

Review

A global horizon scan for urban evolutionary ecology

Brian C. Verrelli , ^{1,*} Marina Alberti , ² Simone Des Roches , ³ Nyeema C. Harris , ⁴ Andrew P. Hendry , ⁵ Marc T.J. Johnson , ⁶ Amy M. Savage , ⁷ Anne Charmantier , ⁸ Kiyoko M. Gotanda , ^{9,10} Lynn Govaert , ¹¹ Lindsay S. Miles , ¹ L. Ruth Rivkin , ^{12,13} Kristin M. Winchell , ¹⁴ Kristien I. Brans , ¹⁵ Cristian Correa , ¹⁶ Sarah E. Diamond , ¹⁷ Ben Fitzhugh , ¹⁸ Nancy B. Grimm , ¹⁹ Sara Hughes , ²⁰ John M. Marzluff , ²¹ Jason Munshi-South , ²² Carolina Rojas , ²³ James S. Santangelo , ¹² Christopher J. Schell , ²⁴ Jennifer A. Schweitzer , ²⁵ Marta Szulkin , ²⁶ Mark C. Urban , ²⁷ Yuyu Zhou , ⁸ and Carly Ziter , ²⁹

Research on the evolutionary ecology of urban areas reveals how human-induced evolutionary changes affect biodiversity and essential ecosystem services. In a rapidly urbanizing world imposing many selective pressures, a time-sensitive goal is to identify the emergent issues and research priorities that affect the ecology and evolution of species within cities. Here, we report the results of a horizon scan of research questions in urban evolutionary ecology submitted by 100 interdisciplinary scholars. We identified 30 top questions organized into six themes that highlight priorities for future research. These research questions will require methodological advances and interdisciplinary collaborations, with continued revision as the field of urban evolutionary ecology expands with the rapid growth of cities.

Emerging challenges in urban evolutionary ecology

Urbanization (see Glossary) is altering ecosystems at a global scale and challenging the future persistence of biodiversity [1–3]. Specifically, demographic predictions suggest that by 2050, urban areas will be home to two-thirds of the human population [4]. With this rapid urbanization, habitats will be irrevocably changed and natural resource extraction will accelerate. These impacts create complex **eco-evolutionary dynamics** that emerge at the intersection of social, political, and cultural systems and technological infrastructure within and among urban areas [5,6]. The field of urban evolutionary ecology has received increasing attention from diverse disciplines to address not only how urbanization changes fundamental evolutionary and ecological processes but also how a more integrated research agenda on evolutionary ecology can reveal the potential feedback of these changes on human and ecosystem health across spatial and temporal scales [7–9]. Because cities share environmental properties that are distinct from other ecosystems, they also provide an ideal system for answering outstanding questions in evolutionary ecology.

Multiple reviews of urban evolutionary ecology research call for developing a shared agenda and guidelines for collaborative initiatives in funding and policy [6,10,11]. Timing is important, as the results of these guidelines will not only shed light on current issues in urban ecosystems but also provide a forward-looking perspective from this burgeoning field relevant to addressing and solving urban problems emerging now and in the future. The current study applied a formalized horizon-scanning protocol (Box 1), which used a survey of interdisciplinary expert opinions (Box 2) to

Highlights

The impact of urbanization on biodiversity has been well documented, yet research into the complex dynamics of ecological and evolutionary processes in urban areas is still in its infancy.

When novel research challenges emerge, a horizon scan exercise is an integrated approach that brings together global interdisciplinary-minded individuals to identify future research questions that can influence new collaborations and funding agenda.

Our horizon scan identified 30 questions for future research in urban evolutionary ecology covering themes in fundamental ecological and evolutionary processes, temporal and spatial scales, sustainability, climate change, sociopolitical and ethical considerations, and innovation in technology.

¹Center for Biological Data Science, Virginia Commonwealth University, Richmond, VA 23284, USA ²Department of Urban Design and Planning, University of Washington, Seattle, WA 98195, USA ³School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195. USA ⁴Applied Wildlife Ecology Lab, Yale School of the Environment, Yale University, New Haven, CT 06511, USA ⁵Department of Biology, Redpath Museum, McGill University, Montreal, QC H3A 0C4. Canada ⁶Department of Biology, Centre for Urban Environments, University of Toronto Mississauga, Mississauga, ON L5L 1C6, Canada

Trends in Ecology & Evolution, Month 2022, Vol. xx, No. xx https://doi.org/10.1016/j.tree.2022.07.012 1
© 2022 Elsevier Ltd. All rights reserved.



identify future challenges ranging across a spectrum of technological, environmental, and sociopolitical dimensions. Here, we present the six broad themes in urban evolutionary ecology (Figure 1) that encompass the 30 top questions that emerged from the horizon scan (Table 1 and Figure 2).

Fundamental processes and mechanisms

Studies increasingly show that cities across the globe are altering fundamental ecological and evolutionary processes. While studied primarily in isolation, these processes may interact in complex ways within cities, creating unique selection pressures and **eco-evolutionary feedbacks** [5]. For example, plant–herbivore and predator–prey interactions [12,13] are altered by urbanization, leading to phenotypic changes in traits ranging from morphological, behavioral, physiological, and life history [14,15]. Urban environments likely also modify sexual selection and thus generate novel mating strategies and preferences [16], which could further shape population dynamics and interactions with other species. However, it is unclear whether these traits are either **exaptations** or novel adaptations to the urban environment [10,17]. In fact, although most adaptations arise from selection on standing genetic variation [18], we know little about how cities influence novel mutation or their long-term effects on organism health [19], despite the importance of mutation in contributing to evolutionary potential.

