REVIEW SUMMARY

EVOLUTION

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PHOTO

Evolution of life in urban environments

Marc T. J. Johnson* and Jason Munshi-South*

BACKGROUND: The extent of urban areas is increasing around the world, and most humans now live in cities. Urbanization results in dramatic environmental change, including increased temperatures, more impervious surface cover, altered hydrology, and elevated pollution. Urban areas also host more non-native species and reduced abundance and diversity of many native species. These environmental changes brought by global urbanization are creating novel ecosystems with unknown consequences for the evolution of life. Here, we consider how early human settlements led to the evolution of human commensals, including some of the most notorious pests and disease vectors. We also comprehensively review how contemporary urbanization affects the evolution of species that coinhabit cities.

ADVANCES: A recent surge of research shows that urbanization affects both nonadaptive and adaptive evolution. Some of the clearest results of urban evolution show that cities elevate the strength of random genetic drift (stochastic changes in allele frequencies) and restrict gene flow (the movement of alleles between populations due to dispersal and mating). Populations of native species in cities often represent either relicts that predate urbanization or populations that established after a city formed. Both scenarios frequently result in a loss of genetic diversity within populations and increased differentiation between populations. Fragmentation and urban infrastructure also create barriers to dispersal, and consequently, gene flow is often reduced among city populations, which further contributes to genetic differentiation between populations.



A gradient in urbanization showing the skyline of Canada's sixth largest city (Mississauga, Canada) on the horizon, and the Credit Valley and the University of Toronto Mississauga campus in the foreground.

The influence of urbanization on mutation and adaptive evolution are less clear. A small number of studies suggest that industrial pollution can elevate mutation rates, but the pervasiveness of this effect is unknown. A better studied phenomenon are the effects of urbanization on evolution by natural selection. A growing num-

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ber of studies show that plant and animal populations experience divergent selection between urban and nonurban environments. This divergent selection has led to adaptive

evolution in life history, morphology, physiology, behavior, and reproductive traits. These adaptations typically evolve in response to pesticide use, pollution, local climate, or the physical structure of cities. Despite these important results, the genetic basis of adaptive evolution is known from only a few cases. Most studies also examine only a few populations in one city, and experimental validation is rare.

OUTLOOK: The study of evolution in urban areas provides insights into both fundamental and applied problems in biology. The thousands of cities throughout the world share some features while differing in other aspects related to their age, historical context, governmental policies, and local climate. Thus, the phenomenon of global urbanization represents an unintended but highly replicated global study of experimental evolution. We can harness this global urban experiment to understand the repeatability and pace of evolution in response to human activity. Among the most important unresolved questions is, how often do native and exotic species adapt to the particular environmental challenges found in cities? Such adaptations could be the difference as to whether a species persists or vanishes from urban areas. In this way, the study of urban evolution can help us understand how evolution in populations may contribute to conservation of rare species, and how populations can be managed to facilitate the establishment of resilient and sustainable urban ecosystems. In a similar way, understanding evolution in urban areas can lead to improved human health. For example, human pests frequently adapt to pesticides and evade control efforts because of our limited understanding of the size of populations and movement of individuals. Applied evolutionary studies could lead to more effective mitigation of pests and disease agents. The study of urban evolution has rapidly become an important frontier in biology, with implications for healthy and sustainable human populations in urban ecosystems.

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REVIEW

EVOLUTION

Evolution of life in urban environments

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Our planet is an increasingly urbanized landscape, with over half of the human population residing in cities. Despite advances in urban ecology, we do not adequately understand how urbanization affects the evolution of organisms, nor how this evolution may affect ecosystems and human health. Here, we review evidence for the effects of urbanization on the evolution of microbes, plants, and animals that inhabit cities. Urbanization affects adaptive and nonadaptive evolutionary processes that shape the genetic diversity within and between populations. Rapid adaptation has facilitated the success of some native species in urban areas, but it has also allowed human pests and disease to spread more rapidly. The nascent field of urban evolution brings together efforts to understand evolution in response to environmental change while developing new hypotheses concerning adaptation to urban infrastructure and human socioeconomic activity. The next generation of research on urban evolution will provide critical insight into the importance of evolution for sustainable interactions between humans and our city environments.

e are living in an increasingly urbanized world, which is altering the environments and life around us. Urbanization is the process by which humans form dense settlements constructed of buildings, roads, and supporting infrastructure. Here, we use the term "urban" to refer to densely populated human settlements and "city" to include large metropolitan centers and towns (1). Fiftyfive percent of people live in cities (1), with urban areas comprising 3% of Earth's land surface (Fig. 1) (2, 3). As the global human population rises, the extent of urbanization will continue to grow (1). Urbanization has large effects on the physical environment, ecosystem processes, and ecology of organisms that live in cities (4, 5). A surge of recent studies suggest that urbanization also alters the evolution of life around us (Fig. 1 and Tables 1 and 2), but our understanding of the importance and prevalence of urban influences on evolution is underdeveloped and forms the focus of our Review.

Urbanization alters abiotic and biotic environments over time and space (Fig. 2). Cities develop gradually, and their impact on the environment can depend on their age, density, size, geographical context, socioeconomics, and governmental policies, among other factors (3, 6). Some of the clearest changes to the physical environment caused by urbanization involve increased impervious surface cover (such as buildings and roads), higher temperatures, as well as elevated air, noise, and light pollution (4). Changes to the biotic environment include increased habitat fragmentation (7), more invasive species, lower diversity, and abundance of some native species (8, 9), and a loss of phylogenetic diversity within communities (10, 11). Urbanization often leads to convergent environments, in which distant cities are more similar to one another than urban areas are to their surrounding nonurban environments (12, 13). Although the ecological effects of urbanization are increasingly understood, how these changes influence evolution have only recently been appreciated (6, 14–16).

