Socio-Eco-Evolutionary Dynamics in Cities

Running Head: Socio-eco-evolutionary dynamics in cities

Simone Des Roches*[1], Kristien Inge Brans[2], Max R. Lambert[3], L. Ruth Rivkin[4,5,6], Amy Marie Savage[7], Christopher J. Schell[8], Cristian Correa[9], Luc De Meester[2,10,11], Sarah E. Diamond[12], Nancy B. Grimm[12], Nyeema C. Harris[14], Lynn Govaert[15,16], Andrew P. Hendry[17], Marc T. J. Johnson[4,5,6], Jason Munshi-South[18], Eric P. Palkovacs[19], Marta Szulkin[20], Mark C. Urban[21], Brian C. Verrelli[22], Marina Alberti[1]

*corresponding author: simone.desroches@gmail.com

[1]Department of Urban Design and Planning, University of Washington, Seattle, WA, USA

[2]Department of Biology, Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium

[3]Department of Environmental Science, Policy, and Management, University of California, Berkeley, Berkeley, CA, USA

[4]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada)

[5]Department of Biology, University of Toronto Mississauga, Mississauga, ON, Canada

[6]Centre for Urban Environments, University of Toronto Mississauga, Mississauga ON, Canada

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

[8]School of Interdisciplinary Arts and Sciences, University of Washington Tacoma, Tacoma, WA, USA

[9]Facultad de Ciencias Forestales y Recursos Naturales, Instituto de Conservación Biodiversidad y Territorio, Universidad Austral de Chile, Valdivia, Chile

[10]Institute of Biology, Freie Universität Berlin, Germany

[11]Leibniz Institut für Gewasserökologie und Binnenfischerei, Berlin, Germany

[12]Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA

[13]School of Life Sciences, Arizona State University, Tempe, AZ, USA

[14]Applied Wildlife Ecology Lab, Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA

[15]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

[16]Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology, Duebendorf, Switzerland

[15]Redpath Museum and Department of Biology, McGill University, Canada

[18]Department of Biological Sciences and Louis Calder Center, Fordham University, Armonk, NY, USA

[19]Department of Ecology & Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA

[20]Centre of New Technologies, University of Warsaw, Poland

[21]Director of the Center of Biological Risk and Professor of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

[22]Center for Life Sciences Education, Virginia Commonwealth University, Richmond, VA, USA

Key Terms:, coupled human-natural systems, anthropogenic, socio-ecological systems, urbanization, adaptation, eco-evo

1

2   DR. SIMONE DES ROCHES (Orcid ID : 0000-0002-5360-8197)

3   DR. CHRISTOPHER JOHN SCHELL (Orcid ID : 0000-0002-2073-9852)

4   DR. SARAH DIAMOND (Orcid ID : 0000-0001-8518-773X)

5   DR. MARC JOHNSON (Orcid ID : 0000-0001-9719-0522)

6   DR. ERIC PALKOVACS (Orcid ID : 0000-0002-5496-7263)

7

8

9   Article type   : Special Issue Perspective

10

11

12   Socio-Eco-Evolutionary Dynamics in Cities

13   *Running Head: Socio-eco-evolutionary dynamics in cities*

14

15   Simone Des Roches*[1], Kristien Inge Brans[2], Max R. Lambert[3], L. Ruth Rivkin[4,5,6], Amy Marie Savage[7],

16   Christopher J. Schell[8], Cristian Correa[9], Luc De Meester[2,10,11], Sarah E. Diamond[12], Nancy B. Grimm[12],

17   Nyeema C. Harris[14], Lynn Govaert[15,16], Andrew P. Hendry[17], Marc T. J. Johnson[4,5,6], Jason Munshi-South[18],

18   Eric P. Palkovacs[19], Marta Szulkin[20], Mark C. Urban[21], Brian C. Verrelli[22], Marina Alberti[1]

19

20   *corresponding author: simone.desroches@gmail.com

21   [1]Department of Urban Design and Planning, University of Washington, Seattle, WA, USA

22   [2]Department of Biology, Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven,

23   Belgium

24   [3]Department of Environmental Science, Policy, and Management, University of California, Berkeley,

25   Berkeley, CA, USA

26   [4]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada)

27   [5]Department of Biology, University of Toronto Mississauga, Mississauga, ON, Canada

28   [6]Centre for Urban Environments, University of Toronto Mississauga, Mississauga ON, Canada

29   [7]Department of Biology & Center for Computational and Integrative Biology, Rutgers University, Camden,

30   NJ, USA

31   [8]School of Interdisciplinary Arts and Sciences, University of Washington Tacoma, Tacoma, WA, USA

32   [9]Facultad de Ciencias Forestales y Recursos Naturales, Instituto de Conservación Biodiversidad y

33   Territorio, Universidad Austral de Chile, Valdivia, Chile

34   [10]Institute of Biology, Freie Universität Berlin, Germany

35   [11]Leibniz Institut für Gewasserökologie und Binnenfischerei, Berlin, Germany

36

37   [12]Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA

38   [13]School of Life Sciences, Arizona State University, Tempe, AZ, USA

39   [14]Applied Wildlife Ecology Lab, Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI,

40   USA

41   [15]Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland

42   [16]Department of Aquatic Ecology, Swiss Federal Institute of Aquatic Science and Technology, Duebendorf,

43   Switzerland

44   [15]Redpath Museum and Department of Biology, McGill University, Canada

45   [18]Department of Biological Sciences and Louis Calder Center, Fordham University, Armonk, NY, USA

46   [19]Department of Ecology & Evolutionary Biology, University of California, Santa Cruz, Santa Cruz, CA, USA

47   [20]Centre of New Technologies, University of Warsaw, Poland

48   [21]Director of the Center of Biological Risk and Professor of Ecology and Evolutionary Biology, University of

49   Connecticut, Storrs, CT, USA

50   [22]Center for Life Sciences Education, Virginia Commonwealth University, Richmond, VA, USA

51

52   **Key Terms:**, coupled human-natural systems, anthropogenic, socio-ecological systems, urbanization,

53   adaptation, eco-evo

54

55

56

57

58

59

60   ## Abstract

61   Cities are uniquely complex systems regulated by interactions and feedbacks between natural

62   and social processes. Characteristics of human society – including culture, economics,

63   technology, and politics – underlie social patterns and activity, creating a heterogeneous

64   environment that can influence and be influenced by both ecological and evolutionary

65   processes. Increasing interest in urban ecology and evolutionary biology has coincided with

66   growing interest in eco-evolutionary dynamics, which encompasses the interactions and

67   reciprocal feedbacks between evolution and ecology. Research on both urban evolutionary

68   biology and eco-evolutionary dynamics frequently focuses on contemporary evolution of species

69   that have potentially substantial ecological – and even social – significance. Still, little research

70   fully integrates urban evolutionary biology and eco-evolutionary dynamics, and rarely do

71   researchers in either of these fields fully consider the role of human social patterns and

72   processes. Because cities are fundamentally regulated by human activities, are inherently

73   interconnected, and are frequently undergoing social and economic transformation, they

74   represent an opportunity for ecologists and evolutionary biologists to study urban "socio-eco-

75   evolutionary dynamics." Through this new framework, we encourage researchers of urban

76   ecology and evolution to fully integrate human social drivers and feedbacks to increase

77   understanding and conservation of ecosystems, their functions, and their contributions to

78   people within and outside cities.

79

80

81

82   Introduction

83   Humans construct and modify their surroundings to support the demands and desires of

84   society (O'Brien & Laland, 2012). This phenomenon is particularly evident in cities, which are

85   currently home to over half of the human population, a percentage predicted to rise to 66% by

86   2050 (UN, 2018). Urban expansion is rapid, with the global city footprint projected to double

87   between 2015 and 2050, largely due to increased urban and suburban sprawl (Barrington-Leigh

88   & Millard-Ball, 2020; Huang, Li, Liu, & Seto, 2019; Liu et al., 2020). As urban areas expand, they

89   are becoming more socially heterogeneous, reflecting an influx of diverse people who bring

90   myriad cultures from around the world (Qadeer, 1997, 2000; Sandercock, 1998). While humans

91   and social processes are affecting all the planet's biomes (Ellis, 2015), it is in urban ecosystems

92   that human density and built habitats are the most pronounced. Cities have thus become

93   representative of an urban "anthrobiome" – a set of ecosystems created and transformed by the

94   people and societies that inhabit and depend on them (M Alberti, 2008; Grimm et al., 2008;

95   Pickett et al., 2001). Cities are unlike any other ecosystems because they are quintessentially

96   built by and for one species: humans – a highly social, interconnected, and omnipresent

97   ecosystem engineer (Smith, 2007). As a result, the study of urban ecosystems should involve

98   novel approaches by urban ecologists and evolutionary biologists to better integrate human

99   social patterns and processes and build a truly synthetic understanding of the evolutionary

100   ecology of cities (Figure 1).

101   **Urban ecosystems** (Definition: Box 1) are abiotically and biotically distinct from non-urban

102   areas in that they feature human-built structures, a high proportion of impervious surface,

103   reduced vegetation cover, elevated pollution levels, and a disproportionately large number of

104   exotic species (Grimm et al., 2008; Seto, Sánchez-Rodríguez, & Fragkias, 2010). They are further

105   characterized by altered patterns of connectivity, resource availability, inter- and intraspecific

106   interactions, temperature, and habitat structure (Groffman et al., 2014; Walsh et al., 2005).

107   Unsurprisingly, research has shown that these urban drivers have substantial effects on both

108   ecological and evolutionary processes (M Alberti, 2016; Donihue & Lambert, 2015; Johnson &

109   Munshi-South, 2017; Szulkin, Munshi-South, & Charmantier, 2020). In many cases, the biological

110   community composition, population demographics (Parris, 2016), phenotypic traits (Merckx,

111   Kaiser, & Van Dyck, 2018), and genetic makeup (Munshi-South, Zolnik, & Harris, 2016) of urban

112   organisms differ substantially from their non-urban counterparts.

113   The structure and composition of urban ecosystems are predominantly a consequence of

114   **human society** (Definition: Box 1), which reflects the complex interplay among culture, economy,

115   politics, and technology (Avolio, Pataki, Trammell, & Endter-Wada, 2018; Collins et al., 2000;

116   Grove, Locke, & O'Neil-Dunne, 2014; Marzluff, 2008). As a result, urban ecological and

117   evolutionary processes are intrinsically influenced by social patterns and processes (Figure 2;

118   Grove et al., 2014; Troy, Grove, & O'Neil-Dunne, 2012). Not only are human activities an

119   underlying driver of ecological and evolutionary processes in cities, these processes feed back to

120   affect human health and wellbeing through **nature's contributions to people** (Definition: Box 1;

121   Díaz et al., 2018), including both ecosystem (Daily, 1997) and "evosystem" (Faith et al., 2010;

122   Faith, Magallón, Hendry, & Donoghue, 2017; Rudman, Kreitzman, Chan, Schluter, & Rudman,

123   2017) services and disservices. These processes may further shape and reshape human attitudes

124   and behaviours towards the environment and biodiversity conservation (Reddy et al., 2017).

125   As cities have grown, so too has interest in the myriad intersections between human life

126   and the lives of other species. During the last three decades, the field of **urban ecology**

127   (Definition: Box 1) has made large strides in integrating human social dimensions into the study

128   of urban ecosystems by fostering new collaborations between natural and social scientists.

129   These collaborations have uniquely explored how urbanization shapes ecological processes,

130   promoting the understanding of cities as ecosystems where humans play a fundamental role in

131   regulating environmental patterns and processes (Alberti, 2008; Liu et al., 2007). Studies on

132   **urban evolutionary biology** (Definition: Box 1) have also increased in recent years (Johnson &

133   Munshi-South, 2017; Rivkin et al., 2019; Szulkin et al., 2020). Although some of the earliest work

134   showing evidence of natural selection focused on urban **adaptive evolution** (Definition: Box 1;

135   Kettlewell, 1958), recent advances in molecular techniques and a broader understanding of the

136   role of gene flow and neutral evolution have contributed to a wealth of research on how **non-**

137   **adaptive evolution** (Definition: Box 1) - including patterns of genetic drift and gene flow -

138   operates in cities (Miles, Rivkin, Johnson, Munshi-South, & Verrelli, 2019; Rivkin et al., 2019;

139   Schmidt, Domaratzki, Kinnunen, Bowman, & Garroway, 2020; Szulkin et al., 2020). Increasing

140   research on urban evolutionary biology has also coincided with the growing field of **eco-**

141   **evolutionary dynamics** (Definition: Box 1), which aims to understand the interactions and

142   feedbacks between evolutionary and ecological processes (Fussmann, Loreau, & Abrams, 2007;

143   Hendry, 2017; Schoener, 2011). Researchers of both urban evolutionary biology and eco-

144   evolutionary dynamics tend to focus on contemporary evolution in species that can have

145   important ecological – or even social – feedbacks (Faith et al., 2010, 2017; Rudman et al., 2017);

146   few, however, have examined the presence and strength of eco-evolutionary dynamics in urban

147   ecosystems (M Alberti, 2015).

148   In recent years, interdisciplinary progress has been made showing how social processes

149   influence ecological dynamics (Band, Cadenasso, Grimmond, Grove, & Pickett, 2005; Liu et al.,

150 2007), how evolutionary dynamics feed back on ecology (Fussmann et al., 2007; Hendry, 2017;

151 Pelletier, Garant, & Hendry, 2009) and how evolutionary dynamics contribute to society (Faith et

152 al., 2010; Palumbi, 2001). However, a general framework for addressing the relationships among

153 all three dimensions – social, ecological, and evolutionary – is still lacking. In particular, little

154 research fully integrates urban evolutionary biology with eco-evolutionary dynamics (but see

155 (Brans, Jansen, et al., 2017) and rarely do either of these fields fully consider the role of human

156 social processes on the eco-evolutionary dynamics in cities (but see Schell et al., *In Revision*). We

157 argue that cities present an opportunity to integrate the fields of social science, ecology, and

158 evolutionary biology for the following reasons: 1) urban ecosystems are biotically and abiotically

159 distinct, potentially resulting in unique effects on ecological and evolutionary dynamics

160 compared to non-urban systems; 2) social patterns and processes are concentrated in cities,

161 where they modify the ecological stage on which evolution takes place, thereby affecting urban

162 eco-evolutionary dynamics; 3) ecological and evolutionary processes in cities are likely to feed

163 back on humans and society; 4) these feedbacks might be magnified or dampened depending on

164 the social and urban contexts in which they occur.

165   The goal of this perspective piece is to provide a "**socio-eco-evolutionary dynamics**"

166 (Definition: Box 1) framework for evolutionary ecologists studying urban ecosystems. We

167 highlight the importance of integrating social patterns, processes, and responses in research on

168 urban ecology, evolutionary biology, and eco-evolutionary dynamics. Further, we use examples

169 from specific study systems and describe how existing frameworks from research in these fields

170 may be extended to include social dimensions. We close by laying the groundwork for future

171 research on urban socio-eco-evolutionary dynamics with a set of empirical and theoretical

172 guidelines and questions.

173

174 **Linking urban social processes with ecology and evolution**

175   Characteristics of human society – demography, culture, governance, economics, and

176 social organization (Odum, 1943; Tipps, 1973) – not only govern interactions among humans, but

177 also influence human interactions with nature. Humans have always engaged in socio-ecological

178 and socio-evolutionary relationships, whether through hunting and gathering, domestication and

179 agriculture, or the use of natural resources to build civilizations and cities (Boivin et al., 2016;

180 Sullivan, Bird, & Perry, 2017). Through these relationships, humans have not only fragmented

181 and connected species' populations, but also constructed and modified their ecological niches. A

182 wealth of research from a diversity of disciplines (e.g., political ecology, cultural anthropology,

183 sociology) has revealed the ubiquity of complex interactions between human society and nature

184 through millennia and across geographic regions (Boivin et al., 2016; Ellis, 2015; O'Brien &

185 Laland, 2012). This research has laid the groundwork for studying the interactions among social,

186 ecological, and evolutionary dynamics in cities.

