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)

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Highlights

- Ecological and evolutionary (hereafter "eco-evolutionary") processes are influenced by urbanization and therefore influence biodiversity in cities
- Cities vary in population and geographic size by many orders of magnitude, and we therefore expect both eco-evolutionary and human cultural processes to scale non-linearly with city size
- We do not expect all processes to scale similarly and correlations among deviations in different attributes (e.g., waterfowl diversity and urban water use) can inform management
- We develop a mechanistic framework to study how scale influences biodiversity through eco-evolutionary and socio-economic mechanisms, and how these relationships might guide biodiversity management in urban areas

Abstract

Many ecological and evolutionary processes are affected by urbanization, but cities vary by orders of magnitude in their human population size and areal extent. 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 process of human environmental modification and is paradoxically both a **biodiversity** filter and facilitator [1,2]. Though the most highly-urbanized habitats are typically dominated by a small number of human commensals, some individuals find refuge in the wide variety of natural "city green space" [3], while others are released and/or cultivated by humans, occasionally forming feral populations [4]. 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 [5]. Urban ecosystems are profitably studied from a perspective that recognizes the reciprocal links between nature and humans [6,7].

Studies of urban ecology vary widely by **city size**, ranging from small towns to the largest **megacities** 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 studied at smaller scales. However, we still lack a comprehensive understanding of how ecological and evolutionary processes that potentially influence biodiversity change with 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 efforts to preserve biodiversity. Similarly, evolutionary processes may vary in response to city size, or could be sensitive to some city size threshold where they could be absent entirely at smaller scales (Box 1). Megacities 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" [8]. 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 [4], and these non-natives tend to thrive in the most modified (by humans) environments [9], 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 2). 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 [5] are likely to have a significant impact on urban biodiversity [10]. Modifications to the biotic and abiotic environment by urban development creates novel selection pressures that have only existed in the past 5,000 years [5]. 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 could influence broader-scale ecological and evolutionary processes via changes in interspecific competition, prey-predator interactions, and genetic diversity in urban habitats. As an example of predator-prey interactions, a freshwater zooplankton community was exposed to either an anadromous or a landlocked population of freshwater fish, resulting in a shift in prey body size, total biomass, and other traits depending on the prey size preferred by the two predators [11]. Because community level eco-evolutionary dynamics have often been studied in a theoretical framework and in experimental microcosms

[12], it is essential to identify these processes in actual urban environments that vary by orders of magnitude in size. There are few empirical studies examining urban-mediated eco-evolutionary dynamics [13]. Such studies are urgently needed as cities expand and species continue adapting to changing landscapes. 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 scales predictably with the log of city size [14]. 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 may be due to geography (e.g., latitudinal gradients) rather than scale. For instance, in Argentina, the difference in urban vs. rural bird diversity appeared to be greater at lower latitudes, with rural areas more diverse toward the equator, yet urban diversity remained constant regardless of latitude [15].

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 requires distinguishing 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 [16]. 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**. Thus, alternative management goals should be applied to large cities that recognize these new dynamic realities [16]. Additionally, large cities may provide opportunities to address unique biodiversity management goals with broader national or international reach. For example, Sydney, Australia's most populous city, contains the most threatened endemic plants and animals of nearly 100 Australian cities evaluated [17]. Some megacities in the United States have become strongholds for non-native species that are imperiled in their native ranges [18].

Cities may now play a disproportionate role in the global conservation of threatened species and the ecosystem services they provide. For example, Australia has four mainland species of flying foxes (family Pteropodidae), large-bodied colonial roosting bats, that are critical long-distance pollinators and seed dispersers [19] and increasingly rely on food resources within urban areas due to habitat destruction across their range [20]. The grey-headed flying fox (*Pteropus poliocephalus*) regularly occurs in cities across eastern Australian, and is undergoing population declines due to habitat loss, roost disturbance, culling and heatwaves [21]. However, 12% of the remaining population of nationally endangered spectacled flying fox (*Pteropus conspicillatus*) occurs within one of the largest cities in its range, where local government policies continue to endanger the species (https://phys.org/news/2020-07-laws-endangered-flying-foxes.html). In this way, larger cities have an opportunity to define unique biodiversity goals that will protect threatened species that provide critical ecological functions such as seed dispersal and pollination services over a much broader geographic scale than the city itself.

Conversely, large cities may play a disproportionate role in the spread of invasive species or pathogens, due to their transport and trade networks [22].

