Review

Eco-evolutionary dynamics in an urbanizing planet

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A great challenge for ecology in the coming decades is to understand the role humans play in eco-evolutionary dynamics. If, as emerging evidence shows, rapid evolutionary change affects ecosystem functioning and stability, current rapid environmental change and its evolutionary effects might have significant implications for ecological and human wellbeing on a relatively short time scale. Humans are major selective agents with potential for unprecedented evolutionary consequences for Earth's ecosystems, especially as cities expand rapidly. In this review, I identify emerging hypotheses on how urbanization drives eco-evolutionary dynamics. Studying how human-driven micro-evolutionary changes interact with ecological processes offers us the chance to advance our understanding of eco-evolutionary feedbacks and will provide new insights for maintaining biodiversity and ecosystem function over the long term.

Expanding the new synthesis

Eco-evolutionary feedbacks (see Glossary) – the reciprocal interactions between ecological and evolutionary dynamics on contemporary timescales – were hypothesized over half a century ago [1], but only recently have they been tested empirically [2]. There is significant evidence that changes in ecological conditions drive evolutionary change in species traits that, in turn, alters ecological interactions [3,4]. However, despite the remarkable progress in studying eco-evolutionary feedbacks over the last decade, empirical studies are still limited and the potential implications for environmental change and the evolution of species are only beginning to emerge [3,5,6]. In particular, we do not know what role human activity plays in the reciprocal interactions between ecological and evolutionary processes.

Earlier assumptions about the different time scales of ecological and evolutionary processes have shaped the unidirectional character of most empirical eco-evolutionary studies and can partly explain our lack of curiosity about the human role in shaping the evolutionary trajectory of planet Earth. However, recent evidence suggests that significant evolutionary change does occur on a short time scale, which urgently challenges both ecologists and evolutionary biologists to redefine the dynamic interplay between the two fields and to understand the interactions between human agency and eco-evolutionary feedback across different levels of biological organization.

Humans are major drivers of micro-evolutionary change [7,8]. In human-dominated environments, selection pressures acting on traits can affect population dynamics by changing organisms' rates of survival or reproductive success, leaving a genetic signature that might affect community dynamics and ecosystem functions [9]. Phenotypic trait changes resulting from changes in gene frequencies might affect population dynamics through changes in demographic rates [10]. Genetic signatures have been observed in the population dynamics of several organisms, including birds, fish, arthropods, rodents, land plants, and algae [7,11]. Effects at the community level might result from predator–prey interactions, parasite–host relationships, mutualism, and competition [12]. These effects drive changes in energy and material fluxes that, in turn, influence ecosystem functions, such as primary productivity, nutrient cycling, hydrological function, and biodiversity [13], which provide essential services for human wellbeing [9].

The emergence and rapid development of cities across the globe might represent a turning point in human-driven eco-evolutionary dynamics in ways we do not yet understand completely. In cities, subtle eco-evolutionary changes are at play – and at an unprecedented pace.

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Glossary

Eco-evolutionary feedbacks: reciprocal interactions between ecological and evolutionary dynamics on contemporary timescales.

Ecosystem: a unit that includes all of the organisms in a given area interacting with the physical environment, so that a flow of energy leads to clearly defined trophic structure, biotic diversity, and material cycles (i.e., exchange of materials between living and nonliving parts).

Ecosystem function: the flux of energy, organic matter, or nutrients in an ecosystem, including the flux of biomass associated with trophic interactions. Functions are expressed as a rate of change of an ecosystem property.

Ecological niche: the functional role and position of a species in the ecosystem including what resources it uses and how it interacts with other species.

Niche construction: the process by which organisms modify components of their environment, such as resource distribution or habitat space, to affect selection pressures on themselves or other organisms in an ecosystem.

Urban: the US Census defines urban agglomerations as having 2500 or more inhabitants, generally with population densities of 1000 or more persons per square mile. In such areas people live at high densities and in high numbers, or the built infrastructure covers a large portion of the land surface.

Urban ecosystems: coupled human–natural systems in which people are the dominant agents and highly dependent beyond its boundaries on large inputs of materials and energy and vast capacities to absorb pollution and waste.

Urbanization simultaneously mediates eco-evolutionary feedback by changing habitat and biotic interactions and by driving socioeconomic transitions toward an increased pace of life. The extraordinary concentration of people and activities in cities provides major opportunities to achieve economies of scale, but it intensifies the use of energy and its environmental impacts. While cities accelerate the transition to efficient technologies, that technological innovation provides access to resources from distant regions, promoting positive feedbacks [14]. Cities are not simply altering biodiversity by reducing the number and variety of native species. Humans are selective agents determining which species can live in cities and causing organisms to undergo rapid evolutionary change. Many organisms, including arthropods, birds, fish, mammals, and plants, are adapting to the new environment by changing their physiology, morphology, and behaviors.

During the last decade, evidence has been growing that species diversity matters to the functioning of ecosystems, but what determines the magnitude of its effect is species identity [15]. By focusing on functional groups, ecological scholars have recently started investigating the extent to which functional substitutions alter a variety of properties such as primary productivity, decomposition rates, and nutrient cycling [16], as well as ecosystem stability and resilience [17]. Biodiversity might provide 'insurance,' a buffer to maintain ecosystem function in the presence of environmental variability, since different species respond differently to environmental fluctuations [17]. Recent studies indicate that 'response diversity' – the variability in responses of species within functional groups – is what sustains ecosystems in the context of rapid environmental change [18].

Humans can affect species composition and their functional roles in ecosystems both directly, by reducing the overall number of species, and selectively, by determining phenotypic trait diversity [19]. Individual species can control processes at both the community and ecosystem levels [20], so diversity might have a strong effect on those processes because changes in diversity affect the probability that these species will occur among potential colonists [21].

By bringing human agency into the study of eco-evolutionary feedback, we can start to articulate and test a series of hypotheses about key mechanisms linking biodiversity and ecosystem function [22] and the potential feedback between evolution and ecosystem dynamics on a human-dominated planet [8,13]. However, to fully appreciate the implications of including humans in such a framework, we need to consider several levels of human interactions with ecological and evolutionary processes.

In this review, I present examples of human-driven eco-evolutionary feedbacks to articulate emerging hypotheses on how urbanization might drive eco-evolutionary dynamics and influence planetary change. By focusing on documented signatures of trait change, I identify emerging mechanisms linking urbanization to eco-evolutionary dynamics and the potential feedbacks on ecosystem function. Then, I elaborate on how evolutionary feedbacks are mediated by co-evolutionary interactions between species or genes, either through strictly genetic co-evolution, or through gene-culture co-evolution. Finally, I discuss how rapid change associated with urbanization can give rise to different feedbacks governing the behavior of evolutionary change and their potential implications for promoting versus buffering potential regime shifts.