Understanding the role of urbanization for evolutionary ecology requires disentangling how landscape changes, temporal change in human-nature interactions, and past ecological and evolutionary legacies influence present-day dynamics. Over longer time periods, organismal changes in response to evolutionary processes altered by humans may ultimately lead to speciation, although it is unknown how common speciation is in cities or the conditions that may favor it in urban areas [20]. Anthropogenic habitat modification has altered ecological and evolutionary processes for at least the past 50 000 years, resulting in species that rely on anthropogenic resources [21], including commensals and domesticated species [22]. In fact, domesticated animals, such as pet cats (*Felis catus*), have severe negative effects on endemic wildlife [23], yet the long-term evolutionary consequences of these predator–prey interactions in cities are not well studied. Studies of these organisms can give

Box 1. Horizon scan protocol

Our horizon scan used a modified Delphi technique [96], consistent with previous horizon scans [97,98]. The main objective of this technique is to conduct iterative evaluations of survey responses (Figure 1). From an international research network on urban eco-evolutionary dynamics (see 'Acknowledgments'), 24 individuals established the 'core' group, with an additional five invited from outside this network to balance backgrounds in ecology, evolutionary biology, environmental science, anthropology, urban planning, policy, and sustainability. The core group (29 authors here) oversaw the horizon-scanning protocol, which generated the survey responses, and provided synthesis for a publication. The survey (Table S1 in the supplemental information online) was designed for participants to provide questions in ecology and evolutionary biology in urban areas for future research directions. The survey also collected voluntary demographic information, anonymized through statistical aggregation, so that responses could not be tied to individual participants.

In September 2020, the survey was emailed to 420 potential participants from 33 countries representing six continents, with responses from 100 participants from 25 countries (Table S2 in the supplemental information online). Our protocol (Figure I) identified potential survey participants from review of the literature on urban ecology and evolutionary biology, with care taken to balance diversity in demographics (e.g., career stage, geography, and discipline) when possible. The 100 respondents provided over 700 questions, which were curated for clarity (e.g., redundancies removed) by a team of seven core individuals. A curated list of 75 questions was presented to the 29 core participants via email to score from 1 (highest) to 5 (lowest) for each of 'novelty' and 'importance' in urban ecology and evolutionary biology. Input on 'novelty' reflected areas not investigated or not thoroughly investigated (e.g., across diverse taxa, geographic areas), whereas, 'importance' reflected areas that, while possibly not novel, are highly valued in the literature and need attention. A 3-day virtual workshop was held in November 2020 for several rounds of small break-out groups and anonymous voting among the 29 core participants in discussing and editing the submitted questions to reach a consensus. A list of 30 questions emerged that were ranked 1–30 by each core participant post-workshop. Consistent with previous horizon scans, the median rank for each question was used to determine the final list (see Table 1 and Figure 2 in main text). After the final ranking, feedback was collected from the core participants to bin and summarize the questions into 'themes' that focused the research directions.

⁷Department of Biology and Center for Computational & Integrative Biology, Rutgers University–Camden, Camden, NJ 08103, USA

⁸CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Montpellier, France

⁹Department of Biological Sciences,

Brock University, St. Catharines,

ON L2S 3A1, Canada

¹⁰Département de Biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

¹¹Leibniz Institute of Freshwater Ecology and Inland Fisheries, 12587 Berlin, Germany

¹²Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON L5L 1C6, Canada

¹³Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2. Canada

¹⁴Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA

¹⁵Department of Biology, Katholieke Universiteit Leuven, 3000 Leuven, Belgium

¹⁶Instituto de Conservación Biodiversidad y Territorio, Centro de Humedales Río Cruces, Universidad Austral de Chile, Valdivia, 5090000, Chile

¹⁷Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA

¹⁸Department of Anthropology, University of Washington, Seattle, WA 98195, USA ¹⁹School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

²⁰School for Environment and Sustainability, University of Michigan,

Ann Arbor, MI 48109, USA ²¹School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA

²²Louis Calder Center & Department of Biological Sciences, Fordham University, Armonk, NY 10504, USA

²³Instituto de Estudios Urbanos y Territoriales, Centro de Desarrollo Sustentable CEDEUS, Pontificia

Universidad Católica de Chile, El Comendador 1916, Providencia,

7500000, Santiago, Chile

²⁴Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA 94720, USA

²⁵Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37917, USA

²⁶Centre of New Technologies, University of Warsaw, Banacha 2c, 02-097, Warsaw, Poland

²⁷Department of Ecology and Evolutionary Biology & Center of Biological Risk,





us a glimpse into the process of organismal change across anthropogenic environments, in some cases leading to populations that are reproductively isolated from their nonurban counterparts [24].

Another focus is the extent to which urbanization has increased or decreased natural connectivity within and among ecosystems, and whether the resulting evolutionary effects can be generalized across cities and taxa [25]. It is unclear how urban drivers (e.g., social, environmental, ecological, and technological) interact to alter population connectivity, and what impact this has on population size and genetic diversity [26], as maintained by source–sink dynamics between urban and nonurban areas [27]. Lastly, incorporating human-mediated gene flow into general models of evolutionary ecology is critical for understanding demography, genetic diversity, and ultimately evolutionary potential [28].

Spatial and temporal scales of drivers and responses

The fast development of cities and their fine-scaled heterogeneity [29] can lead to local selection pressures that create rapid and microgeographic adaptations. This premise suggests that cities are hotspots for evolution, with the potential for novel species interactions that further drive rapid ecological and evolutionary change [25,30]. However, the extent to which cities alter ecological



Box 2. Backgrounds of survey participants

The demographic and disciplinary backgrounds of the 100 survey participants are likely to influence their responses. Although the number of countries from Europe was more represented compared with other continents, more than half of the survey participants came from North America (Table S2 in the supplemental information online). Six countries and 12% of survey participants are from the Global South. Although this sample is geographically biased with respect to total population distribution, it does reflect the distribution of current researchers [83]; researchers from the Global North dominate the field of urban ecology [99]. Although survey participants may reflect the current research domain, they do not represent the overall urban landscape, especially in developing nations. This potential bias could influence the core participants' opinions of research at local scales. For example, while the theme on innovations in technology and methodology discusses research likely to be impactful at a global scale, how it may solve specific problems between and even within areas of North America and Africa was not discussed. Future research directions and their alignment with challenges across sociopolitical structures need to involve greater representation in decision-making [8], as discussed in the 'Concluding remarks' section. Our horizon scan prioritized this issue, as the top-ranked question was focused on social inequalities and their impact on eco-evolutionary dynamics within cities (see Table 1 and Figure 2 in main text).