The relative benefits of different biodiversity management strategies may vary with city size, and in the way biodiversity is measured (Box 2). Depending on the management goal, different forms of urban development may result in different biodiversity outcomes. For example, in a study of butterfly and ground beetle diversity around Tokyo, Japan, **land sharing** (green space interspersed) resulted in larger target insect populations in smaller cities and rural areas, while **land sparing** (green space clustered) resulted in larger populations in the largest cities and in highly urbanized areas [23].

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 [24]. 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 [25]. Care must be taken with small habitat patches to avoid them becoming **ecological traps** [26], given that introduced predators (e.g., domestic cats) also inhabit urban gardens. Biodiversity management approaches that maximize biodiversity outcomes in megacities, for example, opting for “land-sparing” rather than “land-sharing” strategies in more urbanized areas [23,27], may increase the inequity in biodiversity access between socioeconomic groups and also build upon the inherited and ongoing ecological disparities caused by systemic racism, such as redlining [28].

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 ecological and evolutionary processes. 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 [5,13]. Urban development, for example, reduces the size of usable habitat patches and hence increases fragmentation [29]. These habitat modifications reduce dispersal and the frequency of movement [30] and drive genetic drift observed in reduced genetic diversity within patches and greater stochasticity in allele frequencies across patches [5].

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 [31]. 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” [32] whereby there is relaxed predation pressure in urban areas [33]. 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 humans found that urban animals have shorter FIDs than rural conspecifics [34,35]. 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, some studies have revealed local adaptation to relaxed predation pressure as well as to life in urban areas more generally [36]. But, it is important to realize that not all cities have reduced predation risk.

The presence of non-native species may play an important role in ecological and evolutionary processes. The loss of natural predators makes evolutionarily novel domestic cats the main predators on Australian native fauna where cats have been implicated in driving native animals to extinction [37, 38]. Newly introduced species could also modify evolved patterns of interspecific competition [13] which may create mismatches with demographic consequences.

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 [7]. More buildings and roads inhibit movement, reduces dispersal, and are associated with direct mortality [39]. 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 [40]. Artificial night lighting has significant effects on predation, foraging, reproduction, and movement in many species [41,42], and may influence more than one species. For instance, modified prey-predator interactions due to light pollution is likely to change local species composition where light pollution is highest [43]. Air pollution may drive adaptation leading to the evolution of resistant populations, as illustrated by increased DNA mutation rates in urban herring gulls (*Larus argentatus*) compared to those in rural habitats [44]. 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 [45].

The diversity of cultural and socioeconomic drivers (Fig. 1) may have both direct and indirect effects on eco-evolutionary processes as urbanization increases [46]. 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 [47]. 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 [48], 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 [49]. Humans have strong opinions about certain animals [50], and predators may be hunted or hazed in residential areas because of human's fears or anxieties [51]. 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 3) 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 1). Understanding these scaling relationships and their deviations can inform urban biodiversity management across cities (see 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 both predict and to conserve urban biodiversity on a rapidly urbanizing planet.

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GLOSSARY

Biodiversity: Measured in various ways including "richness" or number of (native or non-native) species in an urban area; "functional" or "morphological" diversity [64] which captures the basic processes at work in a given environment, and the roles played by taxa; Genetic/genomic diversity which captures the variety within and between organisms [65]; and "ecosystem diversity" [64] which captures the variation of assemblages of species at different scales. We generally refer to "urban biodiversity" as the biodiversity located within the spatially defined city.

City size: The physical extent of human-dominated landscape around an urban core, including areas of hardscape, residential areas, roads, and associated infrastructure, often including areas of greenspace and preserved land, as well as adjacent municipalities. Related to, but not interchangeable with, total human population or population density. While some studies of urban scaling use Metropolitan Statistical Areas (e.g., [51]), other city datasets use clustering algorithms of the built-environment from satellite images, irrespective of political boundaries, combined with population census data to quantify urban area and population (e.g., Global Human Settlement Database: https://ghsl.jrc.ec.europa.eu).

Community-science: Also known as 'citizen science'. The practice of involving members of the community in collecting biodiversity data.

Ecological traps: Occur when there is a mis-match between environmental cues and habitat quality, which often is a result of rapid environmental change. This leads animals to settle in sub-optimal habitat or make other sub-optimal decisions.

Land sharing: A land management practice whereby there is relatively low intensity urban development that contains small green patches such as parks, gardens, and yards dispersed around the landscape [66].

