magna</i>) ^e	Heat island	Heat tolerance, pace of life syndrome	Strong evidence: Multi-temperature laboratory common garden experiments with multi-generation lab-reared adult organisms	Strong evidence: Urban population water fleas had higher fecundity and total fitness (maximal population growth rate) in a warm laboratory common garden treatment compared with nonurban population water fleas	[50–53]
	Triangulate cobweb spider (<i>Steatoda triangulosa</i>)	Light pollution	Web-building location	Strong evidence: Common garden study on adults reared from the egg stage		[54]
Plants	Ragweed (<i>Ambrosia artemisiifolia</i>) ^e	Pan-urban effects	Flowering phenology	Strong evidence: Single-treatment greenhouse common garden study and fully reciprocal transplant study	Strong evidence: Reciprocal transplant experiment showed that rural population plants have higher total fitness (lifetime reproductive success) in all environments which was not consistent with an adaptive narrative Stronger selection in urban environment, was taken as the core evidence for adaptive urban evolution of flowering phenology	[55]
	Holy hawksbeard (<i>Crepis sancta</i>) ^e	Fragmentation	Seed dispersal, morphological, phenological, and	Strong evidence: Single-treatment greenhouse common garden study and one-way reciprocal transplant	Strong evidence: Genetically-based divergence in dispersal was consistent with predictions from survival costs of	[56–58]

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Table 1. (continued)

CLADE	SPECIES	URBAN DRIVER ^a	FOCAL TRAIT(S)	ELEMENT 1: IS PHENOTYPIC DIVERGENCE GENETICALLY BASED? ^{b,c}	ELEMENT 2: IS THE GENETICALLY-BASED DIVERGENCE ADAPTIVE? ^{b,d}	REFERENCES
			physiological traits	experiment of urban and nonurban populations into the urban environment	dispersal modeling Selection analyses via potential fecundity of plants transplanted to the urban environment were generally consistent with the genetically-based divergence wherein urban population plants were larger, flowered and senesced later, had higher photosynthetic capacity and water-use efficiency, and had higher concentrations of nitrogen in their leaves compared with nonurban population plants	
	Pepperweed (<i>Lepidium virginicum</i>)	Pan-urban effects	Morphological and phenological traits	Strong evidence: Single-treatment greenhouse common garden study Genomic analysis to assess urban a nonurban population genetic structure	Suggestive evidence: Higher fitness of the urban populations compared with nonurban populations in greenhouse conditions that perhaps better mimic urban rather than nonurban conditions Repeated evolution of phenological traits across multiple urbanization gradients	[59]
	Southern crabgrass (<i>Digitaria ciliaris</i>)	Pan-urban effects	Biomass growth	Strong evidence: Low- and high-competition greenhouse common garden study	Suggestive evidence: Increased biomass growth under reduced intraspecific competition typical of urban populations	[60]
	White clover (<i>Trifolium repens</i>)	Snow removal / snow melt leading to cooler winter air temperatures	Hydrogen cyanide production	Strong evidence: Field observations of shifts in the frequency of a strongly genetically determined trait Transplantation of a range of genotypes into urban and nonurban sites	Suggestive evidence: Adaptive nature largely determined from somewhat repeatable pattern of cyanogenesis across multiple urbanization gradients Transplant study found that the direction of selection (via biomass) for greater cyanogenesis during the summer season in the urban environment opposed the genetically-based response of diminished cyanogenesis in urban environments; no evidence of selection on cyanogenesis via seed mass. Selection results do not support an adaptive narrative	[61–64]
Reptiles	Crested anole (<i>Anolis cristatellus</i>)	Habitat structure, heat island	Limb morphology, heat tolerance, arginyl tRNA synthetase	Suggestive / strong evidence depending on the trait: Common garden study found evidence of genetically-based divergence in limb morphology Field-caught lizards exhibit divergence in heat tolerance	Suggestive evidence: Repeated evolution of limb morphology and genes involved in heat tolerance. Locomotor performance in field-caught lizards is most tightly linked to a plastic trait (hind limb length)	[65–67]

Table 1. (continued)

CLADE	SPECIES	URBAN DRIVER ^a	FOCAL TRAIT(S)	ELEMENT 1: IS PHENOTYPIC DIVERGENCE GENETICALLY BASED? ^{b,c}	ELEMENT 2: IS THE GENETICALLY-BASED DIVERGENCE ADAPTIVE? ^{b,d}	REFERENCES
				Allele frequency differences in arginyl tRNA synthetase between urban and nonurban populations		
	Australian water dragon (<i>Intellagama lesueurii</i>)	Pan-urban effects	Behavioral traits	Strong evidence: Common garden study using eggs from wild-collected mothers		[68]

^aThe putative urban agent of natural selection. 'Pan-urban effects' represent when only urban–nonurban comparisons are made.