Ecological changes associated with urbanization have the potential to strongly affect the evolution of urban populations. It was long thought that evolution was too slow to study on time scales relevant to urbanization, but it is now recognized that evolution can be rapid, with observable evolutionary change in as little as two generations (17). Anthropogenic activities in general are known to affect evolutionary processes across a wide range of organisms (18-20), but these results from nonurban environments do not necessarily pertain to urban environments because cities are a unique anthropogenic disturbance. Urbanization causes simultaneous and often predictable largescale changes in numerous abiotic and biotic environmental factors, so that cities represent novel ecosystems with no natural analog. Thus, it is unclear whether previous studies of evolution in nonurban environments are relevant to making predictions about evolution in urban areas (4, 21). Many organisms have evolved adaptations over long periods of time to coinhabit urban areas (22). Rats, pigeons, bed bugs, and cockroaches are just a few of the examples of organisms that have adapted to live in and around human settlements throughout the world (Box 1). A recent wave of evidence shows that urbanization frequently affects adaptive (natural and sexual selection) and nonadaptive (genetic drift and gene flow) evolutionary processes in organisms as diverse as microbes, plants, insects, fish, mammals, and birds (Table 1).

In this Review, we ask whether urbanization affects evolution through a comprehensive review of the evidence for evolutionary change in urban environments and the mechanisms that cause these changes. Because urbanization represents the best and largest-scale unintended evolution experiment, with thousands of cities worldwide, the study of urban evolution makes it possible to tease apart the mechanisms driving evolution at an unprecedented scale. Key examples of urban evolution are summarized in the text as well as in Tables 1 and 2. A comprehensive summary of all species in which urban evolution has been studied is provided in table S1. We then consider how evolution in urban areas can affect the environment and human health. It is increasingly recognized that evolution affects the ecology of populations, communities, and ecosystems (23, 24), but how urban evolution feeds back to affect ecology is unknown (25). Because urban evolution is an emerging area of research with more questions than answers, we highlight the existing challenges and provide a roadmap for future research. Answering these questions goes beyond intellectual curiosity. This knowledge will have important applied implications for conservation, mitigating pests and human disease, and the maintenance of healthy ecosystems.

Does urbanization affect evolution?

At the most basic level, evolution is a change in population allele frequencies from one generation to the next. Mutation, genetic drift, gene flow, and natural or sexual selection can all influence allele frequencies in urban populations. Evolution caused by each of these mechanisms has now been documented in cities by using a diverse array of approaches and organisms (Table 1). By a substantial margin, the influence of urbanization on genetic drift and gene flow has been investigated more extensively than mutation or selection (table S1). Below, we review the evidence for each evolutionary mechanism in urban populations, and identify key unanswered questions.

Our discussion is limited to studies that clearly demonstrate changes in evolutionary processes or patterns in response to urban environments, with direct evidence for allele frequency changes across space or time, or heritable phenotypic changes in urban environments demonstrated through the use of common gardens or the study of Mendelian inherited traits. Many other changes in morphology, behavior, physiology, and gene expression have been reported in urban populations (26), but the genetic basis of these changes has often not been established and may often be explained by phenotypic plasticity, which is an interesting phenomenon in its own right but beyond the scope of this article (14, 27). By limiting our Review to direct evidence for evolution, we

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lay the groundwork for predicting the direction, magnitude, repeatability, and fitness benefits of evolutionary change across urban landscapes (Fig. 2).

Mutation

Evolution from new mutations occurs over much longer time scales than the process of urbanization and is thus unlikely to result in substantial change in response to urbanization on its own. Even so, there are two important aspects of mutation that must be considered. First, environmental changes associated with urbanization may induce mutations or influence genome-wide mutation rates. Second, because mutation is the ultimate source of all genetic variation, it is important to understand whether evolution in urban environments stems from new mutations that occur after urbanization or from preexisting mutations that persist as standing genetic variation within populations. Standing genetic variation is more likely than new mutations to result in rapid adaptive and nonadaptive evolution in response to urbanization (28).

Evidence suggests that urban pollution can increase mutation rates. This occurs whenever changes in the environment act as a mutagen, increasing mutation rates in the germline or within somatic tissues that later differentiate into reproductive tissue. The most extreme examples are cities contaminated with radiation, such as Chernobyl and Fukushima, where mutation rates are consistently higher in plants, animals, and bacteria (29). Even in more typical cases, such as industrial air pollution that increases concentrations of carcinogenic hydrocarbons, mutation rates of repetitive DNA in birds (30) and mammals (31) may be elevated (Fig. 3A). If this is a general urban phenomenon, air pollution could routinely elevate the incidence of deleterious and beneficial mutations within urban populations.

Studies show that evolution in response to urbanization can result from either new mutations that arise after urbanization, or ancestral substitutions that occurred before urbanization and exist as standing genetic variation within populations. For example, it was recently shown that the increase of melanic peppered moths (*Biston betularia*) during the industrial revolution of Europe resulted from a new mutation in the early 1800s after the onset of pollution, which rapidly increased in frequency (*32*). By contrast, adaptation to water pollution in Atlantic killifish (*Fundulus*)

heteroclitus) (33) and tomcod (*Microgadus tomcod*) (34) likely resulted from selection on alleles that were present at low frequency before pollution. Additional examples of evolution from existing genetic variation that predates colonization of urban environments include white clover (*Trifolium repens*) (35, 36), white-footed mouse (*Peromyscus leucopus*) (37), and common blackbird (*Turdus merula*) (Table 1) (38). Although more work is needed, we predict that given the young age and rapid development of cities, adaptive and nonadaptive evolution in cities will typically stem from standing genetic variation.

