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Urban driven phenotypic changes: empirical observations and theoretical implications for eco-evolutionary feedback

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Emerging evidence that cities drive micro-evolution raises the question of whether rapid urbanization of Earth might impact ecosystems by causing systemic changes in functional traits that regulate urban ecosystems' productivity and stability. Intraspecific trait variation—variation in organisms' morphological, physiological or behavioural characteristics stemming from genetic variability and phenotypic plasticity—has significant implications for ecological functions such as nutrient cycling and primary productivity. While it is well established that changes in ecological conditions can drive evolutionary change in species' traits that, in turn, can alter ecosystem function, an understanding of the reciprocal and simultaneous processes associated with such interactions is only beginning to emerge. In urban settings, the potential for rapid trait change may be exacerbated by multiple selection pressures operating simultaneously. This paper reviews evidence on mechanisms linking urban development patterns to rapid phenotypic changes, and differentiates phenotypic changes for which there is evidence of micro-evolution versus phenotypic changes which may represent plasticity. Studying how humans mediate phenotypic trait changes through urbanization could shed light on fundamental concepts in ecological and evolutionary theory. It can also contribute to our understanding of eco-evolutionary feedback and provide insights for maintaining ecosystem function over the long term.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

1. Introduction

Recent studies have shown that humans affect micro-evolutionary change by exerting selection pressures on traits and by affecting population dynamics by changing organisms' rates of survival or reproductive success [1,2]. Such studies raise the question of whether urbanization might cause changes in functional traits that affect ecological function [3–7]. Genetic signals of rapid anthropogenic change have been observed in many organisms including birds, fishes, arthropods, rodents, land plants and algae [8–10]. Effects at the community level might result from predator–prey interactions, parasite–host relationships, mutualism, facilitation or competition [11]. In turn, intraspecific trait variation can impact community structure and drive changes in energy and material fluxes that influence ecosystem functions [5], which provide essential services for human well-being [12] (tables 1 and 2).

For example, the evolution of traits that regulate consumers' demands for resources can affect nutrient cycling [30], plant biodiversity and evolutionary changes of seed dispersers (e.g. *Crepis sancta*) [35] and ecosystem-engineers. For example, ecosystem-engineers include dune and marsh plants [36] and mangroves [37], which have functional roles in maintaining the structures of estuarine and coastal environments. Emerging evidence of rapid evolution and the potential for eco-evolutionary feedback (reciprocal influences of ecology

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Table 1. Examples from literature of phenotypic trait changes in response to urban disturbances. Examples represent adaptive changes, or changes that are hypothesized to be adaptive, with exceptions noted. Genetic basis refers to phenotypic changes for which there is specific evidence of a genetic basis of the trait change, for example via a common garden study.

no.	urban signals		phenotypic trait	genetic basis	refs
	urban disturbance	*mechanism*	*physiological*		
1	social interaction	globalization—movement of mosquito vectors and humans	molecular evolution of genetic-based epidemic activity and disease severity of lineages of dengue	genetic	[13]
2	habitat modification, heterogeneity	habitat fragmentation and urbanization	white-footed mouse (*Peromyscus leucopus*) populations in New York City deviated more strongly from global mean allele frequencies than rural populations. Authors conclude urbanization has substantially altered evolutionary trajectories	genetic	[14]
3	social interaction	insecticide application	differential expression of genes for autogeny, diapause and insecticide resistance in mosquito (*Culex pipiens*)—indications of global and local evolutionary adaptations	genetic	[15]
4	novel disturbance	antibiotic use affects bacteria from urban, industrial wastes dumped into freshwater	evolution of antibiotic resistance in environmental bacteria	genetic	[16]
5	social interaction	insecticide application	resistance to neonicotinoid insecticides in bed bugs (*Cimex lectularius*)		[17]
6	habitat modification	heavy metals pollution	immune system parameters affected in feral pigeons (*Columba livia*)[a]		[18]
7	novel disturbance	man-made pollutants—polychlorinated biphenyls (PCBs)	inherited tolerance to PCBs in mummichog (*Fundulus heteroclitus*)	genetic	[19,20]
			morphological		
8	biotic interaction	altered plant–animal interactions in suburban versus wild sites	floral traits in *Gelsemium sempervirens*, investigated using a common garden experiment	genetic	[21]
9	habitat modification	pollution	flower petal dimensions in a perennial clonal plant species: *Iris pumila*[a]		[22]
10	heterogeneity, biotic interaction	afforestation (more edge habitat), increased urban predators	rounder wings in European starlings (*Sturnus vulgaris*)—heritable wing morphology	genetic	[23]
11	habitat modification	anthropogenic noise	longer, narrower bills, altered vocal performance in house finches (*Haemorhous mexicanus*)		[24]
12	biotic interaction	human-mediated dispersal/range expansion	shell colour in non-native polymorphic land snail (*Cepaea nemoralis*), whose biological invasions and range expansions are facilitated by humans		[25]
			behavioural		
13	heterogeneity	constant access to man-made nesting sites, anthropogenic sources of food	polygyny, polydomy, super-colonial colony structure (invasive characteristics) in house ants (*Tapinoma sessile*)		[26]

