Opinion: Urban biodiversity and the importance of scale

Kenta Uchida [a,*], Rachel V. Blakey [a, b,*,] Joseph R. Burger [c,d*], Daniel S. Cooper [a,*], Chase A. Niesner [a,*], and Daniel T. Blumstein [a,*, †]

[a] *Department of Ecology and Evolutionary Biology, University of California Los Angeles, 621 Young Drive South, Los Angeles, CA 90095-1606, USA*

[b] *La Kretz Center for California Conservation Science, Institute of the Environment and Sustainability, University of California, La Kretz Hall, Los Angeles, CA 90095, USA*

[c] *Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*

[d] *Arizona Institutes for Resilience, University of Arizona, Tucson, AZ 85721, USA*

*Equal contributions by authors

†Corresponding author: Blumstein DT (marmots@ucla.edu)

Email addresses: ku.squirrel@gmail.com (K. Uchida), rachelvblakey@gmail.com (R. V. Blakey), ecoevoburger@arizona.edu (J. R. Burger), dan@cooperecological.com (D. S. Cooper), chasealexander1@gmail.com (C. A. Niesner), marmots@ucla.edu (D. T. Blumstein)

Keywords: urban biodiversity, city scale, eco-evolutionary processes, cultural processes

Highlights

- Eco-evolutionary processes are influenced by urbanization and therefore influence urban biodiversity
- Cities vary in size by many orders of magnitude, and we therefore expect eco-evolutionary and human cultural processes scale non-linearly with city size
- We do not expect all processes to scale similarly and deviations can be informative
- We develop a mechanistic framework to study how scale influences biodiversity through eco-evolutionary mechanisms, and guides urban biodiversity management

Abstract

Many ecological and evolutionary processes are affected by urbanization, but cities vary by orders of magnitude in both their size and degree of development. To quantify and manage urban biodiversity we must understand both how biodiversity scales with city size, and how ecological, evolutionary, and socioeconomic drivers of biodiversity scale with city size. We show how environmental abiotic and biotic drivers as well as human cultural and socioeconomic drivers may act through ecological and evolutionary processes differently at different scales to influence patterns in urban biodiversity. Because relationships likely take linear and non-linear forms, we highlight the need to describe the specific scaling relationships, including deviations and potential inflection points, where different management strategies may successfully conserve urban biodiversity.

What is urban biodiversity, and how does it "scale"?

Urbanization (see Glossary) is an ongoing and dramatic process of environmental modification and is paradoxically both a **biodiversity** filter and facilitator [1-4]. Though many species are unable to dwell widely in the city due to the disruption of their native habitat, some individuals find refuge in the wide variety of natural "city green space" [4,5], while others are released and/or cultivated there by humans, occasionally forming feral populations [6]. The burgeoning study of urban ecology has shown that urbanization has profound impacts on both ecological and evolutionary processes as well as on humans inhabiting urban areas [7]. Urban ecosystems are profitably studied from a perspective that recognizes the reciprocal links between nature and humans [8,9].

Studies of urban systems have been conducted at multiple scales, ranging from small towns to some of the largest urban areas on Earth. An implicit assumption of such studies is that ecological and social processes scale consistently across the great diversity in city size, such that the patterns found in small and mid-sized urban areas would also apply to very large ones. Such an assumption is convenient because if there are general scaling rules of urban attributes, then the ecological, evolutionary, and social processes that occur in very large urban areas can be conveniently studied at smaller scales. However, we still lack a comprehensive understanding of how eco-evolutionary processes that potentially influence biodiversity change by city size. If different ecological, evolutionary, and social characteristics scale differently with city size, management strategies that work at one scale would break down at another, leading to ineffective projects and failure to actually preserve biodiversity. Similarly, evolutionary processes may be different for cities of differing sizes - or could be sensitive to some urban size threshold where they could be absent entirely at smaller scales (Box I). **Megacities** may represent a novel ecosystem and could offer challenges – but also opportunities – for biodiversity conservation.

To conserve urban biodiversity, it is essential to clarify underlying mechanisms of the relationship between city scale and biodiversity. For example, as cities grow larger in extent, they may contain more and larger green patches, and possess higher environmental heterogeneity, both of which are key ecological and evolutionary drivers that underlie urban biodiversity. Within sufficiently large cities, certain natural-cultural systems that scale differently interact to form “cross-scale functional arrangements” [10]. For instance, the diversity of feral populations of exotic birds appears to be related to both abiotic factors (e.g., colonization history, per capita GDP), as well as regional diversity of native species [6], and these non-natives tend to thrive in the most modified (by humans) environments [11], factors which would be expected to scale non-linearly.

From a management perspective, public agencies within larger cities may be able to contribute less funding to biodiversity conservation than smaller ones, as private non-profit groups in large cities might “take up the slack” with less public funding (Box II). Or, small cities may spend far less than would be predicted because they may present a better opportunity for native species from the surrounding area to re-colonize and become established, and may resist non-native species invasions. It may also be the case that beyond a certain size, population pressure on resources of conserved (or simply undeveloped) areas within the largest cities may swamp attempts at protection (signage, fencing, etc.) that would work in smaller cities. Biodiversity management strategies must reflect these emergent and complex relationships that may not scale linearly. Understanding scaling patterns of social and ecological characteristics is essential for municipalities to refine management regimes for desired outcomes.