187

188 *Social drivers of urban ecology*

189   In recent years, urban ecology has emerged as a unified discipline, focusing on the many

190 ways in which urbanization alters abiotic and biotic conditions that influence species

191 interactions, patterns, and processes and how those processes feed back to people via changes

192 in ecosystem services (Collins et al., 2000; Grimm, Grove, Pickett, & Redman, 2000). Intraspecific

193 (communication, mating behaviour, within-species competition) and interspecific (mutualism,

194 predation, herbivory, and among-species competition) interactions - including with humans - can

195 differ significantly between urban and surrounding nonurban habitats (Miles, Breitbart, Wagner,

196 & Johnson, 2019; Pereira-Peixoto, Pufal, Staab, Feitosa Martins, & Klein, 2016; Rodewald,

197 Shustack, & Jones, 2011). Urban ecology has increasingly integrated human social patterns and

198 processes in the study of urban ecosystems (M Alberti, 2008; Grimm et al., 2000; Marzluff, 2008;

199 Tanner et al., 2014), recognizing that cities comprise a mosaic of natural and built habitats with

200 varying disturbance across space and time (Pickett, Cadenasso, Childers, McDonnell, & Zhou,

201 2016; Savage, Hackett, Guénard, Youngsteadt, & Dunn, 2015).

202   Redefining cities as intrinsically **coupled human and natural systems** (also known as

203 CHANS: Box 2) acknowledges not only that social decisions shape urban ecosystems, but also

204 that ecological changes motivate important human decisions (Liu et al., 2007). Decisions and

205 policies made at various social scales - individuals, neighbourhoods, businesses, or municipal and

206 national governments - can both directly regulate and be regulated by urban decision-making

207 and its ecological effects (Pickett et al., 2016). For example, planted trees and gardens regulate

208   air filtration and micro-climates, sump ponds act as stormwater reservoirs, and restored soil and

209   macrophyte communities treat sewage and chemical waste via nutrient uptake and bio- and

210   phytoremediation (Jabeen, Ahmad, & Iqbal, 2009; Zipperer, Morse, & Gaither, 2011). Parks

211   provide recreational and cultural amenities that not only benefit people and reshape ecological

212   processes, but are fundamentally driven by human choices (Ackley, 2014; Bolund & Hunhammar,

213   1999; Leong, Bertone, Bayless, Dunn, & Trautwein, 2016). The CHANS (Box 2) literature has

214   provided a useful framework for studying urban ecology, but it has yet to incorporate

215   evolutionary biology and eco-evolutionary dynamics.

216

217   *Social drivers of urban evolution*

218   A large body of research has revealed that the historical rise of aggregated human

219   communities and subsequent origin of the first cities reflect deep interactions between social

220   and evolutionary processes. The advent of the agrarian societies predating modern cities is

221   reflected in the genomes of humans and domesticated species (O'Brien & Laland, 2012). For the

222   past fifteen thousand years, cultural and agricultural practices have led to strong selection on

223   numerous species (Driscoll, Macdonald, & O'Brien, 2009; Larson & Fuller, 2014) as well as

224   coevolutionary relationships with humans (Jackson, 1996; Leach, 2003). For example,

225   coevolution between humans and crop plants (Perry et al., 2007; Ye, Gao, Wang, Bar-Yosef, &

226   Keinan, 2017) and between humans and livestock (Tishkoff et al., 2007) is associated with the

227   advent of agriculture and the abandonment of nomadic hunter-gatherer lifestyles. For example,

228   genes for lactase that enables dairy consumption (Tishkoff et al., 2007), and amylase that aids

229   starch consumption (Perry et al., 2007), show geographically-spatial and cultural patterns of

230   balancing selection for diverse diets.

231   Historical and contemporary evolutionary patterns in species most closely associated

232   with humans can reflect social, cultural, and even economic trends and trajectories. Indeed,

233   biologists have learned a great deal about evolutionary processes through researching social-

234   evolutionary processes such as domestication. Darwin (1859) built his argument of evolution by

235   natural selection through analogy with artificial selection in the domesticated rock pigeon

236   (*Columba livia*) and other animals. Today, evidence suggests that some of the pigmentation

237 patterns originally favored by fancy pigeon breeders confer an adaptive advantage for urban

238 pigeons (Vickrey et al., 2018), demonstrating the influence of past social preferences on the

239 evolutionary history of a species. Domesticated dogs (*Canis familiarus*), which have undergone

240 thousands of years of artificial selection, still commonly interbreed with wild coyote (*Canis*

241 *latrans*; (Mahan, Gipson, & Case, 1978) and wolf (Pilot et al., 2018) populations. Studies have

242 shown that dogs are often less likely to be neutered and more likely to be abandoned in lower-

243 income urban areas following widespread economic downturns (Morris & Steffler, 2011). Thus,

244 the observed introgression of domestic dog alleles into nearby coyote or wolf populations could

245 potentially be the result of socioeconomic patterns, though this has yet to be directly tested.

246   Some of the classic examples of adaptation by natural selection invoke urban social

247 processes. Pollution and habitat degradation often accompany major technological innovations

248 that are later followed by policies mitigating their damage. For example, during the industrial

249 revolution in the United Kingdom, increasing urban activity deposited a layer of dark soot on the

250 bark of surrounding trees that selected for rarer melanic variants of the commonly light-coloured

251 peppered moth (*Biston betularia*), which became more cryptic and less subject to predation

252 (Cook & Saccheri, 2013; Hof et al., 2016; Kettlewell, 1958). The Clean Air Act, enacted in the UK

253 in 1956, decreased pollutants, leading to an evolutionary reversal whereby light coloured moths

254 again increased in frequency (Cook & Saccheri, 2013). In this iconic natural selection case study,

255 the evolutionary trajectory of urban-adjacent peppered moth populations ostensibly reflected

256 human societal patterns of socio-economic and technological innovations, their impacts, and

257 environmental policy.

258   Today, many evolutionary biologists explore how species respond to novel selection

259 pressures in urban environments (M Alberti, 2015; Donihue & Lambert, 2015; Johnson &

260 Munshi-South, 2017; Szulkin et al., 2020). These selection pressures can vary over fine spatial

261 and temporal scales (Donihue & Lambert, 2015), providing a more realistic context for studying

262 in-situ evolution. For example, populations of killifish (*Fundulus heteroclitus*) from four cities

263 have convergently evolved novel adaptations which confer resistance to toxins in response to

264 pollution in urban estuaries (Reid et al., 2016; Whitehead, Clark, Reid, Hahn, & Nacci, 2017). In

265 another example, white clover (*Trifolium repens*) has shown repeated phenotypic convergence in

266 the loss of cyanogenesis in response to urbanization (Case Study: Box 3a; Johnson et al., 2018;

267 Santangelo, Johnson, & Ness, 2018; Thompson, Renaudin, & Johnson, 2016); There is also

268 increasing evidence for adaptations to stressors such as urban heat islands (Brans & De Meester,

269 2018; Diamond, Chick, Perez, Strickler, & Martin, 2018), which are characteristics that are also

270 reflective of income inequality among urban neighbourhoods (Chakraborty, Hsu, Manya, &

271 Sheriff, 2019). Researchers have also shown that species might be insulated from selection

272 pressures in urban environments that exclude their predators (Rebolo-Ifrán, Tella, & Carrete,

273 2017), though little work has evaluated the evolutionary consequences of such relaxed

274 pressures.

275   Most urban evolutionary biology research to-date has focused on instances of non-

276 adaptive evolution showing, for instance, altered patterns of gene flow and genetic drift in cities

277 (Bullock et al., 2018; Miles, Breitbart, et al., 2019; Schmidt et al., 2020). These genetic patterns

278 can reflect human decisions to construct barriers and corridors that impact the dispersal and

279 thus gene flow of both native and human-affiliated species such as pests, disease vectors, and

280 invasive species (Harris et al., 2016). In particular, overlaying genetic patterns on city maps has

281 led to a more comprehensive understanding of dispersal and relatedness among populations of

282 nuisance species (Combs, Puckett, Richardson, Mims, & Munshi-South, 2018), and thus an ability

283 to predict future spread of pest species and resistance alleles through neighbourhoods (Rost et

284 al., 2009). There is evidence from genetic analyses of neutral genetic variation that native

285 species are negatively affected by urban fragmentation (Delaney, Riley, & Fisher, 2010; Van

286 Rossum, 2008), whereas exotic species can benefit from the deliberate transportation and

287 establishment by humans who favor them for both private and public gardens and parks (Colla &

288 MacIvor, 2017; Trusty, Goertzen, Zipperer, & Lockaby, 2007; Zengeya et al., 2017). Because

289 human decisions and activities structure nearly every aspect of urban ecosystems, studying and

290 quantifying their consequences and feedbacks will be essential for a holistic understanding of

291 evolution in cities.

292

293 **Eco-evolutionary dynamics in cities**

294   The field of eco-evolutionary dynamics emerged from growing evidence of reciprocal

295   feedbacks between ecological and evolutionary processes that are possible when both occur at

296   similar temporal and spatial scales (Hairston, Ellner, Geber, Yoshida, & Fox, 2005; Hendry &

297   Kinnison, 1999; Reznick & Ghalambor, 2001; Thompson, 1998). One of the central tenants of

298   eco-evolutionary dynamics is that evolutionary trait change within species (intraspecific

299   variation) not only influences population dynamics (e.g., migration, reproduction), but also

300   interactions between organisms and their surroundings, thereby affecting ecological patterns

301   and processes like community composition and primary productivity (Des Roches et al., 2018;

302   Fussmann et al., 2007; Hendry, 2017). These altered ecological conditions can then feed back to

303   cause further evolutionary change. These feedbacks are at the centre of experiments and

304   mathematical models of eco-evolutionary dynamics, which have demonstrated their importance

305   and prevalence in controlled laboratory settings as well as natural and altered habitats (Abrams

306   & Matsuda, 1997; Bassar et al., 2010; Harmon et al., 2009; Loeuille & Leibold, 2008; Palkovacs &

307   Post, 2009; Yoshida, Jones, Ellner, Fussmann, & Hairston, 2003). Many of these studies have

308   underscored the importance of rapid evolution and genetic variation in conservation and

309   management strategies for species impacted by anthropogenic threats (Allgeier et al., 2020;

310   Merilä & Hendry, 2013; Nadeau & Urban, 2019; Urban et al., 2016; Wood, Palkovacs, & Kinnison,

311   2018). Still, relatively little research has explicitly examined the existence and role of eco-

312   evolutionary feedbacks in cities (but see Brans et al., 2017). Indeed, conservation in cities will

313   benefit greatly from a better understanding of urban evolution and how it impacts management

314   success .

315   Urban eco-evolutionary feedbacks are particularly relevant because they have the

316   potential to affect a great number of people through ecosystem and "evosystem" services (or

317   "natures contributions to people") and disservices (Bolund & Hunhammar, 1999; Jenerette,

318   Harlan, Stefanov, & Martin, 2011; Pascual et al., 2014). These feedbacks, which can extend

319   beyond the boundaries of cities themselves (Jiang, Deng, & Seto, 2013; Kaufmann et al., 2007;

320   Seto et al., 2010), affect species persistence, abundance, and population demographics, thereby

321   influencing diverse ecological functions and both beneficial and detrimental ecosystem services

322   (Faith et al., 2010). Further, eco-evolutionary feedbacks toward humans can be unevenly

323   distributed within and among cities, leading to unequal distribution of services and disservices

324   across human society (Bolund & Hunhammar, 1999; Jenerette et al., 2011; Pascual et al., 2014).

325   For example, affluent neighbourhoods can have larger, more diverse (Jenerette et al., 2011;

326   Oertli & Parris, 2019), and better interconnected green and blue spaces that support more

327   abundant, genetically variable, and therefore more stable populations of beneficial species such

328   as pollinators (Gill et al., 2016). However, these neighbourhoods can also have a higher

329   proportion of non-native species in gardens and monoculture lawns that are manicured and

330   eradicated of native weeds (Lerman & Warren, 2011; Tallamy, 2020). Green roofs, which are

331   becoming a common feature of newer buildings, can be genetically depauperate and thus

332   harmful to local conspecifics and pollinators unless careful consideration is given to the initial

333   seed stock (Ksiazek-Mikenas, Fant, & Skogen, 2019). Although non-native species might initially

334   boost diversity and ecosystem function (Wilson & Jamieson, 2019), they can become invasive

335   through evolutionary processes such as hybridization (Culley & Hardiman, 2009; Rius & Darling,

336   2014) and introduce novel diseases and pests (Chifflet, Guzmán, Rey, Confalonieri, & Calcaterra,

337   2018; Eritja et al., 2005; Juliano & Philip Lounibos, 2005; Salyer, Bennett, & Buczkowski, 2014)

338   that negatively affect native species (Godefroid, 2001; Shochat, Warren, Faeth, McIntyre, &

339   Hope, 2006; Wania, Kühn, & Klotz, 2006).

340   Some of the most important eco-evolutionary feedbacks on people living in cities occur

341   through the spread of organisms and genes that provide "disservices" such as negative effects

342   on human health and wellbeing (Evans & Wellems, 2002). Again, the burdens of these

343   detrimental feedbacks are unevenly distributed across the urban landscape. For example,

344   rodenticide resistance in brown rats disproportionately affects the lower socio-economic

345   communities that are more burdened by these pests (Case Study Box 3a; Desvars-Larrive et al.,

346   2017). In some cases, humans have coevolved with urban pests such as mosquitos (Kamdem,

347   Fouet, Gamez, & White, 2017; Sabeti et al., 2002) and their malaria-causing pathogens (Case

348   Study Box 3b; Evans & Wellems, 2002). Feedbacks from rapidly evolving pest and pathogen

349   species may be particularly extreme in cities and neighbourhoods where human hosts are living

350   in concentrated areas, such as in lower-income public housing and apartment complexes (Booth

351   et al., 2012; Byers, Lee, Patrick, & Himsworth, 2019; Combs et al., 2018; Koch et al., 2016; Saenz,

352 Booth, Schal, & Vargo, 2012). For example, rampant urban bed bug infestations, again usually in

353 lower income neighbourhoods, are an outcome of higher human density, frequent tenant and

354 resident turnover, increased reliance on public transportation, and the common exchange of

355 second-hand and used goods (Booth et al., 2012). Not only does increased turnover and human-

356 human contact lead to more frequent colonization of these pests, but it also introduces adaptive

357 alleles conferring resistance to common pesticides, thereby further facilitating their spread and

358 persistence (Saenz et al., 2012). Similar transmission of resistance alleles has been documented

359 in other pest and pathogen species such as head lice (Koch et al., 2016), German cockroaches

360 (Wada-Katsumata, Silverman, & Schal, 2013) and malaria (Kamdem et al., 2017). Higher

361 connectivity in urban centres can in some cases promote genetic diversity and persistence in

362 pest and pathogen populations by facilitating gene flow, such as with black widow spiders (Miles,

363 Dyer, & Verrelli, 2018). Explicitly assessing the responses of organisms to features of urban

364 ecosystems such as green space, pollution, waste, and food availability, will improve our

365 understanding of the interface among social, ecological, and evolutionary dynamics in cities.

366   Relatively little research has compared the strength of eco-evolutionary feedbacks

367 between urban and non-urban ecosystems (Miles, Breitbart, et al., 2019). In some cases,

368 feedbacks might be magnified in urban areas: for example, white clover – a common herbaceous

369 plant in urban and parks lawns – has adaptations that likely contribute to its continued

370 persistence in lawns and parks (Case Study Box 3c; Johnson et al., 2018; Thompson et al., 2016),

371 leading to positive feedbacks for beneficial species, such as pollinators and nitrogen-fixing

372 bacteria (Baude et al., 2016; Larson, Kesheimer, & Potter, 2014). Alternatively, feedbacks from

373 evolutionary processes may be overshadowed or weakened due to external forces: for example,

374 *Daphnia* – a genus of ubiquitous freshwater zooplankton – are known to exert strong top-down

375 control on algae and can adapt to increased temperatures in urban ponds (Case Study Box 3d;

376 Brans, Jansen, et al., 2017). However, disturbances, such as extreme heat waves or extensive

377 eutrophication following the build-up of nutrient runoff can compromise *Daphnia*'s capacity to

378 adapt and maintain its algae-controlling ecological function. The loss of this function from the

379 system can initiate drastic shifts in the pond ecosystem, including the spread of toxic algal

380 blooms (Ger et al., 2016) that not only limit the diversity and abundance of insects, amphibians,

381   and submerged vegetation, but also present a public health concern to humans and their pets

382   (Kosten et al., 2012; Thomaz & Cunha, 2010). Feedbacks from species like white clover and

383   *Daphnia* may be more nuanced, though still broadly important for ecosystem function and

384   services in cites.