Integrating humans into eco-evolutionary dynamics

Increasing evidence shows that humans influence evolutionary processes by changing speciation and extinction patterns [23]. Humans are creating and dispersing

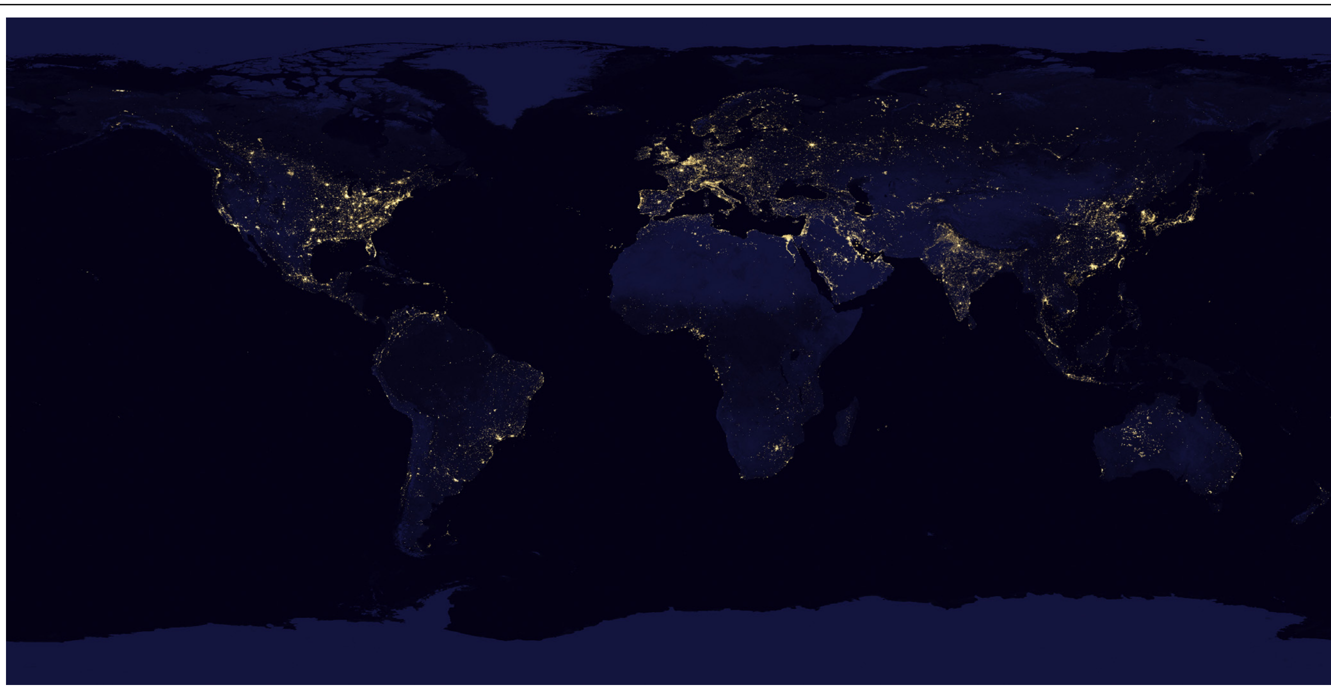

Figure 1. Visible Earth lights 2012 (NASA).

thousands of synthetic compounds and thereby altering bacteria, insects, and other organisms. By hunting, fishing selectively, and reconfiguring the planet's surface, humans have triggered a wave of extinction comparable to the five mass extinctions in Earth's earlier history [24]. The anthropogenic signatures of planet-scale changes are most evident in urbanizing regions (Figure 1). Increasing evidence shows that as humans interact with niche construction through urbanization, they alter the structure and function of communities and ecosystems [25,26]. However, the evolutionary consequences of urbanization and the mechanisms by which dense human settlements affect selective processes are not well known.

Eco-evolutionary biologists have developed several expressions to formalize eco-evolutionary feedback. I revise the general definition from Post and Palkovacs [6] by explicitly identifying urbanization as a variable that intervenes in the interplay between ecological and evolutionary dynamics [27]. Applying the Palkovacs and Hendry [11] framework, we can start to identify urban-driven changes in the attributes of populations, communities, and ecosystems that influence phenotypes via selection and plasticity and via potential feedbacks (Figure 2). Examples of eco-evolutionary feedbacks associated with urbanization (both hypothesized and documented) have been illustrated for many species of birds, fish, plants, mammals, and invertebrates (Table 1).

Building on examples documented in the literature [2,6,8,11], I articulate four overarching hypotheses (H1–H4) linking urbanization to eco-evolutionary dynamics and its potential role in promoting or buffering eco-evolutionary change:

(i) **(H1):** Genetic signatures of urban eco-evolutionary feedback can be detected across multiple taxa and ecosystem functions.
(ii) **(H2):** Through urbanization, humans mediate the interactions and feedback between evolution and ecology in subtle ways by introducing changes in habitat, biotic interactions, heterogeneity, novel disturbance, and social interactions.
(iii) **(H3):** Humans affect eco-evolutionary feedback through both genetic and cultural changes resulting from their 'co-evolutionary dynamics' with other social organisms.