Eco-evolutionary feedbacks are expected and may vary with city size

We suggest that eco-evolutionary feedbacks [12] are likely to have a significant impact on urban biodiversity [13]. Modifications to the biotic and abiotic environment by urban development creates novel selection pressures that have only existed in the past 5,000 years [7]. Thus, we would expect changes in the traits associated with survival, reproductive success, and interspecific interactions to modify population dynamics and community structure. At the same time, urban-mediated alterations of local biodiversity can influence broader-scale ecological and evolutionary processes via changes in interspecific competition, prey-predator interactions, and genetic diversity in urban habitats. For example, change in a predator community could influence the abundance and adaptive phenotypes of prey [14]. Because community level eco-evolutionary dynamics have often been studied in a theoretical framework and experimental microcosms [15], it is essential to identify these processes in actual urban environments that vary by orders of magnitude in size. We must develop deeper insights into these dynamics if we are to better understand and manage expanding urban ecosystems.

There are good reasons to believe that ecological and evolutionary drivers of biodiversity may vary predictably with city size. For example, in Europe, the log of bird species richness has been shown to scale predictably with the log of city size [16]. The slope of the species-area relationship of cities was not significantly different from that of regional species richness, suggesting that patterns of biodiversity seen in “nature” may also apply to certain urban areas. Similarly, changes in the elevation (intercept) of the scaling relationship can inform additional variation, while this is probably due to geographical position rather than scale. For instance, the difference in urban vs. rural bird diversity appears to be greater at lower (i.e., southern-hemisphere) latitudes, with rural areas more diverse, yet urban diversity remained constant regardless of latitude [17].

Scale-dependent biodiversity management

An understanding of how biodiversity scales with city size should influence biodiversity management in two main ways: the opportunities and constraints for goal-setting; and the efficacy and implementation of management.

Defining biodiversity goals in cities is always a challenge. When assessing patterns of urban biodiversity and its management, we must distinguish between biodiversity, biological/evolutionary processes, and the management of each. A common approach is to use surrounding or historical natural ecosystems as a benchmark and to preserve urban genetic, species and ecosystem diversity reference levels [18]. But while restoration of local surrounding or historical biodiversity may be a feasible outcome for smaller cities, as cities grow, they are more likely to develop into novel ecosystems (or will have lost critical components of original ecosystems). Thus, alternative management goals should be applied to large cities that recognize these new realities [18]. Additionally, large cities may provide opportunities to address unique biodiversity management goals with broader national or international reach. For example, Sydney, Australia's largest city, contains the most threatened endemic plants and animals [19]. Megacities in the United States have become strongholds for non-native, but imperiled (in their native range) bird species [20].

Managing urban biodiversity entails weighing the relative importance of biodiversity outcomes between finer (local, regional) and broader (national, global) scales. For example, Australia has four mainland species of flying foxes (family Pteropodidae), large-bodied colonial roosting bats, that regularly form large colonies in urban areas. These nomadic animals once followed seasonal resources including eucalypt flowering and rainforest fruiting events across the country, where they were important seed dispersers and pollinators. Now the fig-tree lined streets of Australian cities provide their most reliable food resource [21]. Given at least one of the flying fox species that regularly occur in cities and range across the eastern Australian continent (*Pteropus poliocephalus*) are undergoing population declines that put them at risk of extinction and are highly vulnerable to climate change [22], cities are likely to now play a disproportionate role in the national conservation of this family and the ecosystem services they provide. In this way, larger cities have an opportunity to define unique biodiversity goals that will influence state and federally protected threatened species that provide critical ecological function such as seed dispersal and pollination services at a national scale. Conversely, large cities may play a disproportionate role in the spread of invasive species or pathogens, due to their transport and trade networks with serious management implications [23].

The relative benefits of different biodiversity management strategies may vary with city size, and in the way biodiversity is measured ([24]; Box II). For example, **land sharing** results in higher population size of target insects in smaller cities, while **land sparing** results in larger insect populations as urbanization expands in extent and urban development intensifies [25].

Recognizing the value of novel resources for biodiversity management includes integrating networks of private gardens into conservation strategies, which has been done in the U.S., the U.K., and Australia with the involvement of “community-science” projects [26]. Scaling is relevant to garden networks given that mobile taxa are likely to be more strongly associated with habitat availability and configuration at scales larger than a single garden [27,28]. Care must be taken with small habitat patches to avoid them becoming ecological traps [39,30], given that introduced predators (e.g., domestic cats) also inhabit urban gardens [31]. Biodiversity management approaches that maximize biodiversity outcomes in megacities, for example, opting for “land-sparing” rather than “land-sharing” strategies in more urbanized areas [25,32], may increase the inequity in biodiversity access between socioeconomic groups by decreasing access to natural resources in low income areas.

A mechanistic model of urban biodiversity

We illustrate how anthropogenically modified abiotic and biotic drivers as well as cultural and socioeconomic drivers act through ecological and evolutionary processes to influence urban biodiversity (Fig. 1). We emphasize that both global abiotic (droughts, fires, the frequency of intense storms, etc.) and biotic drivers act directly on these eco-evolutionary processes, and may act on these drivers directly. And we recognize that there are key feedbacks between drivers and processes, and between biodiversity and processes.