385

386   **Towards an urban socio-eco-evolutionary framework**

387   Despite an inherent spatial and temporal heterogeneity of cities, research on urban

388   ecology and evolutionary biology often defaults to simplistic unidimensional, linear, or

389   dichotomous urban variables (e.g., urban versus nonurban, proportion of built-up area and other

390   land cover classes, human population density) that consider urbanization as a continuous

391   gradient (McPhearson et al., 2016; Moll et al., 2019). Although these aggregate proxies are

392   capable of capturing some urban variation, they often fail to encapsulate the complexity of

393   urban systems that are driven by social and ecological interactions (Alberti et al., In Press; Schell

394   et al., *In Revision*). Acknowledging and incorporating spatial and temporal heterogeneity in these

395   interactions will be important for studying urban eco-evolutionary dynamics. For example,

396   access to food, public transit routes, waste management, and green space usually vary

397   nonlinearly with urban zoning. Further, historical redlining practices that reflect underlying racist

398   policies have led to an uneven distribution of infrastructure and social services that structure the

399   urban ecosystem in many US cities (Grove et al., 2014; Locke et al., 2020; Roman et al.,

400   2018).Below, we argue that study of socio-eco-evolutionary dynamics in cities requires an

401   approach that addresses and acknowledges these complex, multivariate, and heterogeneous

402   stressors. First, we describe how existing phenotypic and genomic approaches for studying eco-

403   evolutionary dynamics might be extended to include the social patterns and processes intrinsic

404   to urban ecosystems. Second, we suggest how the coupled human and natural systems

405   framework – a central tenant of urban ecology – might incorporate evolutionary biology, and by

406   extension, eco-evolutionary dynamics, to help understand socio-ecological processes and

407   feedbacks. Finally, we overview the opportunities for studying socio-eco-evolutionary dynamics,

408   stressing a thorough and systematic identification of the demographic, cultural, political,

409   economic, and technological drivers that shape and are shaped by urban ecology and evolution.

410

411 *Extending eco-evolutionary dynamics to include human society*

412   The concept of the **evolving metacommunity** (Definition: Box 1) is one example of a

413 current framework in evolutionary ecology that can be used to study socio-eco-evolutionary

414 dynamics in urban ecosystems. This framework considers organisms within networks of

415 interconnected populations and communities (Urban & Skelly, 2006). Biological responses to

416 environmental changes are therefore governed by a dynamic interplay between local and

417 regional processes, including species sorting, adaptation, dispersal and gene flow (Urban &

418 Skelly, 2006). Extending the evolving metacommunity theory to incorporate the effects of

419 humans and social dimensions will be an important consideration in studying eco-evolutionary

420 dynamics in urban ecosystems. In these ecosystems, individuals, populations, and communities

421 are nested in a mosaic of habitats that are interconnected and fragmented by human activity

422 and infrastructure. While roads, waterways, and built structures isolate and restrict distribution

423 in some species, they connect and disperse others that are more closely associated with humans

424 (Miles, Rivkin, et al., 2019).

425   Humans might also be uniquely incorporated into evolving metacommunity models as

426 species themselves. As with other interacting species, human populations are characterized by

427 varying abundance and distribution that reflects their interactions with local environments. As

428 important ecosystem engineers (Smith, 2007), humans can impose selection on other species.

429 Other species and their adaptations might also feed back to affect human densities, habitat

430 choices, settlement and movement patterns. At broader spatial scales, urban influences on

431 surrounding environments extend well beyond the geographic boundary of a city, making the

432 hierarchical structure of the evolving metacommunity theory also helpful for studying urban eco-

433 evolutionary dynamics. Including social components like transportation infrastructure,

434 neighbourhood cohesion, and socioeconomic geography, may allow for more accurate

435 predictions. For example, a consideration of international travel networks, national quarantine

436 and customs policies, and trade embargos can help predict the evolution and spread of

437 pathogenic, invasive, and pest species (Helmus, Mahler, & Losos, 2014; Jones et al., 2008; Miles,

438 Rivkin, et al., 2019). While challenging, a thorough incorporation of human social patterns and

439   processes into ecological and evolutionary dynamics will lead to novel insights for understanding

440   urban ecosystems.

441

442   *Extending urban coupled human and natural systems to include evolution*

443   An additional approach to studying socio-eco-evolutionary dynamics in cities is by

444   extending urban ecology's CHANS models (Box 2; Liu et al., 2007) to include evolutionary

445   processes and feedbacks. These models have shown that human socioeconomic and

446   demographic patterns and processes are reflected in infrastructure and other abiotic and biotic

447   features of the urban ecosystem (Schaider, Swetschinski, Campbell, & Rudel, 2019; Tessum et al.,

448   2019). Urban evolution research has simultaneously revealed that these same physical and

449   biological characteristics can influence both the adaptive (Brans & De Meester, 2018; Whitehead

450   et al., 2017) and non-adaptive (Combs et al., 2018; Munshi-South, 2012) evolution of urban

451   species. Indeed, recent work has shown that urban predictor variables that characterize

452   socioeconomic heterogeneity, such as urban heat islands (Brans & De Meester, 2018), and

453   environmental pollutants (Isaksson, 2015; Reid et al., 2016; Wirgin et al., 2011), can drive

454   physiological and life-history adaptations in organisms. Recent work in Baltimore, USA, has

455   shown that tiger mosquitoes (*Aedes albopictus*) in low-income neighbourhoods tend to have

456   larger wing and body sizes - traits linked to increased fecundity, survival, and ultimately spread of

457   disease (Katz, Leisnham, & LaDeau, 2019). The distribution of these human influences is a direct

458   result of socially-driven urban form underpinned by exacerbating legacies of income inequality

459   and segregation over decades and centuries (Grove et al., 2018; Roman et al., 2018). Integration

460   of social processes and their relevant eco-evolutionary feedbacks may therefore serve dual

461   functions; first, by increasing our understanding of the value of ecological and evolutionary

462   processes in cities, and second, by providing the applied tools to mitigate urban disturbances on

463   ecosystems.

464

465   *Opportunities for studying socio-eco-evolutionary dynamics*

466   To fully understand urban eco-evolutionary dynamics, we need to explicitly identify the

467   mechanisms by which human society influences ecology, evolution, and their feedbacks. Urban

468   ecosystems are constantly changing as a result of social decisions and processes such as public

469   policies and private landownership. Humans also interact dynamically within their communities

470   through multiple networks like economic markets and public institutions. For example, urban

471   residents depend on large-scale built infrastructures (e.g., as electric power, water supply, food

472   distribution, and transportation networks) that sustain resource flows within and across cities

473   (Childers et al., 2015). These interactions contribute to unique physical (e.g., sprawl), social (e.g.,

474   cultural and economic segregation), and economic (e.g., land values and use) properties of cities

475   that can affect ecological and evolutionary processes on broad scales.

476   Urban ecosystems are subject to multiple drivers of human-driven environmental change

477   such that they often experience extreme climatic conditions across multiple axes. How different

478   environmental conditions interact with one another and affect urban organisms is highly variable

479   and poorly understood. Consequently, the responses of organisms to urbanization often cannot

480   be predicted based on studies of any environmental condition in isolation. For example,

481   researchers showed that bird life-history traits were better predicted by a simple model that

482   tested the effect of urban vs non-urban habitats compared to models that included four

483   separate environmental variables that were each correlated with urbanization (temperature,

484   humidity, artificial light, and noise). The better fit of the simple model suggests that additional

485   unmeasured variables account for the differences in life-history along urban rural gradients, and

486   thus many ecology, social and evolutionary factors likely need to be included to accurately

487   predict traits changes associated with urbanization (Sprau, Mouchet, & Dingemanse, 2017).

488   Landscape transformation, infrastructure development, and complex social and political

489   networks vary considerably across regions, causing heterogeneity within and among cities that

490   can influence ecological and evolutionary processes (Alberti et al., In Press). For example,

491   variation in land use patterns reflect a complex interplay among homeowners' choices, real

492   estate markets, local businesses, and policy makers (M Alberti, 2008). These interactions can

493   affect the arrangement and proportion of built and natural land cover, thereby influencing

494   organisms and their habitats. Quantifying socio-economic variables can help with the

495   construction and parameterization of urban eco-evolutionary dynamics models (McPhearson et

496   al., 2016). These variables include the distribution of transportation networks (i.e., accessible

497   from municipal resources), built infrastructure (i.e., from urban planning), and land use (i.e.,

498   from GIS and satellite imagery), as well as attributes of human demographics and society (i.e.,

499   from census and other survey data). Participatory science (also called citizen or community

500   science) efforts in particular present an important opportunity both for collecting large-scale

501   eco-evolutionary (Cooper, Dickinson, Phillips, & Bonney, 2007) and socioecological data (Crain,

502   Cooper, & Dickinson, 2014) and for promoting science to the general public using surveys,

503   audiovisual data-collection apps (e.g., SpiderSpotter, Bloomin'Algae, iNaturalist, eBird, iSpot),

504   and other technological platforms (Krasny, Russ, Tidball, & Elmqvist, 2014).

505   The relative predictability of urban sprawl also provides an important avenue for

506   initiating longitudinal studies that collect baseline data and track the development and

507   restoration of landscapes through time (Etterson et al., 2016). In particular, researchers can

508   measure social, ecological, and evolutionary parameters at pre-, intermediate- and post-

509   urbanization time points and at different levels of biological organization, contrasting urbanized,

510   urbanizing, and non-urbanizing sites, within and across cities. These research strategies can

511   enable reconstruction of population genetic and phenotypic diversity and change, as well as

512   community composition and species diversity over time. Socio-demographic and socio-economic

513   changes can be monitored in parallel to determine potential drivers of eco-evolutionary change

514   in cities.

515   Identifying the underlying sources of phenotypic variation is crucial for assessing the

516   relationships and feedbacks among social, ecological, and evolutionary processes in urban

517   ecosystems. Most traits are the product of both genetic and environmental factors. As a result,

518   purely phenotypic studies can confound the inference of eco-evolutionary dynamics if they do

519   not account for the joint effects of plasticity and genetics on phenotypic variation and fitness

520   (Brans, Jansen, et al., 2017; Govaert, Pantel, & De Meester, 2016). The inference of urban

521   evolution in instances of polygenic inheritance, in particular, necessitates standardized common

522   garden or reciprocal transplant experiments to evaluate both the heritability as well as the

523   fitness consequences of supposed urban traits (Thompson et al., 2016). For example,

524   researchers used reciprocal transplants with common ragweed to identify local adaptation and

525   divergent selection between populations in urban and non-urban habitats (Gorton, Moeller, &

526   Tiffin, 2018). Studies like these can be replicated across multiple urban gradients and sampling

527   plots within and among different cities and neighbourhoods to test the ubiquity and

528   convergence of evolutionary trajectories. Variance partitioning metrics (Govaert, 2018; Govaert

529   et al., 2016; Lajoie & Vellend, 2015) can further help disentangle the relative contributions of

530   plasticity and genetics underlying intraspecific trait variation, community ecology, and ecosystem

531   processes (Brans, Govaert, et al., 2017; Stoks, Govaert, Pauwels, Jansen, & Meester, 2016). Such

532   analyses will be essential for understanding socio-eco-evolutionary dynamics.

533

534   **Looking forward: future studies in socio-eco-evolutionary dynamics**

535   Urban ecosystems are fundamentally regulated, transformed, and interconnected by

536   human activity. Thus, integrating human social patterns and processes in urban evolution studies

537   not only presents an opportunity for novel research, but is also imperative for accurately

538   understanding contemporary ecological and evolutionary dynamics in cities. As we move

539   forward, we argue that more fully integrating evolutionary ecology research with the social

540   sciences to address socio-eco-evolutionary questions is critical because:

541   1.   Accurate predictions about urban coupled human and natural systems (CHANS) will

542   require understanding the role of evolution in socio-ecological systems over various

543   timescales.

544   2.   A complete understanding of urban eco-evolutionary dynamics will require an explicit

545   consideration of social patterns and processes.

546   3.   The world is increasingly urbanized and the effects of cities extend beyond their borders.

547   Hence, understanding ecological responses to global change will depend on our ability to

548   address #1 & 2

549

550   **Conclusion**

551   Studies of cities as coupled human and natural systems (CHANS) and of eco-evolutionary

552   dynamics have already provided insights into how urban ecosystems are likely to change over

553   time. We now have the opportunity to leverage these existing bodies of work to create an

554   integrative framework that more fully resembles the simultaneous social, ecological, and

555   evolutionary dynamics in urban ecosystems. We encourage a new collaboration among social

556   scientists, ecologists, and evolutionary biologists to develop more sophisticated questions,

557   increasingly accurate models of urban systems, and garner a greater understanding of dynamics

558   both within and beyond city boundaries. Understanding urban evolutionary biology will have

559   vast implications for socio-ecological policies such as those relating to biodiversity management

560   and ecological restoration as well as human health, wellbeing, and equity. Additionally, we

561   suggest specific, important, and timely questions that can be addressed with an integrated socio-

562   eco-evolutionary framework (Questions: Box 4).

563   Cities provide exciting systems to expand our knowledge of eco-evolutionary dynamics

564   and their social causes and consequences. Studying the social dimensions of eco-evolutionary

565   dynamics in cities will improve our understanding of the complexity of urban biological

566   communities, which will be increasingly crucial for conserving and maximizing ecosystem

567   functions and contributions to people within and outside cities. Urban socio-eco-evolutionary

568   dynamics research provides a unique opportunity to study evolving metacommunities, the

569   interplay between local and regional responses, and the presence and strength of eco-

570   evolutionary feedbacks across multiple taxonomic groups. Just as urban ecology grew to

571   consider the social complexity of cities and eco-evolutionary dynamics integrated the rapid pace

572   of evolution, socio-eco-evolutionary research must recognize the dynamism resulting from the

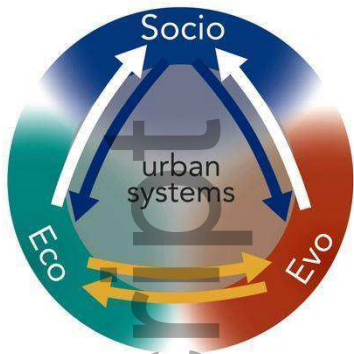573   interplay of social, ecological, and evolutionary dimensions within urban systems.

574

581

582

583

584

Figure 1: Urban ecosystems provide an opportunity to study contemporary evolution and ecological change inherent in eco-evolutionary dynamics (yellow arrows). Because they are fundamentally anthropogenic, eco-evolutionary dynamics in urban ecosystems are strongly linked to human society. Characteristics of human society likely drive (blue arrows) and are impacted by (white arrows) ecological and evolutionary change.