^bBlank fields indicate that no data are available.

^cStudies provide evidence that urban–nonurban phenotypic differences are genetically based rather than being only phenotypically plastic. Strong evidence constitutes F1 common-garden studies or multi-treatment common gardens with measurements of whole-organism or subcellular traits, and/or field observations of shifts in the frequency of a strongly genetically determined trait in response to urbanization. Suggestive evidence often involves the use of later-stage and/or wild-caught organisms that confound interpretation of evolution relative to plasticity.

^dEvidence demonstrating either fitness tradeoffs (i.e., local adaptation) and/or fitness benefits for the urban population, traits under selection, and whether trait changes make adaptive sense based on theory and natural history. Strong evidence comes from reciprocal transplant and/or multi-treatment common-garden experiments that measure fitness. Other data such as patterns of repeated trait variation across urbanization gradients, selection analyses, and inferences on the adaptive nature of the trait from other nonurban studies offer supporting adaptive evidence. Supporting evidence includes the use of fitness proxies, rather than direct fitness measures or only providing supporting data such as selection analyses.

^eOne of six systems showing urban–nonurban phenotypic divergence that is both genetically based and also adaptive.

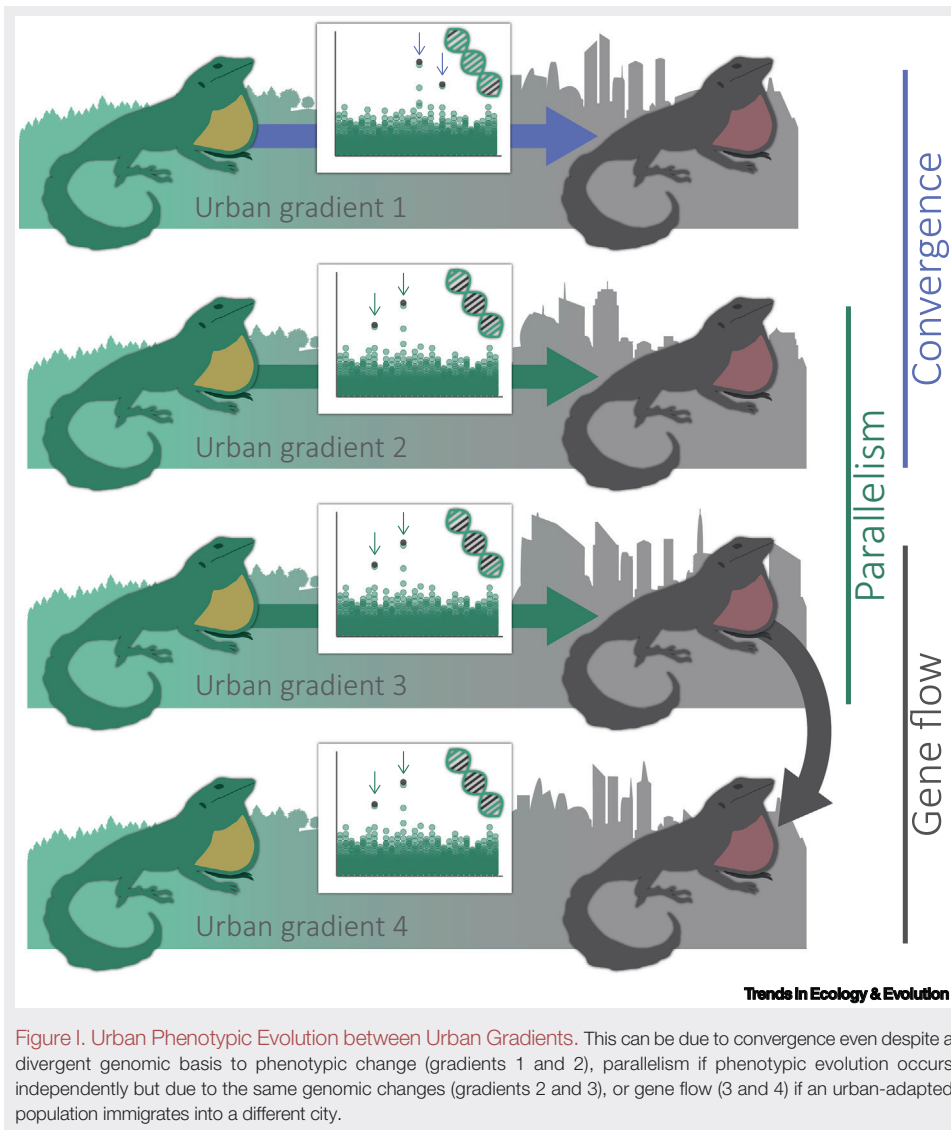
melanism (a highly heritable trait) demonstrated adaptation to urban pollution without experimentation (Table 1). Heritable trait surveys are particularly effective as community (or 'citizen') science projects where community members are deputized to collect phenotypic data and study urban adaptation in their own backyards. For example, community science has successfully shown increased frequencies of heritable color morphs in urban grey squirrels (*Sciurus*