Anthropogenically-modified biotic drivers of biodiversity are crucial to urban biodiversity conservation, and include habitat size, habitat connectivity, the presence of predators, food availability, and more exotic species [33]. A landscape's biotic characteristics, for example, can influence animal movement [34]. Generally, urban development reduces the size of usable habitat patches and hence increases fragmentation [35,36]. These habitat modifications reduce dispersal and the frequency of movement [37] and drive genetic drift observed in reduced genetic diversity within patches and greater stochasticity in allele frequencies across patches [13].

Reduced habitat connectivity may also reduce the frequency of species interactions, which has consequences for urban biodiversity, and this may vary unpredictably with scale. It is easy to envision pollination and seed dispersal dynamics being influenced by isolation within a very large city, such that gene flow and plant diversity are reduced [38,39]. Yet, this might not happen in a smaller city, or within a megacity with large enough patches of natural habitat. Human activity, in some cases, may create a "predator shield" [40,41] whereby there is relaxed predation pressure in urban areas. This reduction of predation risk along an urbanization gradient has led to a suite of phenotypic changes in antipredator behavior. For instance, many studies that quantified flight initiation distance (FID) to an approaching human in urban and rural environments found that urban animals have shorter FIDs than rural conspecifics [42,43]. A release from predation risk permits, in principle, animals to allocate more time to fitness-enhancing activities such as foraging and reproduction, which may contribute to higher population densities. Although this behavioral modification may also be explained by behavioral plasticity [44], some studies have revealed local adaptation to relaxed predation pressure as well as to life in urban areas more generally [45,46].

The presence of non-native species may play an important role in eco-evolutionary processes. Domestic cats, for example, are important predators for many native birds and small mammals [47,48] and cats could create novel threats, as seen in Australia, where they have more than replaced formerly resident predators and been implicated in driving native animals to extinction [49]. Newly introduced species could also modify evolved patterns of interspecific competition [50] which may create mismatches with demographic consequences. However, this simple prediction of decreasing predator-prey interactions in urban areas might not hold if small cities are surrounded by natural habitats, or if large cities have larger patches, that both support predators.

The abiotic urban environment is remarkably different from natural areas in terms of pollution (e.g., air, light, noise), high densities of infrastructure (e.g., roads and buildings), and warmer temperatures attributable to the heat island effect [8]. More buildings and roads inhibit movement, reduces dispersal, and are associated with direct mortality [51]. Modified microclimates create novel challenges to animals and plants. For example, white clover (*Trifolium repens*) has proportionately less cyanogenesis along an urbanization gradient, which results from reduced snow cover and increases in winter temperatures with urbanization [52]. Artificial night lighting has significant effects on predation, foraging, reproduction, and movement in many species [53-55]. For instance, mate choice preferences of females frogs change with increased light levels [56] due to a concomitant reduction in predation risk. In addition, artificial light often creates an ecological trap for insects by attracting predatory birds and frogs [53]. Pollution may drive adaptation leading to the evolution of resistant populations, as illustrated by how industrial air pollution increases DNA mutation rates in urban herring gulls (*Larus argentatus*) compared to those in rural habitats [59]. Importantly, these abiotic drivers may have multi-species effects. For instance, modified prey-predator interactions due to light pollution is likely to change local species composition where light pollution is highest [58]. Additionally, if noise pollution interferes with reproduction (such as by modifying mate preferences, altering song output or preventing species recognition), it may modify sexual selection and increase hybridization [59].

The diversity of cultural and socioeconomic drivers (Fig. 1) may have both direct and indirect effects on eco-evolutionary processes as urbanization increases [60]. Diversity of ownership exists in urban areas (there are both private yards and public parks) and their management will be influenced by cultural demands and societal resources. For example, globally, high income areas are often correlated with higher biodiversity due to unequal distribution of resources across cities resulting from residential segregation and exclusionary zoning practices [61]. Studies in the UK also found that key socioeconomic factors including house type, household size, and age were significant predictors for participation in providing food for birds [62], which, while providing human access to biodiversity, can increase bird populations but also shift community structure towards a greater proportion of urban-adapted and non-native species [63,64]. Humans have strong opinions about certain animals [65], and predators may be hunted or hazed in residential areas because of human's fears or anxieties [66]. Thus, we may see consequences for species composition and ecosystem function due to these cultural biases as large and mid-sized predators play such a key role in ecosystems.

Concluding Remarks

Despite rapid urbanization and growing cities, we lack a general framework to study global urban biodiversity across scales. This mechanistic model can guide future urban biodiversity research (Box III) and management. We challenge future researchers to identify the precise relationships between city size and biodiversity, and that between city size and the drivers that influence biodiversity (Box I). Understanding these scaling relationships and their deviations can inform urban biodiversity management across cities (Outstanding Questions). As cities grow in density and population, green space tends to be lost to urbanization. However, as urban areas expand in extent, their amount of green space may increase, presenting unique management opportunities. Thus, future studies that develop an understanding of these scaling relationships will be essential to forecast and conserve urban biodiversity on a rapidly urbanizing planet.

Acknowledgements

KU is supported by Japan Society for the Promotion of Science. RVB is supported by the La Kretz Center for California Conservation Science at the University of California Los Angeles. JRB is supported by the Bridging Biodiversity and Conservation Science program at the University of Arizona. DTB is supported by the NSF.

