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## **A global horizon scan for urban evolutionary ecology**

Brian Verrelli, Marina Alberti, Simone Des Roches, Nyeema Harris, Andrew Hendry, Marc T.J. Johnson, Amy Savage, Anne Charmantier, Kiyoko Gotanda, Lynn Govaert, et al.

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Verrelli et al: A global horizon scan for urban evolutionary ecology

1 **Title: A global horizon scan for urban evolutionary ecology**

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50  
51 **Keywords:** urbanization, urban ecology, urban evolution, sustainability, socio-political, climate change

52 **Abstract**

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

61

62 **Emerging challenges in urban evolutionary ecology**

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

75 Multiple reviews of urban evolutionary ecology research call for developing a shared agenda and  
76 guidelines for collaborative initiatives in funding and policy [6,10,11]. Timing is important, as the results  
77 of these guidelines will not only shed light on current issues in urban ecosystems, but also provide a

78 forward-looking perspective from this burgeoning field relevant to addressing and solving urban problems  
79 emerging now and in the future. The current study applied a formalized horizon scanning protocol (Box  
80 1), which used a survey of interdisciplinary expert opinions (Box 2) to identify future challenges ranging  
81 across a spectrum of technological, environmental, and socio-political dimensions. Here, we present the  
82 six broad themes in urban evolutionary ecology (Figure 1) that encompass the 30 top questions that  
83 emerged from the horizon scan (Table 1 & Figure 2).

84

### 85 *Fundamental processes and mechanisms*

86 Studies increasingly show that cities across the globe are altering fundamental ecological and  
87 evolutionary processes. While studied primarily in isolation, these processes may interact in complex  
88 ways within cities, creating unique selection pressures and **eco-evolutionary feedbacks** [5]. For example,  
89 plant-herbivore and predator-prey interactions [12,13] are altered by urbanization, leading to phenotypic  
90 changes in traits ranging from morphological, behavioral, physiological, and life history [14,15]. Urban  
91 environments likely also modify sexual selection and thus generate novel mating strategies and  
92 preferences [16], which could further shape population dynamics and interactions with other species.  
93 However, it is unclear whether these traits are either **exaptations** or novel adaptations to the urban  
94 environment [10,17]. In fact, although most adaptations arise from selection on standing genetic variation  
95 [18], we know little about how cities influence novel mutation or their long-term effects on organism  
96 health [19], despite the importance of mutation in contributing to evolutionary potential.

97         Understanding the role of urbanization for evolutionary ecology requires disentangling how  
98 landscape changes, temporal change in human-nature interactions, and past ecological and evolutionary  
99 legacies influence present-day dynamics. Over longer time periods, organismal changes in response to  
100 evolutionary processes altered by humans may ultimately lead to speciation, although it is unknown how  
101 common speciation is in cities or the conditions that may favor it in urban areas [20]. Anthropogenic  
102 habitat modification has altered ecological and evolutionary processes for at least the last 50,000 years,  
103 resulting in species that rely on anthropogenic resources [21], including commensals and domesticated

104 species [22]. In fact, domesticated animals, such as pet cats (*Felis catus*), have severely negative effects  
105 on endemic wildlife [23], yet the long-term evolutionary consequences of these predator-prey interactions  
106 in cities are not well-studied. Studies of these organisms can give us a glimpse into the process of  
107 organismal change across anthropogenic environments, in some cases leading to populations that are  
108 reproductively isolated from their non-urban counterparts [24].

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

116

### 117 *Spatial and temporal scales of drivers and responses*

118 The fast development of cities and their fine-scaled heterogeneity [29] can lead to local selection  
119 pressures that create rapid and microgeographic adaptations. This premise suggests that cities are hotspots  
120 for evolution, with the potential for novel species interactions that further drive rapid ecological and  
121 evolutionary change [25,30]. However, the extent to which cities alter ecological niches and increase  
122 evolutionary potential [28,31] is an empirical question that, once answered, could uncover the scale  
123 dependency of both drivers and responses.

124 The extent to which urban ecological and evolutionary dynamics occurring at various spatial and  
125 temporal scales are species- and city-specific is still relatively unknown. Variable patterns (e.g., spatial  
126 and temporal) of urbanization can reduce or increase colonization rates, genetic drift, and gene flow,  
127 which might determine the relative contribution of adaptive evolution and species-sorting shaping local  
128 communities [5]. For example, high human-mediated dispersal of some species may counteract local  
129 adaptation to cities, whereas others may adapt quickly at fine scales [32,33]. In addition, factors such as

130 age, history, and the pace of urban development may determine the magnitude of evolutionary responses,  
131 such as the strength and direction of selection [34,35]. Empirical studies that collect comparable data  
132 within and among cities with similar and different histories are necessary to relate cities' spatial and  
133 temporal heterogeneity to evolutionary responses [36].

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

143

#### 144 ***Sustainability, health, and well-being***

145 Cities are an important frontier in achieving future global biodiversity and sustainability goals [40]. In  
146 particular, the United Nations Sustainable Development Goals (SDGs), specifically SDG 11 for  
147 sustainable cities and communities, provides an opportunity to link urban evolutionary ecology research  
148 with policies to mitigate environmental crises and promote ecosystem health [4]. For example, cities  
149 could serve as reservoirs for biodiversity that benefit people and nature while also supporting ecosystem  
150 functions, such as decomposition, nutrient recycling, and carbon storage. These processes involve both  
151 ecological and evolutionary mechanisms that underpin ecosystem services such as urban sanitation, water  
152 purification, microclimate modulation, and pollination – all indispensable to well-being [41].

