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Global Change and the Ecology of Cities

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Urban areas are hot spots that drive environmental change at multiple scales. Material demands of production and human consumption alter land use and cover, biodiversity, and hydrosystems locally to regionally, and urban waste discharge affects local to global biogeochemical cycles and climate. For urbanites, however, global environmental changes are swamped by dramatic changes in the local environment. Urban ecology integrates natural and social sciences to study these radically altered local environments and their regional and global effects. Cities themselves present both the problems and solutions to sustainability challenges of an increasingly urbanized world.

Humanity today is experiencing a dramatic shift to urban living. Whereas in 1900 a mere 10% of the global population were urban dwellers, that percentage now exceeds 50% and will rise even more in the next 50 years (Fig. 1). More than 95% of the net increase in the global population will be in cities of the developing world, which will approach the 80% urbanization level of most industrialized nations today (1). In addition, individual cities are growing to unprecedented sizes, with nearly all of these new megacities (>10 million, by convention) in the developing world (Fig. 1). Economic growth and demographic changes will accompany growth in urban populations, especially in populous China and India, producing ever-greater demands on services that nearby and distant ecosystems provide.

Ecologists shunned urban areas for most of the 20th century, with the result that ecological knowledge contributed little to solving urban environmental problems. Recently, however, increasing numbers of ecologists have collaborated with other scientists, planners, and engineers to understand and even shape these ascendant ecosystems. With the advent 10 years ago of National Science Foundation-funded urban research programs in the United States, which built upon but differed from earlier efforts (see references in section 1 of the supporting online material), urban ecology also has begun to change the discipline of ecology. Urban ecology integrates the theory and methods of both natural and social sciences to study the patterns and processes of urban ecosystems. Evolving conceptual frameworks for urban ecology view cities as heterogeneous, dynamic landscapes and as complex, adaptive, socioecological systems, in which the delivery of ecosystem

services links society and ecosystems at multiple scales (2–5).

Urban ecologists seek commonalities among city ecosystems, an understanding of how context shapes the socioecological interactions within them, and their role as both drivers and responders to environmental change. Here, we focus on five major types of global environmental change that affect and are affected by urban ecosystems (Fig. 2): changes in land use and cover, biogeochemical cycles, climate, hydrosystems, and biodiversity. We argue that cities themselves represent microcosms of the kinds of changes that are happening globally, making them informative test cases for understanding socioecological system dynamics and responses to change.

Land-Use and Land-Cover Change Accompanying Urbanization

The unprecedented rates of urban population growth over the past century have occurred on <3% of the global terrestrial surface, yet the impact has been global, with 78% of carbon emissions, 60% of residential water use, and 76% of wood used for industrial purposes attributed to cities (6). Land change to build cities and to support the demands of urban populations itself drives other types of environmental change (Fig. 2).

Urban dwellers depend on the productive and assimilative capacities of ecosystems well beyond their city boundaries—“ecological footprints” tens to hundreds of times the area occupied by a city—to produce the flows of energy, material goods, and nonmaterial services (including waste absorption) that sustain human well-being and quality of life (7, 8). At the same time, large urban agglomerations are fonts of human ingenuity and may require fewer resources on a per capita basis than smaller towns and cities or their rural counterparts (9) (see references in section 2 of the supporting online material; figs. S1 and S2 and table S1).

Even in ancient times, the excessive demands of a highly stratified urban elite led to degradation of productive landscapes and the collapse of otherwise successful societies (e.g., salinization in 3rd millennium BCE Mesopotamia) (10). Although

exacerbated by recent globalization trends, centuries ago the demands of European consumers led to deforestation of colonial lands and more recently, demand for beef from countries of the Western Hemisphere has transformed New World tropical rainforests into grazing land.

It is also at the regional scale that land-use changes driven by and resulting from population movement are most apparent. Perceived opportunities in growing urban centers and lack of opportunities in rural settings, resulting from degraded landscapes and imbalanced economic systems, have made the migrations since the second half of the 20th century the greatest human-environmental experiment of all time (11). In China alone, 300 million more people likely will move to cities, transforming their home landscapes and continuing an already unbelievable juggernaut of urban construction (12). Shortages of construction materials such as metals, coal, cement, and timber are likely to constrain China’s urbanization in the long term, however, and exert pressure on growth of infrastructure globally (13).

Urbanization leads to increased patch fragmentation and diversity (14), which may be expressed as more edges (i.e., interfaces between distinct land-cover types) or smaller patch sizes (e.g., urban, residential, and desert land-use patches averaged 20, 100, and 650 ha, respectively, in central Arizona) (15). Urban land use often leaves a legacy of impact in the ecological characteristics of a landscape. In the city of Phoenix, for example, formerly agrarian lands exhibit unique soil biogeochemical properties after 40 years (16), and other locations in the region still reveal agricultural legacies after centuries (17).