594

595
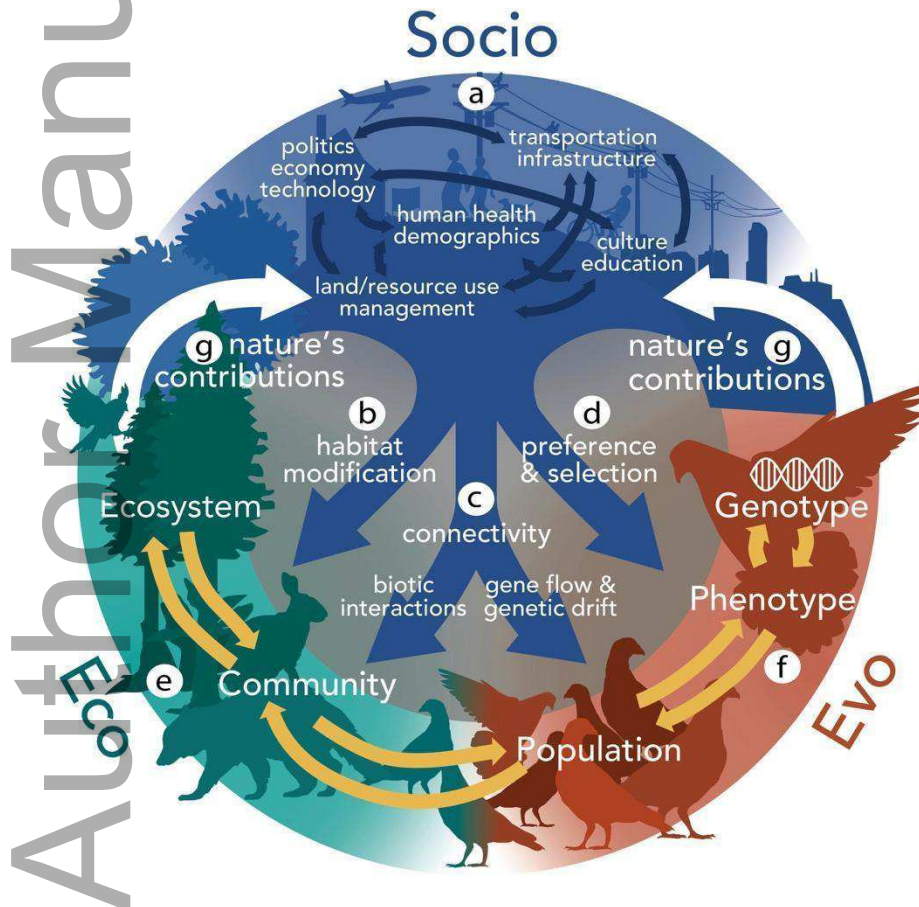
Figure 2: Detailed dynamics among social, ecological, and evolutionary patterns and processes in urban systems. Social patterns and processes (a) encompass a diversity of political, economic and technological drivers that are interrelated with transportation and infrastructure, culture and education, human

599 population demographics, and land/resource use and management. Social drivers affect (b) ecology

600 through habitat modification; (c) ecology (biotic interactions) and evolution (gene flow and genetic drift)

601 through altering connectivity among habitats; and (d) ecology and evolution through selection for

602 preferred genotypes and phenotypes. Ecological (e) and evolutionary (f) dynamics are linked through

603 feedbacks between ecosystems, communities, populations, genotypes and phenotypes. Ecological and

604 evolutionary feedbacks toward society take the form of nature's contributions to people (g) including

605 ecosystem services and disservices.

606 **Boxes**

607

Box 1: Definitions	
Urban Ecosystem	An ecosystem whose biological and physical characteristics are primarily engineered, modified, and constructed by humans. In urban ecosystems, **human society** influences the relationships among organisms and between organisms and the physical environment. Urban ecosystems are characteristic examples of CHANS (Box 2).
Human Society	A group of human beings inhabiting and interacting within a common region, sharing and participating in the same culture (Tischler, 2006) or self-sufficient system that usually persists longer than the life-span of its individual members (Aberle, Cohen, Davis, Levy, & Sutton, 1950).
Urban Ecology	The interdisciplinary study of organismal and ecosystem patterns and processes within and among cities and their relationships with human activities. Urban ecology has increasingly incorporated the study of ecological interactions with **human society** in cities through frameworks such as CHANS (Box 2).
Urban Evolutionary Biology	The study of how urban form and processes shape adaptive (via natural selection) and non-adaptive (via mutation, gene flow, and genetic drift) evolutionary dynamics that occur within or because of cities.
Eco-evolutionary dynamics	The interactions and feedbacks between ecological and evolutionary processes; both the ecological variation that affects evolution *and* the feedbacks of

	evolutionary change on ecological processes. Ecological and evolutionary feedbacks typically center on contemporary **adaptive evolution** of ecologically-relevant traits that alter how organisms interact and function in their ecosystems, for example, influencing their productivity, excretion, or resource consumption (Hendry, 2017).
Socio-eco-evolutionary dynamics	A framework for the integration of social, ecological, and evolutionary patterns and processes that explicitly features the interactions and feedbacks among **human society**, ecology, and both **adaptive** and **non-adaptive evolution**. This framework incorporates human social characteristics, such as economics, culture, and policy, into the study of **eco-evolutionary dynamics** in **urban ecosystems** (Figure 1,2).
Adaptive evolution	The process by which natural selection acts on heritable phenotypic trait variation in a population leading to the increased survival and reproduction (fitness) of individuals with certain trait values.
Non-adaptive evolution	Evolutionary change that is not driven by natural selection, including chance mutation, neutral genetic drift (random changes in the frequency of alleles in a population that is more pronounced in small, isolated populations) and gene flow (the transfer of genetic information among populations due to migration of individuals, gametes, and other propagules.
Nature's contributions to people (NCP)	The essential and often non-replaceable material and assistance (i.e., food, energy, other resources), non-material (i.e., cultural, educational, inspirational) and regulating services (i.e. habitat, climate, and resource maintenance, hazard protection) provided by nature that benefit human existence and wellbeing. The concept of NCP encompasses and extends the former *ecosystem services* (Díaz et al., 2018). Though the new NCP framework does not specifically allude to detrimental feedbacks on humans, authors have also acknowledged *ecosystem disservices*, particularly in **urban ecosystems** (Shackleton et al., 2016). Authors have also recognized *evosystem services* – benefits to humans resulting from evolutionary change (Faith et al., 2010, 2017; Rudman et al., 2017). The concept of NCP is central to **socio-eco-evolutionary dynamics,** as it describes the feedbacks from ecology and evolution toward human society (Figure 2).

Evolving metacommunity framework	A framework describing the spatial context of **eco-evolutionary dynamics** that considers sets of local communities linked by the dispersal of multiple species (a metacommunity) and the change in species interactions with the environment and each other via evolution. This framework integrates community ecology and evolution in local patches with regional dispersal and gene flow among regional patches to understand eco-evolutionary interactions at multiple scales (Urban et al., 2008).

608

609

Box 2: Coupled Human and Natural Systems (CHANS)
Coupled human and natural systems (CHANS) are increasingly pervasive as human activities now influence most natural processes. Researchers recognize CHANS by explicitly acknowledging linked reciprocal interactions between human and natural systems - often characterized by flows of material, energy, and information (Liu et al., 2007; McDonnell & Pickett, 1993). A critical, yet under-recognized component of CHANS is their unexpected feedbacks. These include nonlinear responses and threshold conditions in which system components transition into alternative states, as well as time lags between a stressor and its effects and/or recognition of these effects and the subsequent decisions. Also characteristic of CHANS are emergent properties in which simultaneous changes across multiple variables produce new environmental contexts that cannot be adequately characterized by any single variable or be identified in the human or natural systems alone (Alberti et al., In Press). Given their complex and heterogeneous nature, cities typify CHANS. Urban ecologists have increasingly relied on CHANS conceptual frameworks to understand human-nature connections and dynamics embedded within cities. Doing so has allowed urban ecologists to move from simply studying ecology that occurs within cities to understanding the ecology *of* cities (Grimm et al., 2008, 2000; Pickett et al., 2001). Cities are exemplary CHANS because they are characterized by substantial complexity in ecological, hydrological, and geophysical structure and function across scales as well as complex social hierarchies – from individuals to households, neighbourhoods, municipalities, regions, and nations – with feedbacks occurring within and among various ecological and social scales (Grimm et al., 2008, 2000; Pickett et al., 2001). Because of this complexity, cities and their components cannot simply be understood by measuring human population sizes or densities but require a more comprehensive

assessment of biophysical and social conditions.

610

611

Box 3: Urban Socio-Eco-Evo Dynamics Case Studies

a): Social determinants of rat ecology, evolution, disease transmission, and pest management

Brown, or "Norway" rats (*Rattus norvegicus*) have coinhabited with humans for centuries by exploiting food and built structures (Byers et al., 2019; Gardner-Santana et al., 2009). Brown rats show adaptive resistance to rodenticide commonly used in urban habitats (Desvars-Larrive et al., 2017) and significant genetic differentiation at the city block scale where high traffic roadways limit gene flow across neighbourhoods (Combs, Byers, Himsworth, & Munshi-South, 2019; Combs et al., 2018; Gardner-Santana et al., 2009; Kajdacsi et al., 2013). Garbage management may also influence the population genetic structure of rats such that individuals in resource-rich microhabitats are less likely to disperse and thus aggregate with more closely related kin within small areas (Gardner-Santana et al., 2009). Unsecured food waste, dilapidated structures, and overgrown vegetation all promote increases in rat infestation in urban areas (Murray et al., 2018; M. G. Walsh, 2014) to societal and economic neglect, low-income communities can have the highest aggregation of attractants for brown rats (Byers et al., 2019; Kajdacsi et al., 2013; Murray et al., 2018; Peterson et al., 2020). These dynamics intrinsically link wealth inequality and rat urban ecology. Brown rats are notorious reservoirs of multiple zoonotic pathogens that have myriad negative health implications for humans (Gardner-Santana et al., 2009, p.; Kajdacsi et al., 2013;

Richardson et al., 2017). Brown rats' role as carriers of pathogens underscores the urgent public health priority for socio-eco-evo investigations that inform sustained and efficient pest management practices (Byers et al., 2019; Combs et al., 2019). Recent findings show how rats capitalize on urban centers and can thus inform pest management strategies (Combs et al., 2019). Disenfranchised communities with reduced quality infrastructure should feasibly receive the most targeted and sustained pest control efforts (Peterson et al., 2020). However, many of these

communities are socially and economically neglected, receiving insufficient waste management and public services that would alleviate the conditions that attract brown rats. In combination, these studies demonstrate how social determinants shape ecological conditions that promote rat colonization and adaptation, resulting in negative feedbacks to society in one of the few, fully articulated examples of socio-eco-evolutionary dynamics in cities.
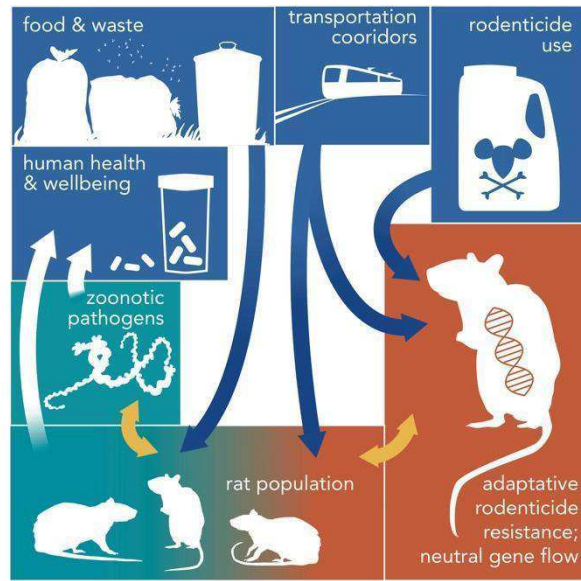
612

613

614

615

616

617

618

619

620

621
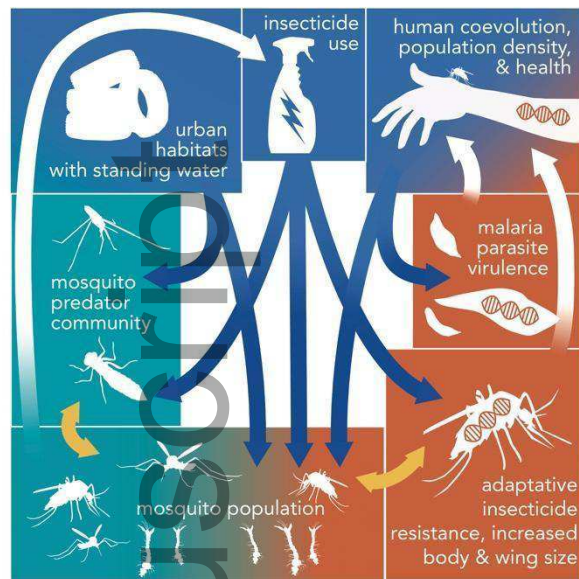
b) Social landscape drivers and pesticides impact mosquito evolution and disease in cities

Mosquitoes (including *Aedes aeqypti* and *Culpex pipiens)* are ubiquitous across the globe, and are prominent vectors for human disease (e.g., Zika virus, Malaria, Dengue fever, West Nile virus; (Kalluri, Gilruth, Rogers, & Szczur, 2007; Rochlin, Turbow, Gomez, Ninivaggi, & Campbell, 2011). Pest management in cities is especially urgent because mosquitoes show accelerated larval growth and increased survivorship in urban environments, due to greater densities of suitable breeding locations 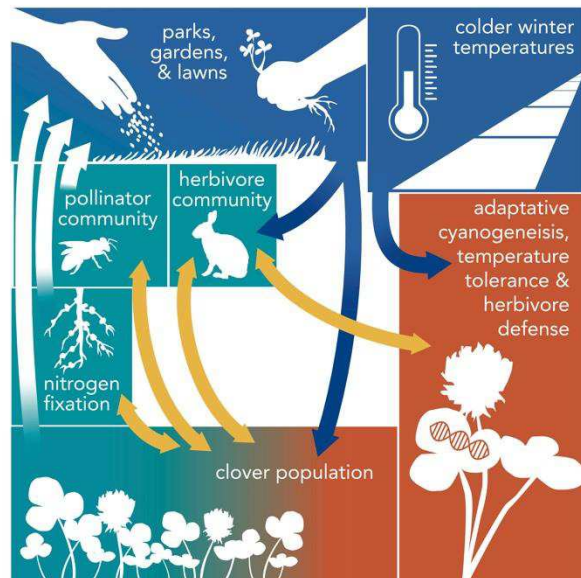(small volumes of standing water), urban heat islands, and reductions in predators due to insecticides and unsuitable habitat (Li, Dicke, Harvey, & Gols, 2014; Wilke et al., 2019). Insecticide application has also promoted resistance, aggravating pest management. Hence, mosquitoes generally tend to experience fitness benefits in cities, increasing the risk of pathogen transmission among humans (Kamdem et al., 2017; Medeiros-Sousa, Fernandes, Ceretti-Junior, Wilke, & Marrelli, 2017). Variation in urban infrastructure, driven by socioeconomics and urban planning, can be linked directly to the ecology and evolution of mosquito species. Low-income cities and neighbourhoods have greater relative proportions of impervious surface cover, leading to more surfaces holding standing water (Ayala & Estrugo, 2014; Rochlin et al., 2011). Accordingly, impoverished neighbourhoods have larger mosquitoes in better condition, with increased survivorship and reproduction (Katz et al., 2019). Recent empirical work further shows that urban residents in low-income neighbourhoods have greater risk of mosquito-borne diseases, specifically West Nile virus in Washington, D.C. and Baltimore, Maryland (LaDeau, Leisnham, Biehler, & Bodner, 2013) and malaria in cities across sub-Saharan Africa (De Silva & Marshall, 2012). Social drivers and may additionally affect the rate of coevolutionary change between mosquito-borne diseases (e.g., *Plasmodium*) and human resistance to those diseases (Ayala & Estrugo, 2014). For example, sickle-cell anemia, a disease characterized by malformed red blood cells, is typically lethal in people who inherit two copies of an allele with a mutation inhibiting hemoglobin production (Allison, 1954). However, heterozygotes (with just one sickle-cell allele) have increased resistance to malaria, leading to the higher prevalence of the allele in urban, suburban, and rural areas where malaria is common (Evans & Wellems, 2002). As countries in malaria-affected

areas continue to urbanize, the close coevolutionary association among humans, mosquitos, and *Plasmodium* species may become an increasingly urban issue.

622
623
624
625
626
627
628
629
630
631
632

c) Clover evolution, repeated loss of cyanogenesis, and urban lawns

The ecology and evolution of white clover (*Trifolium repens*), a perennial, herbaceous plant common in lawns and other human-modified habitats, has been well studied in an urban context. Clover exhibits a Mendelian polymorphism for hydrogen cyanide production (cyanogenesis), which both defends against herbivores and reduces freezing tolerance. White clover repeatedly evolve decreased cyanogenesis in cities, due to putative selection from colder nighttime winter temperatures (Johnson et al., 2018; Santangelo et al., 2018; Thompson et al., 2016). White clover's adaptations might in part lead to their high population densities in cities, where they feed back on the urban ecosystem and society. In particular, clover's mutualistic rhizobial bacteria influence increase soil nitrogen (Hennig & Ghazoul, 2011) and its flowers provide a nectar resource for pollinators (Hicks et al., 2016; Larson et al., 2014; Theodorou et al., 2017). Still, despite its presence in many lawn seed mixes (Bormann, Balmori, & Geballe, 2011), white clover is often considered a weed and removed by homeowners, negatively affecting pollinator communities (Baude et al., 2016; Larson et al.,

2014), the ecosystem-level effects of clover's presence in seed mixes is largely unknown. Because of its strong association with humans, its importance for nutrient cycling and pollinators, and its evolution in cities, the urban white clover system presents an opportunity to study socio-eco-evolutionary dynamics. In particular, research could explore how land use and conversion, homeowner cultural habits, and household income predict clover presence in lawns and thus spatial heterogeneity in pollinator resource availability. If clover is removed, policies could encourage the planting of native species to support its ecosystem functions.