The high variance associated with the ranked questions (see Figure 2 in main text) reflects the diverse disciplinary backgrounds of survey participants. It is not surprising that just over 90% of the participants used the words 'ecology' or 'evolution' to describe their expertise (Table S3 in the supplemental information online). However, while a very small number of participants used additional descriptors for 'evolution' (e.g., 'evolutionary geneticist'), over half of the participants who used 'ecologist' used at least one, and some as many as three additional descriptors (e.g., 'urban/wetland/ecosystem ecologist). Finally, while 22% of the participants used the word 'urban' to define their expertise, the vast majority of this latter group describe themselves as 'urban ecologists/evolutionary ecologists', and never as 'urban evolutionary biologists' alone (Figure S1 in the supplemental information online). These results reflect a growing and emerging discipline previously dominated by urban ecologists [10]. Just as evolutionary biologists, who were not initially focused on urban ecosystems, have entered the field more recently, we anticipate further diversification of the field – with other disciplines, such as engineering, social sciences, and medicine, pursuing the research directions outlined here.

niches and increase evolutionary potential [28,31] is an empirical question that, once answered, could uncover the scale dependency of both drivers and responses.

The extent to which urban ecological and evolutionary dynamics occurring at various spatial and temporal scales are species and city specific is still relatively unknown. Variable patterns (e.g., spatial and temporal) of urbanization can reduce or increase colonization rates, genetic drift, and gene flow, which might determine the relative contribution of adaptive evolution and species sorting shaping local communities [5]. For example, high human-mediated dispersal of some species may counteract local adaptation to cities, whereas others may adapt quickly at fine scales [32,33]. In addition, factors such as age, history, and the pace of urban development may determine the magnitude of evolutionary responses, such as the strength and direction of selection [34,35]. Empirical studies that collect comparable data within and among cities with similar and different histories are necessary to relate cities' spatial and temporal heterogeneity to evolutionary responses [36].

Evolution in natural systems can dampen ecological variation in time and space [37,38]. For example, adaptive evolution can dampen population cycling through time, and local adaptation to harsh environments can homogenize population abundances across spatially heterogeneous landscapes. However, the extent to which evolution stabilizes and homogenizes temporal and spatial heterogeneity in the urban environment is unexplored, although such dampening mechanisms could be counted as an important service to humans when they buffer adverse ecosystem impacts that occur in time or space. Although ecological features can be homogenized across cities globally [36,39], it is unclear whether selective pressures within cities are similar and if convergence in the evolutionary responses across cities is predictable.

Sustainability, health, and well-being

Cities are an important frontier in achieving future global biodiversity and sustainability goals [40]. In particular, the United Nations Sustainable Development Goals (SDGs), specifically SDG 11 for

Glossary

Autonomous systems: include a wide variety of self-learning technologies that can physically operate in environments with minimal human supervision.

Eco-evolutionary dynamics:

interactions between ecological and evolutionary processes that play out on contemporary time scales.

Eco-evolutionary feedbacks: subset of eco-evolutionary dynamics where ecological change causes evolutionary change, which then feeds back to cause additional evolutionary change.

Environmental DNA: genetic material obtained directly from environmental samples, for example, soil, air, sediment, and water.

Exaptations: traits evolved for one role, through either selection or neutrality (i.e., for no function at all in the latter case), and then later 'co-opted' for their current role.

Smart city: approaches that combine information and communication technology to enable citizens to respond more effectively to evolving changes in the urban environment.

Urbanization: the process of converting undeveloped land into cities

and towns where humans become highly concentrated.





Trends in Ecology & Evolution

Figure 1. Emerging research themes in urban evolutionary ecology. Six themes were identified that summarized the 30 questions ranked by core participants (see Box 1 for methods). Keywords reflecting the questions are shown circling a visual reflection of each of the six themes (see Table 1 for the list of questions and their theme names). Abbreviation: SDGs, Sustainable Development Goals.



Table 1. Ranked questions and their themes for research in urban evolutionary ecology

Themes	Questions	Rank
Fundamental processes and mechanisms (Processes)	What are the effects of urbanization on somatic and gametic mutation rates, and how do we mitigate elevated mutation rates in cities?	10
	Under what conditions will urbanization promote or impede speciation, and how does urbanization impact speciation rates?	11
	How does urbanization influence the (co)evolution of species interactions, and do species interactions exacerbate or ameliorate selective pressures associated with urbanization?	13
	To what extent has urbanization led to the evolution of new commensal species, including those that are self-domesticating?	21
	How can cities enhance global eco-evolutionary potential by altering intraspecific and interspecific interactions?	23
	How do urban areas act as genetic sources or sinks in preserving biodiversity?	27
	How is sexual selection altered by urbanization?	30
Spatial and temporal scales of drivers and responses (Scales)	What is the relative importance of evolution in cities in affecting the magnitude and direction of ecological dynamics and patterns, especially compared with nonevolutionary drivers in cities?	6
	What is the spatial and temporal scale of eco-evolutionary dynamics, including in deep time, and how does it differ between urban habitats compared with other nonurban habitats?	8
	How does rapid evolution differ between established and newly developing cities?	17
	What are the relative strengths of individual and interactive effects of drivers of evolution in cities, both genetic and cultural, and do they vary among taxa and across cities?	18
	How does heterogeneity both within the urban environment and between urban and nonurban environments influence eco-evolutionary dynamics?	20
	To what extent can eco-evolutionary signatures that we observe in cities tell us about eco-evolutionary trends at the global scale?	28
Sustainability, health, and well-being (Sustainability)	How do pathogens that cause human disease adapt to the urban environment and how does rewilding and restoration alter our ability to fight disease outbreaks?	2
	How can we harness urban microbiomes for human well-being, for improved soil health and productivity, and to create more sustainable approaches to inform eco-evolutionary dynamics in terrestrial and aquatic systems?	9
	How can eco-evolutionary understanding contribute to the implementation of the Sustainable Development Goals (SDGs), and how will the SDGs influence eco-evolutionary dynamics in cities in different global contexts?	15
Impacts and interactions with climate change (Climate change)	How will climate change and urbanization interact to alter eco-evolutionary dynamics in terms of extreme weather effects on biodiversity and societal consequences in the past and future?	5