Genetic drift

Urbanization is predicted to strongly influence genetic drift, which produces stochastic changes in allele frequencies between generations. Genetic drift is most prominent in small, isolated populations, and thus its evolutionary influence within cities is expected to increase whenever urbanization results in reduced population sizes or greater isolation. Urbanization can cause such reductions in multiple ways, including (i) the loss of natural habitat caused by fragmentation, (ii) founder effects associated with the establishment of new urban populations, and (iii) severe

Table 1. Examples of evolution in noncommensal species in response to urbanization. Columns show species' common and scientific names; the region of study (Africa, AF; Asia, AS; Europe, EU; North America, NA); the maximum number of cities examined in a single study; whether studies examined molecular genetic (G) or heritable phenotypic (P) evolutionary changes; and the mechanisms of evolution examined (mutation, U; genetic drift, D; gene flow, M; selection, S). A comprehensive list and description of species studied is included in table S1.

				Phenotypic/		
Common name	Scientific name	Region	Number of cities	genetic	Mechanism	Citations
			Virus			
Dengue	Dengue virus type 4	NA	-	G	S, D	(58)
			Plants			
Holy hawksbeard	Crepis sancta	EU	1	Р	S	(39, 72, 73)
Virginia pepperweed	Lepidium virginicum	NA	5	G, P	S, M	(83)
White clover	Trifolium repens	NA	4	G, P	S	(36)
			Insect			
Peppered moth	Biston betularia	EU	-	G, P	S	(32, 69, 70, 127)
			Fish			
Killifish	Fundulus heteroclitus	NA	4	G, P	S, D, M	(33, 84, 128, 129)
			Amphibians and reptiles			
Crested anole	Anolis cristatellus	NA	3	Р	S	(82)
Eastern water dragon	Intellagama lesueurii	AU	1	G, P	S, D, M	(75)
Red-backed salamander	Plethodon cinereus	NA	1	G	D, M	(46, 130)
Common wall lizard	Podarcus muralis	EU	1	G	М	(61)
Fire salamander	Salamandra salamandra	EU	2	G	D, M	(47, 131)
			Birds			
House finch	Carpodacus mexicanus	NA	1	G, P	S	(71, 132)
Dark-eyed junco	Junco hyemalis	NA	1	Р	S, D	(76, 81, 111, 133)
Herring gull	Larus argentatus	NA	6	G	U	(30, 126)
Common blackbird	Turdus merula	EU	13	P, G	S, D, M	(38, 51, 78, 134, 135)
			Mammals			
Striped field mouse	Apodemus agrarius	EU	1	G	D, M	(43, 136)
		AF,AS,				
Human	Homo sapiens	EU	17	G	S	(86)
Bobcat	Lynx rufus	NA	1	G	S, D, M	(57)
White-footed mouse	Peromyscus leucopus	NA	1	G	S, D, M	(37, 65, 85, 112, 137, 138)

bottlenecks due to direct selection pressures from humans (such as pesticides). These scenarios are predicted to result in both a loss of genetic diversity within populations and increased differentiation between populations (Fig. 2).

A pervasive outcome of urbanization is fragmentation of habitats used by native species (39, 40), which often leads to a loss of genetic diversity within urban populations (table S1). Urban fragments exist as networks of green spaces such as city parks, community gardens, cemeteries, and other unbuilt land where individuals may become partially or completely isolated. For example, populations of white-footed mice in New York City (NYC), United States, became rapidly differentiated from one another once populations that existed before urbanization were isolated in parks (41). The evolutionary effects of this fragmentation are evident from declines in genome-wide diversity along a 142-km urbanization gradient from forested and rural areas to the urban core (Fig. 3B) (42). Two rodent species in Warsaw, Poland (43), and Dundee, Scotland (44), that are ecologically similar to white-footed mice also exhibited lower genetic diversity within urban populations and greater differentiation between them, when compared with that of rural populations. Species that are poor dispersers may exhibit a much greater loss of genetic diversity because of urbanization. Salamanders are one such group with limited dispersal that are likely to be sensitive to urbanization. For

example, isolated populations of dusky salamanders (Desmognathus fuscus) in NYC (45), red-backed salamanders (Plethodon cinereus) in Montreal, Canada (46), and fire salamanders (Salamandra salamandra) in Oviedo, Spain (47), all exhibited lower genetic diversity and greater genetic structure than those of populations in less urbanized areas. By contrast, animals with greater dispersal capabilities such as birds (48) and larger mammals (49) do not exhibit losses of genetic diversity to the same degree. Overall, decreased genetic diversity within and increased genetic differentiation between urban populations are the most commonly reported patterns of urban evolution (table S1), which may reflect a large and consistent effect of urbanization on genetic drift. A nonexclusive explanation is that conservation geneticists interested in the effects of fragmentation on genetic diversity were among the first to study urban evolution.

Many urban populations are newly established by immigration from surrounding rural areas. Although studies have tested for evidence of reduced genetic variation within urban populations as outlined above, few have examined the consequences of founder effects associated with the establishment of new populations. Red foxes (*Vulpes vulpes*) recently colonized Zurich, Switzerland, which resulted in lower genetic diversity in city foxes compared with that in nearby rural populations (50). Phylogeographic analyses also show that the common blackbird indepen-

Box 1. Archetypes of early urban evolution.