153 Research that integrates evolutionary ecology with urban development creates a direct link  
154 between urban eco-evolutionary dynamics and human and ecosystem health. As the COVID-19 pandemic  
155 demonstrates, the concentration of humans in cities and the interconnectedness of cities can facilitate the

156 spread and evolution of certain diseases [42], and pose an immense challenge to sustainable global health  
157 systems. It is imperative to understand how social heterogeneity and the design of urban landscapes  
158 influences the spread of diseases and their vectors, as well as other established health risks such as urban  
159 heat and elevated pollution [43]. Urban greening can help cool cities and reduce pollution-related health  
160 issues [44], while also maintaining biodiversity and ecosystem functioning [45]. Related, rewilding  
161 projects typically focus on ecological processes, yet more research is needed to investigate how they  
162 influence evolutionary processes and their effects on ecology and human health. For example, green  
163 spaces can reduce gene flow in species, which are well-suited for urban environments (e.g., brown rats,  
164 *Rattus norvegicus*) and that spread human pathogens [46].

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

174

### 175 ***Impacts and interactions with climate change***

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

182 increasingly frequent extreme weather events will require investigations focused on urban long-term  
183 studies.

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

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

202

### 203 ***Politics, governance, culture, their interactions, and their ethical considerations***

204 Political systems and governance arrangements guide urban growth and development in highly variable  
205 ways [63,64] that can shape urban evolutionary ecology. These arrangements can determine the spatial  
206 distribution of environmental burdens and access to amenities, exacerbating social and economic inequity  
207 and oppression [65]. For example, housing and land-use policies have resulted in green spaces being



208 disproportionately located in affluent and primarily white areas within many global cities [8,66,67]. Thus,  
209 investigations into how institutionally-entrenched distributions of urban land-use inequities may influence  
210 ecological properties (e.g., resource distribution or microclimates) and evolutionary change are a high  
211 research priority.

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

224 Although ethics can directly influence research decisions in urban evolutionary ecology, there is  
225 also the potential for ethical considerations to play a role in urban eco-evolutionary outcomes. One often-  
226 overlooked consideration is the moral responsibility of researchers and the role of empathy. For example,  
227 how pro-environmental behaviors have developed over time to influence policy that shapes urban  
228 evolutionary ecology could be thought of as a moral and motivational dilemma [74]. However, decisions  
229 tied to urban areas – such as the magnitude of recycling and composting, programs such as food sharing  
230 or needle exchange, or the distribution of services such as homeless care, community clinics, or street  
231 cleanliness – may have downstream implications for organisms by altering the adaptive landscape. For  
232 example, urban waste recycling practices generate potentially unique pollutants, such as microplastics,  
233 with yet unknown long-term selective pressures linked to water, air, and soil [75]. Interdisciplinary

234 collaborations will help inform how political, institutional, social, cultural, and ethical factors are not only  
235 considered in research, but how they play a direct role in shaping how processes of urban evolutionary  
236 ecology unfold and interact.

237

238 *Innovation in technology and methodology*

239 Advancements in technology and methodology provide unprecedented capacity to enable real-time  
240 monitoring and data analysis for previously unanswered questions in urban evolutionary ecology.

241 Genomic, transcriptomic, and epigenomic tools have not only provided insights into the effects of  
242 urbanization on evolution [76-79], they have also provided the raw materials for downstream  
243 experiments. One example is how genetic technology has been tested for pest control of disease-carrying  
244 organisms [80,81], where manipulating genetic material could shift the evolution and adaptive landscape  
245 of endangered native organisms and their communities [82]. Another example comes from the expected  
246 increase of **autonomous systems** and robotics deployed in urban areas in the coming decades [83],  
247 leading to applications such as weed and pest control that may enhance or hinder plant-pollinator systems  
248 [84]. With the introduction of new artificial agents come unknown consequences, and the need to  
249 characterize the selection regimes that emerge as a natural response [85].

250 A related emerging issue is the abundance of data – both in volume and types – newly generated  
251 to describe urban ecosystems. One solution may be through **smart city** approaches, which have  
252 traditionally focused on enhancing economic efficiency and quality of life for humans [86]. For example,  
253 by integrating evolutionary ecology with engineering and social science in the design and connectivity of  
254 green infrastructure [87,88], we can increase gene flow and population connectivity while also attaining  
255 sustainable development goals in enhancing nature's contribution to people within cities. Just as the  
256 growing field of 'precision medicine' is using artificial intelligence (AI) methodology to find unique  
257 patterns among human genomes, environments, behavior, and social context [89], the same AI  
258 approaches can make sense of complex systems in cities composed of variable environments in space and  
259 time, pollutants/mutagens, genomic structures and phylogenetic relationships. For example, these

260 approaches can be used to monitor biodiversity from **environmental DNA** as well as predict epidemics  
261 from wastewater [83]. The future challenge largely rests in finding ways of translating the massive  
262 amounts of data into impactful and just strategies for management (of species, communities, soil, crops,  
263 urban ecosystems), application (education, infrastructure), and implementation (policies) that will feed  
264 back on nature within cities.

265

### 266 **Concluding remarks**

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

278         Because cities are globally distributed across diverse cultures and histories, this study is a  
279 reminder of the need for international collaborations to rebalance our perspective [64]. For example,  
280 regions of China and the former Soviet republics are urbanizing rapidly, yet knowledge of the ecological  
281 and evolutionary dynamics of those landscapes is limited [90]. Collaboration between scholars from the  
282 Global South and Global North is necessary, and evolutionary ecologists in the North (especially English-  
283 language writers) need to take better stock of research conducted in other parts of the world and published  
284 in other languages [91]. Because cities are best viewed as social-ecological-technological systems [92],

285 interdisciplinary collaborations will help address fundamental questions in urban evolutionary ecology  
286 while ensuring that cities develop in ways that benefit both humans and other organisms.

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

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

309

310

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312

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316 Review Board at the University of Washington (ID# STUDY00010723).