Land sparing: A land management practice whereby urban development is concentrated and large green parks and nature reserves are set aside as habitat that supports biodiversity [66].

Megacity: Megacities are the largest cities which typically contain over 10 million people [67].

Novel ecosystems: A novel ecosystem is composed of invasive and noninvasive species, may be stable or dynamic, and may differ in function from historical ecosystems.

Scale: Quantifiable proportions of urban characteristics that systematically change with city area and/or population size (*sensu* [51]).

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 [68].

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 and human well-being 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 3)?

•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?

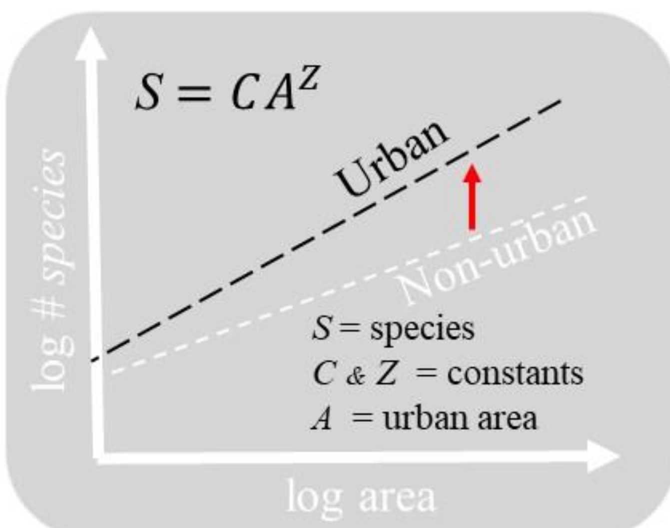
•While both ecological and evolutionary responses to urbanization have been studied, how are eco-evolutionary *dynamics* influenced by cities and how do they formally scale?

Text Boxes

Box 1. A primer on city scaling

Many social and ecological attributes scale with city size. Studying the multiple drivers (Fig. I) 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. I). 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. Some studies show urban environments shift the intercept, C, up resulting in higher Alpha diversity compared to nearby non-urban environments [14] and latitude [2].

Figure I. 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 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 [51]. These scaling relations are necessary to test the causal framework in Fig. I.

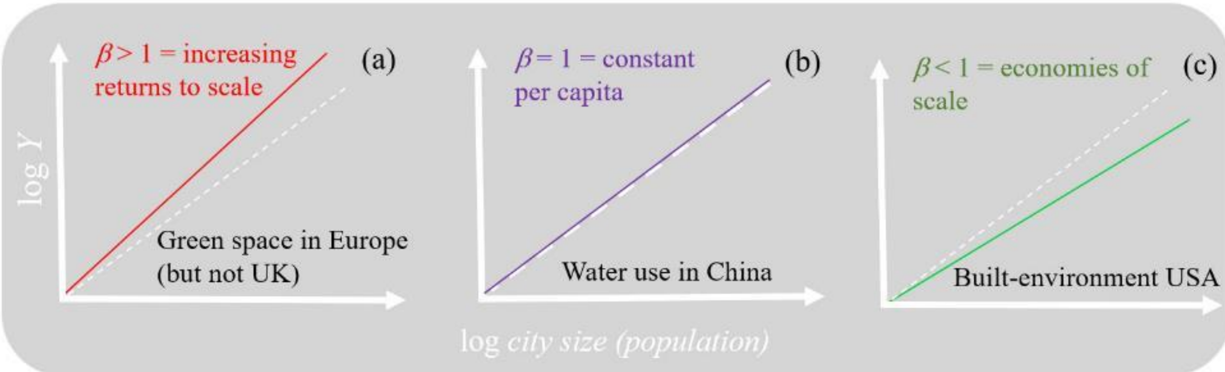
Three classes of urban scaling (Fig. II).

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.