Table 1. (continued)

Themes	Questions	Rank
	What is the effect of urbanization on ecology and evolution in aquatic environments, especially in the context of artificial aquatic infrastructure such as harbors and submersion of cities due to rising sea levels?	16
Politics, governance, culture, their interactions, and their ethical considerations (Sociopolitical)	What is the magnitude of effect of social inequality and systemic oppression in driving ecological and evolutionary dynamics in cities, and how do we ethically and empirically quantify and test this?	1
	To what extent does variation among political systems and governance predict evolutionary responses to, and biodiversity of, urban environments?	3
	How does both biological and cultural evolution in humans differ in the past, present, and future, and how does that human evolution feed back to affect the development of cities and cultures?	7
	How does expanding/enhancing empathy for nature and blue-green infrastructure alter eco-evolutionary processes in urban environments?	14
	How do human diets and behavior impact food webs in urban environments that alter eco-evolutionary dynamics?	19
	How can we more effectively collaborate across disciplines and with communities to incorporate ethics and human cultural sensitivity into the study of urban evolutionary ecology and the implementation and dissemination of research findings?	24
	What role or responsibility do we have as humans for seeking to influence urban eco-evolutionary outcomes?	25
	What role does human society and culture, underpinning the preference and artificial selection for novel traits in pets and ornamentals, have on evolutionary ecology within and among cities?	26
Innovation in technology and methodology (Technology)	What role do genetic manipulations, including genetic engineering, gene editing, and artificial selection, have on the evolution of organisms including humans, and their impact on society and the urban environment?	4
	Will there be synthetic organisms (e.g., drones, robots) that are capable of adapting to the urban environment independent of humans, and if so, how will they reshape the natural environment?	12
	How can automated, high-throughput data collection in cities be used as input to artificial intelligence (AI) to enable discovery and implementation of nature-based solutions?	22
	How can mathematical theory and data synthesis be used to predict urban eco-evolutionary feedbacks?	29

sustainable cities and communities, provides an opportunity to link urban evolutionary ecology research with policies to mitigate environmental crises and promote ecosystem health [4]. For example, cities could serve as reservoirs for biodiversity that benefit people and nature while also supporting ecosystem functions, such as decomposition, nutrient recycling, and carbon storage. These processes involve both ecological and evolutionary mechanisms that underpin ecosystem services such as urban sanitation, water purification, microclimate modulation, and pollination – all indispensable to well-being [41].

CellPress



Trends in Ecology & Evolution

Figure 2. Rank and variance of questions with their themes for research in urban evolutionary ecology. Boxplots reflect the median ranks of the 30 questions by the 29 core participants (Table 1). Box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from the 25th and 75th percentiles, and outliers are represented by dots.

Research that integrates evolutionary ecology with urban development creates a direct link between urban eco-evolutionary dynamics and human and ecosystem health. As the coronavirus disease 2019 (COVID-19) pandemic demonstrates, the concentration of humans in cities and the interconnectedness of cities can facilitate the spread and evolution of certain diseases [42] and pose an immense challenge to sustainable global health systems. It is imperative to understand how social heterogeneity and the design of urban landscapes influences the spread of diseases and their vectors, as well as other established health risks such as urban heat and elevated pollution [43]. Urban greening can help cool cities and reduce pollution-related health issues [44], while also maintaining biodiversity and ecosystem functioning [45]. Related, rewilding projects typically

CelPress

focus on ecological processes, yet more research is needed to investigate how they influence evolutionary processes and their effects on ecology and human health. For example, green spaces can reduce gene flow in species, which are well suited for urban environments (e.g., brown rats, *Rattus norvegicus*) and that spread human pathogens [46].

Another link between urban evolutionary ecology and ecosystem health may be through the understudied world of urban microbiomes. While some soil microbial taxa show reduced abundance and richness in response to urbanization [47], this effect is not universal [48]. Signatures of urbanization have also been detected in animal microbial communities [49], while human microbiomes are known to be less diverse in cities than in rural habitats, with possible repercussions for human autoimmune disorders [50]. However, it is unclear how cities impose selection on humans and other species that is mediated through the microbiome. Research into the influence of urban pollution on local microbial adaptation is needed to understand how to manage, or potentially rewild [51], a range of urban microbial communities for ecosystem health.

Impacts and interactions with climate change

Synergistic effects of urbanization and climate change simultaneously impact organisms, including humans, with complex feedbacks between the two. For example, extreme weather events are exacerbated by both climate change [52] and urbanization [53], with little understanding of whether the effects will be additive or multiplicative [54,55]. As these intensifying disturbances become more common, they are likely to influence genetic diversity [56] and exert strong selective pressures on urban organisms [7]. Thus, understanding the resulting short- and long-term ecological resilience of urban communities to increasingly frequent extreme weather events will require investigations focused on urban long-term studies.

We especially point to the need for research on the evolution of urban pests and diseases, as well as their interactions with hosts and vectors. For example, the invasive Asian tiger mosquito (*Aedes albopictus*), a known vector of chikungunya and dengue viruses [57], is predicted to invade all European countries because it benefits from warming conditions and is well adapted to the urban environment. Research might ask which invasive species possess adaptations for warmer urban conditions and assess the evolutionary potential for novel adaptation to those conditions. Insight sought through historical and archeological analyses could likewise explore novel ecological and evolutionary relationships between humans, pests, and diseases during past eras of rapid climate change [58]. Such retrospective and contemporary research could then inform scenarios and models to better anticipate the evolution and spread of pests and diseases in the urban matrix under various projections of future climate conditions.

Most studies of evolutionary ecology in cities focus on terrestrial organisms, yet changes are also likely in aquatic organisms, particularly in response to changing flow patterns in urban streams [59]; changing temperature in urban streams, ponds, and lakes [60]; and rising sea levels in coastal areas [61]. The last has been the least studied and is therefore emphasized here. In particular, rising sea levels will lead to inundation farther inland and therefore increased salinization of coastal wetlands. It will be important to determine the extent to which freshwater-resident species are able to adapt to those changing conditions. For example, species that have developed adaptations to increased road salt [62] might also have a tolerance to increased sea-water inundation.