Advances in agriculture ~12,000 years ago prompted humans to settle in villages and towns, followed by the development of increasingly dense cities. Even in early cities, certain organisms thrived because they were preadapted for facultative scavenging in human settlements. A subset of these "anthropophiles" evolved into "anthrodependents" because of selection for specialization on anthropogenic resources (90). For example, three widespread commensal rodents—the house mouse (M. musculus), black rat (R. rattus), and brown rat (R. norvegicus)-are archetypal anthrodependents that spread around the world with agriculture and urbanization. Commensalism in the house mouse evolved during the Neolithic Revolution in agricultural areas of the Middle East (Fig. 1), followed by a rapid expansion throughout Eurasia because of their close relationship with humans (119). Black rats evolved in South Asia (Fig. 1) and succeeded in expanding to many places throughout Eurasia because of their preadaptations for living in disturbed areas (120). The brown rat originated in Mongolia (Fig. 1) and initially expanded throughout east and southeast Asia, and then slowly expanded westward into Europe ~500 years ago (92). The most common indoor arthropod pest in urban areas, the German Cockroach (Blatella germanica), also evolved in east and southeast Asia before expanding globally with human commerce; indoor cooking, heating, and cooling technologies may have facilitated their success (121).

Unlike the pests above, rock doves ("pigeons," *C. livia*) were domesticated 5000 to 10,000 years ago as a human food source in southwestern Asia (Fig. 1) (*122*) and became popular throughout Europe and much later in North America. Escapees quickly found their way into cities, with excellent nesting substrates on buildings that resemble their native cliff habitats and an abundance of food subsidies. Feralization probably occurred repeatedly with ongoing gene flow from domestic birds into feral populations, resulting in complex phylogeographic relationships between domestic and free-living pigeons (*122*).

Urbanization also promoted the evolution of parasites that rely on human bodies for food and shelter. The association between bed bugs (*Cimex lectularius*) and humans dates to the cities of ancient Egypt and perhaps earlier (Fig. 1) (123). Humans have also been host to head and body lice (*Pediculus humanus*) throughout their evolutionary history, but settlement in dense urban centers has promoted the contemporary evolution of insecticide resistance in head lice (124). By contrast, infestations by public lice (*Phthiris pubis*) have plummeted in part because of changing habits around adult public hair removal (125), suggesting that this species will decline if it cannot evolve new parasitic strategies.

dently colonized cities across Europe. These multiple founder events resulted in lower genetic diversity in city populations than rural populations (51). As with fragmentation, founder effects may also result in isolation between new urban populations and their source populations. The northern house mosquito (Culex pipiens) likely colonized the underground subway system once in London, UK, and subsequently diverged into a separate form (C. pipiens f. molestus), which is reproductively isolated from and less genetically diverse than surface populations (52). The underground mosquito populations in Chicago and NYC also exhibit lower genetic diversity and greater genetic differentiation than surface populations (53), suggesting that northern house mosquito colonized subway tunnels and sewers multiple times independently around the world. Founder effects may also produce differences between closely related species based on the time since they established urban populations. For example, the vellow-necked mouse (Apodemus flavicollis) colonized Warsaw, Poland, only within the past few decades and consequently exhibits lower genetic diversity and greater genetic structure than those of populations of striped field mouse (A. agrarius) that have occupied Warsaw for more than a century (54). Given the speed and scale of ongoing urbanization around the world (55), new urban populations of a wide range of organisms are likely to become established in coming decades. Urban evolutionary research can produce a framework to understand the population genetic consequences of these processes.

Pest infestations are likely to experience particularly severe bottlenecks in urban species that are exposed to chemical pesticides or other control measures. As an example, bed bugs (Cimex lectularius) sampled throughout cities in the eastern United States show little genetic diversity within populations but are strongly differentiated between populations and show no pattern of isolation by distance (56). These findings indicate that bed bug infestations are associated with bottlenecks resulting from strong founder effects. Pesticide applications can also lead to bottlenecks in urban populations of native animals prone to exposure to these chemicals. Such a case was reported in bobcats (Lynx rufus) occupying urbanized areas of Los Angeles, United States, which experienced a loss of genetic diversity due to habitat fragmentation and severe population bottlenecks associated with consumption of pesticides carried by their rodent prey (57). Although not always intentional, lethal control of pests is likely to produce some of the most drastic losses of genetic variation because of genetic drift.

The studies reviewed here and in Table 1 and table S1 provide ample evidence that fragmentation, founder effects, and human intervention result in greater genetic drift in urban compared with nonurban habitats. This causes a loss of genetic variation within populations and contributes to greater genetic differentiation between urban populations than their nonurban counterparts. Future studies of ongoing colonization of urban areas, and pre- and post-urban



Fig. 1. World map showing cities, the origin of human commensals, and the location of contemporary urban evolution studies. All cities with >300,000 people are shown. The approximate regions of origin of human commensals (Box 1) are shown as blue silhouettes. Urban evolution has been studied in the species and at the locations shown by

comparisons facilitated by DNA from museum specimens, will yield deeper understanding of urban genetic drift (58).