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 II. Illustration of three classes of urban scaling: a) superlinear relationship between population size and green space in Europe [52]**, b) linear relationship between population size and water use in China** [51]**, and c) sublinear relationship between population size and the built environment in the United States** [51]**.**


β > 1 = increasing returns to scale
(a)
Green space in Europe (but not UK)
β = 1 = constant per capita
(b)
Water use in China
β < 1 = economies of scale
(c)
Built-environment USA
log Y
log city size (population)

Box 2: Scaling applications to biodiversity management

Variations and deviations in city scalings will have major consequences for management (Box 1). For example, socio-economic factors such as income may drive variation in water use in cities across countries. A particular city with greater water use than expected for its size, may also have greater waterfowl and aquatic plant diversity, thus revealing direct management implications that can lead to desired outcomes. Moreover, it may not be possible to use insights from studies of smaller cities to manage biodiversity in the largest cities (see [53] 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, large cities have many other things people can do, and such groups are most active in small and mid-sized cities. This is likely to vary in different parts of the world, with higher-income nations promoting more active, expensive projects like brownfields restoration and creation of wildlife corridors through parkland acquisition, and lower-income countries promoting more passive biodiversity restoration such as leaving slivers or even large blocks of habitat undeveloped because they would 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 [54].

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 U.S. 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). This “alphabet soup” of stakeholders exceeds that typically seen in more rural areas where there are fewer (often only federal) entities- such as the U.S. Forest Service, or the U.S. 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?

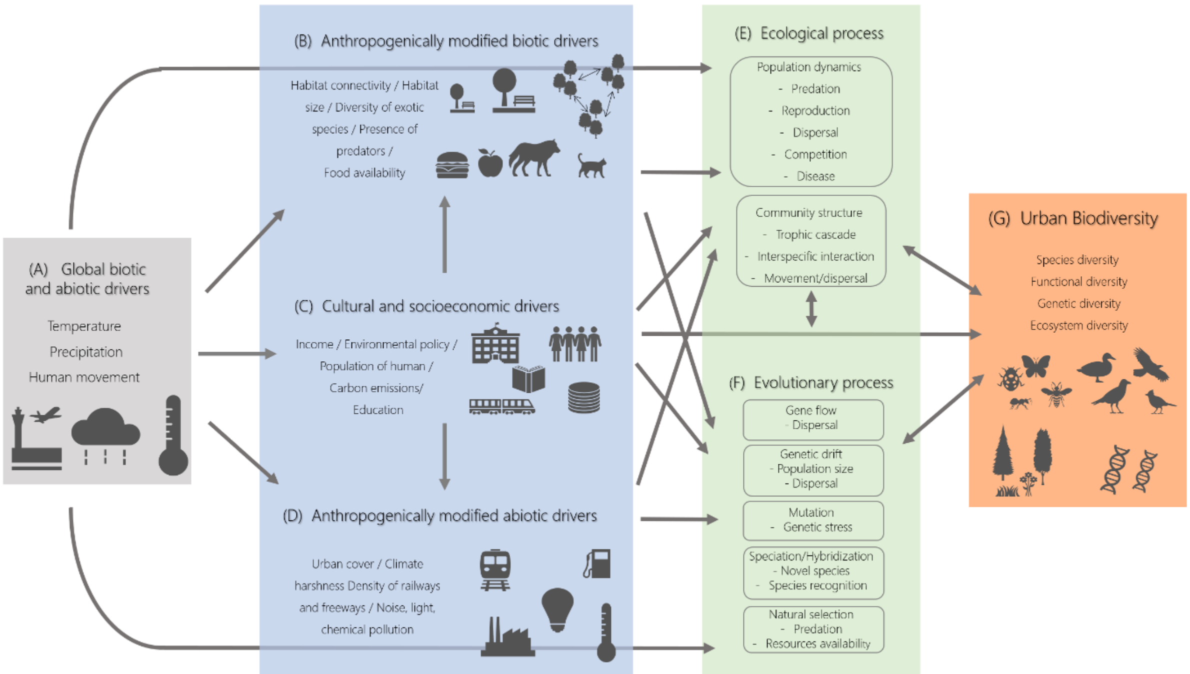
Box 3: **Data opportunities to study the scale of urban biodiversity**

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 [55]. Remotely sensed imagery and lidar provide the means to characterize biodiversity patterns [56], the urban environment [57], and even the human population densities [58] 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., [59]) and have also been used to augment museum collections [60] and work towards global biodiversity monitoring [61]. Environmental DNA, community science, and remotely sensed imagery have been used in combination to map state-level biodiversity [62] and for invasive species management [63]. Combining these emerging techniques should enable us to study the underlying patterns and processes 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 (D) anthropogenically modified abiotic drivers and (C) cultural and socioeconomic drivers) 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.


(A) Global biotic and abiotic drivers
Temperature
Precipitation
Human movement
(B) Anthropogenically modified biotic drivers
Habitat connectivity / Habitat size / Diversity of exotic species / Presence of predators / Food availability
(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