Box 1. Repeated Urban Adaptation

Urban areas have emerged as prime locations for testing fundamental questions in evolutionary biology such as predictability and repeatability [3,24,33,43,59,61,64,67]. Cities are ideal for studying convergence – repeated, independent phenotype evolution either across populations or species in similar environments (Figure 1) – as well as parallel evolution – when convergence results from selection acting through the same genetic and developmental pathways (Figure 1) – because they are predicted to be environmentally homogenized and more similar to each other than to nearby nonurban areas [3].

Common gardens and molecular methods have helped elucidate the existence of, and mechanisms behind, urban convergence and parallelism. For example, common gardens showed repeated evolution of thermal tolerance limits to colder temperatures in acorn ants (*Temnothorax curvispinosus*) in response to urban heat islands in Cleveland and Knoxville (USA) [43]. Molecular methods have facilitated an understanding of the mechanisms underlying parallelism in killifish (*Fundulus heteroclitus*). Molecular evidence demonstrated that killifish tolerance adaptation to polychlorinated biphenyls (PCBs) across multiple North Atlantic urban estuaries is repeatedly and independently linked to the same physiological pathway, providing robust evidence of urban parallelism [16–20] (see Figure 1B in main text).

Observed repeated urban–nonurban phenotypic patterns do not always result from independent adaptation. Gene flow of urban-adapted variants via urban-to-urban dispersal can produce cross-city patterns mimicking convergence (Figure 1). The spread of locally adapted variants among similar environments may be particularly pronounced across cities if focal species are human commensals, particularly because some species, such as black widow spiders (*Latrodectus hesperus*), exhibit substantial cross-city connectivity [70]. For example, a common garden with pepperweed (*Lepidium virginicum*) identified convergent, genetically based urban phenotypes across five North American cities. Nevertheless, genomic data revealed that urban populations are more closely related to each other than to geographically adjacent nonurban areas, suggesting that gene flow, not convergence, among cities results in similar urban phenotypes across cities [59]. In such instances individual urban replicates may no longer be a city, but an entire region. By contrast, population genomic analyses illustrate that each urban–rural Atlantic killifish pairing is a true replicate, supporting parallel urban convergence (see Table 1 in main text).



carolinensis) and grove snails (*Cepaea nemoralis*) (Figure 1C) using SquirrelMapper and SnailSnap digital applications (Table 1). Ongoing research with the Global Urban Evolution (GLUE; <http://www.globalurbanevolution.com/>) project is crowd-sourcing samples to study global convergent evolution (Box 1) in urban white clover (Table 1). We note that, although these surveys demonstrate evolution, they still require manipulations to test whether trait variation is adaptive.

Molecular Approaches

Experiments can provide quantitative insights into genetically heritable urban–nonurban trait variation without specific knowledge of the underlying genetic mechanisms. However, diverse molecular approaches can offer correlative, and occasionally causal, links between specific genes and urban habitats or phenotypes. Although the majority of urban molecular research has