(*Continued*.)

Table 1. (*Continued.*)

no.	urban signals		phenotypic trait	genetic basis	refs
14	social interaction, heterogeneity	supplemental feeding and availability of food resources leading to assortative mating	coevolution with humans of cats (*Felis silvestris catus)* from wildcats *(Felis silvestris)*	genetic	[27]
15	novel disturbance	novel habitat	boldness behaviours (early exploratory behaviour, flight initiation distance) in dark-eyed junco (*Junco hyemalis*)—common garden study	genetic	[28]
16	habitat modification	anthropogenic noise	altered vocal performance in male white crowned sparrows (*Zonotrichia leucophrys*)[a]		[29]
17	habitat modification	p-limited conditions	reduced investment in sex in herbivorous rotifer (*Brachionus calyciflorus*)—common garden study of micro-evolution	genetic	[30]
18	biotic interaction and social interaction	predator–prey differences in coping with proximity of humans	reduced flight distance in prey bird species in urban environments		[31]
19	novel disturbance	novel anthropogenic situations	neophilic and neophobic behaviours in European blackbirds (*Turdus merula*)		[32]
			phenological/life history		
20	heterogeneity, social interaction	climatic amelioration, supplemental feeding	expansion of wintering range of Eurasian blackcaps (*Sylvia atricapilla*)		[33]
21	heterogeneity	city size—resource availability, heat island effect, and artificial light	singing earlier and longer in a paired population study of 54 bird species		[34]

[a] Examples of non-adaptive phenotypic change, or phenotypic change that is hypothesized to not be adaptive.

Table 2. Hypothesized feedback on ecosystem functions and hypothesized effects on humans from examples of phenotypic trait changes listed in table 1.

no. (from table 1)	feedback mechanism	ecosystem function	effect on humans
1–6	disease ecology: disease–host, disease–vector and parasite–host interactions	biotic control	epidemic activity and disease severity of zoonotic and vector-borne diseases
7	trophic effects	provision of raw materials (food)	bioaccumulation of pollutants in food resources, effects on food productivity
8, 9, 12	pollinator–plant interaction and plant–pest interaction	primary productivity	agricultural/crop production
10, 11	trophic interactions, foraging dynamics	nutrient cycling	
13	invasion potential	biotic control	nuisance pests
14, 15, 16, 18, 19	behavioural changes and domestication	biodiversity	animals co-evolved with humans; some may serve as companions or providers of raw materials
17	herbivore grazing pressure on algae, trophic interactions	water quality	clean water for drinking, recreation
20, 21	consumer–resource dynamics	biodiversity	animals that share habitats with humans may spread zoonotic disease, or act as pests by consuming resources. To the extent that people enjoy being in nature and seeing animals, biodiversity in urban settings may also be of cultural value

and evolution) may have significant consequences on ecosystem functions and human well-being on a contemporary timescale [38].