References

1 Aronson, M.F.J. *et al.* (2017) Biodiversity in the city: key challenges for urban green space management. *Front. Ecol. Environ.* 15, 189–196

2 Murthy, A.C. *et al.* (2016) Homogenizing effects of cities on North American winter bird diversity. *Ecosphere* 7, 1–9

3 Sánchez-Bayo, F. and Wyckhuys, K.A.G. (2019) Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* 232, 8–27

4 Goddard, M.A. *et al.* (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol. Evol.* 25, 90–98

5 Lepczyk, C.A. *et al.* (2017) Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. *BioScience* 67, 799–807

6 Dyer, E.E. *et al.* (2017) The Global Distribution and Drivers of Alien Bird Species Richness. *PLoS Biol.* 15, 1–25

7 Rivkin, L.R. *et al.* (2019) A roadmap for urban evolutionary ecology. *Evol. Appl.* 12, 384–398

8 Grimm, N.B. *et al.* (2008) Global change and the ecology of cities. *Science* 319, 756–760

9 Pickett, S.T.A. *et al.* (2011) Urban ecological systems: Scientific foundations and a decade of progress. *J. Environ. Manage.* 92, 331–362

10 Alberti, M. (2018) *Cities That Think Like Planets: Complexity, Resilience, and Innovation in Hybrid Ecosystems*. Seattle: University of Washington Press.

11 Garrett, Kimball L. and Singer, D.S. (1998) Report of the Caifornia bird records comittee: 1995 records. *West. Birds* 29, 133–156

12 Hendry, A.P. *et al.* (2017) Human influences on evolution, and the ecological and societal consequences. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160028

13 Johnson, M.T.J. and Munshi-South, J. (2017) Evolution of life in urban environments. *Science (80).* 358, eaam8327.

14 Palkovacs, E.P. and Post, D.M. (2009) Experimental evidence that phenotypic divergence in predators drives community divergence in prey. *Ecology* 90, 300–305

15 Kokko, H. and López-Sepulcre, A. (2007) The ecogenetic link between demography and evolution: Can we bridge the gap between theory and data? *Ecol. Lett.* 10, 773–782

16 Ferenc, M. *et al.* (2014) Are cities different? Patterns of species richness and beta diversity of urban bird communities and regional species assemblages in Europe. *Glob. Ecol. Biogeogr.* 23, 479–489

17 Filloy, J. *et al.* (2015) Urbanization altered latitudinal patterns of bird diversity-environment relationships in the southern Neotropics. *Urban Ecosyst.* 18, 777–791

18 Hobbs, R.J. *et al.* (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* 24, 599–605

19 Ives, C.D. *et al.* (2016) Cities are hotspots for threatened species. *Glob. Ecol. Biogeogr.* 25, 117–126

20 Shaffer, H.B. (2018) Urban biodiversity arks. *Nat. Sustain.* 1, 725–727

21 Eby, P. (1995) "The biology and management of flying foxes in New South Wales." *New South Wales National Parks and Wildlife Service, Report* 18

22 Lunney, D., Richards, G. & Dickman, C. (2008) *Pteropus poliocephalus*. *The IUCN Red List of Threatened Species* 2008: e.T18751A8554062. Downloaded on 29 June 2020.

23 O’Malia, E.M. *et al.* (2018) Pathways and places associated with nonindigenous aquatic species introductions in the Laurentian Great Lakes. *Hydrobiologia* 817, 23–40

24 Stott, I. *et al.* (2015) Land sparing is crucial for urban ecosystem services. *Front. Ecol. Environ.* 13, 387–393

25 Soga, M. *et al.* (2014) Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *J. Appl. Ecol.* 51, 1378–1386

26 Gonzalez, A. *et al.* (2020) Scaling-up biodiversity-ecosystem functioning research. *Ecol. Lett.* 23, 757–776

27 Chamberlain, D.E. *et al.* (2009) Avian productivity in urban landscapes: A review and meta-analysis. *Ibis.* 151, 1–18

28 Smith, R.M. *et al.* (2006) Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biol. Conserv.* 129, 312–322

29 Hale, R. and Swearer, S.E. (2016) Ecological traps: Current evidence and future directions. *Proc. R. Soc. B Biol. Sci.* 283, 20152647

30 Bruce, R.A. and Richard, H.L. (2006) A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87, 1075–1085

31 Legge, S. *et al.* (2020) We need to worry about Bella and Charlie: the impacts of pet cats on Australian wildlife. *Wildl. Res.* DOI: 10.1071/wr19174

32 Caryl, F.M. *et al.* (2016) Functional responses of insectivorous bats to increasing housing density support “land-sparing” rather than “land-sharing” urban growth strategies. *J. Appl. Ecol.* 53, 191–201

33 McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* 127, 247–260

34 Riley, S.P.D. *et al.* (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conserv. Biol.* 17, 566–576

35 Cadenasso, M.L. *et al.* (2007) Spatial heterogeneity in urban ecosystems: Reconceptualizing land cover and a framework for classification. *Front. Ecol. Environ.* 5, 80–88

36 Dobbs, C. *et al.* (2017) Assessing the drivers shaping global patterns of urban vegetation landscape structure. *Sci. Total Environ.* 592, 171–177

37 Bullock, J.M. *et al.* (2018) Human-Mediated Dispersal and the Rewiring of Spatial Networks. *Trends Ecol. Evol.* 33, 958–970

38 Hennig, E.I. and Ghazoul, J. (2011) Plant-pollinator interactions within the urban environment. *Perspect. Plant Ecol. Evol. Syst.* 13, 137–150