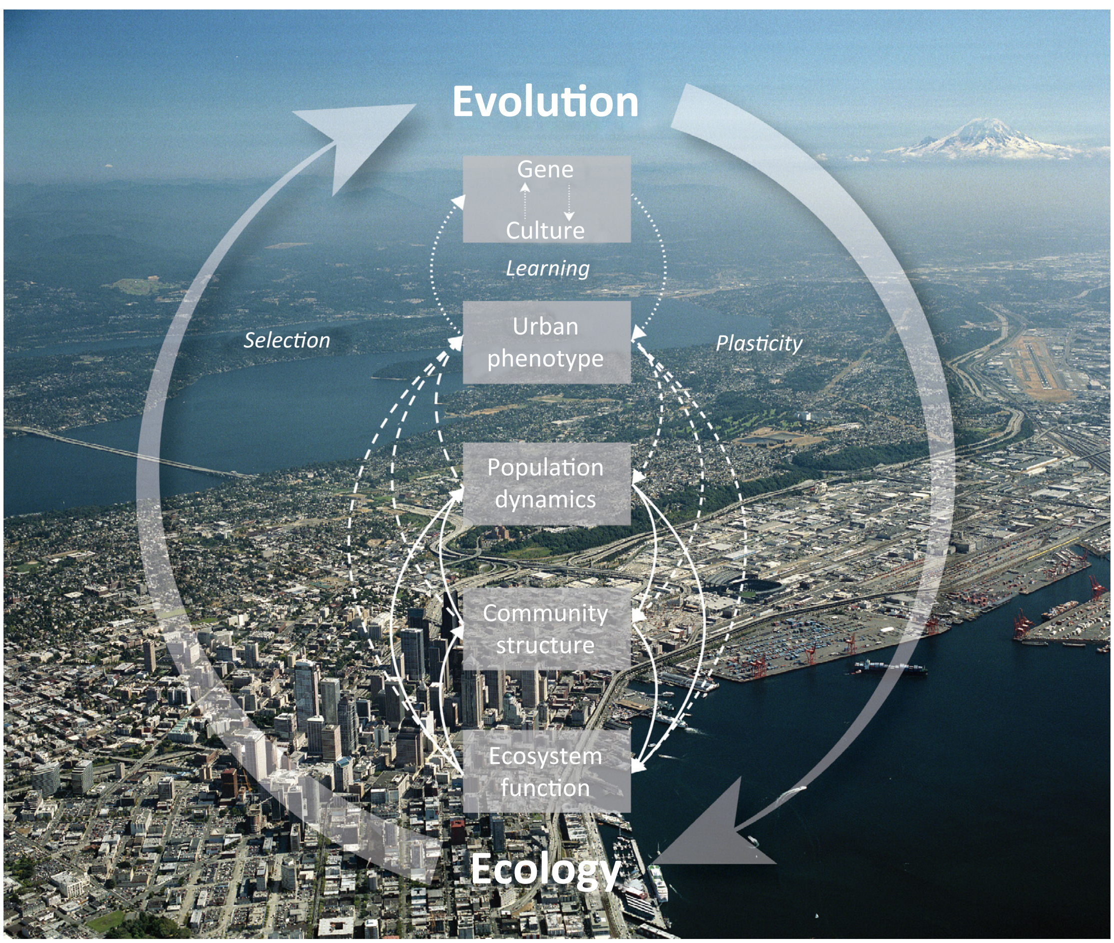

Figure 2. Eco-evolutionary dynamics in urbanizing ecosystems. Changes in gene frequencies might translate into phenotypic trait changes (physiology, morphology, behavior) that affect demographic rates (such as reproduction, survival, or dispersal) and ultimately population dynamics (e.g., numbers of individuals and population persistence), community structure (e.g., species richness or diversity), and ecosystem function (e.g., nutrient cycling, decomposition, and primary productivity) (broken lines). These changes can cascade among levels of ecological organization (continuous lines), and ultimately affect the trajectory of evolution (loops represented by dotted lines). To fully understand the potential implications of eco-evolutionary feedbacks in urbanizing environments, it is critical to expand the framework to include genetic and cultural co-evolution through both inheritance and social learning. (Note: The general framework for eco-evolutionary feedback is adapted from Palkovacs and Hendry [11]. Background photo reproduced, with permission, from Aerolist-photo.com).

Table 1. Examples of urban signatures. Synoptic table of documented examples of cases of trait change in fish, birds, mammals, and plants, their human drivers, and ecological effects

Species	Driver	Traits	Mechanism	Ecological effects	Refs
Fish					
Pacific salmon (*Oncorhynchus* spp.)	Dam construction	Body shape	Phenotypic Genetic	Trophic interactions[a]	[35,36]
Alewife (*Alosa pseudoharengus*)	Dam construction	Gape size Migratory behavior	Phenotypic	Trophic cascade Nutrient subsidies	[6] [82]
Killfish (*Fundulus heteroclitus*)	PCB Contamination	Tolerance to toxicity	Genetic	Trophic cascade	[83]
Largemouth bass (*Micropterus salmoides*)	Recreational fishing	Growth rate Vulnerability to angling	Genetic	Social behavior Trophic interactions[a]	[84] [85]
Top predators (i.e., Atlantic cod, *Gadus morhua*)	Commercial fishing	Fish body size Metabolic rate	Phenotypic	Trophic cascade	[86]
Invertebrates					
Peppered moth (*Biston betularia*)	Industrial pollution Predation	Melanism	Genetic	Biodiversity	[87]
Daphnia (*D. pulex*)	Eutrophication	Resistance to toxins Cyanobacteria	Phenotypic	Trophic cascades[a]	[88]
Daphnia (*D. pulex*)	Hydrological impact on predator–prey interaction	Reproduction	Phenotypic Genetic	Consumer Dynamic[a]	[89]
Earthworms (*Lumbricus rubellus*)	Soil contamination, trace elements, (i.e., arsenic)	Tolerance to metals	Phenotypic Genetic	Nutrient Cycling[a]	[90]
Birds					
Dark-eyed junco (*Junco hyemalis*)	Heat island	Tail feathers	Genetic	Biodiversity Seed dispersal Biotic control	[31]
Song birds	Fragmentation	Wing shape	Phenotypic	Metapopulation dynamics[a]	[32]
European blackcap (*Sylvia atricapilla)*	Supplemental feeding	Wing shape Beak shape	Phenotypic	Niche diversification[a]	[33]
Great tits (*Parus major*)	Noise	Song acoustic-adaptation	Genetic	Biodiversity	[91]
European blackbirds (*Turdus merula*)	Artificial light	Stress response behavior	Genetic	Metapopulation dynamics[a]	[19]
Mammals					
Red fox (*Vulpes vulpes*)	New food	Body size	Genetic	Trophic Dynamic	[92]
White-footed mouse (*Peromyscus leucopus*),	Fragmentation	Protein coding Immune system	Genetic	Population growth Diseases	[38]
Plants					
Plants	Elevated CO_2 concentration	Leaf nitrogen composition	Phenotypic	Consumer dynamics[a]	[88]
Populus	Habitat modification	Leaf tannin levels	Genetic	Nutrient cycling	[93]
Weed (*Crepis sancta*)	Fragmentation	Dispersal	Genetic	Metapopulation dynamics[a]	[39]

[a]Hypothesized.

(iv) **(H4):** The hybrid nature of urban ecosystems – resulting from co-evolving human and natural systems – is a source of 'innovation' in eco-evolutionary processes.

Detecting the genetic signatures of urban evolutionary change

Urbanization alters natural habitats, leading to new 'selection pressures' and 'phenotypic plasticity' (Figure 3). The significant decrease in biodiversity in cities is only the most apparent of several more subtle changes associated with urbanization that have the potential to affect genetic diversity [19,22,25]. Habitat modification and fragmentation might lead to genetic differentiation. New predators and competitors affect species interactions. Exposure to new pathogens in cities alters host–pathogen interactions and can influence species fitness via the immune system. Diverse forms of pollution (from toxins to noise and light) can favor species that adapt more efficiently to these new conditions. Furthermore, the socioeconomic transitions and technological shifts associated with urbanization significantly affect the scale and pace of ecological change, leading to rapid evolution beyond the cities' boundaries.

The new selection regimes have significant consequences for microevolutionary changes. At the same time, the extreme turnover in biological communities might prevent the genetic differentiation of urban populations and impede evolutionary responses to the novel selective forces associated with urbanization [28]. Urbanization also induces phenotypic responses via phenotypic plasticity, but it might require genetic adaptation [19,29]. Heritable differences can accumulate (genetic accommodation) and plastic responses can generate new selection pressures