Human-driven evolutionary change is particularly evident in cities and urbanizing regions. Although urban areas represent only 3–5% of the total land surface, more than 50% of Earth's human population lives in cities [39]. In urbanizing regions, the socio-economic transitions toward an increased pace of life and intensity of human activities may accelerate the rates and increase the magnitudes of landscape-level anthropogenic changes. The extraordinary concentration of people and activities in cities provides major opportunities to achieve economies of scale, but it also intensifies the use of energy and its environmental impacts both locally and globally. Cities affect phenotypic change locally by altering natural habitat and biotic interactions. Yet the increase in pace of life for humans in cities and their activities has far reaching consequences. While cities accelerate the transition to efficient technologies, the energy demands of the city remain reliant on the extraction of resources from distant regions, which may impact the ecology and evolution of urban flora and fauna on a global scale [40]. For example, the process of transporting resources can increase the rate of introductions of non-native species, which impact native biological communities, e.g. marine invasive species transported in ballast water of ships [41]. Additionally, the transportation of distant resources may support continued technological expansion and associated pollution, which has the potential to exert selective pressure, e.g. changing the frequency of melanistic genes in peppered moths (*Biston betularia*) [42].

Despite significant progress in the past two decades in understanding the rules governing community assembly and the functional implications of environmental change, the roles of evolutionary change in community dynamics have received little attention until very recently. Even less attention has been given to explaining these dynamics in urbanizing regions. Yet emerging evidence of reciprocal feedbacks between community interactions and evolutionary processes raise important questions regarding the potential for rapid evolutionary change in urbanizing regions that affect ecosystem functioning and stability [5,7]. Current rapid environmental change associated with urbanization and its evolutionary effects might have significant implications for ecosystem function and human well-being on a relatively short timescale.

In this review, we seek to develop a theoretical framework to systematically describe the eco-evolutionary effects of urbanization. Accurate and precise terminology to describe urban ecosystems and eco-evolutionary dynamics is important because our ability to articulate these concepts circumscribes the ways in which we are able to frame hypotheses and conduct empirical studies. Herein, we define and provide examples of five urban disturbances: habitat modification, social interaction, biotic interaction, heterogeneity and novel disturbances [2]. We review recent empirical evidence that these disturbances can drive phenotypic trait changes in urban organisms. In our review of empirical evidence, we are broadly inclusive of evidence of phenotypic changes linked to urban anthropogenic disturbances. Such changes create the potential for eco-evolutionary feedback, if the observed changes are in fact genetic. However, we caution that phenotypic change is not synonymous with evolutionary change; urban-driven changes in the attributes of populations, communities and ecosystems influence phenotypes via selection and plasticity [9]. Furthermore, some phenotypic changes are adaptive, and some are maladaptive responses to environmental disturbances. Throughout this review, we will indicate phenotypic change examples for which there is a known genetic basis for the trait or for which there is evidence via common garden studies, versus examples for which the genetic basis of a phenotypic trait change is unknown. We conclude with theoretical implications of how changes in functional traits may affect ecosystem processes and have eco-evolutionary feedback in urbanizing regions.

2. Framing eco-evolutionary dynamics on an urbanizing planet

As ecologists and evolutionary biologists provide new evidence of the dynamic interplay between ecology and evolution [38], it becomes critical that we investigate how human agency mediates eco-evolutionary dynamics. Without considering interactions and feedback between human and ecological systems, our understanding of eco-evolutionary feedback and its implications for ecosystem function and human well-being on a contemporary scale remains limited. Although a few recent studies of evolutionary change have examined anthropogenic drivers [1,8], few have focused on the role of urbanization [2,43].

Acknowledging the role of human agency in eco-evolutionary dynamics requires that we examine the history of the human habitat from Neolithic settlements to industrial and post-industrial cities. As humans urbanize land, novel biotic and abiotic conditions emerge. Emerging ecological conditions are governed by either historical processes (e.g. forest succession) or novel anthropogenic processes (e.g. urban sprawl). As ecosystems become increasingly dominated by human action, such novel processes may initiate new feedback mechanisms.

The ecological state of a given place can be described along abiotic and biotic axes of change, ranging from natural to anthropogenic (novel) habitat. To understand the dynamics of novel coupled human–natural systems, we add a third axis: social interactions and associated socio-economic and technological transitions [44]. Today, different cities occupy different positions within this multidimensional space.