39 Theodorou, P. *et al.* (2020) Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11, 1–13

40 Møller, A.P. (2012) Urban areas as refuges from predators and flight distance of prey. *Behav. Ecol.* 23, 1030–1035

41 Smith, J.A. *et al.* (2017) Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proc. R. Soc. B Biol. Sci.* 284, 20170433

42 Samia, D.S.M. *et al.* (2015) Increased tolerance to humans among disturbed wildlife. *Nat. Commun.* 6, 1-8

43 Uchida, K. *et al.* (2019) Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behav. Ecol.* 30, 1583–1590

44 McCleery, R.A. (2009) Changes in fox squirrel anti-predator behaviors across the urban-rural gradient. *Landsc. Ecol.* 24, 483–493

45 Møller, A.P. (2008) Flight distance of urban birds, predation, and selection for urban life. *Behav. Ecol. Sociobiol.* 63, 63–75

46 Lowry, H. *et al.* (2013) Behavioural responses of wildlife to urban environments. *Biol. Rev.* 88, 537–549

47 Bonnington, C. *et al.* (2013) Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species. *J. Appl. Ecol.* 50, 15–24

48 Loss, S.R. *et al.* (2013) The impact of free-ranging domestic cats on wildlife of the United States. *Nat. Commun.* 4, 1396

49 Legge, S. *et al.* (2017) Enumerating a continental-scale threat: How many feral cats are in Australia? *Biol. Conserv.* 206, 293–303

50 Alberti, M. *et al.* (2017) Urban driven phenotypic changes: Empirical observations and theoretical implications for eco-evolutionary feedback. *Philos. Trans. R. Soc. B Biol. Sci.* 372, 20160029.

51 Carvalho, F. *et al.* (2018) The effects of a motorway on movement behaviour and gene flow in a forest carnivore: Joint evidence from road mortality, radio tracking and genetics. *Landsc. Urban Plan.* 178, 217–227

52 Thompson, K.A. *et al.* (2016) Urbanization drives the evolution of parallel clines in plant populations. *Proc. R. Soc. B Biol. Sci.* 283, 20162180

53 Longcore, T. and Rich, C. (2004) Ecological light pollution. *Front. Ecol. Environ.* 2, 191–198

54 Gaston, K.J. *et al.* (2013) The ecological impacts of nighttime light pollution: A mechanistic appraisal. *Biol. Rev.* 88, 912–927

55 Lao, S. *et al.* (2020) The influence of artificial night at night and polarized light on bird-building collisions. *Biol. Conserv.* 241, 108358

56 Rand, A.S. *et al.* (1997) Light Levels Influence Female Choice in Túngara Frogs : Predation Risk Assessment ? *Copeia*, 1997, 447–450

57 Yauk, C.L. and Quinn, J.S. (1996) Multilocus DNA fingerprinting reveals high rate of heritable genetic mutation in herring gulls nesting in an industrialized urban site. *Proc. Natl. Acad. Sci. U. S. A.* 93, 12137–12141

58 Gaston, K.J. and Holt, L.A. (2018) Nature, extent and ecological implications of night-time light from road vehicles. *J. Appl. Ecol.* 55, 2296–2307

59 Grabenstein, K.C. and Taylor, S.A. (2018) Breaking barriers: Causes, consequences, and experimental utility of human-mediated hybridization. *Trends Ecol. Evol.* 33, 198–212

60 Des Roches, S. *et al.* (2020) Socio-eco-evolutionary dynamics in cities. *Evol. Appl.* DOI: 10.1111/eva.13065.

61 Kuras, E.R. *et al.* (2020) Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis. *Landsc. Urban Plan.* 198, 103799

62 Davies, Z.G. *et al.* (2012) Household factors influencing participation in bird feeding activity: A national scale analysis. *PLoS One* 7, e39692

63 Fuller, R.A. *et al.* (2008) Garden bird feeding predicts the structure of urban avian assemblages. *Divers. Distrib.* 14, 131–137

64 Reynolds, S.J. *et al.* (2017) Garden bird feeding: Insights and prospects from a north-south comparison of this global Urban phenomenon. *Front. Ecol. Evol.* 5, 24

65 Soga, M. and Gaston, K.J. (2020) The ecology of human–nature interactions. *Proc. R. Soc. B Biol. Sci.* 287, 20191882

66 van Eeden, L.M. *et al.* (2018) Managing conflict between large carnivores and livestock. *Conserv. Biol.* 32, 26–34

67 Bettencourt, L.M.A. *et al.* (2007) Growth, innovation, scaling, and the pace of life in cities. *Proc. Natl. Acad. Sci. U. S. A.* 104, 7301–7306

68 Bettencourt, L.M.A. *et al.* (2010) Urban scaling and its deviations: Revealing the structure of wealth, innovation and crime across cities. *PLoS One* 5, e13541

69 Borgström, S.T. *et al.* (2006) Scale mismatches in management of urban landscapes. *Ecol. Soc.* 11

70 Stavros, E.N. *et al.* (2017) ISS observations offer insights into plant function. *Nat. Ecol. Evol.* 1, 0194

71 Schneider, F.D. *et al.* (2017) Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nat. Commun.* 8, 1441

72 Alonzo, M. *et al.* (2014) Urban tree species mapping using hyperspectral and lidar data fusion. *Remote Sens. Environ.* 148, 70–83