633
634
635
636
637
638
639
640
641
642
643
644
645
646
647
648
649
650
651

d) Daphnia evolution, eutrophication, urban heat islands, and trophic cascades
Daphnia are common zooplankton species in urban, rural, and natural freshwater ponds and lakes across the globe. They vary in several intraspecific life history, behavioural, and physiological traits that can elicit strong ecosystem-level effects. *D. magna* show reduced body size, higher heat tolerance, faster pace-of-life, and altered stress physiology in urban populations compared to rural populations, which are most likely adaptations to warmer temperatures (Brans & De Meester, 2018; Brans, Jansen, et al., 2017).
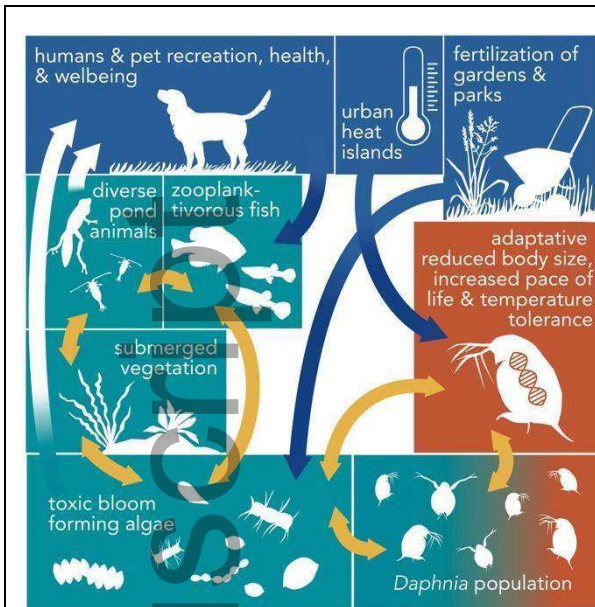
Smaller average body size in urban zooplankton communities including *Daphnia* can have cascading effects on the pond ecosystem (Gianuca, Pantel, & De Meester, 2016). While increased *Daphnia* thermal tolerance allows them to persist and suppress algae populations, smaller body size diminishes their capacity to do so (Gianuca et al., 2016). Reduced top-down effects from primary consumers can result in disappearance of emergent and submerged vegetation, eutrophication, and decline in amphibians, invertebrates, and overall pond biodiversity (Blaustein et al., 2011; Huisman et al., 2018; Landsberg, 2002; Paerl & Otten, 2013). Algal blooms will likely increase with climate change and urbanization (Paerl & Huisman, 2009; Teurlincx et al., 2019; Waajen, Faassen, & Lürling, 2014) causing toxic conditions that are harmful for humans and pets (Huisman et al., 2018; Reid et al., 2019). Persistence of *D. magna* in urban and natural ponds is thus crucial for human health and wellbeing. Yet certain actions taken by humans can directly lead to their demise (Paerl & Huisman, 2009; Teurlincx et al., 2019; Waajen et al., 2014). For example, fertilizer runoff and removal of submerged vegetation can result in anoxic conditions, fatal to *D. magna* and other zooplankton (Peretyatko, Teissier, De Backer, & Triest, 2009). Further, stocking of zooplanktivorous fish can reduce Daphnia abundance and thus their ability to control algae populations (Peretyatko et al., 2009). Shifts toward eutrophic pond ecosystems can negatively impact human psychological well-being, hydrological balance, climate mitigation, nutrient retention, and bio- and phytoremediation of toxicants from the environment (Reid et al., 2019). Thus, human management, monitoring, and mitigation of local environmental conditions like warming and nutrient runoff are crucial for the maintenance of urban pond ecosystems (Paerl & Otten, 2013; Peretyatko et al., 2009).

652

653

654

655

656

657

658

659

660

661

662

663

664

665

Box 4: Outstanding questions that could be addressed using a socio-eco-evolutionary framework

Integrating insights from social sciences, ecology, and evolutionary biology can help us address critical questions about urban systems. This understanding will likely feed back to improve our knowledge and predictions about how ecosystems respond to global change. Here, we propose ten key questions to inform an integrated socio-eco-evolutionary framework.

1. How can incorporating methods from the social sciences improve our understanding of eco-evolutionary dynamics?

2. How do socio-eco-evolutionary dynamics scale with the spatial redistribution and generation lengths of humans and associated organisms across space and time?

3. What is the relevance and magnitude of evolutionary feedbacks to ecological and social patterns and processes in different urban contexts?

4. Can we predict the ways that interspecific interactions will influence eco-evolutionary dynamics in cities and the ways in which social drivers will modify these dynamics and patterns?

5. How important are local dynamics and species identity to eco-evolutionary dynamics in cities? What are the components of a cohesive theory that is relevant to all or most urban systems, and when do local ecology, culture and politics idiosyncratically shape outcomes?

6. How can eco-evolutionary dynamics feed back to influence social processes in cities? In what ways

---

can social systems change in response to evolutionary changes that are induced by urbanization?

7. How can this multidimensional framework help us better understand the resilience of urban ecosystems to pulse disturbances, such as extreme weather events, and ramping disturbances, such as climate change?

8. What elements of human social constructs (e.g. socioeconomic, cultural, religious, philosophical, political, aesthetic, etc.) are likely to impact socio-eco-evolutionary dynamics?

9. Under what circumstances are eco-evolutionary processes stronger or weaker in urban compared to non-urban areas?

10. How do socio-eco-evolutionary changes in cities affect the influences of cities on surrounding landscapes?

666
667
668
669
670
671 **References**

672 Aberle, D. F., Cohen, A. K., Davis, A. K., Levy, M. J., & Sutton, F. X. (1950). The functional
673   prerequisites of a society. *Ethics*, *60*(2), 100–111. Retrieved from JSTOR.
674 Abrams, P. A., & Matsuda, H. (1997). Prey adaptation as a cause of predator-prey cycles.
675   *Evolution*, *51*(6), 1742–1750.
676 Ackley, J. W. (2014). *Bringing nature to humans: How to evaluate the next generation of urban*
677   *parks and green spaces*. *7*, 9.
678 Alberti, M. (2008). *Advances in urban ecology: Integrating humans and ecological processes in*
679   *urban ecosystems*. Boston: Springer.
680 Alberti, M. (2015). Eco-evolutionary dynamics in an urbanizing planet. *Trends in Ecology &*
681   *Evolution*, *30*, 114–126.

682 Alberti, M. (2016). *Cities that think like planets: Complexity, resilience, and innovation in hybrid*

683   *ecosystems*. Seattle: University of Washington Press.

684 Allgeier, J. E., Cline, T. J., Walsworth, T. E., Wathen, G., Layman, C. A., & Schindler, D. E. (2020).

685   Individual behavior drives ecosystem function and the impacts of harvest. *Science*

686   *Advances*, *6*(9), eaax8329. https://doi.org/10.1126/sciadv.aax8329

687 Allison, A. C. (1954). Protection afforded by sickle-cell trait against subtertian malarial infection.

688   *British Medical Journal*, *1*(4857), 290–294.

689 Avolio, M. L., Pataki, D. E., Trammell, T. L. E., & Endter-Wada, J. (2018). Biodiverse cities: The

690   nursery industry, homeowners, and neighborhood differences drive urban tree

691   composition. *Ecological Monographs*, *88*(2), 259–276.

692   https://doi.org/10.1002/ecm.1290

693 Ayala, R., & Estrugo, A. (2014). Assessing the effects of climate and socioeconomic factors on

694   vulnerability to vector-borne diseases in Latin America. *IDB Working Paper Series, No.*

695   *IDB-WP-497*.

696 Band, L. E., Cadenasso, M. L., Grimmond, C. S., Grove, J. M., & Pickett, S. T. A. (2005).

697   Heterogeneity in urban ecosystems: Patterns and process. In *Ecosystem Function in*

698   *Heterogeneous Landscapes* (pp. 257–278). https://doi.org/10.1007/0-387-24091-8_13

699 Barrington-Leigh, C., & Millard-Ball, A. (2020). Global trends toward urban street-network

700   sprawl. *Proceedings of the National Academy of Sciences*, *117*(4), 1941–1950.

701   https://doi.org/10.1073/pnas.1905232116

702 Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., … Reznick,

703   D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes.

704   *Proceedings of the National Academy of Sciences*, *107*(8), 3616–3621.

705   https://doi.org/10.1073/pnas.0908023107

706 Baude, M., Kunin, W. E., Boatman, N. D., Conyers, S., Davies, N., Gillespie, M. A. K., … Memmott,

707   J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in

708   Britain. *Nature*, *530*(7588), 85–88. https://doi.org/10.1038/nature16532

709 Blaustein, A. R., Han, B. A., Relyea, R. A., Johnson, P. T. J., Buck, J. C., Gervasi, S. S., & Kats, L. B.

710   (2011). The complexity of amphibian population declines: Understanding the role of

711   cofactors in driving amphibian losses. *Annals of the New York Academy of Sciences*,

712   *1223*(1), 108–119. https://doi.org/10.1111/j.1749-6632.2010.05909.x

713   Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., … Petraglia,

714   M. D. (2016). Ecological consequences of human niche construction: Examining long-

715   term anthropogenic shaping of global species distributions. *Proceedings of the National*

716   *Academy of Sciences*, *113*(23), 6388–6396.

717   Bolund, P., & Hunhammar, S. (1999). Ecosystem services in urban areas. *Ecological Economics*,

718   *29*(2), 293–301. https://doi.org/10.1016/S0921-8009(99)00013-0

719   Booth, W., Saenz, V. L., Santangelo, R. G., Wang, C., Schal, C., & Vargo, E. L. (2012). Molecular

720   markers reveal infestation dynamics of the Bed Bug (Hemiptera: Cimicidae) within

721   apartment buildings. *Journal of Medical Entomology*, *49*(3), 535–546.

722   https://doi.org/10.1603/ME11256

723   Bormann, F. H., Balmori, D., & Geballe, G. T. (2011). *Redesigning the American lawn: A search*

724   *for environmental harmony*. Yale University Press.

725   Brans, K. I., & De Meester, L. (2018). City life on fast lanes: Urbanization induces an evolutionary

726   shift towards a faster lifestyle in the water flea Daphnia. *Functional Ecology*, *32*(9),

727   2225–2240. https://doi.org/10.1111/1365-2435.13184

728   Brans, K. I., Govaert, L., Engelen, J. M. T., Gianuca, A. T., Souffreau, C., & De Meester, L. (2017).

729   Eco-evolutionary dynamics in urbanized landscapes: Evolution, species sorting and the

730   change in zooplankton body size along urbanization gradients. *Philosophical*

731   *Transactions of the Royal Society B: Biological Sciences*, *372*(1712).

732   https://doi.org/10.1098/rstb.2016.0030

733   Brans, K. I., Jansen, M., Vanoverbeke, J., Tüzün, N., Stoks, R., & De Meester, L. (2017). The heat

734   is on: Genetic adaptation to urbanization mediated by thermal tolerance and body size.

735   *Global Change Biology*, *23*, 5218–5227.

736   Bullock, J. M., Bonte, D., Pufal, G., da Silva Carvalho, C., Chapman, D. S., García, C., … Delgado,

737   M. M. (2018). Human-mediated dispersal and the rewiring of spatial networks. *Trends in*

738   *Ecology and Evolution*, *33*(12), 958–970.

739 Byers, K. A., Lee, M. J., Patrick, D. M., & Himsworth, C. G. (2019). Rats about town: A systematic

740   review of rat movement in urban ecosystems. *Frontiers in Ecology and Evolution*, *7*.

741   https://doi.org/10.3389/fevo.2019.00013

742 Chakraborty, T., Hsu, A., Manya, D., & Sheriff, G. (2019). Disproportionately higher exposure to

743   urban heat in lower-income neighborhoods: A multi-city perspective. *Environmental*

744   *Research Letters*, *14*(10), 105003. https://doi.org/10.1088/1748-9326/ab3b99

745 Chifflet, L., Guzmán, N. V., Rey, O., Confalonieri, V. A., & Calcaterra, L. A. (2018). Southern

746   expansion of the invasive ant *Wasmannia auropunctata* within its native range and its

747   relation with clonality and human activity. *PLoS ONE*, *13*(11).

748   https://doi.org/10.1371/journal.pone.0206602

749 Childers, D. L., Cadenasso, M. L., Grove, J. M., Marshall, V., McGrath, B., & Pickett, S. T. A.

750   (2015). An ecology for cities: A transformational nexus of design and ecology to advance

751   climate change resilience and urban sustainability. *Sustainability*, *7*(4), 3774–3791.

752   https://doi.org/10.3390/su7043774

753 Colla, S. R., & MacIvor, J. S. (2017). Questioning public perception, conservation policy, and

754   recovery actions for honeybees in North America: Questioning public perception.

755   *Conservation Biology*, *31*(5), 1202–1204. https://doi.org/10.1111/cobi.12839

756 Collins, J. P., Kinzig, A., Grimm, N. B., Fagan, W. F., Hope, D., Wu, J., & Borer, E. T. (2000). A new

757   urban ecology: Modeling human communities as integral parts of ecosystems poses

758   special problems for the development and testing of ecological theory. *American*

759   *Scientist*, *88*(5), 416–425. Retrieved from JSTOR.

760 Combs, M., Byers, K., Himsworth, C., & Munshi-South, J. (2019). Harnessing population genetics

761   for pest management: Theory and application for urban rats. *Human–Wildlife*

762   *Interactions*, *13*(2). https://doi.org/10.26077/0bcx-v339

763 Combs, M., Puckett, E. E., Richardson, J., Mims, D., & Munshi-South, J. (2018). Spatial

764   population genomics of the brown rat (Rattus norvegicus) in New York City. *Molecular*

765   *Ecology*, *27*(1), 83–98. https://doi.org/10.1111/mec.14437

766   Cook, L. M., & Saccheri, I. J. (2013). The peppered moth and industrial melanism: Evolution of a

767   natural selection case study. *Heredity*, *110*(3), 207–212.

768   https://doi.org/10.1038/hdy.2012.92

769   Cooper, C. B., Dickinson, J., Phillips, T., & Bonney, R. (2007). Citizen science as a tool for

770   conservation in residential ecosystems. *Ecology and Society*, *12*(2). Retrieved from

771   JSTOR.

772   Crain, R., Cooper, C., & Dickinson, J. L. (2014). Citizen science: A tool for integrating studies of

773   human and natural systems. *Annual Review of Environment and Resources*, *39*(1), 641–

774   665. https://doi.org/10.1146/annurev-environ-030713-154609

775   Culley, T. M., & Hardiman, N. A. (2009). The role of intraspecific hybridization in the evolution of

776   invasiveness: A case study of the ornamental pear tree *Pyrus calleryana*. *Biological

777   Invasions*, *11*(5), 1107–1119. https://doi.org/10.1007/s10530-008-9386-z

778   Daily, G. C. (1997). *Nature's services* (Vol. 3). Island Press, Washington, DC.

779   Darwin, C. (1859). On the origins of species by means of natural selection. In *London: Murray*.

780   London: John Murray.

781   De Silva, P. M., & Marshall, J. M. (2012). Factors contributing to urban malaria transmission in

782   sub-saharan africa: A systematic review. *Journal of Tropical Medicine*, *2012*, 819563.

783   https://doi.org/10.1155/2012/819563

784   Delaney, K. S., Riley, S. P. D., & Fisher, R. N. (2010). A rapid, strong, and convergent genetic

785   response to urban habitat fragmentation in four divergent and widespread vertebrates.