3. Mechanisms linking urban patterns to phenotypic change

Increasing evidence in urban ecology describes how urban development changes landscape composition, biogeochemical cycles and disturbance regimes. Urban development can also facilitate introductions of invasive species (e.g. competitors, hosts, pathogens and predators), creating novel habitats. Urban environments can facilitate genetic differentiation by bringing together species that were previously isolated, or isolating populations through habitat transformation [45,46]. The development of partial reproductive isolation between populations can be linked to social learning and plasticity, as there is increasing evidence for learned mate preferences potentially being important in the early stages of population divergence and speciation [47–50]. For some populations, urbanization results in landscape-level changes that increase their likelihood of extinction [51]. In addition to the changes in the physical template (e.g. by building infrastructure and diverting the flow of bodies of water), humans in cities modify the availability of resources and their variability over time, buffering their effects on community structure (e.g. lawns are watered year-round to protect against seasonal drought) [52]. Furthermore, cities amplify telecoupled interactions (social, economic and environmental interactions occurring over large distances) and the impact of human activities on distant places [53]. The latter expands the impact of urban-driven eco-evolutionary change beyond city boundaries.

Alberti [2] identifies five mechanisms by which humans in urbanizing environments drive phenotypic changes in organisms. Although each mechanism can be identified as an independent driver, their consequences cannot be understood in isolation and mechanisms often overlap. In urban environments, selective changes are caused by the combined effect of changes in landscape composition and pattern (e.g. loss of forest cover and connectivity) and processes (e.g. biogeochemical and nutrient cycling) and changes in biotic interactions (e.g. predation). Humans in cities also mediate eco-evolutionary interactions by introducing novel disturbances and altering the heterogeneity of land cover [54]. Cities and their habitats are shaped by human social interactions and cultural evolution [55], with significant consequences for co-evolution between humans and other species, e.g. between humans and crows (*Corvus brachyrhynchos*) [56].

(a) Habitat modification

Perhaps, the most evident change driven by urbanization is rapid large-scale land cover conversion and effects on native vegetation: extensive loss, isolation and simplification [54]. The matrix of built environments can form isolated vegetation patches, reducing or eliminating their connectivity. As a consequence of reduced connectivity, the movement of resources and organisms across the landscape can be hampered or obstructed completely. Human activities also drive direct and indirect changes in the distribution of resources, which might result in changes in their availability across an urban-to-rural gradient. Additional urban stressors that can contribute to phenotypic trait changes include night light pollution and environmental contaminants such as trace metals [57].

Phenotypic trait changes in response to habitat modification may represent coping mechanisms or non-adaptive direct responses to urban stressors. For example, concentrated pollutants that are taken up by flowering plants may negatively affect plant growth [22]. Because this direct result of pollution influences flowers, the reproductive organs of plants, subsequent effects on fitness of the affected plants are possible [22]. Several model organisms are instructive in their evolutionary responses to landscape modification. For example, heritable tolerance to environmental contaminants associated with urbanization has been observed in mummichogs (*Fundulus heteroclitus*) [19,20]. Birds are a focus of many studies documenting phenotypic trait changes in response to urbanization; afforestation and increased concentrations of predators in urban areas have influenced wing morphology in urban European starlings (*Sturnus vulgaris*) [23], traffic mortality may be selecting for narrower wings and associated increased agility in cliff swallows (*Petrochelidon pyrrhonota*) that nest under bridges [58], house finches (*Haemorhous mexicanus*) have evolved longer and narrower bills and altered vocal performance in response to anthropogenic noise in urban environments [24], and white crowned sparrows (*Zonotrichia leucophrys*) have adapted to anthropogenic noise by singing at higher minimum frequencies and with reduced bandwidth [29]. Community structure is influenced by urban habitat modification; the urban fringe is home to edge-adapted generalists—species that are able to use a variety of natural and human-generated resources for their survival [54].