Box 2. The Complex Role of Plasticity in Adaptive Urban Evolution

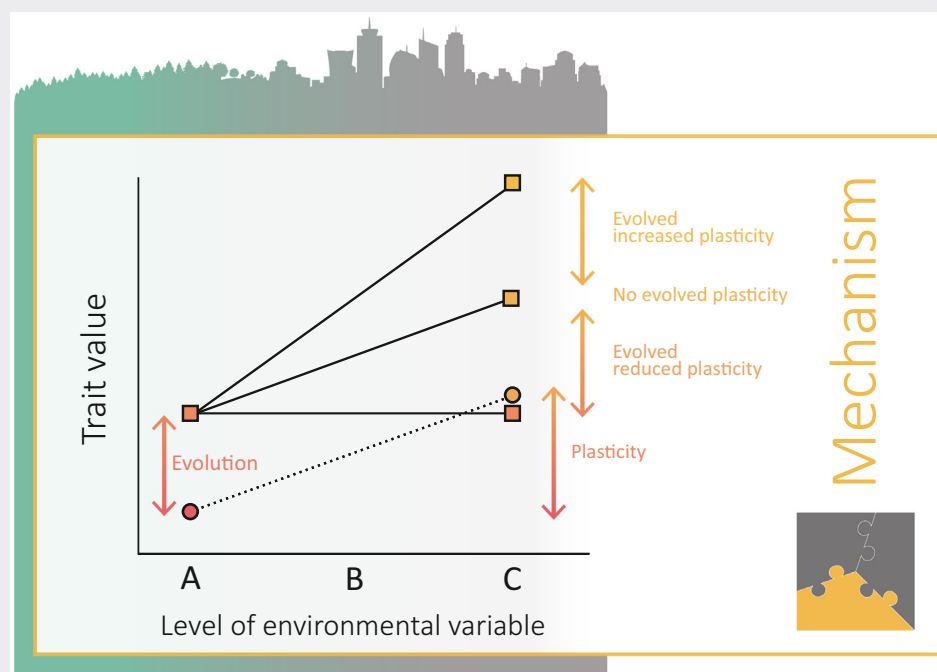
How plasticity might permit or impede organisms entering, persisting, and adapting to cities has not yet been explicitly examined. Interestingly, several examples offer evidence that plasticity has evolved in urban landscapes (Figure I), although these shifts are only putatively adaptive [24,35,42,52,53]. Crucially, phenotypic plasticity highlights the importance of accurate narratives and of carefully considering and addressing alternative hypotheses underlying urban phenotypes.

Attributing Adaptation

Identifying urban adaptation necessitates disentangling plastic responses from genetically based, evolved changes in populations [3,78]. In phenotype-only studies of urban organisms, the null hypothesis should be that the urban phenotypes result from plasticity [69]. The alternative hypothesis is that urban phenotypes are genetically based. Nevertheless, evolution and plasticity are not mutually exclusive (Figure I). Common gardens and reciprocal transplants enable the isolation of genetically based and plastic effects of the source environment on urban phenotypes (see Figure 1A,B in main text). Multiple experimental treatment conditions allow urban phenotypic variation to be partitioned into plastic and genetic components [52]. Care should be taken when possible to use at least F1 or subsequent generations to minimize field effects and potential **transgenerational plasticity** (see Table 1 in main text).