Politics, governance, culture, their interactions, and their ethical considerations

Political systems and governance arrangements guide urban growth and development in highly variable ways [63,64] that can shape urban evolutionary ecology. These arrangements can determine the spatial distribution of environmental burdens and access to amenities, exacerbating social

CellPress

and economic inequity and oppression [65]. For example, housing and land-use policies have resulted in green spaces being disproportionately located in affluent and primarily white areas within many global cities [8,66,67]. Thus, investigations into how institutionally entrenched distributions of urban land-use inequities may influence ecological properties (e.g., resource distribution or microclimates) and evolutionary change are a high research priority.

Another focus is understanding urban ecological and evolutionary dynamics in cultural contexts across space and time. Specifically, the historical characteristics of place, people, culture, and history might shape present ecological and evolutionary processes [68] and offer input to models that make more realistic future predictions [69]. We must also differentiate between biological evolution and cultural evolution as they encompass different traits, underlying mechanisms and units of inheritance, such that cultural evolution can proceed at faster rates than biological evolution [70]. For example, increasing economic prosperity in cities often results in changing nutritional land-scapes that produce greater quantities of urban food waste. Such waste can, in turn, influence wildlife behavior and population structure when animals expand into urban habitats and alter their feeding behaviors and diets [71]. While urban evolutionary dynamics have generally been understood according to biological traits, integrating cultural niche construction into urban evolutionary models is needed to conceptualize urban ecosystems from historical and contemporary perspectives [72,73].

Although ethics can directly influence research decisions in urban evolutionary ecology, there is also the potential for ethical considerations to play a role in urban eco-evolutionary outcomes. One often-overlooked consideration is the moral responsibility of researchers and the role of empathy. For example, how proenvironmental behaviors have developed over time to influence policy that shapes urban evolutionary ecology could be thought of as a moral and motivational dilemma [74]. However, decisions tied to urban areas – such as the magnitude of recycling and composting, programs such as food sharing or needle exchange, or the distribution of services such as homeless care, community clinics, or street cleanliness – may have downstream implications for organisms by altering the adaptive landscape. For example, urban waste recycling practices generate potentially unique pollutants, such as microplastics, with yet unknown long-term selective pressures linked to water, air, and soil [75]. Interdisciplinary collaborations will help inform how political, institutional, social, cultural, and ethical factors are not only considered in research, but how they play a direct role in shaping how processes of urban evolutionary ecology unfold and interact.

Innovation in technology and methodology

Advancements in technology and methodology provide unprecedented capacity to enable real-time monitoring and data analysis for previously unanswered questions in urban evolutionary ecology. Genomic, transcriptomic, and epigenomic tools have provided not only insights into the effects of urbanization on evolution [76–79] but also the raw materials for downstream experiments. One example is how genetic technology has been tested for pest control of disease-carrying organisms [80,81], where manipulating genetic material could shift the evolution and adaptive landscape of endangered native organisms and their communities [82]. Another example comes from the expected increase of **autonomous systems** and robotics deployed in urban areas in the coming decades [83], leading to applications such as weed and pest control that may enhance or hinder plant-pollinator systems [84]. With the introduction of new artificial agents come unknown consequences and the need to characterize the selection regimes that emerge as a natural response [85].

A related emerging issue is the abundance of data – both in volume and types – newly generated to describe urban ecosystems. One solution may be through **smart city** approaches, which have



traditionally focused on enhancing economic efficiency and quality of life for humans [86]. For example, by integrating evolutionary ecology with engineering and social science in the design and connectivity of green infrastructure [87,88], we can increase gene flow and population connectivity while also attaining SDGs in enhancing nature's contribution to people within cities. Just as the growing field of 'precision medicine' is using artificial intelligence (AI) methodology to find unique patterns among human genomes, environments, behavior, and social context [89], the same AI approaches can make sense of complex systems in cities composed of variable environments in space and time, pollutants/mutagens, genomic structures, and phylogenetic relationships. For example, these approaches can be used to monitor biodiversity from **environmental DNA** as well as predict epidemics from wastewater [83]. The future challenge largely rests in finding ways of translating the massive amounts of data into impactful and just strategies for management (of species, communities, soil, crops, urban ecosystems), application (education, infrastructure), and implementation (policies) that will feed back on nature within cities.

Concluding remarks

In this first horizon scan for urban evolutionary ecology research, a core team of diverse researchers prioritized over 700 research questions into 30 key questions and grouped them into six major themes. These themes highlight the important topics and breadth of research directions that are priorities for future investigation. For example, fundamental processes such as species interactions and mutation rates might be uniquely affected within and among urbanized areas. Additionally, eco-evolutionary feedbacks could have applied implications in the context of climate change and sustainability given the global extent of rapid urbanization and its local and regional impacts [65]. We anticipate that innovations in technology and methodology in addressing large and diverse datasets will emerge from these research directions. In addition, it will be vital to not only integrate ethical considerations into these research areas but also evaluate how social and political biases associated with race, culture, and religion directly feed back into urban evolutionary ecology outcomes.

Because cities are globally distributed across diverse cultures and histories, this study is a reminder of the need for international collaborations to rebalance our perspective [64]. For example, regions of China and the former Soviet republics are urbanizing rapidly, yet knowledge of the ecological and evolutionary dynamics of those landscapes is limited [90]. Collaboration between scholars from the Global South and Global North is necessary, and evolutionary ecologists in the North (especially English-language writers) need to take better stock of research conducted in other parts of the world and published in other languages [91]. Because cities are best viewed as social–ecological–technological systems [92], interdisciplinary collaborations will help address fundamental questions in urban evolutionary ecology while ensuring that cities develop in ways that benefit both humans and other organisms.