73 Wardrop, N.A. *et al.* (2018) Spatially disaggregated population estimates in the absence of national population and housing census data. *Proc. Natl. Acad. Sci. U. S. A.* 115, 3529–3537

74 Callaghan, C.T. *et al.* (2020) Avian trait specialization is negatively associated with urban tolerance. *Oikos* DOI: 10.1111/oik.07356

75 Spear, D.M. *et al.* (2017) Citizen science as a tool for augmenting museum collection data from urban areas. *Front. Ecol. Evol.* 5, 86

76 Kissling, W.D. *et al.* (2018) Building essential biodiversity variables (EBVs) of species distribution and abundance at a global scale. *Biol. Rev.* 93, 600–625

77 Lin, M. *et al.* (2020) A biodiversity composition map of California derived from environmental DNA metabarcoding and Earth observation. *bioRxiv* DOI: https://doi.org/10.1101/2020.06.19.160374

78 Larson, E.R. *et al.* (2020) From eDNA to citizen science: emerging tools for the early detection of invasive species. *Front. Ecol. Environ.* 18, 194-202.

79 Gaston, K. J., & Spicer, J. I. (2013). *Biodiversity: an introduction*. John Wiley & Sons.

80 Maclaurin, J., & Sterelny, K. (2008). *What is biodiversity?*. University of Chicago Press.

81 Lin, B.B. and Fuller, R.A. (2013) Sharing or sparing? How should we grow the world's cities? *J. Appl. Ecol.* 50, 1161–1168

82 United Nations Department of Economic and Social Affairs Population Division (2018) *World Urbanization Prospects*, 12

83 Seto, K.C. *et al.* (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U. S. A.* 109, 16083–16088

GLOSSARY

Biodiversity: Biodiversity can be measured in many ways that include simple measurements of variation in the number of species space and time, as well as species richness within urban areas. “Functional” or “morphological” diversity [79] captures the basic processes at work in a given environment, and the roles played by taxa. Genetic/genomic diversity captures the variety within and between organisms [80], and, “ecosystem diversity” [79] captures the variation of assemblages of species at different scales.

Land sharing: An urban land management practice whereby there is relatively low intensity urban development that contains small green patches such as parks, gardens, and yards [81].

Land sparing: An urban land management practice whereby urban development is concentrated and large green parks and nature reserves are set aside as habitat that supports biodiversity [81].

Megacity: Megacities are the largest cities which typically contain over 10 million people [82].

Urbanization: The process of anthropogenic transformation of wildlands to the built environment where people live and work. Urban areas have been rapidly expanding globally and have been associated with concomitant biodiversity loss [83].

OUTSTANDING QUESTIONS

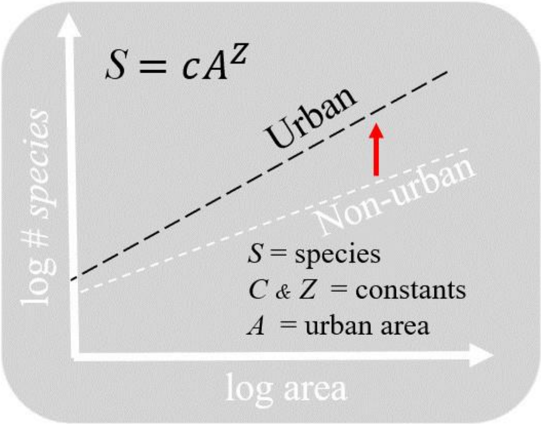
- What is the goal of urban biodiversity management? Is it to sustain local biodiversity or to create a new urban biodiversity? Or, is it to enhance human well-being from biodiversity? Can urban biodiversity management achieve biodiversity goals at multiple scales (local, regional, global)?
- What are the scaling relationships between anthropogenic drivers and eco-evolutionary drivers of biodiversity with city size? How do these vary by countries and regions? And how do deviations in these scaling relationships reflect different cultures and policies?
- What are the costs and benefits to urban biodiversity conservation and management ("green gentrification"), and how might environmental justice be integrated into urban biodiversity management at multiple scales?
- How can scaling relationships, once identified, inform best management strategies applied at different scales?
- How can global data infrastructures facilitate socio-ecological and biodiversity compilation, standardization, and management to facilitate the study of urban biodiversity scaling (Box III)?
- How might increasing and then shrinking/urbanization influence future urban biodiversity?
- How do we better understand emergent properties of urban areas as new ecosystems develop?
- What specific scale-dependent relationships are associated with whether a species declines or expands?

Text Boxes

Box I. A primer on city scaling

Many social and ecological attributes scale with city size. Studying the multiple drivers (Fig. B1) of urban biodiversity requires characterizing these scaling relationships so that cities varying in size by many orders of magnitude can be compared. The species-area relationship is illustrative (Fig. 1). The number of species, S, scales as a function of urban area, A, with scaling constants C and Z. Deviations in these scalings provide a means of normalizing for city size and comparing social-ecological drivers impacting urban biodiversity. Studies show urban environments shift the intercept, C, up resulting in higher Alpha diversity compared to nearby non-urban environments [16] and latitude [2].

Figure B1. Generalized species-urban area relationship contrasting possible relationships in urban and non-urban areas



Scaling has other implications for the physical, biological, and social characteristics of cities. Scaling relationships take power-law form

$$Y(t) = Y_o(t)\ City\ Size(t)^{\beta}$$

Where Y at time t is a quantifiable city characteristic, such as green space, or economic GDP, Y_o is a constant (intercept), and X is typically city population size or total area at time t. β the scaling exponent reveals emergent dynamics that take place across cities of different sizes. These scaling relations are necessary to test the causal framework in Fig. B1.