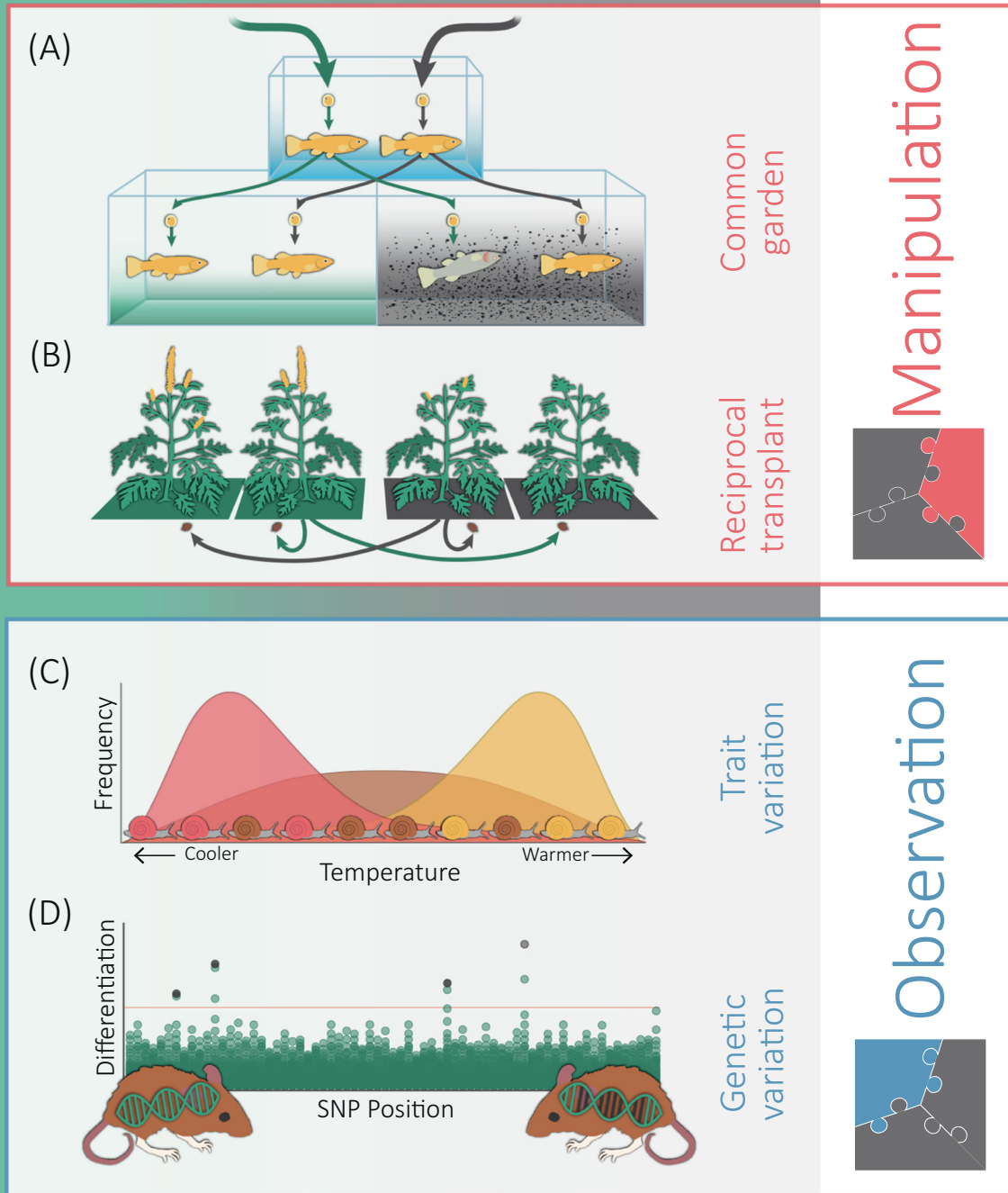
Mechanism

The role plasticity plays in structuring urban biodiversity remains largely unexplored. Plasticity may facilitate urban adaptation in various ways. Plasticity can allow entry into urbanized landscapes by overcoming environmental filtering from urban stressors. Plasticity can also allow persistence by 'buying time' for populations to adapt [78]. Finally, it can also provide novel phenotypic variation on which selection may act, for example through the release of cryptic genetic variation in urban environments [79]. Depending on whether plasticity is favored, enhanced plastic responses (e.g., **polyphenisms**) or canalization of plastic phenotypes (**genetic assimilation**) can further refine phenotypes (**genetic accommodation**) [80]. Such determinations generally rely on the tradeoffs between the cost of producing urban phenotypes and the match of the phenotype to novel urban conditions [81]. Although usually considered at the within-generation scale, plastic effects might have important effects between generations – so-called transgenerational plasticity. Such effects will only be beneficial in the urban environment if future conditions can be anticipated by previous generations [82]. Importantly, however, although plasticity could facilitate urban adaptation, plasticity can also shield phenotypic variation from selection, thus impeding urban adaptation [83].



Trends in Ecology & Evolution

Figure I. Plasticity and Evolution in Urban Environments. Experiments using multiple urban treatment levels offer unique opportunities to test for the underlying genetic-based, evolved basis and plastic contributions to urban phenotypes, including whether urbanization leads to the evolution of enhanced or reduced plasticity. Circles and squares represent different source populations.



focused on non-adaptive processes (e.g., gene flow) [5], molecular approaches are becoming increasingly popular for studying urban adaptation.

Molecular methods, especially candidate gene and genomic techniques, are useful for generating hypotheses about urban adaptation. In candidate gene approaches, one or a few genes of interest are sequenced based on hypothesized associations with urbanization. For example, genotypic divergence in harm avoidance, fear, or novelty-seeking behaviors across urbanization gradients in various bird species [98,99] suggest urban adaptation to human activity. Genomic approaches, which have become increasingly popular for inferring urban adaptation, use extensive sequence data to infer loci that may have experienced natural selection. These methods can be especially useful for generating hypotheses about traits that are otherwise challenging to measure, such as physiology [100,101]. For instance, researchers have used transcriptomics to identify loci related to metabolic functions in white-footed mice (*Peromyscus leucopus*) (Figure 1D), thereby setting the stage for experiments to explicitly test adaptation to urban pollution and altered dietary conditions [102,103].