317

318 **Declaration of interests**

319

320 No interests are declared.

321

322 **Glossary**

323

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

326

327 **Eco-evolutionary dynamics:** interactions between ecological and evolutionary processes that play out on  
328 contemporary time scales

329

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

332

333 **Environmental DNA:** genetic material obtained directly from environmental samples, e.g., soil, air,  
334 sediment, and water

335

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

338

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

341

342 **Urbanization:** the process of converting undeveloped land into cities and towns where humans become  
343 highly concentrated

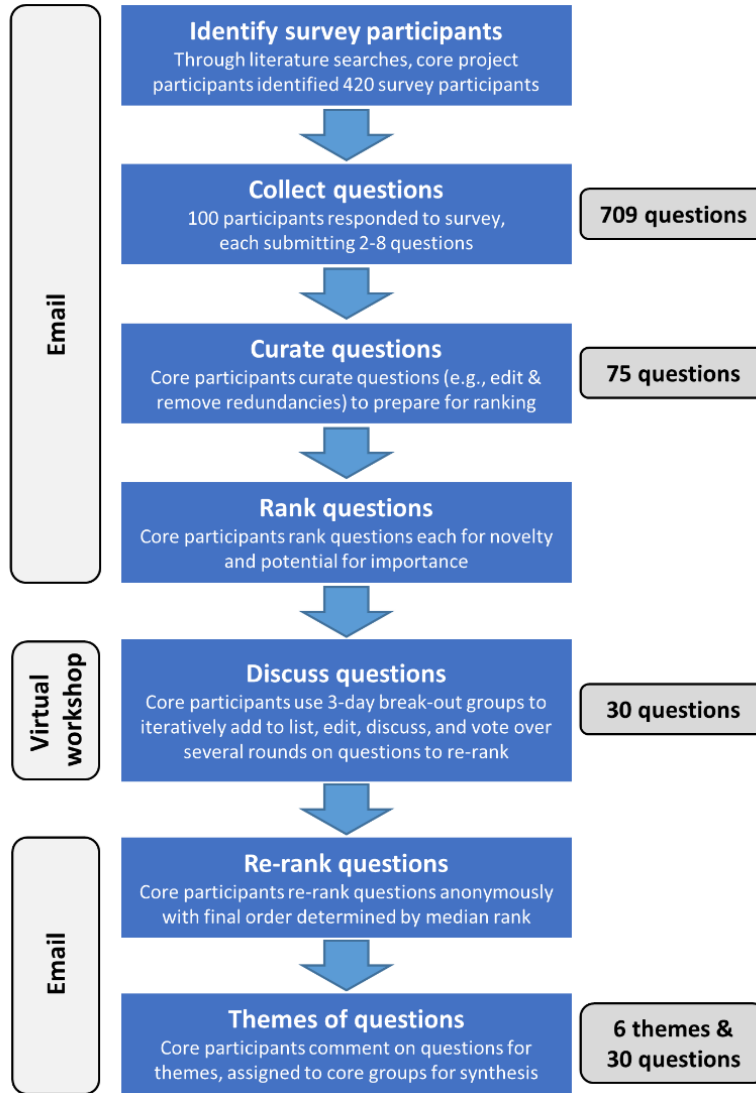
344 **Box 1. Horizon scan protocol**

345 Our horizon scan used a modified Delphi technique [96], consistent with previous horizon scans [97,98].  
346 The main objective of this technique is to conduct iterative evaluations of survey responses (Figure I).  
347 From an international research network on urban eco-evolutionary dynamics (see “Acknowledgements”),  
348 24 individuals established the “core” group, with an additional five invited from outside this network to  
349 balance backgrounds in ecology, evolutionary biology, environmental science, anthropology, urban  
350 planning, policy, and sustainability. The core group (29 authors here) oversaw the horizon-scanning  
351 protocol, which generated the survey, identified survey participants, evaluated the survey responses, and  
352 provided synthesis for a publication. The survey (Table S1) was designed for participants to provide  
353 questions in ecology and evolutionary biology in urban areas for future research directions. The survey  
354 also collected voluntary demographic information, anonymized through statistical aggregation, so that  
355 responses could not be tied to individual participants.

356 In September 2020, the survey was emailed to 420 potential participants from 33 countries  
357 representing six continents, with responses from 100 participants from 25 countries (Table S2). Our  
358 protocol (Figure I) identified potential survey participants from review of the literature on urban ecology  
359 and evolutionary biology, with care taken to balance diversity in demographics (e.g., career stage,  
360 geography, and discipline) when possible. The 100 respondents provided over 700 questions, which were  
361 curated for clarity (e.g., redundancies removed) by a team of seven core individuals. A curated list of 75  
362 questions was presented to the 29 core participants via email to score from 1 (highest) to 5 (lowest) for  
363 each of “novelty” and “importance” in urban ecology and evolutionary biology. Input on “novelty”  
364 reflected areas not investigated or not thoroughly (e.g., across diverse taxa, geographic areas), whereas,  
365 “importance” reflected areas that while possibly not novel, are highly valued in the literature and need  
366 attention. A three-day virtual workshop was held in November 2020 for several rounds of small break-out  
367 groups and anonymous voting among the 29 core participants in discussing and editing the submitted  
368 questions to reach a consensus. A list of 30 questions emerged that were ranked 1-30 by each core  
369 participant post-workshop. Consistent with previous horizon scans, the median rank for each question was  
370 used to determine the final list (Table 1 & Figure 2). After the final ranking, feedback was collected from  
371 the core participants to bin and summarize the questions into “themes” that focused the research  
372 directions.  
373

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**Figure I.** Protocol summary for identifying and reviewing questions for the horizon scan exercise.