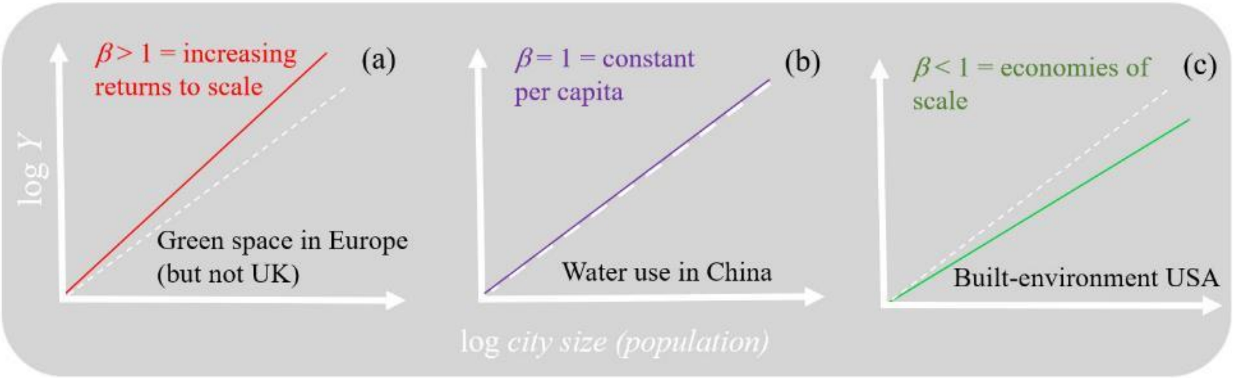
Three classes of urban scaling (Fig. B2).

a) Superlinear scaling: $\beta > 1$, resulting in increasing returns to scale with city size and is characteristic of attributes associated with human interactions GDP, innovation, infectious disease cases, crime (e.g., [67]).

b) Isometric scaling: $\beta = 1$, resulting in constant per capita values in Y irrespective of city size. Most resource use and waste production (CO_2 emissions) show isometry.

c) Sublinear scaling: $\beta < 1$, resulting in economies of scale – a systematic decrease of per capita values with city size. This is analogous to Kleiber's law in biological scaling. In some studies, infrastructure characteristics of cities such as road surfaces and electrical cables, scale $\beta < 1$.

Figure B2. Three classes of urban scaling: a) superlinear, b) linear, and c) sublinear



Box II: Scaling applications to biodiversity management

Variations and deviations in scaling would have major consequences for management (Box 1). It may not be possible to use insights from studies of smaller cities to manage biodiversity in the largest cities (see [68] for examples of city scaling and deviations from expected values). Larger cities may host both greater economic and social capital, as well as open space, to achieve higher level biodiversity goals. For example, as cities expand in extent, conservation projects (such as the number of habitat restoration work days across the urban area) may become more numerous, effective and widespread, since the pool of people interested in conservation is sufficiently large to support multiple active conservation groups. Or, perhaps conservation activity doesn't scale predictably - perhaps large cities become overwhelmed with human activity, and such groups are most active in small and mid-sized cities (we acknowledge that determining their "effectiveness" should be a separate endeavor, outside the scope of this paper). This is likely to vary in different parts of the world, with wealthy nations promoting more active, expensive projects like brownfields restoration and creation of wildlife corridors through parkland acquisition, and less-wealthy areas promoting more passive biodiversity restoration such as leaving slivers or even large blocks of habitat undeveloped because they lack the resources to develop them. However, we recognize that integration of local scale and regional scale biodiversity goals (cross-scale management), and research on this integration, remains limited [69].

From a management perspective, large urban areas tend to have multiple agencies responsible for the management of large urban green spaces (the Los Angeles River, for example, has Federal, regional, state, and municipal agencies and utilities, as well as dozens of local non-profit community groups, all devoted to flood control, biodiversity preservation and water quality along its 50-mile length through the urbanized Los Angeles Basin). This "alphabet soup” of stakeholders exceeds that typically seen in more rural areas where there are fewer entities- such as the U.S. Forest Service, or the Bureau of Land Management - controlling most of the surrounding and interstitial open space around small cities (and thus, its biodiversity). Whether these differences - as influenced by city size - result in different patterns of biodiversity conservation at different scales is a critically important question. For example, would a city 10x the size of another city requires 10x more agency funding to maintain high biodiversity levels?