Urban-driven trait changes have the potential to feed back on ecological functions such as biodiversity and net primary productivity (NPP). Emerging patterns of species diversity reflect changes in productivity along the urban-to-rural gradient [59]. Several studies show that NPP mediates the relationship between urban land cover change and the richness of animal and plant species, and that the relationship varies with taxon specific traits (e.g. dispersal capacities of species) and coarse- versus fine-grained habitat structure [60].

Phenotypic trait changes resulting from habitat modification might have both direct and indirect influences on humans and human well-being. For example, habitat fragmentation associated with urbanization has altered the evolutionary trajectory of the white-footed mouse (*Peromyscus leucopus*), which is host for ticks that can cause Lyme disease in humans [14].

(b) Biotic interactions

Urbanization alters the way species are distributed and interact with each other [61]. Causes include human-mediated dispersal of invasive species in cities, and community-level effects stemming from organisms having different tolerances and affinities to proximity to humans. Urban development alters species distributions and biotic interactions [62] by creating new opportunities and challenges for species competition and predation.

Community-level urban-driven effects include increases in native and non-native predators near human settlements (e.g. high rates of nest predation of migratory songbirds [63]), which may affect other native species. Invasion of non-native species can lead to colonization [64]. Among many examples, McDonnell *et al.* [65] found lower levels of earthworm densities in the rural forests along a 140 km urban-to-rural environmental gradient originating in New York City, compared with the urban forests, probably because of introduced species. As urbanization converts extensive coniferous forest into a mixture of shrub and altered forest, the opportunistic Bewick's wren (*Thryomanes bewickii*) encroaches and competes with the native Pacific wren (*Troglodytes pacificus*) [66]. Differences between the abilities of predators and prey to cope with proximity to humans may result in reduced flight distances of prey species in urban environments, because they do not have to avoid predators to the same extent as in natural habitats [31]. Altered biotic interactions have the potential to affect community composition and trophic interactions, with potential feedback on nutrient cycling and reduced biotic control of prey birds in urban areas.

(c) Heterogeneity

Humans in cities change the heterogeneity of habitat quality and resource availability in space and time. Urban heterogeneity emerges from the interactions among biotic, abiotic and social complexes and from the interactions of these with the built environment [67]. Humans in cities design 'human habitats' intentionally to support human functions and human well-being. Because cities are designed to meet the needs of a specific species (humans), cities have lower diversity of microclimates and of habitat niches than most natural habitats. An example of change in temporal heterogeneity is the buffering effect created by microclimatic changes associated with urbanization [52]. Availability of supplemental food in urban habitats may also buffer urban organisms from environmental stochasticity in resource availability.

Patch heterogeneity in urban landscape might explain the evolution of dispersal traits in urban populations of *Crepis sancta* [35]. Cheptou *et al*. [35] show that this species has evolved to produce a greater proportion of non-dispersing plants in urban areas compared with their unfragmented surroundings. Habitat fragmentation also contributes to reduction in connectivity, which can isolate populations and therefore accelerate rates of adaptation, genetic drift or extinction [68]. The fragmentation of lands has well-documented negative consequences for local biodiversity of wildlife. Fragmentation affects the community composition of wildlife and plants in patches, with the potential for large impacts on species of intermediate or low mobility [68].

The biodiversity of species in urbanizing regions is greatly affected by the quality of the land and the template of resources. In natural environments, heterogeneity allows for greater niche differentiation, hence more species. In urban environments, the larger number of small patches characterized by differentiation of environmental condition does not necessarily imply greater diversity of species [69]. Instead, habitat changes associated with urbanization selectively affect urban species composition, driving the homogenization of ecological structure and functions [70]. Cities still retain native species, but because of loss of sensitive species from the core of the city, the richness of bird and plant species (the number of species per square kilometre) in cities has significantly declined worldwide over the past few centuries of urbanization [71].

Habitats designed to reduce variability in resource availability to meet the needs of humans may unwittingly facilitate pest species that take advantage of homogeneity in resource availability. For example, access to man-made nesting sites and anthropogenic food resources are implicated in the evolution of invasive characteristics in house ants (*Tapinoma sessile*), including super-colonial colony structure [26]. Supplemental foods may also increase associations between humans and species they find to be aesthetically pleasing, such as birds that visit feeding stations [33]. The wintering range of Eurasian blackcaps (*Sylvia atricapilla*) has expanded in urban regions, for example, where city dwellers enjoy their company [66]. If urban bird populations become excessively dense, this may have important potential implications for human health because urban birds can harbour zoonotic pathogens [72].