Gene flow

Urban areas can have diverse effects on the dispersal of individuals and their alleles (gene flow). Features of urban landscapes that impede gene flow (such as roads, buildings, and rivers) may facilitate genetic divergence between populations on opposite sides of a barrier, in combination with genetic drift or selection (Fig. 2). Even incomplete barriers, such as smaller roads or manicured green spaces, may restrict connectivity between urban populations (*59*). By contrast, urban features that increase gene flow (such as habitat corridors) may homogenize allele frequencies, increase genetic diversity within populations, and erode differentiation between populations.

Many of the examples of urban genetic drift described above result from barriers, particularly impervious surfaces such as roads and buildings, that restrict gene flow between urban habitat fragments. Several recent studies have incorporated molecular markers and sophisticated landscape models of resistance to dispersal to quantify how these barriers and other landscape features affect gene flow in and between urban and nonurban environments (60). For example, the largest barrier to gene flow for the common wall lizard (Podarcis muralis) in Trier, Germany, is a river (Fig. 3C). Buildings and canopy cover further restrict gene flow through the city, whereas urban vineyards and rocky substrates facilitate movement (Fig. 3C) (61). Song sparrows (Melospiza *melodia*) also exhibit reduced gene flow owing to conversion of their native habitat to urban land cover with greater than 50% impervious surface. The sparrows disperse through such urbanized habitat at a lower rate, and the resultant genetic differentiation between populations increases with age of urbanization (48). A study conducted on a native insect similarly reported that urban impervious surfaces limit regional gene flow in a bumble bee (*Bombus vosnesenskii*) (62). These examples indicate that urbanization, particularly impervious surfaces and natural barriers, strongly affect gene flow in many species.

Although restricted gene flow is a common outcome of urbanization (table S1), some species may be unaffected by urban areas. Urbanization does not impede gene flow among populations of a globally rare butterfly endemic to barrier islands of coastal North Carolina, United States, but dispersal is restricted by major natural landscape features such as open water (63). Insectmediated gene flow among individuals of a tropical tree species (Koompassia malaccensis) is maintained between forest reserves and botanical gardens in Singapore, even across >2.5 km of impervious surface (64). Gene flow of multiple rodent species (44, 65) and at least one marsupial (66) is facilitated by corridors of natural vegetation within cities. In some cases, urban parks act as sources of genetic diversity to surrounding areas. This is seen in the great tit (Parus major), for which populations in Barcelona, Spain, contain more genetic variation in city parks than that in nearby forests, and gene flow from urban to nonurban populations is greater than the re-

black silhouettes. Only one location is shown when multiple cities were studied within a single species. The legend shows how variation in dot size and color correspond to human population sizes within cities. The species and locations shown are a representative subset of the studies in table S1.

> verse (67). These results show that although urbanization can create dispersal barriers, some features of urban environments (such as natural vegetation) facilitate gene flow, at least to a level similar to nonurban environments.

> Gene flow can maintain genetic diversity and reduce genetic differentiation between urban populations but may also slow or prevent local adaptation. Behavioral phenotypes, the structure and composition of landscape elements, and differences in dispersal ability and habitat tolerance between species all influence realized connectivity across urban landscapes. Recent progress in landscape genetics provides tools with which to quantify structural and functional connectivity that influence gene flow in urban areas and to identify genotypes that are strongly associated with specific urban landscape features (59). Such genotype-by-environment associations may underlie traits that are locally adapted, even under moderate or high rates of gene flow. However, to date no studies of urban gene flow have replicated findings across multiple cities, and most have only included one species (54, 68). Greater replication will be necessary to identify general landscape trends that facilitate or impede the movement of alleles within and through cities and how this may facilitate or counteract local adaptation.

Natural selection

A key question in urban evolutionary biology is whether populations adapt to urban environments. At one level, the answer to this question is obviously "yes." A small but prominent subset of taxa have adapted to be specialists of human environments (I, 22). But as cities become larger and increase in number, will more organisms adapt to an urban lifestyle? If such adaptations are common, then it may allow populations to colonize, persist, and even thrive in human-dominated landscapes.

Several studies show that environmental changes associated with urbanization alter phenotypic selection. Kettlewell's study of peppered moth was the first to show that urbanization can affect selection on populations (69). In the 19th and early 20th centuries, industrial pollution coated the bark of trees with dark soot sur-





rounding cities of the UK and Europe. Kettlewell's experiments showed that the dark morph of peppered moth was harder for birds to locate on trees in polluted areas, which resulted in higher daily survival than the wild-type lightcolored morph (69). This selection was reversed after pollution abatement in the mid-1900s, with stronger selection against the dark morph compared with wild type (70). Urbanization can also alter selection on animal morphology. For example, urbanization in Tucson, United States, alters selection on beak morphology of house finches (Carpodacus mexicanus) (71), which rely on sunflower seeds at bird feeders in cities-a food that is larger and harder than their natural foods in surrounding desert habitats. This change in diet caused directional selection for longer and wider beaks in the urban population, traits associated with stronger bite force. By contrast, nonurban desert populations experienced selection for shorter bills of intermediate width. Last, urbanization can affect selection on dispersal traits, as seen in the plant holv hawksbeard (Crepis sancta) (72). In fragmented landscapes of Montpellier, France, impervious surfaces are extensive and inhospitable. C. sancta exhibits heritable variation for the production of nondispersing seeds (versus dispersing seeds), and there is selection in favor of reduced dispersal in fragmented urban habitats (72). Although these studies clearly show that urbanization can alter selection on phenotypic traits, populations may not always evolve in response to selection, and thus it is necessary to explicitly quantify adaptive changes to urbanization.