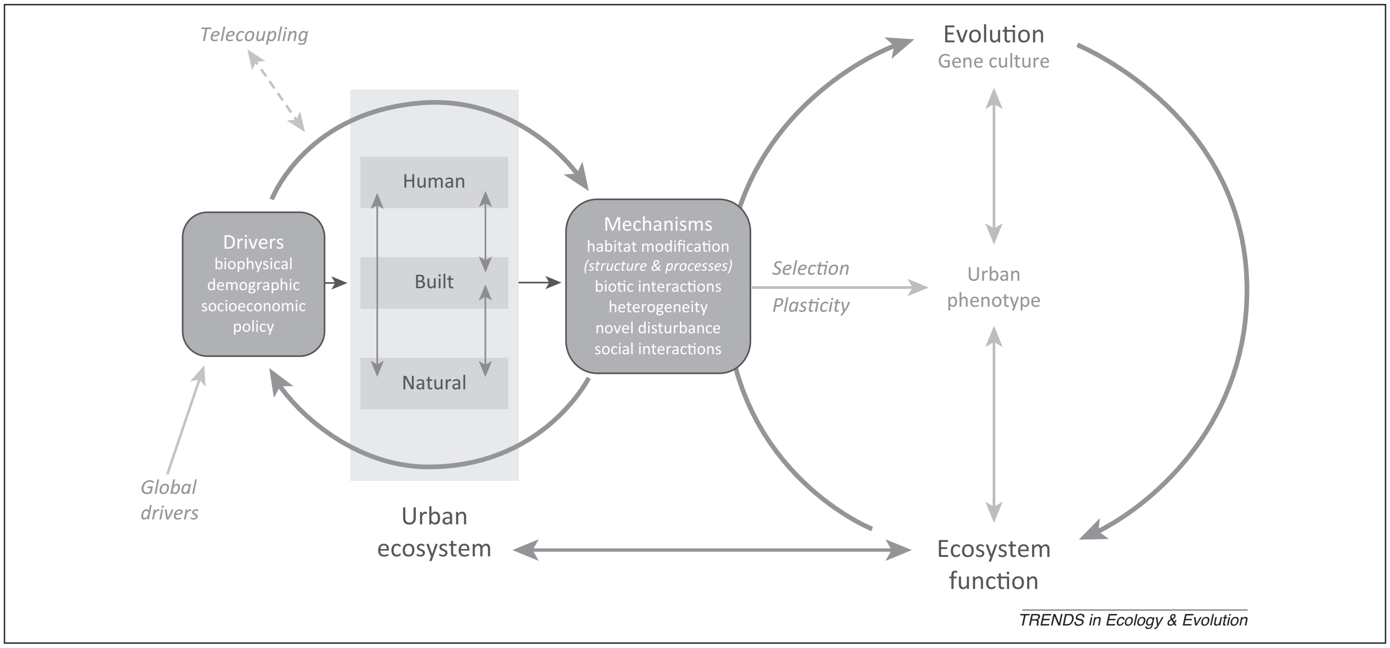

Figure 3. A conceptual framework of urban eco-evolutionary feedback. An integrated model to identify key mechanisms linking urban ecosystem dynamics to eco-evolutionary feedback. Key human drivers of change (e.g., climate, demographics, economics, and policy) influence eco-evolutionary dynamics through interactions between the human, natural and built system components of the urban ecosystem. Highlighted are the emerging mechanisms of how urbanization drives eco-evolutionary dynamics: Habitat change (structure and processes), biotic interactions, heterogeneity, novel disturbances, and social interactions.

[30]. Complex genetic and cultural co-evolution between species and between humans and other organisms also plays important roles through social learning [25].

Several studies have documented rapid human-driven trait changes (Table 1) [7,8], but only a few specifically examine the role of urbanization (Box 1). Hendry *et al.* [7] indicate that human-driven trait changes occur roughly twice as fast as those driven by nonanthropogenic forces. Recent reviews of adaptive evolution in urban ecosystems have started to document studies of specific organisms [25] and to synthesize a spectrum of applied techniques [26]. Examples of urban-driven eco-evolutionary feedbacks (both hypothesized and documented) have been illustrated for many species of birds [31–33], fish [34–37], rodents [38], plants [39–41], and amphibians, as well as for diverse invertebrates [6]. A few notable examples (e.g., *Daphnia*) are revealing the reciprocal causal mechanisms that drive the interactions between organisms and their environments, as new selective pressures can alter the population dynamics of multiple prey species, reconfigure trophic interactions, and ultimately, affect multiple ecosystem functions [13]. Understanding the mechanisms by which species successfully adapt to human-driven changes and urban environments is critical to anticipating future evolutionary trajectories of an urbanizing planet.

Emerging urban eco-evolutionary mechanisms

Urbanization mediates eco-evolutionary feedbacks through several filters that operate simultaneously across multiple scales. Urban development changes habitat structure and biogeochemical cycles, modifies disturbance regimes, and introduces species (e.g., hosts, pathogens, and predators), creating novel habitats (Figure 3). Urban environments can facilitate speciation by bringing together species that were previously isolated, or by isolating populations through habitat transformation [19]. Changes in habitat and selective forces increase the chances of extinction [25]. In addition to the changes in the physical template, humans in cities modify the availability of resources and their variability over time, buffering their effects on the community structure [28]. Although each filter can be identified as an independent driver, their consequences cannot be understood in isolation. Furthermore, cities increase the pace of life [14] and amplify telecoupled interactions and the impact of human activities on distant places [42].

Mechanisms by which urbanization affects evolutionary dynamics

Hypotheses about how humans in urbanizing environments impact eco-evolutionary feedbacks can be articulated around key mechanisms that influence species diversity and ecosystem function, and ultimately, human wellbeing [19,28]. In urban environments, selective changes are caused by the combined effects of changes in habitat structure (i.e., loss of forest cover and connectivity) and processes (i.e., biogeochemical and nutrient cycling) and changes in biotic interactions (i.e., predation). Humans in cities also mediate eco-evolutionary interactions by introducing novel disturbances and altering habitat heterogeneity [43] (Box 2). These mechanisms vary on an urban gradient (Box 3). Complex interactions resulting from the changes in habitat and biotic interactions, coupled with the emerging spatial and temporal patterns of resource availability, might produce new trophic dynamics (i.e., shifts in control from top–down to bottom–up [28]). In urban ecosystems, however, changes in the ecological dynamics are only part of the picture. What makes urban ecosystems unique is the presence of people. Cities are shaped by social interactions [44] and cultural evolution

Box 1. Urban eco-evolutionary examples

The best known case of urban eco-evolution is the darker color of the peppered moth (*Biston betularia*) in the 1800s, associated with industrialization [87]. Recently, in San Diego, California, USA, the dark-eyed Junco, *Junco hyemalis*, has adapted its tail feathers [31]. Wing shapes in songbirds have evolved in response to forest fragmentation in North America [32]. Food sources and the buffering of resource variability have led to changes in migratory behavior and wing shapes in the European Black Cap, *Sylvia atricapilla* [33]. Great tits are among bird species that have changed the frequency of their notes to adapt to the noise present in urban environments [90].

Urbanization causes rapid evolution of seed sizes and seed dispersal [39,40]. Cheptou *et al.* [39] show that the weed *Crepis sancta* disperses a significantly lower proportion of its seeds in urban patches than in unfragmented surroundings. Riba *et al.* [41] found evidence that the seeds of *Mycelis muralis* were less able to disperse by wind in fragmented landscapes. Plants' increased tolerance for heavy metals in urban microhabitats or brownfields is another example of rapid evolution.

Several scholars have documented evidence of changes in the morphological attributes of fish in response to the construction of dams and habitat changes [34–37]; they also show how natural selection in the body size of the Pacific salmon (*Oncorhynchus* spp.) affects salmon population dynamics, community interactions, and ecosystem process (fluxes of salmon biomass). Ample evidence for the potential impact of selection pressures on trophic interactions is provided by the evolutionary changes of a keystone aquatic herbivore, *Daphnia* [88]. Selection pressures influencing the composition of zooplankton communities result from the significant changes in biogeochemical cycles and physical templates that occur in urbanizing catchment areas, leading to rapid evolutionary change.