(d) Novel disturbance

In urban ecosystems, novel disturbances (resulting from intentional and unintended change) emerge from human actions affecting resource availability (i.e. water and nutrients), ecosystem productivity and species diversity [73]. Increasing evidence shows how urbanization modifies existing disturbance regimes (e.g. through fire and flood management) and creates novel ones (e.g. new or disrupted dispersal pathways). McKinney [54] has documented how human-induced disturbances in urban environments maintain urban habitats at an early successional stage. The interactions of multiple disturbances and fragmentation of urban habitats results in a number of possible succession paths across habitat patches [69].

The response to novel scenarios in anthropogenic environments has resulted in behavioural adaptations, for example in European blackbirds (*Turdus merula*). Such behavioural changes, which are implicated in the success of species in urban areas, include changes in neophilic and neophobic behaviours, novelty seeking versus novelty avoiding behaviours, respectively [32]. In urban areas, organisms encounter novel environmental contaminants. For example, dumping of industrial and urban waste into bodies of freshwater has been implicated in the evolution of antibiotic resistance in environmental bacteria [16]. Evolution of antibiotic resistance has the potential to increase the prevalence of antibiotic resistance in pathogens which infect humans [16].

(e) Social interactions

Urbanization drives change in social interactions among people [55] and between people and other species [51]. Bettencourt & West [40] have documented how with urbanization, we can observe a consistent increase in the pace of life for humans; we hypothesize that increased human activity will contribute to increased environmental change and selective pressure on the organisms in urban areas. Cities exhibit scaling relationships similar to those that biologists have found for organisms' molecular, physiological, ecological and life-history attributes, but in cities instead of 'sublinear scaling' (e.g. metabolic rate), increasing social interactions shows 'superlinear' environmental changes. The bigger the city, the faster its pace of human-driven environmental change [40]. Furthermore, with urbanization, coupled human–natural interactions are more frequent, and occur at higher speeds [74]. The phenomenon of telecoupling—interactions between distant natural and human systems [53]—might amplify urban-driven phenotypic changes beyond city boundaries and accelerate ecosystem changes. Yet, the lack of systematic studies across multiple urban regions makes it particularly challenging to understand the potential global eco-evolutionary implications and feedback associated with urbanization. In some cases, phenotypic changes that have resulted from direct human agency have consequences for human well-being. For example, insecticide resistance in mosquitoes (*Culex pipiens*) has developed in response to insecticide application [15].

4. Multidimensional urban influences on phenotypic traits

Building on emerging evidence and hypothesized outcomes of urban-driven evolutionary change for wildlife and plants [2,45,51,52,75], we develop general hypotheses about how the multidimensional urban influences on species traits can increase the total strength of selection on a given trait and can increase selection on a greater number of traits.

(1) *Rates of phenotypic change are greater in urban than non-urban contexts*. The interplay between rapid changes in the biotic and abiotic environment associated with urbanization leads to the expectation of an increase in the strength of selection on a given trait and on a greater number of traits [2].

(2) *Urban patterns of spatial and temporal heterogeneity lead to genetic divergence between urban and non-urban populations.* Allele frequencies in urban and non-urban population will differ due to the complex and dynamic interplay between abiotic, biotic and social heterogeneity and their interactions with built systems characterizing urbanizing regions [67]. Alternatively, migration between non-urban and urban areas and human-mediated dispersal of organisms might counteract this genetic differentiation [52].

(3) *Urban-driven evolutionary changes emerge from genetic and cultural mechanisms resulting from co-evolutionary dynamics between humans and other organisms* [2,51] A significant role in evolutionary change is played by culture variations in phenotypes acquired directly and indirectly though social learning. Many species of mammals, birds, fishes and insects have learned novel behaviours, such as diet, foraging skills and anti-predator behaviour [51]. Urban settings provide unique opportunities for learning novel behaviours.