786   *PLoS ONE*, *5*(9). https://doi.org/10.1371/journal.pone.0012767

787   Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., … Palkovacs,

788   E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology &

789   Evolution*, *2*, 57–64. https://doi.org/10.1038/s41559-017-0402-5

790   Desvars-Larrive, A., Pascal, M., Gasqui, P., Cosson, J.-F., Benoît, E., Lattard, V., … Vourc'h, G.

791   (2017). Population genetics, community of parasites, and resistance to rodenticides in

792   an urban brown rat (*Rattus norvegicus*) population. *PLOS ONE*, *12*(9), e0184015.

793   https://doi.org/10.1371/journal.pone.0184015

794   Diamond, S. E., Chick, L. D., Perez, A., Strickler, S. A., & Martin, R. A. (2018). Evolution of thermal

795   tolerance and its fitness consequences: Parallel and non-parallel responses to urban

796   heat islands across three cities. *Proceedings of the Royal Society B: Biological Sciences*,

797   *285*(1882), 20180036. https://doi.org/10.1098/rspb.2018.0036

798   Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., … Shirayama, Y.

799   (2018). Assessing nature's contributions to people. *Science (New York, N.Y.)*, *359*(6373),

800   270–272. https://doi.org/10.1126/science.aap8826

801   Donihue, C. M., & Lambert, M. R. (2015). Adaptive evolution in urban ecosystems. *AMBIO*,

802   *44*(3), 194–203. https://doi.org/10.1007/s13280-014-0547-2

803   Driscoll, C. A., Macdonald, D. W., & O'Brien, S. J. (2009). From wild animals to domestic pets, an

804   evolutionary view of domestication. *Proceedings of the National Academy of Sciences*,

805   *106*(Supplement 1), 9971–9978. https://doi.org/10.1073/pnas.0901586106

806   Ellis, E. C. (2015). Ecology in an anthropogenic biosphere. *Ecological Monographs*, *85*(3), 287–

807   331.

808   Eritja, R., Escosa, R., Lucientes, J., Marquès, E., Molina, R., Roiz, D., & Ruiz, S. (2005). Worldwide

809   invasion of vector mosquitoes: Present European distribution and challenges for Spain.

810   *Biological Invasions*, *7*(1), 87–97. https://doi.org/10.1007/s10530-004-9637-6

811   Etterson, J. R., Franks, S. J., Mazer, S. J., Shaw, R. G., Gorden, N. L. S., Schneider, H. E., … Weis, A.

812   E. (2016). Project Baseline: An unprecedented resource to study plant evolution across

813   space and time. *American Journal of Botany*, *103*(1), 164–173.

814   https://doi.org/10.3732/ajb.1500313

815   Evans, A. G., & Wellems, T. E. (2002). Coevolutionary genetics of plasmodium malaria parasites

816   and their human hosts. *Integrative and Comparative Biology*, *42*(2), 401–407.

817   https://doi.org/10.1093/icb/42.2.401

818   Faith, D. P., Magallón, S., Hendry, A. P., Conti, E., Yahara, T., & Donoghue, M. J. (2010).

819   Evosystem services: An evolutionary perspective on the links between biodiversity and

820   human well-being. *Current Opinion in Environmental Sustainability*, *2*(1–2), 66–74.

821   https://doi.org/10.1016/j.cosust.2010.04.002

822   Faith, D. P., Magallón, S., Hendry, A. P., & Donoghue, M. J. (2017). Future benefits from

823   contemporary evosystem services: A response to Rudman et al. *Trends in Ecology and*

824   *Evolution*, *32*(10), 717–719. https://doi.org/10.1016/j.tree.2017.07.005

825   Fussmann, G. F., Loreau, M., & Abrams, P. A. (2007). Eco-evolutionary dynamics of communities

826   and ecosystems. *Functional Ecology*, *21*(3), 465–477. https://doi.org/10.1111/j.1365-

827   2435.2007.01275.x

828   Gardner-Santana, L. C., Norris, D. E., Fornadel, C. M., Hinson, E. R., Klein, S. L., & Glass, G. E.

829   (2009). Commensal ecology, urban landscapes, and their influence on the genetic

830   characteristics of city-dwelling Norway rats (*Rattus norvegicus*). *Molecular Ecology*,

831   *18*(13), 2766–2778. https://doi.org/10.1111/j.1365-294X.2009.04232.x

832   Ger, K. A., Urrutia-Cordero, P., Frost, P. C., Hansson, L.-A., Sarnelle, O., Wilson, A. E., & Lürling,

833   M. (2016). The interaction between cyanobacteria and zooplankton in a more eutrophic

834   world. *Harmful Algae*, *54*, 128–144. https://doi.org/10.1016/j.hal.2015.12.005

835   Gianuca, A. T., Pantel, J. H., & De Meester, L. (2016). Disentangling the effect of body size and

836   phylogenetic distances on zooplankton top-down control of algae. *Proceedings of the*

837   *Royal Society B: Biological Sciences*, *283*(1828), 20160487.

838   https://doi.org/10.1098/rspb.2016.0487

839   Gill, R. J., Baldock, K. C. R., Brown, M. J. F., Cresswell, J. E., Dicks, L. V., Fountain, M. T., … Potts,

840   S. G. (2016). Chapter four - protecting an ecosystem service: Approaches to

841   understanding and mitigating threats to wild insect pollinators. In G. Woodward & D. A.

842   Bohan (Eds.), *Advances in Ecological Research* (pp. 135–206).

843   https://doi.org/10.1016/bs.aecr.2015.10.007

844   Godefroid, S. (2001). Temporal analysis of the Brussels flora as indicator for changing

845   environmental quality. *Landscape and Urban Planning*, *52*(4), 203–224.

846   https://doi.org/10.1016/S0169-2046(00)00117-1

847   Gorton, A. J., Moeller, D. A., & Tiffin, P. (2018). Little plant, big city: A test of adaptation to

848   urban environments in common ragweed (Ambrosia artemisiifolia). *Proceedings of the*

849   *Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2018.0968

850   Govaert, L. (2018). Eco-evolutionary partitioning metrics: A practical guide for biologists.

851   *Belgian Journal of Zoology*, *148*(2), 167–202. https://doi.org/10.3929/ETHZ-B-

852   000316056

853   Govaert, L., Pantel, J. H., & De Meester, L. (2016). Eco-evolutionary partitioning metrics:

854   Assessing the importance of ecological and evolutionary contributions to population and

855   community change. *Ecology Letters*, *19*(8), 839–853. https://doi.org/10.1111/ele.12632

856   Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X. M., & Briggs, J. M.

857   (2008). Global change and the ecology of cities. *Science*, *319*, 756–760.

858   Grimm, N. B., Grove, J. G., Pickett, S. T. A., & Redman, C. L. (2000). Integrated approaches to

859   long-term studies of urban ecological systems. *BioScience*, *50*(7), 571–584.

860   https://doi.org/10.1641/0006-3568(2000)050[0571:iatlto]2.0.co;2

861   Groffman, P. M., Cavender-Bares, J., Bettez, N. D., Grove, J. M., Hall, S. J., Heffernan, J. B., …

862   Steele, M. K. (2014). Ecological homogenization of urban USA. *Frontiers in Ecology and*

863   *the Environment*, *12*(1), 74–81. https://doi.org/10.1890/120374

864   Grove, J. M., Locke, D. H., & O'Neil-Dunne, J. P. M. (2014). An ecology of prestige in new york

865   city: Examining the relationships among population density, socio-economic status,

866   group identity, and residential canopy cover. *Environmental Management*, *54*(3), 402–

867   419. https://doi.org/10.1007/s00267-014-0310-2

868   Grove, J. M., Ogden, L., Pickett, S., Boone, C., Buckley, G., Locke, D. H., … Hall, B. (2018). The

869   legacy effect: Understanding how segregation and environmental injustice unfold over

870   time in baltimore. *Annals of the American Association of Geographers*, *108*(2), 524–537.

871   https://doi.org/10.1080/24694452.2017.1365585

872   Hairston, N. G., Ellner, S. P., Geber, M. A., Yoshida, T., & Fox, J. A. (2005). Rapid evolution and

873   the convergence of ecological and evolutionary time. *Ecology Letters*, *8*(8), 1114–1127.

874   https://doi.org/10.1111/j.1461-0248.2005.00812.x

875   Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B., & Schluter, D. (2009).

876   Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*,

877   *458*(7242), 1167–1170. https://doi.org/10.1038/nature07974

878 Harris, S. E., Xue, A. T., Alvarado-Serrano, D., Boehm, J. T., Joseph, T., Hickerson, M. J., &
879   Munshi-South, J. (2016). Urbanization shapes the demographic history of a native
880   rodent (the white-footed mouse, Peromyscus leucopus) in New York City. *Biology*
881   *Letters*, *12*(4). https://doi.org/10.1098/rsbl.2015.0983

882 Helmus, M. R., Mahler, D. L., & Losos, J. B. (2014). Island biogeography of the Anthropocene.
883   *Nature*, *513*(7519), 543–546. https://doi.org/10.1038/nature13739

884 Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton: Princeton University Press.

885 Hendry, A. P., & Kinnison, M. T. (1999). Perspective: The pace of modern life: Measuring rates
886   of contemporary microevolution. *Evolution*, *53*(6), 1637–1653.
887   https://doi.org/10.1111/j.1558-5646.1999.tb04550.x

888 Hennig, E. I., & Ghazoul, J. (2011). Plant–pollinator interactions within the urban environment.
889   *Perspectives in Plant Ecology, Evolution and Systematics*, *13*(2), 137–150.
890   https://doi.org/10.1016/j.ppees.2011.03.003

891 Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, M. A., Kunin, W. E., … Stone, G.
892   N. (2016). Food for pollinators: Quantifying the nectar and pollen resources of urban
893   flower meadows. *PLOS ONE*, *11*(6), e0158117.
894   https://doi.org/10.1371/journal.pone.0158117

895 Hof, A. E. van't, Campagne, P., Rigden, D. J., Yung, C. J., Lingley, J., Quail, M. A., … Saccheri, I. J.
896   (2016). The industrial melanism mutation in British peppered moths is a transposable
897   element. *Nature*, *534*(7605), 102–105. https://doi.org/10.1038/nature17951

898 Huang, K., Li, X., Liu, X., & Seto, K. C. (2019). Projecting global urban land expansion and heat
899   island intensification through 2050. *Environmental Research Letters*, *14*(11), 114037.
900   https://doi.org/10.1088/1748-9326/ab4b71

901 Huisman, J., Codd, G. A., Paerl, H. W., Ibelings, B. W., Verspagen, J. M. H., & Visser, P. M. (2018).
902   Cyanobacterial blooms. *Nature Reviews Microbiology*, *16*(8), 471–483.
903   https://doi.org/10.1038/s41579-018-0040-1

904 Isaksson, C. (2015). Urbanization, oxidative stress and inflammation: A question of evolving,
905   acclimatizing or coping with urban environmental stress. *Functional Ecology*, *29*(7), 913–
906   923. https://doi.org/10.1111/1365-2435.12477

907   Jabeen, R., Ahmad, A., & Iqbal, M. (2009). Phytoremediation of heavy metals: Physiological and

908   molecular mechanisms. *Botanical Review*, *75*(4), 339–364.

909   https://doi.org/10.1007/s12229-009-9036-x

910   Jackson, F. (1996). The coevolutionary relationship of humans and domesticated plants.

911   *American Journal of Physical Anthropology*, *101*(S23), 161–176.

912   https://doi.org/10.1002/(SICI)1096-8644(1996)23+<161::AID-AJPA6>3.0.CO;2-8

913   Jenerette, G. D., Harlan, S. L., Stefanov, W. L., & Martin, C. A. (2011). Ecosystem services and

914   urban heat riskscape moderation: Water, green spaces, and social inequality in Phoenix,

915   USA. *Ecological Applications*, *21*(7), 2637–2651. https://doi.org/10.1890/10-1493.1

916   Jiang, L., Deng, X., & Seto, K. C. (2013). The impact of urban expansion on agricultural land use

917   intensity in China. *Land Use Policy*, *35*, 33–39.

918   https://doi.org/10.1016/j.landusepol.2013.04.011

919   Johnson, M. T. J., & Munshi-South, J. (2017). The evolution of life in urban environments.

920   *Science*, *358*(6363). https://doi.org/10.1126/science.aam8327

921   Johnson, M. T. J., Prashad, C. M., Lavoignat, M., & Saini, H. S. (2018). Contrasting the effects of

922   natural selection, genetic drift and gene flow on urban evolution in white clover

923   (Trifolium repens). *Proceedings of the Royal Society B: Biological Sciences*, *285*(1883),

924   20181019. https://doi.org/10.1098/rspb.2018.1019

925   Jones, K. E., Patel, N. G., Levy, M. A., Storeygard, A., Balk, D., Gittleman, J. L., & Daszak, P.

926   (2008). Global trends in emerging infectious diseases. *Nature*, *451*(7181), 990–993.

927   https://doi.org/10.1038/nature06536

928   Juliano, S. A., & Philip Lounibos, L. (2005). Ecology of invasive mosquitoes: Effects on resident

929   species and on human health. *Ecology Letters*, *8*(5), 558–574.

930   https://doi.org/10.1111/j.1461-0248.2005.00755.x

931   Kajdacsi, B., Costa, F., Hyseni, C., Porter, F., Brown, J., Rodrigues, G., … Caccone, A. (2013).

932   Urban population genetics of slum-dwelling rats (*Rattus norvegicus*) in Salvador, Brazil.

933   *Molecular Ecology*, *22*(20), 5056–5070. https://doi.org/10.1111/mec.12455

934   Kalluri, S., Gilruth, P., Rogers, D., & Szczur, M. (2007). Surveillance of arthropod vector-borne

935   infectious diseases using remote sensing techniques: A review. *PLoS Pathogens*, *3*(10).

936   https://doi.org/10.1371/journal.ppat.0030116

937   Kamdem, C., Fouet, C., Gamez, S., & White, B. J. (2017). Pollutants and insecticides drive local

938   adaptation in African malaria mosquitoes. *Molecular Biology and Evolution*, *34*(5), 1261–

939   1275. https://doi.org/10.1093/molbev/msx087

940   Katz, G., Leisnham, P. T., & LaDeau, S. L. (2019). *Aedes albopictus* body size differs across

941   neighborhoods with varying infrastructural abandonment. *Journal of Medical*

942   *Entomology*, *57*, 615–619. https://doi.org/10.1093/jme/tjz170

943   Kaufmann, R. K., Seto, K. C., Schneider, A., Liu, Z., Zhou, L., & Wang, W. (2007). Climate

944   response to rapid urban growth: Evidence of a human-induced precipitation deficit.

945   *Journal of Climate*, *20*(10), 2299–2306. https://doi.org/10.1175/JCLI4109.1

946   Kettlewell, H. B. D. (1958). A survey of the frequencies of *Biston betularia* (L.) (Lepidoptera) and

947   its melanic forms in Great Britain. *Heredity*, *12*, 51–72.

948   Koch, E., Clark, J. M., Cohen, B., Meinking, T. L., Ryan, W. G., Stevenson, A., … Yoon, K. S. (2016).

949   Management of head louse infestations in the united states—A literature review.

950   *Pediatric Dermatology*, *33*(5), 466–472. https://doi.org/10.1111/pde.12982

951   Kosten, S., Huszar, V. L. M., Bécares, E., Costa, L. S., Donk, E. van, Hansson, L.-A., … Scheffer, M.

952   (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global*

953   *Change Biology*, *18*(1), 118–126. https://doi.org/10.1111/j.1365-2486.2011.02488.x

954   Krasny, M. E., Russ, A., Tidball, K. G., & Elmqvist, T. (2014). Civic ecology practices: Participatory

955   approaches to generating and measuring ecosystem services in cities. *Ecosystem*

956   *Services*, *7*, 177–186. https://doi.org/10.1016/j.ecoser.2013.11.002

957   Ksiazek-Mikenas, K., Fant, J. B., & Skogen, K. A. (2019). Pollinator-mediated gene flow connects

958   green roof populations Across the urban matrix: A paternity analysis of the self-

959   compatible forb *Penstemon hirsutus*. *Frontiers in Ecology and Evolution*, *7*.