Providing a further example of rapid evolution with potential consequences for human health, Harris *et al.* [38] studied white-footed mice (*Peromyscus leucopus*) in the New York metropolitan area. Their study is one of the first to report candidate genes exhibiting signatures of directional selection in divergent urban ecosystems. These mice are the critical hosts for black-legged ticks, which carry and spread the bacterium that causes Lyme disease. Superabundant mouse populations allow more ticks to survive and lead to predictable spikes in human exposure to Lyme (Figure I).

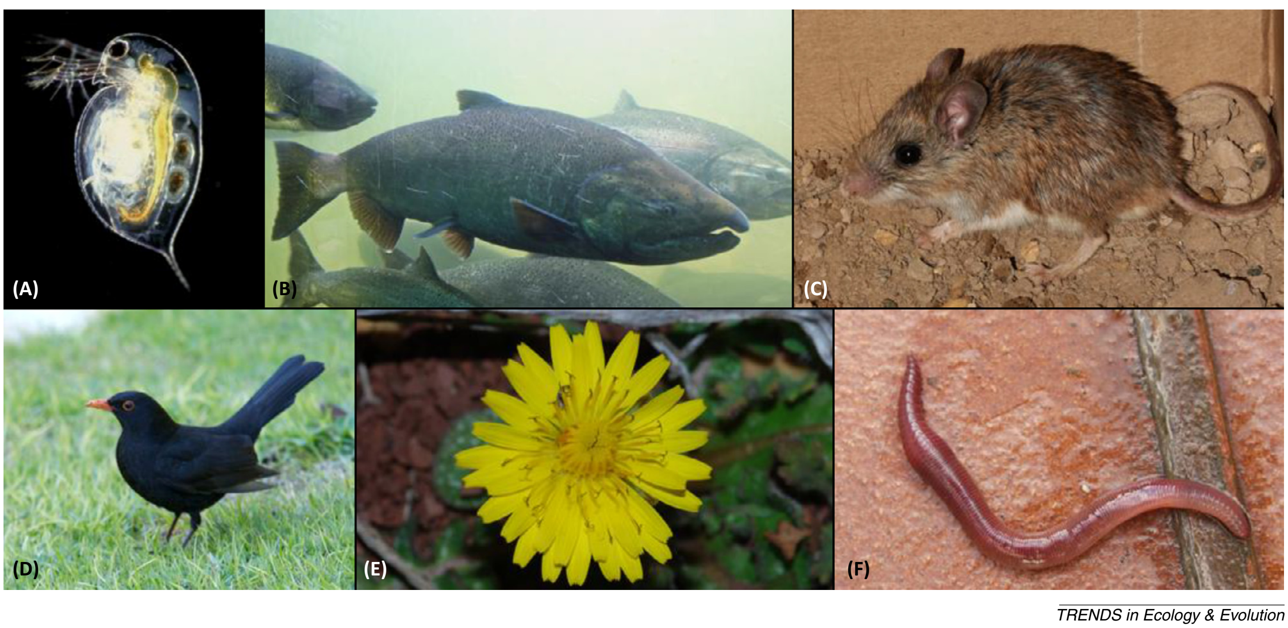

Figure I. **(A)** The water flea *Daphnia*, which plays a pivotal role in the functioning of pelagic freshwater food webs [89]. **(B)** Pacific salmon (*Oncorhynchus* spp.) provide important subsidies of marine-derived nutrients to rivers, lakes, and streams [35,36]. **(C)** The white-footed mouse (*Peromyscus leucopus*), a common resident of New York City's forest fragments, exhibits signatures of directional selection in urban ecosystems [38]. **(D)** European blackbirds (*Turdus merula*) show differential behavior traits in response to urbanization [19]. **(E)** *Crepis sancta*'s seed dispersal has evolved rapidly [39]. **(F)** Earthworms have adapted genetically to a series of soil contaminants (*Lumbricus rubellus*) [90]. Reproduced, with permission, from Paul Heber (A), Michael Jefferies (B), J.N. Stuart (C), Lip Kee (D), Bernard Dupont (E), and Belteguese (F).

[25], with significant consequences for co-evolution between humans and other species, and for the pace of change [14]. One such consequence is the phenomenon of telecoupling: the emerging interactions between distant natural and human systems [42] which expand the edge of the urban-driven eco-evolutionary change beyond the city itself, and accelerate its dynamic.

Habitat modification

Land cover conversion and rapid loss of native habitat are major drivers of micro-evolutionary change. Habitat patches and their species communities are often isolated from each other by a matrix of built environments. The fragmentation of natural patches is one of the best-known impacts of human activities on the diversity, structure, and distribution of vegetation, as well as on the movement of resources and organisms among natural patches. New barriers make dispersal difficult and potentially penalize less mobile organisms [45]. Furthermore, changes in productivity – the rate at which energy flows through an ecosystem – might explain patterns of species diversity along the urban-to-rural gradient [46], although studies have produced contradictory results. Net Primary Production (NPP) mediates the relationship between anthropogenic land cover change and the richness of both faunal and plant species, but the relationship varies with taxa and scale, and across biomes [47]. Human activities drive direct and indirect changes in the distribution of resources, which can peak at the urban fringe, simultaneously reducing their variability.

Box 2. The homogenization hypothesis

The effect that human actions have on spatial heterogeneity in urbanizing regions is well documented, but we know less about how heterogeneity varies with scale, partly because studies have tended to focus primarily on aggregated measures [22]. At the scale of meters or below, urbanization might reduce the heterogeneity of land cover, but at the patch level, it might introduce highly heterogeneous new biophysical conditions as the varied behaviors of landowners result in fragmented management patterns. As the scale increases we could observe a further reduction in heterogeneity due to consistent patterns of urban development and habitat fragmentation. McKinney [43] advanced the hypothesis that urbanization causes global homogenization. As cities expand, urban regions are maintained in a state of disequilibrium from the local natural environment, so that habitats across urban sites are more similar to each other than to their respective adjacent natural environments [53].

Urban management and the built infrastructure can artificially reduce the variation – in both space and time – of resource availability, thus altering seasonal variations and dampening temporal variability [28]. Some species thrive when they have less variation to endure, and their urban populations rise. A well known example is the grey-headed flying fox (*Pteropus poliocephalus*), a large nomadic bat from eastern Australia, which became established in Melbourne, Australia when a heat island effect led to long-term climatic changes. Parris and Hazell [94] found that human activities have increased temperatures and effective precipitation in central Melbourne, creating a more suitable climate for the fox to camp. Changed habitat, with more water and food available, interacts with biotic, trophic, and genetic processes, and might help some species adapt to urban environments.

Changes in temporal variability in urban ecosystems are driven by both human structures and high inputs of resources. A good example of change in temporal heterogeneity is the buffering effect that microclimatic changes associated with urbanization can have on habitat: in temperate cities, heat islands can extend the growing season, but in desert cities they can cause extended droughts. Shochat *et al.* [28] report that the heat island in Phoenix, Arizona, USA, has increased the stress on cotton plants (*Gossypium hirsutum*). Highly managed green areas in temperate cities, such as Seattle, Washington, USA, and irrigation in semi-arid cities, such as Salt Lake City, Utah, USA, provide water for plants throughout the year with subtle effects on wildlife.