Nevertheless, genotype–phenotype and genotype–environment associations do not inherently confirm the genetic basis of a trait (which requires procedures such as gene knockouts) and necessitate experiments to determine whether urban phenotypes are differentiated, heritable, and linked to fitness. As such, researchers must take care in exploring and inferring urban adaptation based solely on molecular data. For example, a study on bobcats (*Lynx rufus*) in Los Angeles, California, USA found evidence for selection at several immune loci following an urban mange outbreak [104]. This study provides evidence of selection that correlated with a disease event; however, evidence of selection does not mean that adaptation necessarily occurred. By contrast, work on coyotes (*Canis latrans*) in New York, New York, USA failed to detect evidence of selection on immune genes [105]. The authors attribute this result to minimal evidence of urban disease, but the point remains that studies of selection on particular genes do not necessarily provide evidence for adaptation, either by failing to detect selection or by not taking further steps to link the selection to adaptive evolutionary responses. Finally, researchers studying water dragons (*Intellagama lesueurii*) in parks in Brisbane, Australia showed both urban–nonurban morphological divergence in field-collected lizards and differentiation at neutral genetic loci [106], but were careful to discuss multiple plausible neutral, plastic, and adaptive explanations for this molecular and morphological divergence [106].

Integrating Methods

Integrating insights from multiple non-manipulative and manipulative approaches is often ideal for demonstrating and contextualizing urban adaptation. To date, this has only been accomplished in a few systems (Table 1). For instance, studies on mosquitoes (*Anopheles gambiae*)

Figure 1. Methodological Approaches to Studying Urban Adaptation. Diverse methods have been employed to infer adaptive evolution in cities. Manipulative experiments offer the most direct evidence of adaptive evolutionary change in cities. Common gardens (A) with killifish (*Fundulus heteroclitus*) have demonstrated repeated local adaptation to polychlorinated biphenyl (PCB) contamination across cities, and reciprocal transplants (B) with ragweed plants (*Ambrosia artemisiifolia*) demonstrated local adaptation where urban ragweed has higher reproductive success in urban habitats compared to nonurban ragweed. Observational studies, both of phenotypes and genotypes, can provide insights into urban evolutionary change but often cannot demonstrate that genetically based differences are adaptive. Observed variation (C) in shell color, a genetically heritable trait in grove snails (*Cepea nemoralis*), found more yellow shells in urban heat islands and more pink shells in cooler regions, although further experiments will be necessary to understand whether evolutionary shifts in shell color frequencies are adaptations to urban heat islands. Observational genomic analyses (D) of white-footed mice (*Peromyscus leucopus*) have identified single nucleotide polymorphisms (SNPs) in genomic regions that are associated with metabolic functions, and experimental work will be necessary to show whether urban mice are adapted to metabolizing toxins and urban food sources.

and killifish integrate common gardens and molecular approaches across multiple cities and ontogenetic or generational scales to understand adaptation to urban contaminants, and studies on white clover and holy hawksbeard plants have explored urban adaptation using combinations of transplant, common-garden, candidate gene, and selection gradient approaches (Table 1).

Although common gardens and reciprocal transplants are ideal for testing urban adaptation, they are impractical, if not impossible, for many species, especially those that are protected, large, or long-lived. In urban areas, transplants may also be untenable owing to potential vandalism or restrictive issuing of permits. In these cases, creatively integrating methods – such as molecular approaches coupled with field observations (genotype–phenotype rather than only genotype–environment associations) can provide evidence consistent with urban adaptation [107]. For example, researchers identified genotypes associated with greater plasticity in thermal physiology in urban wild-collected crested anole lizards (*Anolis cristatellus*) using RNA-seq, and provided preliminary evidence of urban heat-island adaptation [67]. Even so, manipulative studies will be necessary to test for innate urban–nonurban heat-tolerance differences in these anoles.

We emphasize that, for systems where manipulative experiments are feasible, integrating other approaches is not a replacement for manipulations – these offer the strongest insights for understanding urban adaptation. Alternatively, for inferring urban adaptation in taxa such as soil fungi (Table 1), where generation times are nebulous and measuring fitness is challenging owing to sexual and asexual changes, integrating methods may be essential for understanding urban adaptation.

Common Issues in Identifying Urban Adaptation

Growth and Development

The choice of life stage has profound effects on testing and interpreting adaptation (Table 1). For transplants and common gardens, organisms must experience test environments from early developmental stages because using older and/or wild-collected organisms can confound developmental and environmental plastic effects with evolutionary divergence (Box 2 and Table 1). For example, the use of wild-collected larvae (rather than embryos) complicates inferences about urban adaptation to pollution and pesticides for mosquitoes and to urban lighting for ermine moths (*Yponomeuta cagnagella*) (Table 1). The need to minimize environmental effects on development may be particularly crucial in urban environments where organisms are simultaneously exposed to myriad novel conditions that may make discerning plastic and genetic effects on traits in wild-collected individuals more difficult than in nonurban conditions.