A growing number of studies report divergent phenotypic evolution between urban and nonurban environments in response to selection. Most studies of urban-induced phenotypic evolution have focused on a single city (table S1). These studies show that urban populations can diverge from nonurban populations in a wide diversity of traits (Table 1), including life-history (72, 73), morphology (71, 74, 75), physiology (34, 76, 77), behavior (78, 79), and reproductive traits (39, 80, 81). Heritable phenotypic divergence is typically attributed to adaptive evolution in response to altered selection between urban and nonurban environments. Although many of these examples are likely adaptive, changes in selection are rarely quantified directly (71, 72), and nonadaptive processes such as genetic drift and restricted gene flow are pervasive and may explain divergence across a single city (2, 37).

Parallel evolution of populations experiencing similar environments is the hallmark of adaptation in response to natural selection. Thus, studies that compare divergence in heritable phenotypic traits between urban and nonurban environments across multiple cities provide a strong test of whether populations can adapt to urbanization. Several studies have taken such an approach. For example, across three cities of Puerto Rico, crested anoles (*Anolis cristatellus*) evolve longer limbs and more toe lamellae in urban environments, traits thought to increase locomotory performance on artificial surfaces



Fig. 3. Examples of how urbanization affects evolution. (A) Pollution from steel mills in industrial cities causes higher mutation rates in herring gull (*Larus argentatus*) as compared with nonindustrial cities or rural areas (mean \pm 95% confidence interval) (30, 126). (B) Increased urbanization leads to more impervious surfaces, which is associated with stronger genetic drift and decreased genetic diversity in white-footed mice (*P. leucopus*) (37). (C) A

major river, buildings, and woodlands increase resistance to gene flow in the common wall lizard (*Podarcus muralis*) (61), whereas urban vineyards and rocky substrates facilitate movement and decrease resistance to gene flow. The large white triangle in the top left contains no information about gene flow. (**D**) Clines in minimum winter temperatures from rural to urban areas select for genotypes with decreased chemical defenses in white clover (*Trifolium repens*) (36).

(82). Across four large cities in North America, urban white clover consistently evolved decreased antiherbivore chemical defenses in cities compared with suburban and rural populations (Fig. 3D) (36). This evolution was attributed to decreased snow and colder winter temperatures in cities than rural areas, which selected against lower freezing tolerance in chemically defended plants. Across five large North American cities, urban populations of Virginia pepperweed (Lepidium virginicum) exhibited heritable changes toward faster growth. larger size, earlier flowering, and greater fitness than rural populations (83). Last, killifish repeatedly evolved tolerance to polychlorinated biphenyls (PCBs) in urban polluted waters but not in nonpolluted sites (33, 84). Each of these systems show evidence of parallel evolution across multiple cities and therefore represent our strongest evidence for adaptive phenotypic evolution in response to urbanization.

The application of molecular and genomic technologies to the study of urban evolution has made it possible to identify molecular signatures of selection in response to urbanization. For example, white-footed mouse shows evidence of positive selection in several candidate genes in urban environments (*85*). Many of these candidate genes have immune, toxicological, or metabolic functions, suggesting that urbanization alters pathogen or chemical exposure, or results in dietary changes, in urban deer mice. A candidate gene approach in common blackbird found that urban birds were diverged at the *SERT* gene, which affects harm-avoidance behaviors (*38*). In

10 of the 12 cities studied, urban birds showed lower frequency of the most common *SERT* allele found in rural populations. Similar differences are found in swans at the dopamine receptor gene *DRD4*, in which allelic variation is associated with decreased wariness to humans in urban areas (79). Humans also show evidence of molecular adaptations to urban living, for which an allele that confers resistance to human diseases (such as tuberculosis or leprosy) is at higher frequencies in older cities where there is likely a longer history of exposure to these diseases (*86*). These studies provide compelling evidence for adaptive molecular evolution, but how they relate to evolution of phenotypic traits is often unclear.

The gold standard for studies of adaptive evolution is linking genetic mechanisms with phenotypic evolution in response to natural selection. Three studies have convincingly demonstrated this link. The first is the classic peppered moth system, in which the insertion of a transposable element into the gene *cortex* disrupts normal pigmentation patterning (32). The second is white clover (36), in which the evolution of decreased chemical defenses in cities (Fig. 3D) is caused by a simple Mendelian polymorphism, controlled by the epistatic interaction between CYP79D15 and Li to produce hydrogen cyanide (87, 88). The third is killifish, in which repeated evolution of PCB resistance is caused by convergent evolution in an aryl hydrocarbon receptor gene (33). Future research should combine the study of parallel adaptive changes across multiple urban/nonurban comparisons with the molecular mechanisms underlying these changes.

The studies reviewed here and in Table 1 provide direct evidence that populations frequently adapt in response to urbanization. These adaptations often relate to genes and traits that are predicted to provide fitness advantages in novel urban environments. These novel environmental challenges in urban areas typically relate to pollution, pesticides, altered physical structures, climate, and social environments associated with anthropogenic activity. Despite these advances, there exist major gaps in our understanding of how populations adapt to urban environments (Future directions, below).

Evolutionary research can improve urban environments and human health

Most of our examples of evolution have focused on noncommensal species that persist in or colonize cities (Table 1), but the evolution of human commensals that are restricted to cities is equally important and may have applied consequences for human health. These species have been referred to as "urban exploiters" (21), "synurbic" (89), or "anthrodependent" (90) and include several pests, parasites, and pathogens that take advantage of human subsidies. In Box 1, we survey the ancient evolution of commensalism and parasitism in early cities that produced urban specialists such as rats, pigeons, bed bugs, and cockroaches.