A much-debated urban-planning assumption holds that the form of cities follows the function of land-use patterns, leading to a diversity of land-use arrangements (18). However, a recent study of four Chinese cities found convergent urban form in shape, size, and growth rates despite varying economic and political drivers (19). Land-use policies (i.e., zoning, master plans, growth boundaries) help determine urban form and its impact, but a long-term study of the Seattle region found that growth-management efforts to increase housing densities within growth boundaries had the unintended consequence of encouraging low-density housing sprawl in rural and wildland areas just beyond those boundaries (20).

Urban ecology at the local scale centers on the relationships among urban design and construction, ecosystem services delivered in the new system, responses of people and their institutions to evolving opportunities, and actions that drive further change in the system (2, 3, 5). The “edge” of the city expands into surrounding rural landscape, inducing changes in soils, built structures, markets, and informal human settlements, all of which exert pressure on fringe ecosystems. These peri-urban environments are the glue that link

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core cities in extended urbanized regions. Indeed, urban planner Robert Lang has suggested that cities are no longer independent but represent a limited number of dominant megapolitan regions across the globe—coalitions of urban centers and increasingly built-up intervening regions (21). The next frontier in urban ecology is to understand urbanization in the context of biophysical, economic, or political settings. Continental or global comparisons among cities might productively be based on this megapolitan concept.

Altered Biogeochemical Cycles in Cities and Their Regional-to-Global Effects

Urban areas are both responsible for, and respond to, changes in biogeochemical cycles (Fig. 2). The concentration of transportation and industry in urban centers means that cities are point sources of CO₂ and other greenhouse gases, which affect Earth's climate, as well as trace gases such as NO, NO₂, O₃, SO₂, HNO₃, and various organic acids (22, 23). Regionally, air pollution in particular influences nutrient cycling and primary production in adjacent, exposed ecosystems. The disproportionate location of cities along rivers and coastlines makes these areas important contributors to eutrophication.

Wastes generated in cities and entering air and water transport affect biogeochemical cycles from local to global scales, with the extent of influence depending on the vectors by which materials are carried away from their source. For example, the 20 largest U.S. cities each year contribute more CO₂ to the global atmosphere than the total land area of the continental United States can absorb (24). The concept of urban metabolism analogizes a city to an organism that takes in food and other required resources and releases wastes to the environment (8, 25). Scientists debate the appropriateness of the metabolism analogy (25), but its greatest utility has been in quantifying the longitudinal trends in consumption and waste generation of expanding cities (26). This and other studies show large increases over two decades in the throughput of materials such as the food-waste stream, import and solid-

waste accumulation or decomposition of paper and plastics, and tremendous growth in demand for building materials. In Beijing, for example, total carbon emitted from solid-waste treatment increased by a factor of 2.8 from 1990 to 2003 (27).

Pollution generation by cities is of increasing concern when urbanization outpaces societal capacity to implement pollution-control measures. For example, in the United States, emissions controls somewhat counterbalance the increased

driving distances resulting from urban sprawl (28); however, increased coal burning and automobile use accompanying economic expansion in some Chinese cities have had serious air-pollution consequences (29). Nutrient loads from rapidly urbanizing regions to rivers and coastal ecosystems in the developing world show large increases where sewage treatment is lacking or inadequate (30). However, although urbanization and economic expansion outpace environmental controls in the developing world, waste from the most affluent cities remains a primary driver of altered biogeochemical cycles globally.

Cities themselves show symptoms of the biogeochemical imbalances that they help to create at coarser scales. For example, cities experience high acid and N deposition and elevated atmospheric concentrations of CO₂, CH₄, and O₃, which can produce both growth-enhancing and growth-inhibiting effects on organisms (31). Elemental mass balances can frame this problem, because they identify potential excesses of inputs over outputs and likely sinks within the urban landscape (8, 22, 32). Cities are hot spots of accumulation of N, P, and metals (8, 33) and, consequently, harbor a pool of material resources. Could high-nutrient, treated wastewater substitute for commercial N fertilizers to supply crops and lawns with nitrogen, for example? In Phoenix, using nitrate-rich groundwater to irrigate fields could reduce needed fertilizer by >100 kg/ha (34). A small (but growing) proportion of the copper extracted globally is recycled, yet increasing the reuse and recycling of cop-

per and other metals would do much to stem the rapid rise in demand from sources increasingly difficult to extract (33). Such reuse also would alleviate problems of metal accumulation in soils (35).