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379 **Box 2. Backgrounds of survey participants**

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

395 The high variance associated with the ranked questions (Figure 2) reflects the diverse disciplinary  
396 backgrounds of survey participants. It is not surprising that just over 90% of the participants used the  
397 words "ecology" or "evolution" to describe their expertise (Table S3). However, while a very small  
398 number of participants used additional descriptors for "evolution" (e.g., "evolutionary geneticist"), over  
399 half of the participants who used "ecologist" used at least one, and some as many as three additional  
400 descriptors (e.g., "urban/wetland/ecosystem ecologist"). Finally, while 22% of the participants used the  
401 word "urban" to define their expertise, the vast majority of this latter group describe themselves as "urban  
402 ecologists/evolutionary ecologists", and never as "urban evolutionary biologists" alone (Figure S1). These  
403 results reflect a growing and emerging discipline previously dominated by urban ecologists [10]. Just as  
404 evolutionary biologists, who were not initially focused on urban ecosystems, have entered the field more  
405 recently, we anticipate further diversification of the field – with other disciplines, such as engineering,  
406 social sciences, and medicine, pursuing the research directions outlined here.  
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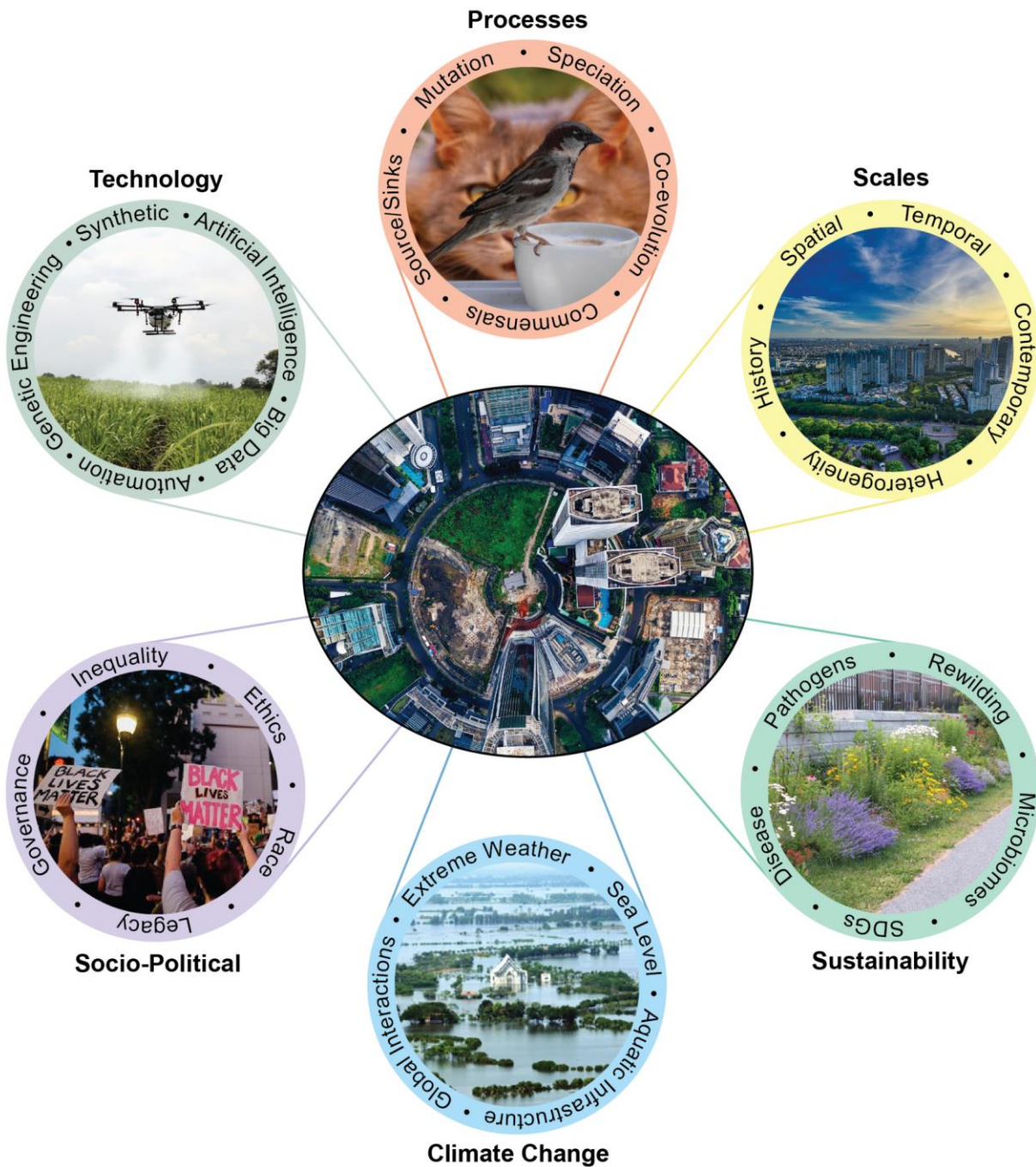
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**Table 1. Ranked questions and their themes for research in urban evolutionary ecology.**

Themes	Questions	Rank
<b>Fundamental processes &amp; mechanisms</b> (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
<b>Spatial &amp; temporal scales of drivers and responses</b> (Scales)	What is the relative importance of evolution in cities in affecting the magnitude and direction of ecological dynamics and patterns, especially compared to non-evolutionary 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 to other non-urban 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 non-urban 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
<b>Sustainability, health, &amp; wellbeing</b> (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 wellbeing, 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
<b>Impacts &amp; interactions with climate change</b> (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
	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
<b>Politics, governance, culture, their interactions, &amp; their ethical considerations</b> (Socio-Political)	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 in the 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
<b>Innovation in technology &amp; methodology</b> (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