In addition to analyzing the historical relationships between humans and their pests (91, 92),

evolutionary analyses have been used to understand the contemporary dynamics of urban infestations (Table 2). For example, German cockroaches (Blatella germanica) randomly mate within individual urban apartments but exhibit genetic differentiation and isolation-by-distance between apartments within a single building and between buildings because of restricted gene flow (93). Bed bug infestations stem from founder events and migrate readily through single residential buildings (94), but genetic drift results in strong genetic differentiation between bed bug populations in nearby buildings (56). Gene flow is high among brown rats (Rattus norvegicus) living in cities (95, 96), although landscape features that prevent dispersal cause geographical clusters of relatedness. These studies not only provide important insight into the evolution of human commensals but also have applications to human society. Understanding gene flow in urban areas provides information on the spatial and temporal scales of pest management that maximize success. Although most pest control is typically implemented at the scale of individual properties, interventions that use information on gene flow and the spatial scale of relatedness among individuals are more likely to sustainably reduce pest populations.

Knowledge of urban evolutionary phenomena may be used to improve current environmental and public health practices in cities or manipulate evolutionary dynamics of the species that live in or around our homes (97). For example, the diverse adaptations of pesticide resistance in commensal rodents (98), bed bugs (99), cockroaches (100), mosquitoes (101), and many other pests indicate that evolutionary principles need to inform best practices for pest control. The evolutionary processes underlying these arms races have been understood for decades (102). Most effort has focused on developing next-generation poisons (for example, new warfarin derivatives targeted at rodents), which are effective in the short-term but may ultimately fail and have unintended negative consequences for wildlife (57). A renewed research focus on integrated pest management that aims to alter human behaviors promoting pests, remove or restrict access to pest habitats, and promote communities of native species that resist infestation may slow adaptation of pests in urban environments (103). Emerging technologies-such as chemical scents that manipulate pest or prey behavior (104) and synthetic gene drives (intentional release of alleles that are preferentially inherited) to alter sex ratios in wild populations (105)-will likely be used against urban pests in the near future. These techniques will require proven efficacy and careful risk management before implementation.

Evolutionary modeling of gene flow and drift could also be used to achieve ecological goals in cities. Such approaches would have major implications for the design of "green" and "gray"

Table 2. Contemporary evolution of human commensals in urban environments. Columns show species' common and scientific names, the evolutionary processes studied, and corresponding references

Common name	Scientific name	Evolutionary processes	References	
	Blatella germanica	Selection: Sugar-baited pesticides impose selection that	(93, 100, 139, 140)	
		causes evolution of glucose aversion.		
		Genetic drift: Pesticide treatment and founder events cause		
German cockroach		bottlenecks.		
		Gene flow: Genetic differentiation increases with spatial scale,		
		being lowest within buildings, higher between buildings,		
		and greatest between cities and continents.		
	Cimex lectularius	Selection: Insecticide application drives evolution of resistance.	(56, 94, 123, 141–144)	
		Genetic drift: Population bottlenecks cause a loss of genetic		
Bed bug		diversity within populations.		
		Gene flow: Limited dispersal contributes to high genetic		
		differentiation between populations.		
Northern house mosquito	<i>Culex pipien</i> s (molestus)	Selection: Underground populations do not require a blood	(52, 53, 145, 146)	
		meal to lay eggs, lack a winter diapause and are reproductively		
		isolated from aboveground populations.		
		Genetic drift: Underground populations have less		
		genetic diversity and are genetically differentiated from		
		aboveground populations.		
Rock dove (aka "pigeon")	Columba livia	Selection: Darker morphs (with white rumps) exhibit lower	(147–150)	
		predation to falcons, higher survival as young when exposed to		
		lead, and greater defense against parasites.		
House mouse	Mus musculus	Gene flow: Populations exhibit patterns of early dispersal and	(119)	
		population expansion, followed by patterns that mirror		
		human migration and settlement patterns.		
	Pediculus humanus	Selection: Increased frequency of resistance to pesticides	(124)	
Head and body lice		through time, which is related to mutations in		
		the VSSC α -subunit gene.		
	Rattus norvegicus	Selection: Evolve resistance to warfarin pesticides through	(92, 95, 98, 151, 152)	
		mutations in VKORCI.		
		Genetic drift: Populations exhibit little evidence of inbreeding.		
Norway rat		Gene flow: There is moderate genetic differentiation		
		and genetic clustering of populations, which is attributed to limited		
		dispersal and natural barriers to gene flow.		
	Rattus rattus	Gene flow: Populations exhibit substantial genetic clustering	(120)	
Black rat		and patterns of dispersal and population expansion that reflect		
		human dispersal and settlement.		

urban infrastructure. Networks of green spaces, even small community gardens or residential backyards (106), have quantifiable positive effects on biodiversity (107). These green spaces also influence gene flow between city parks (65), and interventions to change the extent, quality, or spatial arrangement of these green spaces will influence the movement of organisms and their genes. Evolutionary analyses of genetic variation may also guide choices about lineages that could be used to construct ecological communities in and around cities. Of particular interest will be lineages with a high potential for local adaptation in cities or high capacity for phenotypically plastic responses promoting acclimation or tolerance of urban conditions (108). More drastic interventions such as assisted migration or rewilding of habitats in and around cities would particularly benefit from analyses of evolutionary potential (109).