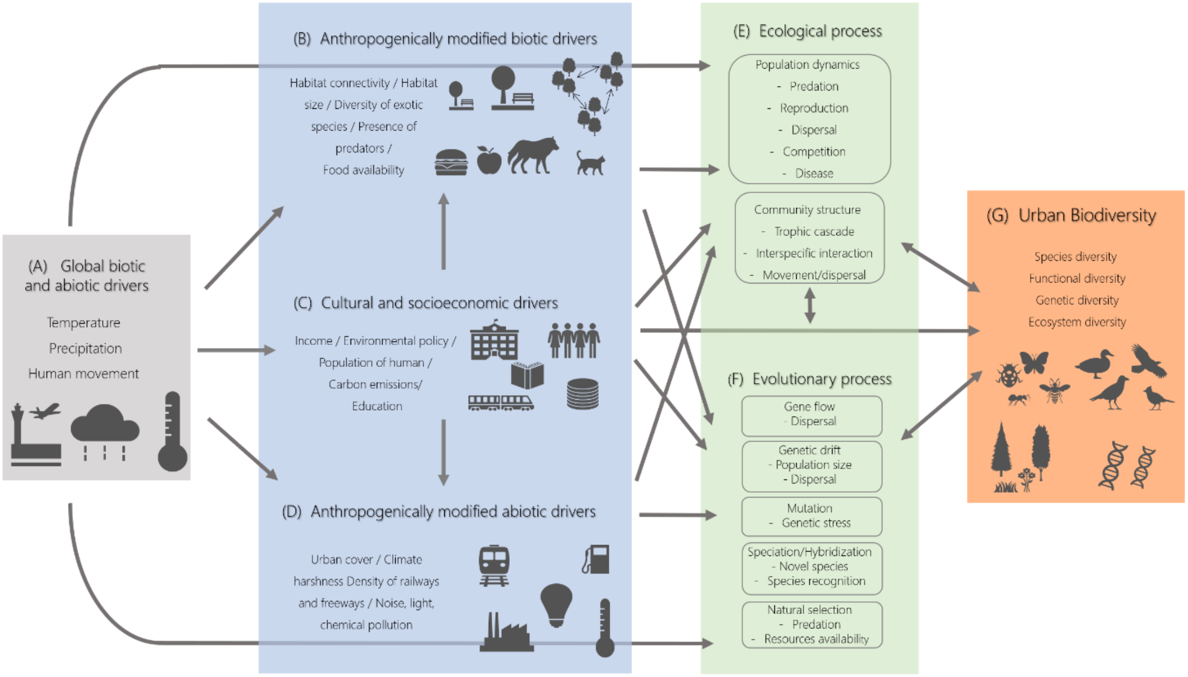
Box III: **Data opportunities to study the scale of urban biodiversity**

Investigations of biodiversity scale relationships have been hampered in the past by a lack of consistent and globally available biodiversity data. The growth of community science, remote methods of biodiversity surveillance, and international partnerships in urban ecology are rapidly filling this data gap. Global remote sensing products are increasing in their spatial and temporal resolution, and their ability to characterize the structure and function of landscapes [70]. Remotely sensed imagery and lidar provide the means to characterize biodiversity patterns [71], the urban environment [72], and even the human population densities [73] in areas where on-the-ground data are scarce. Global community science programs, such as iNaturalist and eBird have allowed large-scale analyses of urban ecology (e.g., [74]) and have also been used to augment museum collections [75] and work towards global biodiversity monitoring [76]. Environmental DNA, community science, and remotely sensed imagery have been used in combination to map state-level biodiversity [77] and for invasive species management [78]. Combining these emerging techniques should enable us to study the underlying patterns and processes mechanisms of urban biodiversity and identify scaling relationships between city size and eco-evolutionary processes.

Figure 1

Figure 1. A causal model of urban eco-evolutionary processes linked to biodiversity

Our goal is to illustrate how environmental factors influence eco-evolutionary processes to drive urban biodiversity. To inform biodiversity management in urban environments, we focus on (B) anthropogenically modified biotic drivers (e.g., Habitat connectivity, Habitat size, Human density, Diversity of exotic species, Presence of predators, Food availability), (D) anthropogenically modified abiotic drivers (e.g., Urban cover, Density of railways and freeways, Noise, light, and chemical pollution, Climate harshness, Heterogeneity in these factors), and (C) cultural and socioeconomic drivers (e.g., Income, Environmental policies, Human population, Human movement, Carbon emissions, Education) as main factors that drive eco-evolutionary processes. Decreased numbers of natural predators, for example, allows prey species to allocate more time to foraging, may increase intraspecific competition, and may have cascading effects which change population dynamics and community structure. These biotic drivers also modify predation pressure and may influence gene flow through changing movement behavior of prey species. Because the urban environment is designed to meet social and economic demands, culture and socioeconomic factors drive the eco-evolutionary processes directly and indirectly via influencing biotic/abiotic drives. Since each driver is related to more than one eco-evolutionary processes, we casually connected drivers, eco-evolutionary processes, and biodiversity. We also acknowledge that (A) global-scale environmental factors have an important role as direct and indirect drivers of urban eco-evolutionary processes.


(B) Anthropogenically modified biotic drivers
Habitat connectivity / Habitat size / Diversity of exotic species / Presence of predators / Food availability
(A) Global biotic and abiotic drivers
Temperature
Precipitation
Human movement
(C) Cultural and socioeconomic drivers
Income / Environmental policy / Population of human / Carbon emissions/ Education
(D) Anthropogenically modified abiotic drivers
Urban cover / Climate harshness Density of railways and freeways / Noise, light, chemical pollution
(E) Ecological process
Population dynamics
- Predation
- Reproduction
- Dispersal
- Competition
- Disease
Community structure
- Trophic cascade
- Interspecific interaction
- Movement/dispersal
(F) Evolutionary process
Gene flow
- Dispersal
Genetic drift
- Population size
- Dispersal
Mutation
- Genetic stress
Speciation/Hybridization
- Novel species
- Species recognition
Natural selection
- Predation
- Resources availability
(G) Urban Biodiversity
Species diversity
Functional diversity
Genetic diversity
Ecosystem diversity