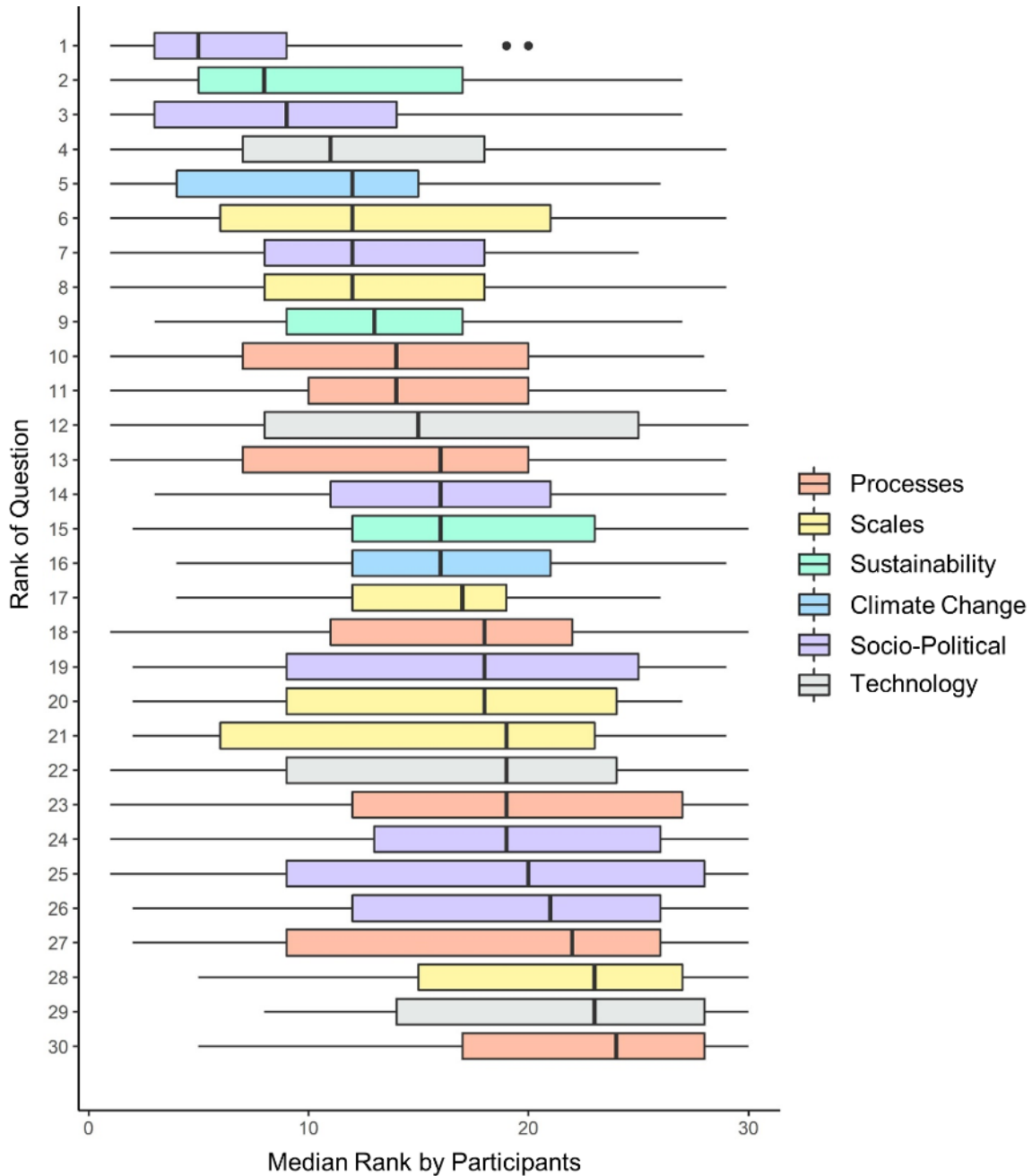
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410 **Figure 1. Emerging research themes in urban evolutionary ecology.** Six themes were identified that  
411 summarized the 30 questions ranked by core participants (see Box 1 for methods). Keywords reflecting  
412 the questions are shown circling a visual reflection of each of the six themes (see Table 1 for the list of  
413 questions and their theme names).  
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418 **Figure 2. Rank and variance of questions with their themes for research in urban evolutionary**  
 419 **ecology.** Boxplots reflect the median ranks of the 30 questions by the 29 core participants (see Table 1).  
 420 Box limits indicate the 25th and 75th percentiles, whiskers extend 1.5 times the interquartile range from  
 421 the 25th and 75th percentiles, and outliers are represented by dots.  
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Verrelli et al: A global horizon scan for urban evolutionary ecology

There is not a separate section for “Outstanding Questions” for our submission. In accordance with a standard “horizon scan”, the main objective of our study is to collect recommendations and analyze questions for future research. This list of questions can be found in Table 1.



**Editor's comments:**

1. Image files are needed for all figure files, including the Box figure - see notes below. I can't accept the article without these.

**Author response:** Image files have been submitted for all three figures.

2. In Box 1, you need to refer to the box figure. It is Figure I (Roman numeral) and the figure needs a short caption. See box 2 of this article for an example [https://www.cell.com/trends/ecology-evolution/fulltext/S0169-5347\(22\)00089-1](https://www.cell.com/trends/ecology-evolution/fulltext/S0169-5347(22)00089-1)

**Author response:** The Figure in Box 1 has now been labeled "Figure I" with a short caption provided (line 374), and is cited within Box 1 (line 346).

3. Pet cats needs a species name. Please check this throughout.

**Author response:** The species name for cats (*Felis catus*) has been added (line 104), and all other common/species names have been resolved throughout.

4. Suppl. Info. Table 1. Don't vertically centre the continent names. It looks like Austria - Germany are part of Asia.

**Author response:** Thank you for seeing this. The continent names are now appropriately justified.

**Reviewers' Comments:**

Reviewer #3: Verrelli et al. present a horizon scan of urban evolutionary ecology and address key questions for the future of urban evolutionary ecology. The revisions to the methodology address much of the reviewers questions. However, I do not agree with the authors' decision to not publish the survey. The original survey that was sent out to the 420 participants (e.g., how the open-ended questions were asked, the demographic questions and possible responses) should be published in the supplementary material, as is common in publications that utilize survey methodology. Many horizon scans minimally publish this information, as well as the responses (e.g., your 709 questions), and each step of distilled responses (e.g., your 75 questions), all of which are needed here.

**Author response:** We have made the survey questions that were analyzed available in Supplementary Information Table S1, which is now cited in Box 1 (line 352).

Other points:

1. "novelty" and "importance" are still not defined in Box 1.

**Author response:** We have now provided a sentence to clarify in Box 1 (line 363): "Input on "novelty" reflected questions not investigated or not thoroughly (e.g., across diverse taxa, geographic areas), whereas, "importance" reflected questions that while possibly not novel, are highly valued in the literature and need attention."