Human management of urban landscapes is often highly heterogeneous within cities, depending on the financial resources to purchase plants, fertilizer, and even water, land cover (including impervious surfaces), and the relevant organiza-

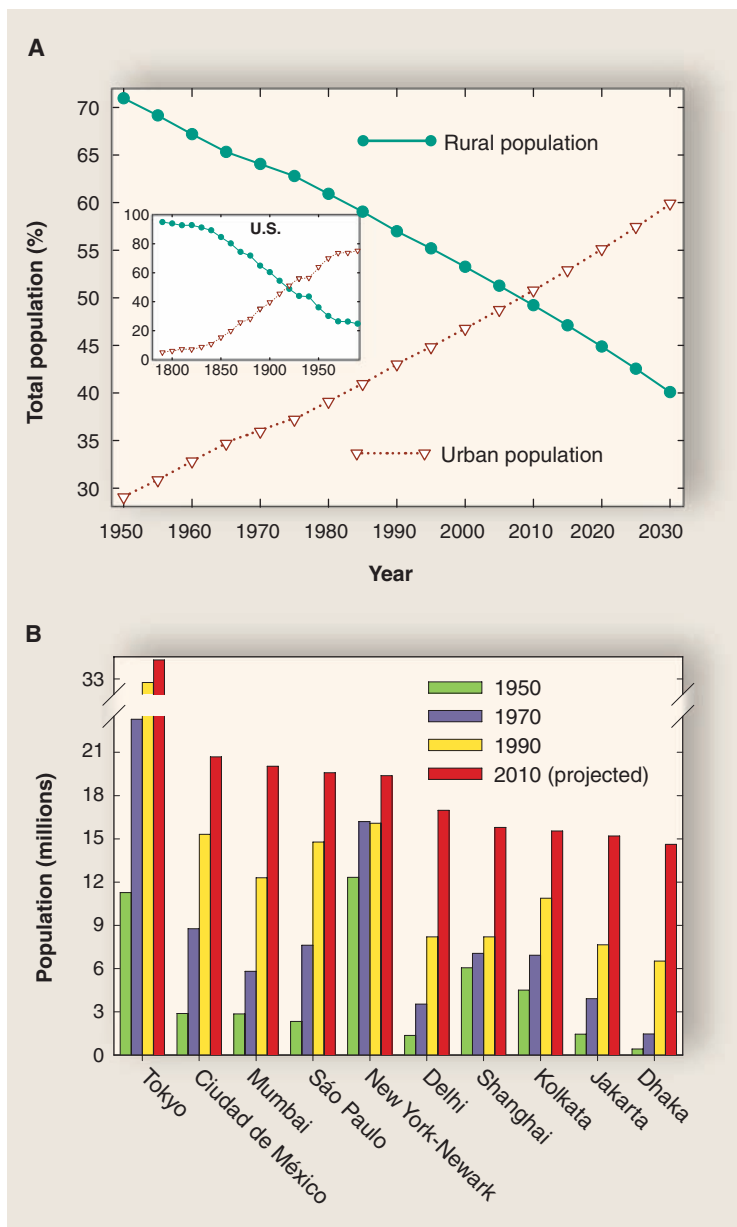


Fig. 1. (A) Change in world urban and rural population (%) from 1950 to 2030 (projected); plotted from data in (1). Inset shows comparable data for the United States from 1790 to 1990; plotted from data in (73). **(B)** Change in population of the 10 largest urban agglomerations from 1950 to 2010 (projected), ranked from left (largest) to right by their projected population size in 2010: Tokyo, Japan; Ciudad de México, Mexico; Mumbai, India; São Paulo, Brazil; New York–Newark, USA; Delhi, India; Shanghai, China; Kolkata, India; Jakarta, Indonesia; Dhaka, Bangladesh. Data are from (1).

Cities

tional level at which management is applied (e.g., household, neighborhood, city). For example, soil-nutrient concentrations across desert metropolitan regions can vary considerably because of legacy factors mentioned previously, as well as urban structure (impervious land cover) and landscape choices (lawns, tree cover, etc.) (36). Certain features of streams are more effective than others in retaining nutrients (37). For some atmospheric pollutants, localized variation in human behavior is less important than the collective, temporal behavior of the population—for example, in driving habits that produce daily or weekly cycles of particulate, CO₂, NO_x, or O₃ plumes (38).

Urbanization and Climate Change

Undoubtedly, urban centers, especially those in the developed world, are the primary source of greenhouse-gas emissions and thus are implicated in global climate change. Yet, the top-down influence of global climate change on cities may be overshadowed by local changes in climate that accompany urbanization (Fig. 2): increased minimum temperatures and sometimes reduced maxima, reduced or increased precipitation, and weekly cycles.