Biotic interactions

Urban development creates new opportunities and challenges for species competition and predation, both as exotic species are introduced and as invasive species migrate in, taking advantage of poorly integrated communities and patches in the urban setting. This sometimes results in a colonization process, as more frequent introductions of exotic species translate into invasions [48]. Examples of this phenomenon abound [25]. Along a 140-km urban-to-rural environmental gradient originating in New York City, McDonnell *et al.* [49] found lower levels of both earthworm biomass and abundance in the urban forests compared to the rural forests, likely because of introduced species. Urbanization also alters the way species are distributed and interact with each other [50]. Marzluff [51] developed a series of testable hypotheses about how urbanization affects colonization and extinction in determining local diversity and found that, while diversity still emerges as the balance between extinction and colonization, species invasion plays a prominent role [51].

Heterogeneity

Cities are 'human habitats' and are designed and managed to best support human functions. This is why we find less diversity in microclimates and species among urban sites, compared to other adjacent natural ecosystems (Box 2). The diversity of species in urbanizing regions is greatly affected by the quality of habitat and the template of resources. Habitat heterogeneity allows for greater niche differentiation, and hence, more species. Humans in cities affect habitat quality and resource availability by changing their heterogeneity in space and time. An example of change in temporal heterogeneity is the buffering effect created by microclimatic changes associated with urbanization. Heat islands can extend the growing season in temperate cities, but extend droughts in desert urban areas [28]. Despite the high numbers of small patches with different environmental conditions [52], habitat changes associated with urban land uses act as filters in urban species composition, with clear winners and losers and losses of native species, driving the homogenization of ecological structure and functions [53]. However, cities still retain native species worldwide [54].

Novel disturbance

Ecosystem disturbances affect resource availability (i.e., water and nutrients), ecosystem productivity, and species diversity [55]. Urbanization modifies existing disturbance regimes (e.g., through fire and flood management) and creates novel disturbances (e.g., new or disrupted dispersal pathways or introduced species). Human-induced disturbances in urban environments maintain urban habitats at an early successional stage [43,49]. Furthermore, the patchy distribution of urban habitats, combined with the varying degree of human-induced disturbances, results in a number of succession paths across habitat patches [52]. Cardinale *et al.* [15] suggest that disturbance can moderate relationships between biodiversity and ecosystem functioning in two ways. It can increase the chance that diversity generates unique system properties, and it can suppress the probability of ecological processes being controlled by a single taxon.

Social interactions

Urbanization also changes the dynamics of social interactions among people [44] and between people and other species [25]. Perhaps the most significant quality that distinguishes cities from other systems is the pace of change. By examining a large set of data on a diversity of aspects that characterize urban regions, Bettencourt and West [14] observed that, while cities exhibit scaling relationships similar to those that biologists have found for organisms' molecular, physiological, ecological, and life-history attributes, some relationships have no analog in natural systems. In nature, the networks and interactions that sustain biological organisms and ecosystems are dominated by economies of scale or 'sublinear scaling.' In cities, environmental changes are driven by social interactions that operate in exactly the opposite fashion, showing 'superlinear scaling.' The larger the city, the faster its pace of life [44].

Box 3. Urban ecological gradients

Patterns of development produce different landscape signatures – spatial and temporal changes in ecosystem processes that, in turn, influence biodiversity [68] – that vary along an urban-to-rural gradient ranging from the urban core to suburban and exurban areas to rural and intact forest. Emerging hypotheses on the mechanisms linking urbanization patterns to changes in species traits are based on the evidence that patterns of urbanization affect natural habitat and biotic interactions across the urban-to-rural gradient in subtle ways [49]. The hypothesized urban landscape signatures are represented in Figure I in relationship to each mechanism for which some initial evidence supports its varying along a hypothetical urban gradient (x axis) [22,67].

Ecosystem functions along a gradient of urbanization are simultaneously affected by changes in habitats and biotic interactions (Figure I). Rates of forest conversion and loss of native habitat will be the highest at the urban fringe since forest conversion has already occurred at the urban core. Forest connectivity declines as we move closer to the urban core. Resource availability is kept artificially high at the urban fringe because of human inputs, but the variability of available resources will decline. Disturbances increase with urbanization [67].

We can expect a steady decline in native species and an increase in extinction toward the urban core; meanwhile the colonization by early successional and synanthropic species will peak at the urban fringe and then decline at the urban core [51]. Predation will decline towards the urban core, although not steadily due to predation by urban pets. Parasitism will be higher closer to the urban core. Humans might facilitate parasites in the suburbs, for example by putting out bird nest boxes. Insect species that are facilitated in 'nature' by woodpeckers are facilitated in suburbs by woodpeckers, people, and other birds; for example, chickadees and swallows nest in nest boxes and lights. We can expect that novel competitions will emerge as landscapes urbanize [25].

Together, habitat modification and changes in biotic interactions lead to evolutionary responses in species and ecosystem functions. In cities, humans modify the mechanisms that control the spatial and temporal variability of nutrient sources and sinks [68,95]. In New York, urban forests exhibit faster rates of litter decomposition and nitrification than rural forests [49]. The heat island effect and the introduction and colonization of (nonnative) earthworms in the urban forests were hypothesized to drive these results. However, empirical studies of the underlying processes and mechanisms linking urbanization patterns and ecosystem dynamics are still extremely limited [68].