(4) *Genetic divergence in urbanizing regions will scale with the proportion of the plant and animal populations that are urban.* Interplay between biotic and social interactions might lead to rapid genetic divergence. Evidence shows that increase in land cover change and social interactions scale with city size. The urban matrix acts as a significant barrier to gene flow compared with other matrices. The greatest influence on genetic divergence occurs when the proportion of non-urban organisms is small compared with the urban population, and influence will scale with city size [75].

(5) *'Hybridization' between historical and novel habitats in urban ecosystems might explain their ability to maintain ecosystem functions over periods of rapid environmental change* [2]. In genetics, novel phenotypes in interspecific hybrids may emerge from the interactions of two genomes. We hypothesize that 'hybrid' human–natural ecosystems may display analogous tendencies, and may be able to accumulate differences in structure while maintaining pre-existing ecosystem functions.

5. Eco-evolutionary feedback and human well-being

By explicitly linking urban development to changes in traits that affect ecosystem function, we can start to map the eco-evolutionary implications of urbanization for ecosystem function and human well-being. In urban settings, phenotypic changes driven by urbanization could affect a variety of ecosystem functions such as biodiversity, food security and the availability of natural resources that support human well-being.

Urbanization mediates eco-evolutionary feedback through several mechanisms that operate on multiple scales. Efforts to explore the link between urban-driven phenotypic change and their effects on ecosystem functions in urbanizing regions are relatively nascent [2,43,51]. Insights from the study of ecological and evolutionary dynamics in response to climate change [76] may serve as a basis for formulation of hypotheses about eco-evolutionary dynamics in urbanizing regions. Examples of ecosystem functions relevant to both ecosystem and human well-being include nutrient cycling and primary productivity regulated by consumers' traits that control their demand for resources. Change in species trait might also affect ecosystem stability and resilience. The physical structure of estuarine and coastal environments, within which many cities are located, is maintained by a diversity of organisms particularly dune and marsh plants, mangroves and seagrasses. Evolution in traits underlying their ecosystem-engineering effects has potentially significant functional impacts on coastal resilience. An example of a direct impact on human health is that of white-footed mice in the New York metropolitan area. Studies by Munshi-South *et al.* [14,77–79] and Harris *et al.* [80]. show signals of directional selection in urban ecosystems for these mice which are the critical hosts for black-legged ticks (*Ixodes scapularis*) that carry the Lyme disease bacterium *Borrelia burgdorferi*, leading to spikes of human exposure to this organism.

Insight from the study of evolutionary change in urban regions could help scholars reconcile key theoretical concepts, including niche construction and community assembly, and redefine Hutchinson's 'realized niche' in an urbanizing planet [2].

6. Conclusion

Cities provide a natural laboratory for understanding eco-evolutionary dynamics in an urbanizing world and could represent microcosms of alternative futures for the planet. They are also ideal laboratories for studying interactions between human and other species, ecological niche construction and eco-evolutionary feedback. As a first step to quantifying the urban signal of eco-evolutionary dynamics, development of standardized empirical studies in which focal species are monitored along urban-to-rural gradients is required. The repeated or replicated observations of eco-evolutionary feedbacks in urban regions could further illuminate whether some characteristics of urban development override city-specific environmental alterations and cause an emerging signal of eco-evolutionary feedback across the globe.

Rethinking evolutionary processes on an urbanizing planet requires acknowledging the reciprocal interactions between selection and environmental changes. We can also shed light on innovation in evolutionary processes and the processes by which an organism improves its environment to enhance its persistence [81]. Finally, by considering the strong and reciprocal evolutionary forces that shape the urban environment and its inhabitants, we may also come to better view our own evolution. Humans are, after all, an urban species that is also presumably rapidly evolving. How far might we already be along the road leading from *Homo sapiens* to *Homo urbanus* [82]? Recognizing and studying the eco-evolutionary feedback between humans and their urban world may afford us greater ability to predict the ecological and evolutionary impacts of urbanization.

Competing interests. We declare we have no competing interests.

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