960   https://doi.org/10.3389/fevo.2019.00299

961   LaDeau, S. L., Leisnham, P. T., Biehler, D., & Bodner, D. (2013). Higher mosquito production in

962   low-income neighborhoods of baltimore and washington, dc: Understanding ecological

963   drivers and mosquito-borne disease risk in temperate cities. *International Journal of*

964   *Environmental Research and Public Health*, *10*(4), 1505–1526.

965   https://doi.org/10.3390/ijerph10041505

966 Lajoie, G., & Vellend, M. (2015). Understanding context dependence in the contribution of

967   intraspecific variation to community trait–environment matching. *Ecology*, *96*(11),

968   2912–2922. https://doi.org/10.1890/15-0156.1

969 Lambert, M. R., & Donihue, C. M. (2020). Urban biodiversity management using evolutionary

970   tools. *Nature Ecology & Evolution*, 1–8. https://doi.org/10.1038/s41559-020-1193-7

971 Landsberg, J. H. (2002). The effects of harmful algal blooms on aquatic organisms. *Reviews in*

972   *Fisheries Science*, *10*(2), 113–390. https://doi.org/10.1080/20026491051695

973 Larson, G., & Fuller, D. Q. (2014). The evolution of animal domestication. *Annual Review of*

974   *Ecology, Evolution, and Systematics*, *45*(1), 115–136. https://doi.org/10.1146/annurev-

975   ecolsys-110512-135813

976 Larson, J. L., Kesheimer, A. J., & Potter, D. A. (2014). Pollinator assemblages on dandelions and

977   white clover in urban and suburban lawns. *Journal of Insect Conservation*, *18*(5), 863–

978   873. https://doi.org/10.1007/s10841-014-9694-9

979 Leach, H. M. (2003). Human domestication reconsidered. *Current Anthropology*, *44*(3), 349–

980   368. https://doi.org/10.1086/368119

981 Leong, M., Bertone, M. A., Bayless, K. M., Dunn, R. R., & Trautwein, M. D. (2016). Exoskeletons

982   and economics: Indoor arthropod diversity increases in affluent neighbourhoods.

983   *Biology Letters*, *12*(8). https://doi.org/10.1098/rsbl.2016.0322

984 Lerman, S. B., & Warren, P. S. (2011). The conservation value of residential yards: Linking birds

985   and people. *Ecological Applications*, *21*(4), 1327–1339. https://doi.org/10.1890/10-

986   0423.1

987 Li, Y., Dicke, M., Harvey, J. A., & Gols, R. (2014). Intra-specific variation in wild *Brassica oleracea*

988   for aphid-induced plant responses and consequences for caterpillar-parasitoid

989   interactions. *Oecologia*, *174*, 853–862.

990   Liu, J., Dietz, T., Carpenter, S. R., Alberti, M., Folke, C., Moran, E., … Taylor, W. W. (2007).

991   Complexity of coupled human and natural system. *Science*, *317*(5844), 1513–1516.

992   https://doi.org/10.1126/science.1144004

993   Liu, X., Huang, Y., Xu, X., Li, X., Li, X., Ciais, P., … Zeng, Z. (2020). High-spatiotemporal-resolution

994   mapping of global urban change from 1985 to 2015. *Nature Sustainability*, 1–7.

995   https://doi.org/10.1038/s41893-020-0521-x

996   Locke, D. H., Hall, B., Grove, J. M., Pickett, S. T. A., Ogden, L. A., Aoki, C., … O'Neil-Dunne, J. P.

997   M. (2020). Residential housing segregation and urban tree canopy in 37 US Cities.

998   *SocArXiv*.

999   Loeuille, N., & Leibold, M. A. (2008). Ecological consequences of evolution in plant defenses in a

1000   metacommunity. *Theoretical Population Biology*, *74*(1), 34–45.

1001   https://doi.org/10.1016/J.TPB.2008.04.004

1002   Alberti, M, Palkovacs, E. P., Des Roches, S., De Meester, L., Brans, K. I., Govaert, L., … Verrelli, B.

1003   C. (In Press). The complexity of urban eco-evolutionary dynamics. *BioScience*.

1004   Mahan, B. R., Gipson, P. S., & Case, R. M. (1978). Characteristics and distribution of coyote x

1005   dog hybrids collected in Nebraska. *The American Midland Naturalist*, *100*(2), 408–415.

1006   https://doi.org/10.2307/2424840

1007   Marzluff, J. M. (2008). Island biogeography for an urbanizing world: How extinction and

1008   colonization may determine biological diversity in human-dominated landscapes. In

1009   *Urban Ecology* (pp. 355–371). https://doi.org/10.1007/978-0-387-73412-5_23

1010   McDonnell, M. J., & Pickett, S. (1993). *Humans as components of ecosystems: The ecology of*

1011   *subtle human effects and populated areas*. New York: Springer Science & Business

1012   Media.

1013   McPhearson, T., Pickett, S. T. A., Grimm, N. B., Niemelä, J., Alberti, M., Elmqvist, T., … Qureshi,

1014   S. (2016). Advancing urban ecology toward a science of cities. *BioScience*, *66*(3), 198–

1015   212. https://doi.org/10.1093/biosci/biw002

1016   Medeiros-Sousa, A. R., Fernandes, A., Ceretti-Junior, W., Wilke, A. B. B., & Marrelli, M. T. (2017).

1017   Mosquitoes in urban green spaces: Using an island biogeographic approach to identify

1018   drivers of species richness and composition. *Scientific Reports*, *7*(1), 1–11.

1019   https://doi.org/10.1038/s41598-017-18208-x

1020 Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients

1021   at both community and intraspecific level in macro-moths. *Global Change Biology*, *24*(8),

1022   3837–3848. https://doi.org/10.1111/gcb.14151

1023 Merilä, J., & Hendry, A. P. (2013). Climate change, adaptation, and phenotypic plasticity: The

1024   problem and the evidence. *Evolutionary Applications*, *7*, 1–14.

1025   https://doi.org/10.1111/eva.12137

1026 Miles, L. S., Breitbart, S. T., Wagner, H. H., & Johnson, M. T. J. (2019). Urbanization shapes the

1027   ecology and evolution of plant-arthropod herbivore interactions. *Frontiers in Ecology*

1028   *and Evolution*, *7*(AUG). https://doi.org/10.3389/fevo.2019.00310

1029 Miles, L. S., Dyer, R. J., & Verrelli, B. C. (2018). Urban hubs of connectivity: Contrasting patterns

1030   of gene flow within and among cities in the western black widow spider. *Proceedings of*

1031   *the Royal Society B: Biological Sciences*, *285*(1884), 20181224.

1032   https://doi.org/10.1098/rspb.2018.1224

1033 Miles, L. S., Rivkin, L. R., Johnson, M. T. J., Munshi-South, J., & Verrelli, B. C. (2019). Gene flow

1034   and genetic drift in urban environments. *Molecular Ecology*, *28*(18), 4138–4151.

1035   https://doi.org/10.1111/mec.15221

1036 Moll, R. J., Cepek, J. D., Lorch, P. D., Dennis, P. M., Tans, E., Robison, T., … Montgomery, R. A.

1037   (2019). What does urbanization actually mean? A framework for urban metrics in

1038   wildlife research. *Journal of Applied Ecology*, *56*(5), 1289–1300.

1039   https://doi.org/10.1111/1365-2664.13358

1040 Morris, G. D., & Steffler, J. (2011). Was pet relinquishment related to foreclosure?: A spatial

1041   research note from California during the height of foreclosure. *The Social Science*

1042   *Journal*, *48*(4), 739–745. https://doi.org/10.1016/j.soscij.2011.03.010

1043 Munshi-South, J. (2012). Urban landscape genetics: Canopy cover predicts gene flow between

1044   white-footed mouse (*Peromyscus leucopus*) populations in New York City. *Molecular*

1045   *Ecology*, *21*(6), 1360–1378. https://doi.org/10.1111/j.1365-294X.2012.05476.x

1046   Murray, M. H., Fyffe, R., Fidino, M., Byers, K. A., Ríos, M. J., Mulligan, M. P., & Magle, S. B.

1047   (2018). Public complaints reflect rat relative abundance across diverse urban

1048   neighborhoods. *Frontiers in Ecology and Evolution*, *6*.

1049   https://doi.org/10.3389/fevo.2018.00189

1050   Nadeau, C. P., & Urban, M. C. (2019). Eco-evolution on the edge during climate change.

1051   *Ecography*, ecog.04404. https://doi.org/10.1111/ecog.04404

1052   O'Brien, M. J., & Laland, K. N. (2012). Genes, culture, and agriculture: An example of human

1053   niche construction. *Current Anthropology*, *53*(4), 434–470.

1054   https://doi.org/10.1086/666585

1055   Odum, H. W. (1943). Sociology in the contemporary world of today and tomorrow. *Social*

1056   *Forces*, *21*(4), 390–396. https://doi.org/10.2307/2571170

1057   Oertli, B., & Parris, K. M. (2019). Review: Toward management of urban ponds for freshwater

1058   biodiversity. *Ecosphere*, *10*(7). https://doi.org/10.1002/ecs2.2810

1059   Paerl, H. W., & Huisman, J. (2009). Climate change: A catalyst for global expansion of harmful

1060   cyanobacterial blooms. *Environmental Microbiology Reports*, *1*(1), 27–37.

1061   https://doi.org/10.1111/j.1758-2229.2008.00004.x

1062   Paerl, H. W., & Otten, T. G. (2013). Harmful cyanobacterial blooms: Causes, consequences, and

1063   controls. *Microbial Ecology*, *65*(4), 995–1010. https://doi.org/10.1007/s00248-012-

1064   0159-y

1065   Palkovacs, E. P., & Post, D. M. (2009). Experimental evidence that phenotypic divergence in

1066   predators drives community divergence in prey. *Ecology*, *90*(2), 300–305.

1067   Palumbi, S. R. (2001). Humans as the world's greatest evolutionary force. *Science*, *293*(5536),

1068   1786–1790.

1069   Parris, K. M. (2016). *Ecology of urban environments*. John Wiley & Sons.

1070   Pascual, U., Phelps, J., Garmendia, E., Brown, K., Corbera, E., Martin, A., … Muradian, R. (2014).

1071   Social equity matters in payments for ecosystem services. *BioScience*, *64*(11), 1027–

1072   1036. https://doi.org/10.1093/biosci/biu146

1073   Pelletier, F., Garant, D., & Hendry, A. P. (2009). Eco-evolutionary dynamics. *Philosophical*

1074   *Transactions of the Royal Society B: Biological Sciences*, *364*(1523), 1483–1489.

1075   https://doi.org/10.1098/rstb.2009.0027

1076   Pereira-Peixoto, M. H., Pufal, G., Staab, M., Feitosa Martins, C., & Klein, A.-M. (2016). Diversity

1077   and specificity of host-natural enemy interactions in an urban-rural interface. *Ecological*

1078   *Entomology*, *41*(3), 241–252. https://doi.org/10.1111/een.12291

1079   Peretyatko, A., Teissier, S., De Backer, S., & Triest, L. (2009). Restoration potential of

1080   biomanipulation for eutrophic peri-urban ponds: The role of zooplankton size and

1081   submerged macrophyte cover. *Hydrobiologia*, *634*(1), 125–135.

1082   https://doi.org/10.1007/s10750-009-9888-4

1083   Perry, G. H., Dominy, N. J., Claw, K. G., Lee, A. S., Fiegler, H., Redon, R., … Stone, A. C. (2007).

1084   Diet and the evolution of human amylase gene copy number variation. *Nature Genetics*,

1085   *39*(10), 1256–1260. https://doi.org/10.1038/ng2123

1086   Peterson, A. C., Ghersi, B. M., Campanella, R., Riegel, C., Lewis, J. A., & Blum, M. J. (2020).

1087   Rodent assemblage structure reflects socioecological mosaics of counter-urbanization

1088   across post-Hurricane Katrina New Orleans. *Landscape and Urban Planning*, *195*,

1089   103710. https://doi.org/10.1016/j.landurbplan.2019.103710

1090   Pickett, S. T. A., Cadenasso, M. L., Childers, D. L., McDonnell, M. J., & Zhou, W. (2016). Evolution

1091   and future of urban ecological science: Ecology in, of, and for the city. *Ecosystem Health*

1092   *and Sustainability*, *2*, e01229. https://doi.org/10.1002/ehs2.1229

1093   Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V., Zipperer, W. C., &

1094   Costanza, R. (2001). Urban ecological systems: Linking terrestrial, ecological, physical,

1095   and socioeconomic components of metropolitan areas. *Annual Review of Ecology and*

1096   *Systematics*, *32*, 127–157.

1097   Pilot, M., Greco, C., vonHoldt, B. M., Randi, E., Jędrzejewski, W., Sidorovich, V. E., … Wayne, R.

1098   K. (2018). Widespread, long-term admixture between grey wolves and domestic dogs

1099   across Eurasia and its implications for the conservation status of hybrids. *Evolutionary*

1100   *Applications*, *11*(5), 662–680. https://doi.org/10.1111/eva.12595

1101   Qadeer, M. A. (1997). Pluralistic planning for multicultural cities: The Canadian practice. *Journal*

1102   *of the American Planning Association*, *63*(4), 481–494.

1103   https://doi.org/10.1080/01944369708975941

1104   Qadeer, M. A. (2000). *Urban planning and multiculturalism: Beyond sensitivity*.

1105   https://doi.org/10.25316/IR-249

1106   Rebolo-Ifrán, N., Tella, J. L., & Carrete, M. (2017). Urban conservation hotspots: Predation

1107   release allows the grassland-specialist burrowing owl to perform better in the city.

1108   *Scientific Reports*, *7*(1), 1–9. https://doi.org/10.1038/s41598-017-03853-z

1109   Reddy, S. M. W., Montambault, J., Masuda, Y. J., Keenan, E., Butler, W., Fisher, J. R. B., …

1110   Gneezy, A. (2017). Advancing conservation by understanding and influencing human

1111   behavior. *Conservation Letters*, *10*(2), 248–256. https://doi.org/10.1111/conl.12252

1112   Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., … Cooke, S. J.

1113   (2019). Emerging threats and persistent conservation challenges for freshwater

1114   biodiversity. *Biological Reviews*, *94*(3), 849–873. https://doi.org/10.1111/brv.12480

1115   Reid, N. M., Proestou, D. A., Clark, B. W., Warren, W. C., Colbourne, J. K., Shaw, J. R., …

1116   Whitehead, A. (2016). The genomic landscape of rapid repeated evolutionary

1117   adaptation to toxic pollution in wild fish. *Science*, *354*(6317), 1305–1308.

1118   https://doi.org/10.1126/science.aah4993

1119   Reznick, D. N., & Ghalambor, C. K. (2001). The population ecology of contemporary adaptations:

1120   What empirical studies reveal about the conditions that promote adaptive evolution.

1121   *Genetica*, *112–113*, 183–198.

1122   Richardson, J. L., Burak, M. K., Hernandez, C., Shirvell, J. M., Mariani, C., Carvalho-Pereira, T. S.

1123   A., … Caccone, A. (2017). Using fine-scale spatial genetics of Norway rats to improve

1124   control efforts and reduce leptospirosis risk in urban slum environments. *Evolutionary*

1125   *Applications*, *10*(4), 323–337. https://doi.org/10.1111/eva.12449

1126   Rius, M., & Darling, J. A. (2014). How important is intraspecific genetic admixture to the success

1127   of colonising populations? *Trends in Ecology & Evolution*, *29*(4), 233–242.

1128   https://doi.org/10.1016/j.tree.2014.02.003

1129   Rivkin, L. R., Santangelo, J. S., Alberti, M., Aronson, M. F. J., Keyzer, C. W. de, Diamond, S. E., …

1130   Johnson, M. T. J. (2019). A roadmap for urban evolutionary ecology. *Evolutionary*

1131   *Applications*, *12*(3), 384–398. https://doi.org/10.1111/eva.12734

1132   Rochlin, I., Turbow, D., Gomez, F., Ninivaggi, D. V., & Campbell, S. R. (2011). Predictive mapping

1133   of human risk for West Nile Virus (WNV) based on environmental and socioeconomic

1134   factors. *PLoS ONE*, *6*(8). https://doi.org/10.1371/journal.pone.0023280

1135   Rodewald, A. D., Shustack, D. P., & Jones, T. M. (2011). Dynamic selective environments and

1136   evolutionary traps in human-dominated landscapes. *Ecology*, *92*(9), 1781–1788.