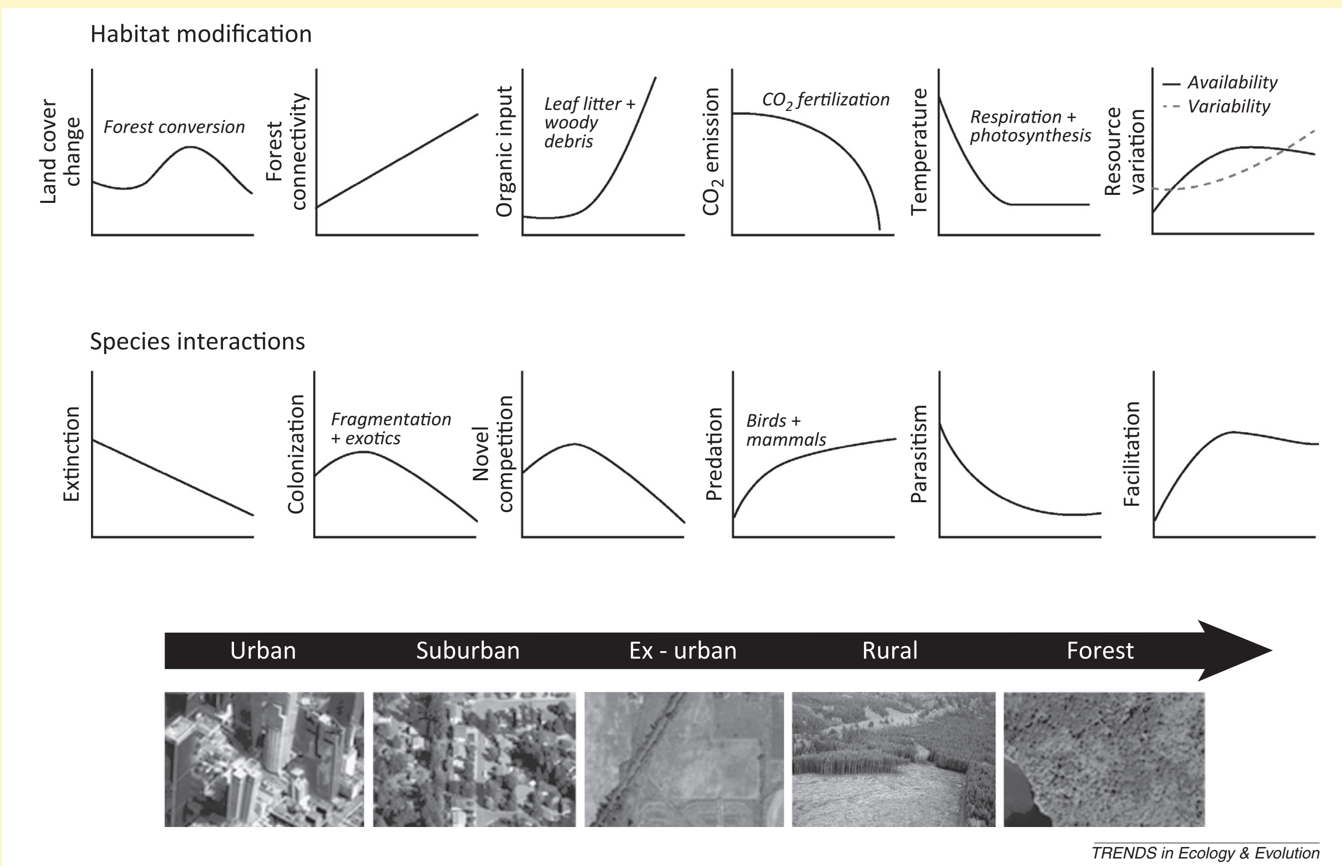

Figure I. Hypothesized urban landscape signatures emerging from the literature representing the relationships of key mechanisms associated with habitat modification and species interactions represented on the y-axes and an hypothetical urban–natural gradient. The hypothesized signatures are intended to highlight the complexity of the relationships and do not apply across all urban–natural gradients in regions where the wild lands would be steppe, savanna, or desert.

Telecoupling

Cities are networked far beyond their own physical edges. Their functions depend on highly interconnected infrastructures and on flows of material, energy, and information from proximate (e.g., hydroelectric dams) and distant regions (e.g., trade and telecommunication). Distant coupled human–natural interactions are more prevalent, and occur at higher speeds [42]. Such complex interactions in telecoupled systems make it particularly challenging to understand the potential eco-evolutionary implications and feedback associated with urbanization and to anticipate potential crossings of thresholds and outcomes. On a human-dominated planet, telecoupling challenges the ecosystem concept implied in eco-evolutionary studies to expand both its boundaries and relationships to include distant interactions and the new potential cross-scale feedback [42].

Mechanisms by which evolutionary change affects urban ecosystems

Researchers are increasingly documenting how phenotypic evolution might affect ecosystem functions [16]. Individual trait variation has significant implications for ecosystems' productivity and their stability, thus – according to Matthews *et al.* [13] – it represents a natural intersection point between evolutionary biology and ecosystem science.

Linking phenotypic evolution to urban population and community dynamics

Table 2 identifies examples of potentially heritable traits for which there is evidence of evolutionary response to environmental changes driven by urbanization and that might directly or indirectly affect ecosystem functions [11,13,28]. The evolution of the traits of organisms that control ecosystem processes could lead to significant changes in ecosystem functions through their ability to alter their environment and their selective regimes [3]. For example, primary productivity is associated with consumer traits that regulate their demand for resources. Evolution in such traits can affect nutrient cycling, and ultimately, the magnitude and spatial distribution of primary production [56]. Seed dispersers have a significant impact on plant diversity and their functional role in urban ecosystems. A great diversity of organisms modify the physical structure of estuarine and coastal environments, particularly dune and marsh plants, mangroves, seagrasses, kelps, and infauna. Evolution in traits underlying their ecosystem-engineering effects has potentially significant functional impacts.

Matthews *et al.* [13] examine how the evolution of ecosystem-effect traits can directly or indirectly affect ecosystem functions by influencing ecosystem processes via the environmental, population, and community dynamics. For example, as plants' photosynthetic traits evolve, that could in turn alter the rates of primary production and carbon sequestration in terrestrial ecosystems. CO_2 concentrations can also affect the growth rate and phenotype of algae, which could alter the rates of primary production and carbon sequestration in aquatic ecosystems [57].

Urbanization also exerts selective pressures on traits that underlie species interactions (e.g., foraging traits, defense traits), driving changes in community dynamics that control ecosystem functions. New selective forces in urban environments can alter the population dynamics of predators and reconfigure the trophic interactions between predator individuals and their prey and the flux of organic matter in ecosystems [58].

Mapping phenotypic evolution to urban ecosystem function

Scholars have documented how urbanization affects primary productivity, nutrient cycling, hydrological function, and biodiversity through direct and subtle changes in climatic, hydrologic, geomorphic, and biogeochemical processes and biotic interactions [22,28]. Simultaneously, increasing interest is emerging among scientists to study contemporary evolution in urban ecosystems [19,25,26]. By explicitly linking urban development to heritable traits that affect ecosystem functions, we can start to map the eco-evolutionary implications of human-induced trait changes for those species that play an important functional role in communities and ecosystems and identify the existing gaps in knowledge (Table 2) [17]. The scale at which species perform different ecosystem functions could be a key to understanding the relationship between urbanization, functional diversity, and ecosystem stability [59].

Co-evolutionary dynamics in hybrid ecosystems

Cities evolve through a complex series of interactions involving a vast number of different components, agents, and decisions. In this section, I hypothesize that co-evolutionary processes can have a significant impact on the evolutionary process and the adaptive capacity of coupled human–natural systems because of the potential for change and innovation. Humans provide opportunities for evolutionary change [26,60]. Human activity can also facilitate 'reverse speciation' by inhibiting the process of species divergence [61]. Eco-evolutionary feedbacks are mediated by co-evolutionary interactions between species or genes; these can include strictly genetic-co-evolution or gene-culture-co-evolution [62].

Expanding the spectrum of phenomena that can cause evolutionary change to include developmental bias and niche construction would more effectively represent the complex dynamic of interactions that takes place between co-evolution and eco-evolutionary feedback in a human-dominated world [63]. A significant role 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 behaviors, such as diet, foraging skills, and anti-predator behavior [64].

In cities, completely novel interactions between human and ecological processes might produce novel ecological conditions and unprecedented expressions, leading to new ecological patterns, processes, and functions. An example is the interaction between seed dispersal and road transportation in urban environments. As humans become agents for dispersing seeds, they facilitate competition between species, helping determine which species thrive. Meanwhile, the structures and infrastructure that humans build provide new vectors and pathways for seed dispersal and new habitats that determine their survival. Vehicles alter the mechanisms and patterns of seed dispersal in urban areas, making it far easier for nondispersing seeds to spread, sometimes farther than 5 miles [65]. Humans also provide unintentional novel habitats: abandoned rail corridors and vacant lots.