2. rewilding vs. urban greening. This has been clarified in the text, but the Figure still has "rewilding". I see that the question specifically addresses rewilding and restoration, so leaving "rewilding" in the figure works, but I would argue that urban greening as a whole is more impactful on urban ecological and evolutionary processes as rewilding is a very small part of urban greenspace design, management, etc.

Also, not to be too picky, but the picture you chose for this is a designed garden, not a "rewilding", so this also confuses your point.

**Author response:** We agree that “rewilding” may currently be a “very small part of urban greenspace design” as the reviewer says here; however, we note that in looking forward on the “horizon” (i.e., not current research), our review of the questions submitted found several focused on novel ways to “rewild” urban areas. One example is the microbiome research we noted as a novel direction in rewilding. Lastly, we will note that the picture provided for “rewilding” in Figure 1 can indeed be an example of “rewilding”. For example, although it may be a garden design, the intention here (as we noted in the text) could be to design urban spaces that “rewild” areas for pollinators in new ecological interactions within cities.

3. still not following the empathy argument - particularly where it comes to "moral responsibility of researchers" as your examples are not specific to research fields, but to policy and management actions.

**Author response:** We have several individuals within our core group who participate in socio-cultural research in urban areas and its impact on eco-evolutionary outcomes. This growing literature (as cited) and our review of it shows that humans often make decisions that come from “moral and motivational” perspectives, as we note. That is, the “moral dilemma” as we point out is whether researchers make decisions in urban areas that consider not just research outcomes but socio-cultural impacts they have, and downstream, how these decisions can affect eco-evolutionary outcomes. We previously provided specific examples in the text in this theme that are not just policy- or management-related but also related to the “adaptive landscape” to help explain what these eco-evolutionary outcomes related to moral decisions could be in the future.

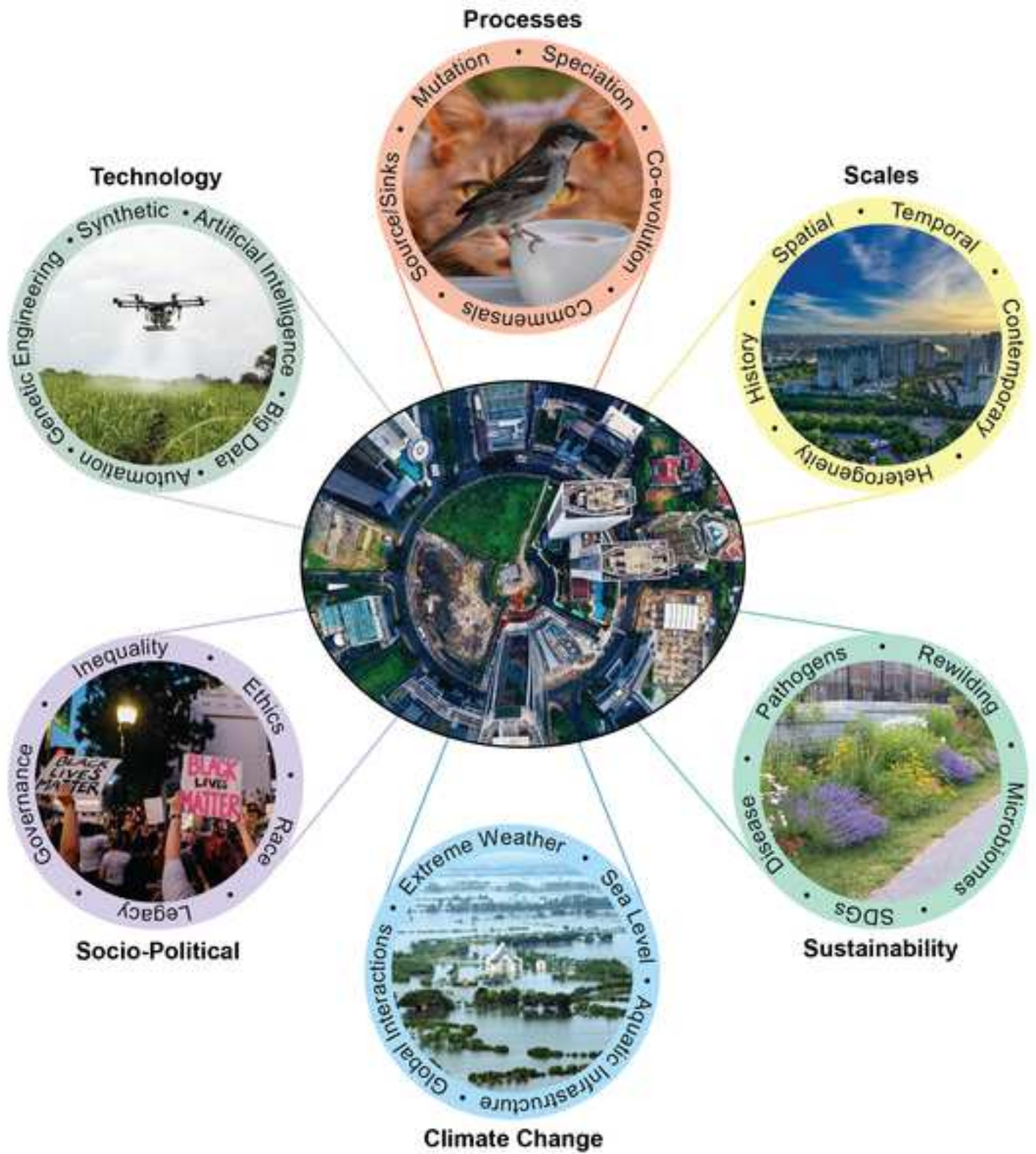
4. Line 281 - while I whole-heartedly agree with this paragraph, I argue one way to address these issues is to start at the top - with the author list. Inviting scientists from institutions in these underrepresented regions into these types of working groups and co-authoring is key to incorporating diverse socio-political, cultural and scientific perspectives.