There are multiple challenges to realizing these research priorities. Accounting for heterogeneity among cities is one such challenge, as are the needs to consider historical contexts and sociopolitical, economic, and racist legacies, even when studying evolutionary ecology. This means confronting financial, social, and geographic barriers to research, particularly in regions with limited resources and infrastructure. Horizon scans are designed to prioritize future research directions, yet we also must recognize research of high importance today. For example, this scan highlighted current global issues, such as social injustice and the COVID-19 pandemic, and their potential scaled effects on urban evolutionary ecology. In this respect, we recognize the need to constantly revise these research priorities to changes in the global landscape.

Despite the challenge, research in urban evolutionary ecology offers opportunities for advancing fundamental and applied science. First, the concentration of diverse people and non-human biota



in urban-built environments facilitates new collaborations to incorporate insights from disciplines across the life and social sciences, as well as physical sciences (e.g., climate scholars) and humanities (e.g., architects and historians) [6,8,93]. Second, while frequent and ongoing management actions in cities provide challenges to urban research [94], cities may also offer future opportunities for designing field manipulations that are challenging in natural areas. For example, new parks might alternate between connected and unconnected patches to test hypotheses about connectivity without needing to alter rural habitats. Third, research in cities offers the potential of new-found socioecological, and not just biological, discoveries to enhance human well-being and improve sociopolitical issues in urban settings where the majority of people are projected to reside in the coming decades [95]. Ultimately, these opportunities could expose city dwellers to the excitement of evolutionary ecology, such as through community science activities, and encourage them to pursue careers in these disciplines.

Acknowledgments

This study is a collaborative effort of the National Science Foundation Research Coordination Network (RCN): Eco-Evolutionary Dynamics in an Urban Planet: Underlying Mechanisms and Ecosystem Feedbacks (DEB 1840663). The study protocol and survey were approved in advance by the Institutional Review Board at the University of Washington (ID# STUDY00010723).

Declaration of interests

No interests are declared.

Supplemental information

Supplemental information associated with this article can be found online https://doi.org/10.1016/j.tree.2022.07.012.

References

- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260
- McDonald, R.I. et al. (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141, 1695–1703
- Alberti, M. (2015) Eco-evolutionary dynamics in an urbanizing planet. *Trends Ecol. Evol.* 30, 114–126
- United Nations, Department of Economic and Social Affairs, Population Division (2019) World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420), United Nations, New York
- Alberti, M. et al. (2020) The complexity of urban eco-evolutionary dynamics. *BioScience* 70, 772–793
- 6. Des Roches, S. et al. (2021) Socio-eco-evolutionary dynamics in cities. Evol. Appl. 14, 248–267
- 7. Johnson, M.T.J. and Munshi-South, J. (2017) Evolution of life in urban environments. *Science* 358, eaam8327
- Schell, C.J. *et al.* (2020) The ecological and evolutionary consequences of systemic racism in urban environments. *Science* 369, eaay4497
- 9. Szulkin, M. et al. (2020) Urban Evolutionary Biology (1st edn), Oxford University Press
- Rivkin, L.R. et al. (2019) A roadmap for urban evolutionary ecology. Evol. Appl. 12, 384–398
- Diamond, S.E. and Martin, R.A. (2021) Evolution in cities. *Annu. Rev. Ecol. Syst.* 52, 519–540
- Miles, L.S. *et al.* (2019) Urbanization shapes the ecology and evolution of plant-arthropod herbivore interactions. *Front. Ecol. Evol.* 7, 310
- Brans, K.I. *et al.* (2021) Cryptic eco-evolutionary feedback in the city: urban evolution of prey dampens the effect of urban evolution of the predator. *J. Anim. Ecol.* 91, 514–526
- 14. Gotanda, K.M. (2020) Human influences on antipredator behaviour in Darwin's finches. J. Anim. Ecol. 89, 614–622
- Santangelo, J.S. *et al.* (2020) Predicting the strength of urban-rural clines in a Mendelian polymorphism along a latitudinal gradient. *Evol. Lett.* 4, 212–225
- Halfwerk, W. et al. (2019) Adaptive changes in sexual signalling in response to urbanization. Nat. Ecol. Evol. 3, 374–380

- McDonnell, M.J. and Hahs, A.K. (2015) Adaptation and adaptedness of organisms to urban environments. *Annu. Rev. Ecol. Syst.* 46, 261–280
- Barrett, R. and Schluter, D. (2008) Adaptation from standing genetic variation. *Trends Ecol. Evol.* 23, 38–44
- Marchetti, F. et al. (2020) A return to the origin of the EMGS: rejuvenating the quest for human germ cell mutagens and determining the risk to future generations. *Environ. Mol. Mutagen.* 61, 42–54
- Halfwerk, W. (2021) How should we study urban speciation? Front. Ecol. Evol. 8, 573545
- Sullivan, A.P. et al. (2017) Human behaviour as a long-term ecological driver of non-human evolution. Nat. Ecol. Evol. 1, 0065
- 22. Ravinet, M. et al. (2018) Signatures of human-commensalism in the house sparrow genome. Proc. R. Soc. B 285, 20181246
- Legge, S. et al. (2020) We need to worry about Bella and Charlie: the impacts of pet cats on Australian wildlife. Wildl. Res. 47, 523–539
- Booth, W. et al. (2015) Host association drives genetic divergence in the bed bug, *Cimex lectularius*. Mol. Ecol. 24, 980–992
- 25. Miles, L.S. et al. (2019) Gene flow and genetic drift in urban environments. *Mol. Ecol.* 28, 4138–4151
- Gustafson, K.D. et al. (2019) Genetic source-sink dynamics among naturally structured and anthropogenically fragmented puma populations. Conserv. Genet. 20, 215–227
- Tassone, E.E. *et al.* (2021) Evolutionary stability, landscape heterogeneity, and human land-usage shape population genetic connectivity in the Cape Floristic Region biodiversity hotspot. *Evol. Appl.* 14, 1109–1123
- Wood, Z.T. et al. (2021) The importance of eco-evolutionary potential in the Anthropocene. *BioScience* 71, 805–819
- Zhou, W. et al. (2017) Shifting concepts of urban spatial heterogeneity and their implications for sustainability. *Landsc. Ecol.* 32, 15–30
- Gallo, T. *et al.* (2019) Urbanization alters predator-avoidance behaviours. *J. Anim. Ecol.* 88, 793–803
- Alberti, M. et al. (2017) Global urban signatures of phenotypic change in animal and plant populations. Proc. Natl. Acad. Sci. U. S. A. 114, 8951–8956
- 12 Trends in Ecology & Evolution, Month 2022, Vol. xx, No. xx