Eco-evolution and innovation in hybrid ecosystems

Urban ecosystems are not simply complex coupled human–natural systems [66]. They are hybrids [67,68] – and that fact has an enormous impact on the eco-evolutionary dynamics of coupled human–natural systems. It is their hybrid nature that makes them unstable and unpredictable, but also capable of innovating [44], allowing coupled human–natural systems to co-evolve and change [69]. Novel interactions in urban ecosystems might trigger unprecedented dynamics and unpredictable change with significant implications for system function and dynamics

Table 2. Mapping urban-driven heritable traits change to ecosystem function. Documented heritable trait changes, urban drivers, and hypothesized eco-evolutionary feedback mechanisms

Urban habitat		Heritable trait	Eco-evolutionary feedback		Refs
Habitat modification	Biotic interactions		Ecosystem function	Feedback mechanism	
		Physiological			
CO_2 Concentration		Photosynthetic rate (Algae)	Primary productivity Nutrient cycling	CO_2 effect on algae growth rate and phenotype	[57]
CO_2 concentration	Food web and Trophic interaction	Leaf nitrogen composition (Plants)	Nutrient cycling	Herbivore density and feeding behavior	[96]
Toxic chemicals	Trophic interaction	Endocrine system/ hormones (Fish)	Nutrient cycling Biodiversity	Impaired signaling pathways	[82,97]
Toxic chemicals Noise Light	Trophic Interaction	Endocrine system/ hormones (Birds)	Biotic Control Seed Dispersal Biodiversity	Impaired reproductive and Immune functions	[97]
Metals		Tolerance to metals (Earthworms)	Nutrient cycling Decomposition	Increased numbers and biomass of earthworms	[90]
Nutrient loads Eutrophication	Trophic cascade	Resistance to toxic cyanobacteria (*Daphnia*)	Primary productivity Nutrient cycling	Consumer-resource dynamics	[88]
		Morphological			
Hydrological connectivity	Trophic interactions Predator–prey interaction	Body shape/ size (Fish)	Biodiversity Nutrient cycling	Effects on life history of zooplankton *Daphnia*	[98]
Emissions Heat		Plumage (Birds)	Biodiversity	Colonization	[31]
Forest fragmentation Food	Novel competition	Wing shape (Birds)	Biotic control Seed dispersal Biodiversity	Niche diversification Metapopulation dynamic	[32,33]
		Behavioral			
Hydrological connectivity	Trophic interactions	Migratory propensity (Fish)	Nutrient cycling Biodiversity	Relative energetic or survival costs of migration	[99]
Forest fragmentation	Competition for food Predation risk	Foraging (Birds)	Biodiversity	Efficiency in exploiting food resources	[28]
Artificial lighting Noise	Competition for territories	Syndromes (neophilic and neophobic) (Birds)	Biodiversity	Colonization	[100]
Heat island Food	Predation risk	Migratory propensity (Birds)	Biodiversity Biotic control	Meta population dynamic	[19]
		Phenological/Life history			
Heat island Artificial lighting Food	Breeding density	Time and duration of reproduction (Birds)	Biodiversity	Colonization	[19]
Hydrological connectivity	Predator–prey interaction	Time and reproductive effort (*Daphnia*)	Primary productivity Nutrient cycling	Consumer-dynamic	[98]
Fragmentation		Dispersal (Seeds)	Biodiversity Nutrient cycling	Metapopulation dynamics	[39]

[70]. At the same time, novelty in hybrid systems is a key component of reorganization and renewal. Complex systems provide multiple possible solutions for a given evolutionary problem [71]. In hybrid systems, that capacity allows the system to accumulate differences and still maintain preexisting functions. In genetics, this is a fundamental source of novelty. Novel phenotypes in interspecific hybrids emerge from the interactions of two divergent genomes [72]. Despite the emerging divergence, their molecular co-evolution ensures that their functions are maintained.

In these tightly coupled systems, the opportunities for resilience and adaptation emerge from the inherent uncertainty of complex cross-scale human–environment interactions, which vary in both space and time. In studying genetic networks in biological systems, Torres-Sosa *et al.* [73] found that critical systems exhibit important properties that allow robustness and flexibility: quick information processing, collective responses to perturbations, and the ability to integrate a wide range of external stimuli without saturation. Such interactions in urban systems are highly influenced by technology and infrastructure [74]. A key factor governing such interactions might be the lag time between human decisions and their impact, delayed and distributed over long distances [66], because it regulates the relationships between humans and natural resources through both physical and social mechanisms.

Although evolutionary biologists have recognized that the interactions in hybrids are a significant source of innovation in co-evolutionary processes, most researchers have seen the hybrid nature of urban ecosystems as a threat to ecosystem stability and resilience. By contrast, Hypothesis 4 (H4) suggests that hybrid ecosystems can represent a source of innovation in eco-evolutionary processes [67]; hybrid mechanisms are essential to maintain ecosystem functions while simultaneously allowing systems to co-evolve and change. Understanding the bases of these newly generated interactions is central to understanding co-evolution and adaptation in hybrid systems.

Concluding remarks

From a planetary perspective, the emergence and rapid expansion of cities across the globe could represent another turning point in the life of our planet [75]. For most of its history, Earth has experienced long periods of relative stability, dominated primarily by negative feedbacks. However, the recent increase in positive feedback (i.e., climate change), and the emergence of evolutionary innovations (i.e., novel metabolisms) [76], could trigger transformations on the scale of the Great Oxidation [77].

The increasing complexity and interdependence of socioeconomic networks and rapid telecoupling can produce 'tipping cascades' in the Earth's system, leading to unexpected regime shifts [75,78,79]. Only a formidable collaboration among scientists can address major questions such as these: What role do humans play in the evolution of Earth? Can the emergence and rapid development of cities change the course of Earth's evolution? Might different patterns of urbanization alter the effect of human action on eco-evolution? Can urbanization determine the probability of crossing thresholds that will trigger abrupt change on a planetary scale? How can research tackle such questions in new and productive ways?

In this article, I have argued that to begin to address these questions, we need to consider several levels of human interactions with ecological and evolutionary processes. First, what influence do humans have on population dynamics and community assembly? Second, how do human settlements influence heritable trait changes that support ecosystem functions? Third, we should expand the notion of eco-evolution to consider both the genetic and cultural co-evolution of human–natural systems [25,63]. A fourth level of inquiry should focus on how human-driven eco-evolutionary feedbacks affect ecosystem stability and regime shifts [67].

By integrating humans into the study of eco-evolutionary feedbacks, ecological scholars might be able to reconcile key theoretical concepts including niche construction and community assembly, and redefine Hutchinson's [80] 'realized niche' in an urbanizing planet [27]. Doing so could also resolve important puzzles in island biogeography and explain contradictory empirical results [51,81]. Rethinking evolutionary processes in a human-dominated world also implies expanding the notion of evolutionary causes beyond those that directly change gene frequencies, to acknowledge reciprocal causation between selection and environmental changes and the significant role of phenotypic plasticity [4,63], including characteristics that organisms acquire through social learning [64] in directing evolutionary change [63].

I contend that studying how humans mediate eco-evolutionary feedback through urbanization can contribute significantly to progress and synthesis in evolution and ecology.

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