The most direct method of minimizing environmental and transgenerational (Box 2) effects is by generating and testing F1 and F2 offspring reared in the test environment. Naturally, controlled rearing is only possible for species that can survive and reproduce under manipulated conditions in feasible timeframes. Notably, a recent meta-analysis of animals concluded that maternal effects are approximately half as strong as additive genetic variation (although their strength decreased across development) [108]. Therefore, having parent generations spend a long developmental acclimation period in the test treatment might substantially minimize maternal effects, especially because maternal effects can have substantial impacts on urban phenotypes [109]. Experiments incorporating parental acclimation have been carried out with urban water fleas, acorn ants, damselflies, and killifish in response to heat islands and pollution (Table 1).

Box 3. Space and Time in Urban Adaptation

Spatial and temporal variation can shape evolutionary outcomes. Such variation is particularly pronounced in and among cities owing to heterogeneity in abiotic, biotic, and social conditions [111,112]. Researchers can maximize or minimize urban heterogeneity depending on the particular urban adaptation question.

For example, research on urban ragweed (*Ambrosia artemisiifolia*) adaptation explicitly incorporated variable urban source habitats including bike paths, road medians, abandoned lots, and riverbanks to account for urban heterogeneity and to examine pan-urban adaptation [55]. By contrast, research on water flea and acorn ant adaptation to heat islands specifically selected sites to isolate heat-island effects from other urban factors [41,42,51]. Urban site selection such as this allows direct evolutionary comparisons within and between cities. Work on clover has used distance from the city center as the site selection criterion, and this therefore assesses pan-urban effects but without explicitly addressing urban site variation or hypothesized drivers of adaptation [61].

How cities are used with respect to minimizing or maximizing local versus regional site variation has important implications for interpreting urban adaptation, from pan-urban or patch-level urban agents of selection. These considerations might have important, predictable consequences for the use of cities as testbeds of convergent evolution (Box 1) because convergence perhaps more likely occurs when urban site variation is minimized. Specifically, although multiple selection gradients (e.g., heat islands) occur systematically across the globe, individual cities, and even habitats within cities, are complex and are impacted by diverse social and biophysical factors. Urban heterogeneity may therefore impede cities from acting as replicate selection environments, even if similar phenotypes are observed. Such spatial and temporal heterogeneity highlights the importance of careful experimental design in studying urban convergence.

Temporal variation is also essential to consider in urban adaptation research. Further, with the heightened role that humans play in shaping evolutionary responses within cities [111,112], the provenance of the species under study must also be considered. Whether cities developed around existing populations (thus allowing many generations of urban adaptation) versus the entry or re-entry of species (which might then have fewer generations to adapt to city life) can strongly impact on the interpretation of whether populations can and are adapting to cities. Because humans construct and modify cities, urbanization offers a unique opportunity to document the rates of adaptation [3], but few studies, except research on urban dark-eyed juncos (*Junco hyemalis*) [11], explicitly assess the speed of urban adaptation. Although humans readily document many facets of urbanization, it may be more challenging to know the age of urban populations. Introduction experiments may therefore prove to be useful tools for studying rates of adaptive urban evolution.

Fitness

Establishing fitness consequences associated with urban populations or phenotypes is essential for demonstrating urban adaptation. Composite fitness measures of survival and fecundity offer the greatest inferences of local adaptation [84] but have seldom been used for urban organisms (Table 1). Fitness proxies, such as biomass, growth rate, performance, and body condition, are commonly used in urban adaptation studies, but are difficult to translate into survival or reproductive success and thus adaptation. For instance, work on *Anolis* lizards assessed urban–nonurban differences in locomotor performance, a fitness proxy. However, because the lizards were wild-collected, the relative influences of developmental plasticity (i.e., lizard limbs grow differently in cities because they develop while running on urban surfaces) and evolution cannot be untangled, especially because a common garden showed that the primary morphological correlate of locomotor performance (hindlimb leg length) is plastic rather than genetically based [65,66]. In addition, work on clover has used seed set and biomass as proxies that do not necessarily translate directly into reproductive success [61].

The distinction between absolute and relative fitness also must be assessed in common gardens or transplants [110]. This is especially important for urban populations that might have higher relative fitness than nonurban populations when raised in urban environments (i.e., are urban-adapted), but both populations could have lower fitness in the urban environment than in the nonurban environment (i.e., are maladapted), as with blue tits [86]. Note, however, that fitness could also be higher for both populations owing to factors such as enemy release or nutrient supplementation, which are especially prevalent in urban environments. Accounting for spatial and temporal variation in urban selective pressures (Box 3) is particularly important for

understanding absolute and relative fitness, both among urban sites and between urban and nonurban environments.