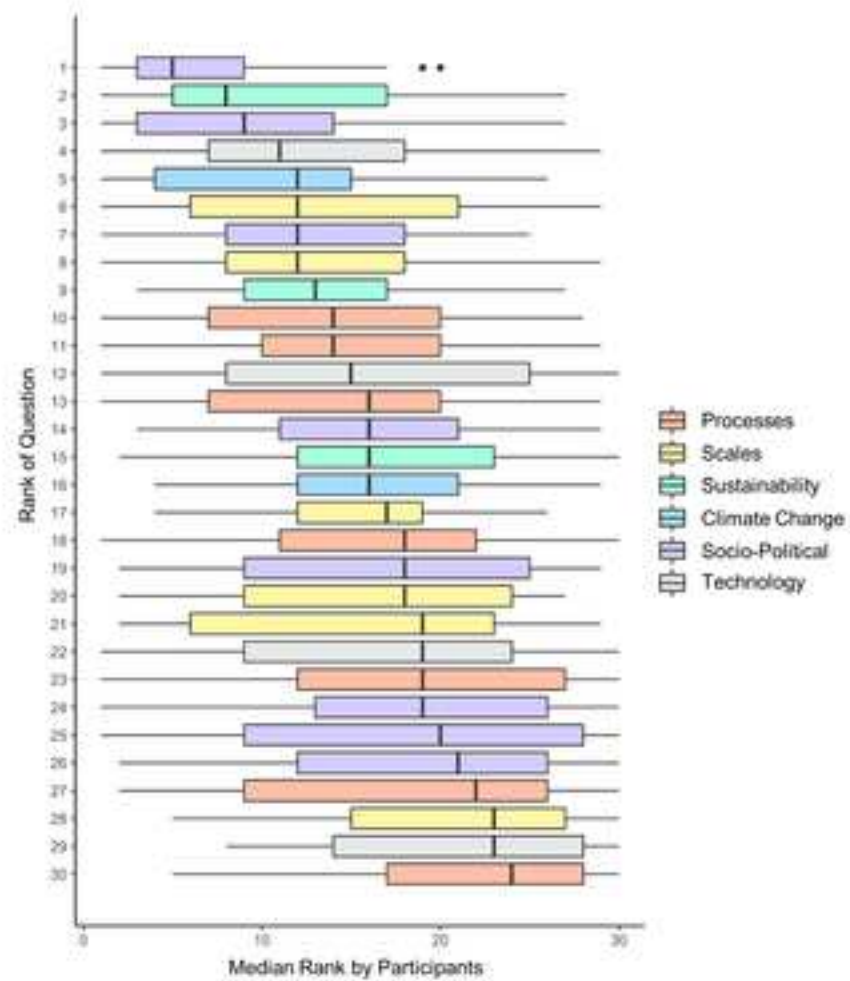
**Author response:** We completely agree that incorporating diversity from ethnic, geographic, and discipline perspectives at the top is the way to go. This point is reflected in this noted paragraph in the concluding remarks of “...this study is a reminder of the need for international collaborations to rebalance our perspective” and “Collaboration between scholars from the Global South and Global North is necessary”. Additionally, in Box 2 we also discuss specifically the inherent bias of survey and core participants in horizon scans when current research groups do not match the current landscape, something pointed out by other horizon scans too (and which we cited). In this respect, to the best of our ability, our recruitment for the core group over many months did prioritize diversity in all three of these areas of ethnicity, geography, and discipline consistent with whom is currently conducting urban eco-evo research across career stages. In fact, our consortium and this horizon scan has built new bridges and brought in new students from backgrounds with which we had previously not interacted. Thus, these movements bring new hope and we strongly embrace future opportunities with those in the field as diversity continues to grow with this expanding discipline.

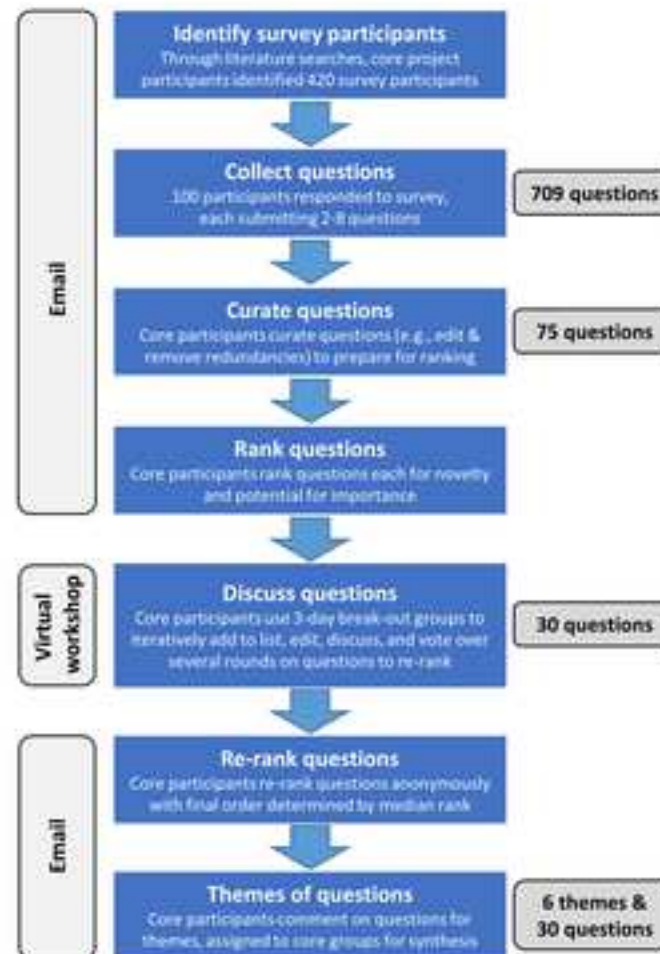
Verrelli et al: A global horizon scan for urban evolutionary ecology

### **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, socio-political and ethical considerations, and innovation in technology.