1137   https://doi.org/10.1890/11-0022.1

1138   Roman, L. A., Pearsall, H., Eisenman, T. S., Conway, T. M., Fahey, R. T., Landry, S., …

1139   Staudhammer, C. (2018). Human and biophysical legacies shape contemporary urban

1140   forests: A literature synthesis. *Urban Forestry & Urban Greening*, *31*, 157–168.

1141   https://doi.org/10.1016/j.ufug.2018.03.004

1142   Rost, S., Pelz, H.-J., Menzel, S., MacNicoll, A. D., León, V., Song, K.-J., … Müller, C. R. (2009).

1143   Novel mutations in the VKORC1 gene of wild rats and mice – a response to 50 years of

1144   selection pressure by warfarin? *BMC Genetics*, *10*(1), 4. https://doi.org/10.1186/1471-

1145   2156-10-4

1146   Rudman, S. M., Kreitzman, M., Chan, K. M. A. A., Schluter, D., & Rudman, S. M. (2017).

1147   Evosystem services: Rapid evolution and the provision of ecosystem services. *Trends in*

1148   *Ecology and Evolution*, *32*(6), 403–415. https://doi.org/10.1016/j.tree.2017.02.019

1149   Sabeti, P. C., Reich, D. E., Higgins, J. M., Levine, H. Z. P., Richter, D. J., Schaffner, S. F., … Lander,

1150   E. S. (2002). Detecting recent positive selection in the human genome from haplotype

1151   structure. *Nature*, *419*(6909), 832–837. https://doi.org/10.1038/nature01140

1152   Saenz, V. L., Booth, W., Schal, C., & Vargo, E. L. (2012). Genetic analysis of bed bug populations

1153   reveals small propagule size within individual infestations but high genetic diversity

1154   across infestations from the eastern united states. *Journal of Medical Entomology*,

1155   *49*(4), 865–875. https://doi.org/10.1603/ME11202

1156   Salyer, A., Bennett, G. W., & Buczkowski, G. A. (2014). Odorous house ants (*Tapinoma sessile*)

1157   as back-seat drivers of localized ant decline in urban habitats. *PLOS ONE*, *9*(12),

1158   e113878. https://doi.org/10.1371/journal.pone.0113878

1159   Sandercock, L. (1998). *Towards Cosmopolis: Planning for Multicultural Cities*. Chichester: John

1160   Wiley and Sons.

1161   Santangelo, J. S., Johnson, M. T. J., & Ness, R. W. (2018). Modern spandrels: The roles of genetic

1162   drift, gene flow and natural selection in the evolution of parallel clines. *Proceedings of*

1163   *the Royal Society B: Biological Sciences*, *285*(1878), 20180230.

1164   https://doi.org/10.1098/rspb.2018.0230

1165   Savage, A. M., Hackett, B., Guénard, B., Youngsteadt, E. K., & Dunn, R. R. (2015). Fine-scale

1166   heterogeneity across Manhattan's urban habitat mosaic is associated with variation in

1167   ant composition and richness. *Insect Conservation and Diversity*, *8*(3), 216–228.

1168   https://doi.org/10.1111/icad.12098

1169   Schaider, L. A., Swetschinski, L., Campbell, C., & Rudel, R. A. (2019). Environmental justice and

1170   drinking water quality: Are there socioeconomic disparities in nitrate levels in U.S.

1171   drinking water? *Environmental Health*, *18*(1), 3. https://doi.org/10.1186/s12940-018-

1172   0442-6

1173   Schell, C. J., Dyson, K., Fuentez, T. L., Des Roches, S., Woelfle-Erskine, C. A., Harris, N. C., &

1174   Lambert, M. R. (*In Revision*). The eco-evolutionary consequences of social inequality.

1175   *Science*.

1176   Schmidt, C., Domaratzki, M., Kinnunen, R. P., Bowman, J., & Garroway, C. J. (2020). Continent-

1177   wide effects of urbanization on bird and mammal genetic diversity. *Proceedings of the*

1178   *Royal Society B: Biological Sciences*, *287*(1920), 20192497.

1179   https://doi.org/10.1098/rspb.2019.2497

1180   Schoener, T. W. (2011). The newest synthesis: Understanding the interplay of evolutionary and

1181   ecological dynamics. *Science*, *331*(6016), 426–429.

1182   Seto, K. C., Sánchez-Rodríguez, R., & Fragkias, M. (2010). The new geography of contemporary

1183   urbanization and the environment. *Annual Review of Environment and Resources*, *35*(1),

1184   167–194. https://doi.org/10.1146/annurev-environ-100809-125336

1185   Shackleton, C. M., Ruwanza, S., Sinasson Sanni, G. K., Bennett, S., De Lacy, P., Modipa, R., …

1186   Thondhlana, G. (2016). Unpacking Pandora's Box: Understanding and categorising

1187   ecosystem disservices for environmental management and human wellbeing.

1188   *Ecosystems*, *19*(4), 587–600. https://doi.org/10.1007/s10021-015-9952-z

1189   Shochat, E., Warren, P. S., Faeth, S. H., McIntyre, N. E., & Hope, D. (2006). From patterns to

1190   emerging processes in mechanistic urban ecology. *Trends in Ecology & Evolution*, *21*,

1191   186–191. https://doi.org/10.1016/j.tree.2005.11.019

1192   Smith, B. D. (2007). The Ultimate Ecosystem Engineers. *Science*, *315*(5820), 1797–1798.

1193   https://doi.org/10.1126/science.1137740

1194   Sprau, P., Mouchet, A., & Dingemanse, N. J. (2017). Multidimensional environmental predictors

1195   of variation in avian forest and city life histories. *Behavioral Ecology*, *28*(1), 59–68.

1196   https://doi.org/10.1093/beheco/arw130

1197   Stoks, R., Govaert, L., Pauwels, K., Jansen, B., & Meester, L. D. (2016). Resurrecting complexity:

1198   The interplay of plasticity and rapid evolution in the multiple trait response to strong

1199   changes in predation pressure in the water flea Daphnia magna. *Ecology Letters*, *19*(2),

1200   180–190. https://doi.org/10.1111/ele.12551

1201   Sullivan, A. P., Bird, D. W., & Perry, G. H. (2017). Human behaviour as a long-term ecological

1202   driver of non-human evolution. *Nature Ecology and Evolution*, *1*(3).

1203   https://doi.org/10.1038/s41559-016-0065

1204   Szulkin, M., Munshi-South, J., & Charmantier, A. (2020). *Urban Evolutionary Biology*. Oxford

1205   University Press.

1206   Tallamy, D. W. (2020). *Nature's Best Hope*. Retrieved from

1207   https://www.workman.com/products/natures-best-hope

1208   Tanner, C. J., Adler, F. R., Grimm, N. B., Groffman, P. M., Levin, S. A., Munshi-South, J., … Wilson,

1209   W. G. (2014). Urban ecology: Advancing science and society. *Frontiers in Ecology and the*

1210   *Environment*, *12*(10), 574–581. https://doi.org/10.1890/140019

1211   Tessum, C. W., Apte, J. S., Goodkind, A. L., Muller, N. Z., Mullins, K. A., Paolella, D. A., … Hill, J. D.

1212   (2019). Inequity in consumption of goods and services adds to racial–ethnic disparities

1213   in air pollution exposure. *Proceedings of the National Academy of Sciences of the United*

1214   *States of America*, *116*(13), 6001–6006. https://doi.org/10.1073/pnas.1818859116

1215 Teurlincx, S., Kuiper, J. J., Hoevenaar, E. C., Lurling, M., Brederveld, R. J., Veraart, A. J., … de

1216   Senerpont Domis, L. N. (2019). Towards restoring urban waters: Understanding the main

1217   pressures. *Current Opinion in Environmental Sustainability*, *36*, 49–58.

1218   https://doi.org/10.1016/j.cosust.2018.10.011

1219 Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. E., & Paxton, R. J.

1220   (2017). The structure of flower visitor networks in relation to pollination across an

1221   agricultural to urban gradient. *Functional Ecology*, *31*(4), 838–847.

1222   https://doi.org/10.1111/1365-2435.12803

1223 Thomaz, S. M., & Cunha, E. R. da. (2010). The role of macrophytes in habitat structuring in

1224   aquatic ecosystems: Methods of measurement, causes and consequences on animal

1225   assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia*, *22*(02), 218–

1226   236. https://doi.org/10.4322/actalb.02202011

1227 Thompson, J. N. (1998). Rapid evolution as an ecological process. *Trends in Ecology & Evolution*,

1228   *13*(8), 329–332. https://doi.org/10.1016/S0169-5347(98)01378-0

1229 Thompson, K. A., Renaudin, M., & Johnson, M. T. J. (2016). Urbanization drives the evolution of

1230   parallel clines in plant populations. *Proceedings of the Royal Society B: Biological*

1231   *Sciences*, *283*(1845), 20162180. https://doi.org/10.1098/rspb.2016.2180

1232 Tipps, D. C. (1973). Modernization theory and the comparative study of societies: A critical

1233   perspective. *Comparative Studies in Society and History*, *15*(2), 199–226. Retrieved from

1234   JSTOR.

1235 Tischler, H. (2006). *Introduction to Sociology*. Cengage Learning.

1236 Tishkoff, S. A., Reed, F. A., Ranciaro, A., Voight, B. F., Babbitt, C. C., Silverman, J. S., … Deloukas,

1237   P. (2007). Convergent adaptation of human lactase persistence in Africa and Europe.

1238   *Nature Genetics*, *39*(1), 31–40. https://doi.org/10.1038/ng1946

1239 Troy, A., Grove, J. M., & O'Neil-Dunne, J. (2012). The relationship between tree canopy and

1240   crime rates across an urban-rural gradient in the greater Baltimore region. *Landscape*

1241   *and Urban Planning*, *106*(3), 262–270.

1242   https://doi.org/10.1016/j.landurbplan.2012.03.010

1243 Trusty, J. L., Goertzen, L. R., Zipperer, W. C., & Lockaby, B. G. (2007). Invasive Wisteria in the

1244   Southeastern United States: Genetic diversity, hybridization and the role of urban

1245   centers. *Urban Ecosystems*, *10*(4), 379–395. https://doi.org/10.1007/s11252-007-0030-y

1246 UN. (2018). *Revision of World Urbanization Prospects*. Retrieved from

1247   https://www.un.org/development/desa/publications/2018-revision-of-world-

1248   urbanization-prospects.html

1249 Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., … others. (2016).

1250   Improving the forecast for biodiversity under climate change. *Science*, *353*, aad8466.

1251 Urban, M. C., Leibold, M. A., Amarasekare, P., Meester, L. D., Gomulkiewicz, R., Hochberg, M.

1252   E., … others. (2008). The evolutionary ecology of metacommunities. *Trends in Ecology*

1253   *and Evolution*, *23*, 311–317.

1254 Urban, M. C., & Skelly, D. K. (2006). Evolving metacommunities: Toward an evolutionary

1255   perspective on metacommunities. *Ecology*, *87*, 1616–1626.

1256 Van Rossum, F. (2008). Conservation of long-lived perennial forest herbs in an urban context:

1257   Primula elatior as study case. *Conservation Genetics*, *9*(1), 119–128.

1258   https://doi.org/10.1007/s10592-007-9314-2

1259 Vickrey, A. I., Bruders, R., Kronenberg, Z., Mackey, E., Bohlender, R. J., Maclary, E. T., … Shapiro,

1260   M. D. (2018). Introgression of regulatory alleles and a missense coding mutation drive

1261   plumage pattern diversity in the rock pigeon. *ELife*, *7*, e34803.

1262   https://doi.org/10.7554/eLife.34803

1263 Waajen, G. W. A. M., Faassen, E. J., & Lürling, M. (2014). Eutrophic urban ponds suffer from

1264   cyanobacterial blooms: Dutch examples. *Environmental Science and Pollution Research*,

1265   *21*(16), 9983–9994. https://doi.org/10.1007/s11356-014-2948-y

1266 Wada-Katsumata, A., Silverman, J., & Schal, C. (2013). Changes in taste neurons support the

1267   emergence of an adaptive behavior in cockroaches. *Science*, *340*(6135), 972–975.

1268   https://doi.org/10.1126/science.1234854

1269 Walsh, C. J., Roy, A. H., Feminella, J. W., Cottingham, P. D., Groffman, P. M., & Morgan, R. P.

1270   (2005). The urban stream syndrome: Current knowledge and the search for a cure.

1271   *Journal of the North American Benthological Society*, *24*(3), 706–723.

1272   https://doi.org/10.1899/04-028.1

1273 Walsh, M. G. (2014). Rat sightings in New York City are associated with neighborhood

1274   sociodemographics, housing characteristics, and proximity to open public space. *PeerJ*,

1275   *2*, e533. https://doi.org/10.7717/peerj.533

1276 Wania, A., Kühn, I., & Klotz, S. (2006). Plant richness patterns in agricultural and urban

1277   landscapes in Central Germany—Spatial gradients of species richness. *Landscape and*

1278   *Urban Planning*, *75*(1–2), 97–110. https://doi.org/10.1016/j.landurbplan.2004.12.006

1279 Whitehead, A., Clark, B. W., Reid, N. M., Hahn, M. E., & Nacci, D. (2017). When evolution is the

1280   solution to pollution: Key principles, and lessons from rapid repeated adaptation of

1281   killifish (*Fundulus heteroclitus*) populations. *Evolutionary Applications*, *10*(8), 762–783.

1282   https://doi.org/10.1111/eva.12470

1283 Wilke, A. B. B., Chase, C., Vasquez, C., Carvajal, A., Medina, J., Petrie, W. D., & Beier, J. C. (2019).

1284   Urbanization creates diverse aquatic habitats for immature mosquitoes in urban areas.

1285   *Scientific Reports*, *9*(1), 1–11. https://doi.org/10.1038/s41598-019-51787-5

1286 Wilson, C. J., & Jamieson, M. A. (2019). The effects of urbanization on bee communities

1287   depends on floral resource availability and bee functional traits. *PLOS ONE*, *14*(12),

1288   e0225852. https://doi.org/10.1371/journal.pone.0225852

1289 Wirgin, I., Roy, N. K., Loftus, M., Chambers, R. C., Franks, D. G., & Hahn, M. E. (2011).

1290   Mechanistic basis of resistance to PCBs in Atlantic Tomcod from the Hudson River.

1291   *Science*, *331*(6022), 1322–1325. https://doi.org/10.1126/science.1197296

1292 Wood, Z., Palkovacs, E., & Kinnison, M. (2018). Eco-evolutionary feedbacks from non-target

1293   species influence harvest yield and sustainability. *Scientific Reports*, *8*, 6389.

1294   https://doi.org/10.1038/s41598-018-24555-0

1295 Ye, K., Gao, F., Wang, D., Bar-Yosef, O., & Keinan, A. (2017). Dietary adaptation of FADS genes in

1296   Europe varied across time and geography. *Nature Ecology & Evolution*, *1*, 167.

1297   https://doi.org/10.1038/s41559-017-0167

1298   Yoshida, T., Jones, L. E., Ellner, S. P., Fussmann, G. F., & Hairston, N. G. (2003). Rapid evolution

1299   drives ecological dynamics in a predator – prey system. *Nature*, *424*(July), 303–306.

1300   https://doi.org/10.1038/nature01767

1301   Zengeya, T., Ivey, P., Woodford, D. J., Weyl, O., Novoa, A., Shackleton, R., … van Wilgen, B.

1302   (2017). Managing conflict-generating invasive species in South Africa: Challenges and

1303   trade-offs. *Bothalia - African Biodiversity & Conservation*, *47*(2), 1–11.

1304   https://doi.org/10.4102/abc.v47i2.2160

1305   Zipperer, W., Morse, W., & Gaither, C. (2011). Linking social and ecological systems. In J.

1306   Niemela (Ed.), *Urban ecology: Patterns, processes, and adaptations* (pp. 298–308).

1307   Oxford: Oxford University Press.

1308