In reviewing the urban adaptation literature, we found that fitness is seldom assessed, even when traits are shown to be heritable (Table 1 and supplemental information online). Further, relative versus absolute fitnesses are rarely contextualized in relation to one another. In particular, the nonurban context (e.g., agricultural versus natural areas) with which an urban population is compared may influence interpretations of relative and absolute fitness. Indeed, the studies we identified as demonstrating urban adaptation compared urban populations to both agricultural [55–59] and natural [34–37,47] populations. However, these different nonurban contexts are rarely discussed, although they could possibly shape interpretations of urban adaptation.

Concluding Remarks: Urban Adaptationists

Urban adaptation offers exciting prospects for advancing fundamental questions in biology (see Outstanding Questions). However, we found that few systems conclusively demonstrate urban adaptation, although an increasing number offer exciting preliminary evidence. Studies have regularly emphasized urban adaptation based solely on phenotypic or molecular variation, and it was often unclear whether evolution had occurred, and much less whether variation was adaptive. Evolutionary research in general is fraught with hyper-adaptationist narratives, often with insufficient evidence [69,113]. The urban adaptation research program described previously [3], expanded upon here, provides a firm basis for assessing urban adaptation. Comprehensive understanding of urban adaptation, in part, remains obscured because adaptationist terminology is inconsistently and inaccurately applied. We are encouraged, however, by appropriately circumspect language in many studies reporting evidence consistent with, but not conclusive proof of, urban adaptive evolution, and we applaud researchers for reporting negative urban adaptation findings [61,86,114,115]. Although rigorously identifying urban adaptation is essential, it is equally important to report when species do not adapt to cities because this is equally relevant for conserving and managing urban biodiversity [77].

Misunderstanding of urban adaptation in part stems from popularization of the term **urban adapter** – which implies evolutionary processes despite its original intended use in a more ecological or colloquial sense [116]. In addition, although conflating **exaptations** with true adaptations is not unique to urban research, doing so has contributed substantially to confusion about whether urban phenotypes exist because they facilitate colonization of urban areas (i.e., are exaptations) or whether they are real urban adaptations. For instance, work on mammals has described a series of traits associated with urban species as facilitating 'urban adaptation' [117] although these traits are more accurately labeled 'urban exaptations' [118]. Furthermore, the urban literature commonly uses the evolutionarily ambiguous term **preadaptation** [119,120] to describe traits that are exaptations. Although the use of 'adapt' in its colloquial sense pre-dates its biological use by centuries, 'adaptation' has a particular meaning in biology. We suggest that the relatively loose, colloquial use of 'adapt' and its derivatives by biologists has obstructed our synthetic understanding of evolution in urban environments.

Urban adaptation narratives are increasingly common not only in scientific discourse but also in popular books [121], news stories [122], and blogs (e.g., <https://urbanevolution-litc.com/>). It is therefore essential that urban researchers accurately and carefully employ adaptationist rhetoric. Urban adaptation offers unique opportunities to teach evolutionary principles to the public by using organisms in their own backyard, but only if those stories accurately portray biological phenomena [77]. For better or worse, scientists also increasingly inform themselves about scientific advances through non-academic media [123,124], meaning that inaccurate adaptationist

Outstanding Questions

Urban adaptation is typically studied relative to 'baseline' nonurban environments. How does microgeographic variation in site selection (e.g., local vs regional land use, forest vs agricultural nonurban sites) impact on adaptive inferences?

Urban ecosystems are composed of species communities that do not have natural analogs. How important is provenance (species that persist through urbanization vs species that secondarily invade post-urbanization) for evolutionary outcomes? What traits determine why some species are found in cities whereas others are not?

What are the relative contributions of adaptation, plasticity, and exaptations in structuring urban biodiversity?

Are urban abiotic factors stronger selective agents than biotic factors?

Does adapting to one selective agent make an organism more or less likely to adapt to another?

How prevalent is urban maladaptation, and how do populations recover or fail to recover from urban maladaptation?

Is urban adaptation reversible if a selective pressure is mitigated or removed?

How prevalent is convergent or parallel urban adaptation, and when do other urban selective agents mediate convergence?

To what extent does urban adaptation influence eco-evolutionary dynamics (communities, ecosystem functions, and ecosystem services) and vice versa?

Human society affects all aspects of cities. How does human social heterogeneity shape urban adaptation and urban eco-evolutionary dynamics?

messaging may further mislead researchers about the state of knowledge about urban adaptation. Narratives shape the way researchers understand a field and ask new questions [113], and continued synthetic inquiry into urban evolutionary biology therefore requires careful and accurate narratives. When and how adaptation shapes evolving urban biodiversity remains an exciting and pressing issue in an era of relentless and unprecedented urbanization [125].

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Supplemental Information

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