Supplemental Information

**A global horizon scan for urban evolutionary ecology**

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**Table S1. Survey questions analyzed for the horizon scan.**

<b>Number</b>	<b>Question</b>
1	What do you think will be the most important and novel (i.e., unasked and unaddressed) research questions specifically in "urban evolutionary ecology" in 10-100 years? (provide up to 8 responses)
2	Using any keywords that you prefer, how would you briefly describe your professional/research expertise? (provide up to 3 responses)
3	What is your country of residence?



**Table S2. Reported country of residence of survey respondents (91 reporting of 100 respondents).**

<b>Continent</b>	<b>Country</b>	<b>Count</b>
Africa	South Africa	1
Asia	China	2
	Japan	2
Europe	Singapore	1
	Austria	1
	Denmark	1
	Estonia	1
	Finland	2
	France	3
	Germany	2
	Italy	1
	Netherlands	1
	Poland	1
	Portugal	1
	Spain	1
	Sweden	3
	Switzerland	2
North America	Canada	12
	Mexico	2
	United States of America	41
Oceania	Australia	2
	New Zealand	2
South America	Chile	3
	Colombia	1
	Brazil	2
<b>Total</b>		<b>91</b>

**Table S3. Keywords provided by survey participants in response to how they would describe their professional/research expertise (94 reporting of 100 respondents).**

<b>Participant</b>	<b>keyword (1)</b>	<b>keyword (2)</b>	<b>keyword (3)</b>
1	ecologist	science policy	animal behaviour
2	evolutionary biology	genetics	animal behaviour
3	insect ecophysiologicalist	evolutionary ecologist	behavioral ecologist
4	molecular ecologist	population geneticist	behavioral ecologist
5	ecologist	ecophysiologicalist	behavioural ecologist
6	ecologist	microbiologist	biochemist
7	evolutionary ecology	population genomics	biodiversity
8	landscape ecology	anthropology/archaeology	climate change
9	ecologist	urban design	community scientist
10	population geneticist	evolutionary biologist	computational biologist
11	contemporary evolution	eco-evolutionary dynamics	conservation genetics
12	evolutionary ecologist	invertebrate zoologist	data science
13	ecologist	species interactions	dispersal
14	genetics/ genomics	molecular biology	ecology
15	plant ecologist	plant ecophysiologicalist	ecosystem processes
16	landscape ecologist	urban ecologist	ecosystem service
17	ecologist	environmental science	ecosystem services
18	evolutionary ecologist	biologist	empirical
19	ecologist	biostatistician	entomologist
20	community ecologist	global change ecologist	evolutionary ecologist
21	ecologist	behavioral ecologist	evolutionary ecologist
22	population geneticist	human evolution	evolutionary ecologist
23	urban ecologist	ecotoxicologist	evolutionary ecologist
24	urban ecologist	landscape ecologist	geography
25	ecologist	evolutionary biologist	global change
26	ecologist	landscape geneticist	herpetologist
27	community ecologist	applied ecologist	insect biologist
28	environmental scientist	landscape ecologist	land change dynamics
29	ecologist	urban ecologist	landscape ecologist
30	ecologist	community ecology	landscape ecology
31	evolutionary ecologist	species interactions	mutualism
32	evolutionary ecologist	quantitative geneticist	ornithologist
33	anthropology	hazards/ disasters	philosophy
34	animal ecologist	evolutionary ecologist	physiologist
35	evolutionary biologist	botanist	plant
36	quantitative geneticist	population geneticist	plant
37	evolutionary ecologist	botanist	plant-insect
38	evolutionary ecology	community ecology	plant-insect interactions

39	plant geneticist	quantitative geneticist	population geneticist
40	evolutionary biologist	ecologist	population genetics
41	household ecology	cities	rapid evolution
42	archaeologist	anthropologist	social scientist
43	conservation biologist	evolutionary biologist	urban ecologist
44	evolutionary biology	population genomics	urban ecology
45	urban ecology	urban biodiversity	urban environmental planning
46	urban evolutionary biologist	urban biologist	urban evolutionary ecologist
47	ecologist	forester	urban planning
48	ecosystems ecologist	urban ecologist	wetland ecologist
49	evolutionary biologist	ecologist	wildlands manager
50	ornithologist	urban ecologist	wildlife scientist
51	ethologist	urban ecologist	zoologist
52	evolutionary biologist	behavioural ecologist	
53	urban wildlife planner	biologist	
54	population biologist	ecologist	
55	ecologist	entomologist	
56	behavioural ecologist	evolutionary biologist	
57	botanist	evolutionary biologist	
58	ecologist	evolutionary biologist	
59	evolutionary ecologist	evolutionary biologist	
60	evolutionary ecologist	evolutionary biologist	
61	ecology	evolutionary biology	
62	ecologist	insects	
63	ecologist	interdisciplinary	
64	urban ecologist	landscape ecologist	
65	landscape ecologist	landscape geneticist	
66	ecologist	lepidopterist	
67	archaeologist	modeler	
68	restoration ecologist	plant ecology	
69	evolutionary biologist	population genetics	
70	evolutionary geneticist	protistologist	
71	evolutionary ecologist	quantitative geneticist	
72	geographer	remote sensing	
73	forester	socio-ecologist	
74	evolutionary ecologist	theoretician	
75	evolutionary ecologist	urban evolutionary biology	
76	evolutionary ecologist	urban evolutionary ecologist	
77	environmental policy	urban politics	
78	ecologist		
79	ecologist		
80	ecologist		
81	ecologist		

82	ecologist
83	ecologist
84	ecologist
85	ecologist and ecophysiologicalist
86	environmental engineer
87	evolutionary biologist
88	evolutionary ecologist
89	evolutionary ecologist
90	evolutionary ecologist
91	historical ecologist
92	plant evolutionary biologist
93	urban ecology
94	urban ecology

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**Figure S1. Intersection of keywords reflecting reported expertise of survey respondents.** From the keywords provided by 94 of the 100 respondents (see Table S3), we examined the number of individuals using any form of the the word “ecology” (eco), “evolution” (evo), or “urban”. For example, 31 individuals used the word “ecology” without “evolution” or “urban”, whereas, only 6 individuals used the words “ecology”, “evolution”, and “urban”.