Future directions

Our understanding of how urbanization affects evolution is in its infancy, with more questions than answers. Of the 192 studies included in table S1, more than half were published in the past 5 years. There are many interesting questions that can be addressed through the study of urban evolution, such as examining whether urbanization causes rapid speciation, or whether cities are hotspots for hybridization. However, we argue that three unresolved questions are most important to advancing urban evolutionary biology.

How frequently do populations adapt to cities?

Although evidence is accumulating that urbanization affects the evolution of species, it is unclear how frequently evolution results from adaptation to novel urban ecosystems versus nonadaptive evolution. When adaptation is implicated, an additional consideration is to tease apart adaptive evolution in constitutively expressed traits, adaptive phenotypic plasticity, and nongenetic plastic responses that allow individuals to acclimate to urban environments. This question is important because adaptive evolution and some forms of phenotypic plasticity result in increased fitness, which can facilitate a population's persistence in urban environments. A major limitation is that most studies have examined evolution in a small number of populations in a single city (Table 1 and table S1), where drift, restricted gene flow, and selection can all lead to divergence between urban and nonurban populations. Sampling multiple cities assesses the generality of adaptive and nonadaptive evolutionary processes, including how differences in the size, culture, socioeconomics, and history of cities affect evolution. Sampling multiple cities also tests whether populations exhibit parallel or convergent evolution because of similar selection pressures across cities. A related limitation is that most studies are from temperate regions (Fig. 1), so whether urbanization leads to similar changes in tropical, arid, or boreal climates is largely unknown.

Three additional shortcomings of past studies further limit our insight into whether popula-

tions frequently adapt to cities. First, explicit measures of natural or sexual selection in urban and nonurban environments are rare (71, 110, 111). More striking is that the fitness benefits of putative adaptations are rarely tested experimentally between urban and nonurban environments (36). Such studies are required to provide direct evidence for the effects of urbanization on adaptive evolution. Second, few studies examine how both the genotype and phenotype of populations evolve and adapt to urban environments (33). A genotype-to-phenotype approach provides a mechanistic understanding of urban adaptation and the basis for future predictions. Third, there is a need to understand the relative roles of selection, drift, and gene flow in affecting evolutionary processes of urban populations. Given that urbanization often causes fragmentation and population bottlenecks, drift and restricted gene flow are predicted to be more prevalent in urban populations than elsewhere (16). Studies of selection in urban environments may therefore need to account for drift and demographic changes in urban areas that may confound genomic signatures of selection (112). Urban evolution studies to date have typically used microsatellite markers to understand drift and gene flow. These markers are suitable for basic estimates of genetic diversity, differentiation, and gene flow, but larger data sets of genome-wide variation will be necessary to estimate parameters under more complex demographic scenarios. The adoption of genome-wide SNPs, whole exomes, and whole-genome resequencing will improve the ability of researchers to identify genes and pathways under selection in urban environments.

Are there consequences of urban evolution for conservation and human health?

Although the effects of urbanization on the ecology of species and ecosystems are increasingly understood (4), the role that urban evolution plays in conservation, ecosystem processes, and human health are virtually unknown (25). Adaptive evolution can have positive feedbacks on the fitness of individuals and the growth of populations (113). Thus, if rare and endangered species can adapt to urban environments, this could facilitate conservation efforts to protect these species. Potential models for such studies include Peregrine Falcons (Falco peregrinus) nesting in cities (114), prairie dogs that use urban habitats (115), and cliff plants that grow on urban substrates (116). As outlined above, understanding how urbanization affects evolutionary processes of human commensals can also help mitigate the spread of human pests and diseases by designing strategies that improve the efficacy of population control and prevent the spread of pesticide resistance.

Can we use urban evolutionary biology to design cities that are more sustainable?

A major goal in urban ecology is to create cities that are more resilient to environmental perturbation (such as climate change and invasive species) and sustainable for humans and nonhuman urban dwellers alike (5). Understanding and facilitating evolution in urban environments is an important consideration in this regard. For example, facilitating the maintenance of genetic diversity within populations promotes not only adaptation but has immediate positive effects on the diversity and stability of communities and ecosystems (117). Increased genetic diversity frequently leads to greater species diversity at multiple trophic levels (118) and promotes beneficial ecosystem services such as resistance to invasive species and greater primary productivity (117). Research is needed that examines the features of cities, including management and design practices, that influence evolutionary processes and have beneficial effects on the persistence of native populations and communities. Meeting this need will require educating the public, city planners, and policy-makers about the importance of evolutionary biology. The study of urban evolution offers a distinct and powerful opportunity for such education efforts while improving sustainability of our cities.

To address these questions, the next generation of urban evolutionary biology requires largescale rigorous studies that take a global approach. We make five specific recommendations for future studies of urban evolution: (i) Maximize the number of cities studied to test for the generality and convergence of urban evolutionary processes and patterns. (ii) Select cities in such a way as to allow identification of specific urban features (such as city size, percent impervious surface, climate, and socioeconomics) that affect evolutionary processes and patterns. (iii) Increase the number of populations sampled along urban to nonurban gradients so as to maximize the statistical power to detect evolutionary divergence. (iv) Conduct experiments to understand the ecological mechanisms underlying evolution in urban environments. (v) Take a global approach to urban evolution in order to understand how urbanization is affecting evolution of species throughout the world.

We anticipate an exciting proliferation of research on urban evolution over the next decade. This research will bring about advances to fundamental problems in evolutionary biology, given that urban environments provide large-scale, globally replicated "natural" experiments to understand how environmental change affects evolution. Urban evolutionary biology will also lead to novel solutions to conservation, pest and disease prevention, and improvements to human health.

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SUPPLEMENTARY MATERIALS

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