- Combs, M. et al. (2018) Urban rat races: spatial population genomics of brown rats (*Rattus norvegicus*) compared across multiple cities. Proc. R. Soc. B 285, 20180245
- Johnson, M.T.J. *et al.* (2018) Contrasting the effects of natural selection, genetic drift and gene flow on urban evolution in white clover (*Trifolium repens*). *Proc. R. Soc. B* 285, 20181019
- Ossola, A. *et al.* (2021) Valuing the role of time in urban ecology. *Front. Ecol. Evol.* 9, 620620
- Wei, X. et al. (2021) Long-term urbanization impacts the easterm golden frog (*Pelophylax plancy*) in Shanghai City: demographic history, genetic structure, and implications for amphibian conservation in intensively urbanizing environments. *Evol. Appl.* 14, 117–135
- Santangelo, J.S. et al. (2022) Global urban environmental change drives adaptation in white clover. Science 375, 1275–1281
- Kinnison, M.T. et al. (2015) Cryptic eco-evolutionary dynamics: cryptic eco-evolutionary dynamics. Ann. N. Y. Acad. Sci. 1360, 120–144
- Urban, M.C. *et al.* (2020) Evolutionary origins for ecological patterns in space. *Proc. Natl. Acad. Sci. U. S. A.* 117, 17482–17490
 Groffman, P.M. *et al.* (2017) Ecological homogenization of residence of the second sec
- dential macrosystems. *Nat. Ecol. Evol.* 1, 0191
- Arneth, A. et al. (2020) Post-2020 biodiversity targets need to embrace climate change. Proc. Natl. Acad. Sci. U. S. A. 117, 30882–30891
- Otto, I.M. et al. (2020) Social tipping dynamics for stabilizing Earth's climate by 2050. Proc. Natl. Acad. Sci. U. S. A. 117, 2354–2365
- Nuñez, M.A. et al. (2020) Invasion science and the global spread of SARS-CoV-2. Trends Ecol. Evol. 35, 642–645
- Douglas, I. (2012) Urban ecology and urban ecosystems: understanding the links to human health and well-being. *Curr. Opin. Environ. Sustain.* 4, 385–392
- Mei, P. et al. (2021) Air pollution, human health and the benefits of trees: a biomolecular and physiologic perspective. Arboric. J. 43, 19–40
- Lepczyk, C.A. et al. (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience* 67, 799–807
- Byers, K.A. et al. (2021) Using genetic relatedness to understand heterogeneous distributions of urban rat-associated pathogens. Evol. Appl. 14, 198–209
- Epp Schmidt, D.J. *et al.* (2017) Urbanization erodes ectomycorrhizal fungal diversity and may cause microbial communities to converge. *Nat. Ecol. Evol.* 1, 0123
- Reese, A.T. *et al.* (2016) Urban stress is associated with variation in microbial species composition — but not richness — in Manhattan. *ISME J.* 10, 751–760
- Danko, D. et al. (2021) A global metagenomic map of urban microbiomes and antimicrobial resistance. Cell 184, 3376–3393.e17
- 50. Blaser, M.J. (2014) The microbiome revolution. J. Clin. Invest. 124, 4162–4165
- Mills, J.G. *et al.* (2017) Urban habitat restoration provides a human health benefit through microbiome rewilding: the Microbiome Rewilding Hypothesis. *Restor. Ecol.* 25, 866–872
- AghaKouchak, A. et al. (2020) Climate extremes and compound hazards in a warming world. Annu. Rev. Earth Planet. Sci. 48, 519–548
- Yang, X. et al. (2017) Contribution of urbanization to the increase of extreme heat events in an urban agglomeration in east China. *Geophys. Res. Lett.* 44, 6940–6950
- Lahr, E.C. et al. (2018) Getting ahead of the curve: cities as surrogates for global change. Proc. R. Soc. B 285, 20180643
- Avilés-Rodríguez, K.J. et al. (2021) Phenotypic response to a major hurricane in Anolis lizards in urban and forest habitats. Biol. J. Linn. Soc. 133, 880–895
- Schmidt, C. et al. (2020) Continent-wide effects of urbanization on bird and mammal genetic diversity. Proc. R. Soc. B 287, 20192497
- Benedict, M.Q. et al. (2007) Spread of the tiger: global risk of invasion by the mosquito Aedes albopictus. Vector Borne Zoonotic Dis. 7, 76–85
- Penny, D. and Beach, T.P. (2021) Historical socioecological transformations in the global tropics as an Anthropocene analogue. *Proc. Natl. Acad. Sci. U. S. A.* 118, e2022211118
- Kern, E.M.A. and Langerhans, R.B. (2018) Urbanization drives contemporary evolution in stream fish. *Glob. Chang. Biol.* 24, 3791–3803

- Brans, K.I. et al. (2018) Urban hot-tubs: local urbanization has profound effects on average and extreme temperatures in ponds. Landsc. Urban Plan. 176, 22–29
- Tully, K. et al. (2019) The invisible flood: the chemistry, ecology, and social implications of coastal saltwater intrusion. *BioScience* 69, 368–378
- Hintz, W.D. and Relyea, R.A. (2019) A review of the species, community, and ecosystem impacts of road salt salinisation in fresh waters. *Freshw. Biol.* 64, 1081–1097
- 63. Elmqvist, T. et al. (2019) Sustainability and resilience for transformation in the urban century. *Nat. Sustain.* 2, 267–273
- 64. Hughes, S. and Hoffmann, M. (2020) Just urban transitions: toward a research agenda. *Wiley Interdiscip. Rev. Clim. Chang.* 11, e640
- 65. United Nations Environment Programme and United Nations Human Settlements Programme (UN-Habitat) (2021) Global Environment for Cities-GEO for Cities: Towards Green and Just Cities, UNEP, Nairobi
- Kronenberg, J. et al. (2020) Environmental justice in the context of urban green space availability, accessibility, and attractiveness in postsocialist cities. *Cities* 106, 102862
- Venter, Z.S. *et al.* (2020) Green Apartheid: urban green infrastructure remains unequally distributed across income and race geographies in South Africa. *Landsc. Urban Plan.* 203, 103889
- Tuckett, Q.M. et al. (2021) Domestication and feralization influence the distribution and phenotypes of escaped ornamental fish. *Biol. Invasions* 23, 1033–1047
- 69. Larmuseau, M.H.D. et al. (2019) A historical-genetic reconstruction of human extra-pair paternity. Curr. Biol. 29, 4102–4107.e7
- Milot, E. and Stearns, S.C. (2020) Selection on humans in cities. In Urban Evolutionary Biology (Szulkin, M. et al., eds), pp. 268–288, Oxford University Press
- 71. Lee, V.E. and Thornton, A. (2021) Animal cognition in an urbanised world. *Front. Ecol. Evol.* 9, 633947
- Marzluff, J.M. (2012) Urban evolutionary ecology. In Urban Bird Ecology and Conservation (Lepczyk, C.A. and Warren, P.S., eds), pp. 286–308, University of California Press
- Riede, F. (2019) Niche construction theory and human biocultural evolution. In *Handbook of Evolutionary Research in Archaeology* (Prentiss, A.M., ed.), pp. 337–358, Springer International Publishing
- Turaga, R.M.R. et al. (2010) Pro-environmental behavior: rational choice meets moral motivation. Ann. N. Y. Acad. Sci. 1185, 211–224
- Yang, H. et al. (2018) Waste management, informal recycling, environmental pollution and public health. J. Epidemiol. Community Health 72, 237–243
- Campbell-Staton, S.C. et al. (2020) Parallel selection on thermal physiology facilitates repeated adaptation of city lizards to urban heat islands. *Nat. Ecol. Evol.* 4, 652–658
- Miles, L.S. et al. (2020) Ovarian transcriptomic analyses in the urban human health pest, the Western black widow spider. *Genes (Basel)* 11, 87
- Perrier, C. et al. (2020) Adaptation genomics in urban environments. In Urban Evolutionary Biology (Szulkin, M. et al., eds), pp. 74–90, Oxford University Press
- Watson, H. et al. (2021) Urbanization is associated with modifications in DNA methylation in a small passerine bird. Evol. Appl. 14, 85–98
- Kyrou, K. et al. (2018) A CRISPR–Cas9 gene drive targeting doublesex causes complete population suppression in caged Anopheles gambiae mosquitoes. Nat. Biotechnol. 36, 1062–1066
- Buchthal, J. et al. (2019) Mice against ticks: an experimental community-guided effort to prevent tick-borne disease by altering the shared environment. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 374, 20180105
- Kumar, R. et al. (2019) CRISPR-based genome editing in wheat: a comprehensive review and future prospects. *Mol. Biol. Rep.* 46, 3557–3569
- Goddard, M.A. *et al.* (2021) A global horizon scan of the future impacts of robotics and autonomous systems on urban ecosystems. *Nat. Ecol. Evol.* 5, 219–230
- Potts, S.G. et al. (2018) Robotic bees for crop pollination: why drones cannot replace biodiversity. Sci. Total Environ. 642, 665–667
- Gulsrud, N.M. et al. (2018) 'Rage against the machine'? The opportunities and risks concerning the automation of urban green infrastructure. Landsc. Urban Plan. 180, 85–92



CellPress

Trends in Ecology & Evolution

- 86. Bibri, S.E. (2019) On the sustainability of smart and smarter cities in the era of big data: an interdisciplinary and transdisciplinary literature review. J. Big Data 6, 25
- MacIvor, J.S. et al. (2016) Phylogenetic ecology and the greening of cities. J. Appl. Ecol. 53, 1470–1476
- Zohrabi, N. et al. (2021) Towards sustainable food security: an interdisciplinary approach. In 2021 IEEE SmartWorld, Ubiquitous Intelligence & Computing, Advanced & Trusted Computing, Scalable Computing & Communications, Internet of People and Smart City Innovation (SmartWorld/SCALCOM/UIC/ATC/IOP/ SCI), pp. 463–470
- Álvarez-Machancoses, Ó. *et al.* (2020) On the role of artificial intelligence in genomics to enhance precision medicine. *Pharmacogenom. Pers. Med.* 13, 105–119
- Jiang, Y. et al. (2018) Urban pluvial flooding and stormwater management: a contemporary review of China's challenges and "sponge cities" strategy. Environ. Sci. Policy 80, 132–143
- Khelifa, R. *et al.* (2022) A solution for breaking the language barrier. *Trends Ecol. Evol.* 37, 109–112

- Markolf, S.A. et al. (2018) Interdependent infrastructure as linked social, ecological, and technological systems (SETSs) to address lock-in and enhance resilience. *Earth's Future* 6, 1638–1659
- McPhearson, T. *et al.* (2016) Advancing urban ecology toward a science of cities. *BioScience* 66, 198–212
- Aronson, M. *et al.* (2017) Biodiversity in the city: key challenges for urban green space management. *Front. Ecol. Environ.* 15, 189–196
 Kardan, O. *et al.* (2015) Neighborhood greenspace and health in
- a large urban center. *Sci. Rep.* 5, 11610 96, Mukheriee, N. *et al.* (2015) The Delohi technique in ecology and
- biological conservation: applications and guidelines. *Methods Ecol. Evol.* 6, 1097–1109
- Ricciardi, A. et al. (2017) Invasion science: a horizon scan of emerging challenges and opportunities. *Trends Ecol. Evol.* 32, 464–474
- Sutherland, W.J. et al. (2022) A horizon scan of global biological conservation issues for 2022. Trends Ecol. Evol. 37, 95–104
- Dobbs, C. *et al.* (2019) Urban ecosystem services in Latin America: mismatch between global concepts and regional realities? *Urban Ecosyst.* 22, 173–187