The best-documented example of anthropogenic climate modification is the urban heat island (UHI) effect: Cities tend to have higher air and surface temperatures than their rural surroundings (39), especially at night. Several characteristics of urban environments alter energy-budget parameters and can affect the formation of the UHI. These include land-cover pattern, city size (usually related to urban population size), increased impervious surfaces (low albedo, high heat capacity), reduced areas covered by vegetation and water (reduced heat loss due to evaporative cooling), increased surface areas for absorbing solar energy due to multistory buildings, and canyon-like heat-trapping morphology of high-rises. The UHI is a local phenomenon with negligible effect on global climate (40), but its magnitude and effects may represent harbingers of future climates, as already-observed temperature increases within cities exceed the predicted rise in global temperature for the next several decades. Kalnay and Cai (41) estimated that urbanization and other land-use changes accounted for half of the observed reduction in diurnal temperature range and an increase in mean air temperature of 0.27°C in the continental United States during the past century. By comparison, downtown temperatures for the United States have increased by 0.14° to 1.1°C per

decade since the 1950s (42). Research on the effects of elevated temperature on remnant ecosystems (e.g., parks and open space) within cities, particularly when other variables are controlled [e.g., (31)], may contribute much to our ability to predict how ecosystems will respond to global climate change (43).

UHI affects not only local and regional climate, but also water resources, air quality, human health, and biodiversity and ecosystem functioning (42). Urban warming in hot climates exerts heat stress on organisms, including humans, and may influence water resources by changing the surface-energy balance, altering not only heat fluxes but also moisture fluxes near the surface. UHI may induce the formation of photochemical smog and create local air-circulation patterns that promote dispersion of pollutants away from the city. In warm regions (and

Although local temperature changes may exert greater influence on urban ecosystems than global temperature increases at present, other aspects of regional and global climate change pose risks to cities. In particular, coastal cities would be exposed to rising sea level and any increased hurricane frequency caused by climate change. Thus, one important aspect of achieving urban sustainability is strengthening our ability to respond to the changing relation between urbanization and climate. For cities to effectively respond to global climate change, both mitigation and adaptation strategies—and economic markets for them—will be required.

Human Modifications of Hydrologic Systems

Throughout history, cities have sprung up along rivers and deltas, precisely because of the available water. Seldom are these waterways left

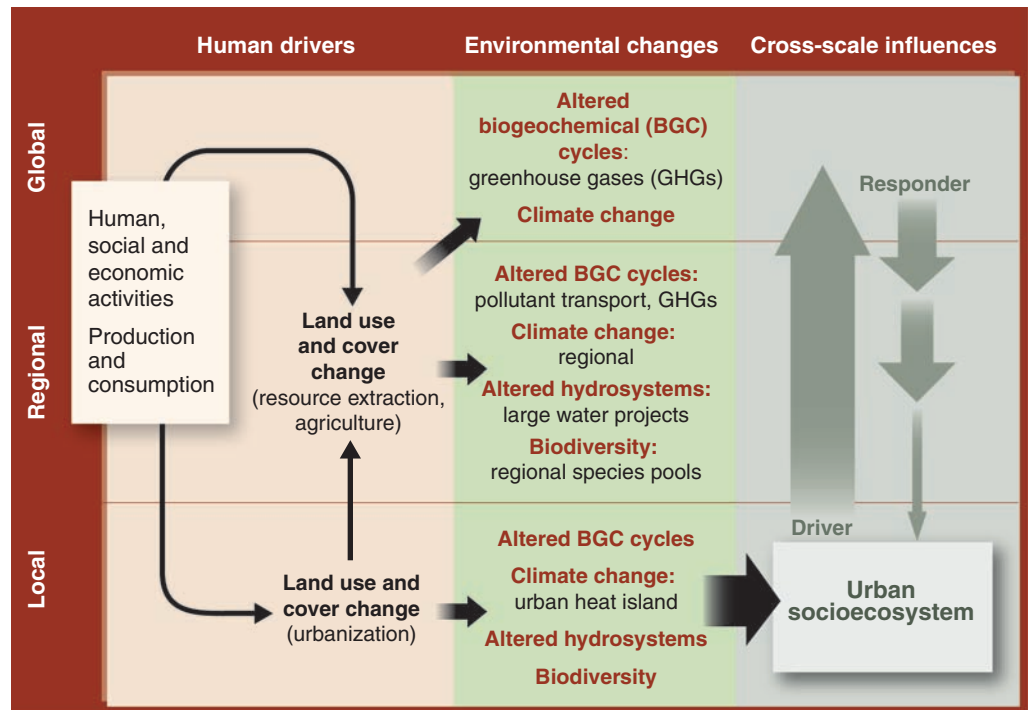


Fig. 2. Framework showing urban socioecosystem (lower right) as a driver of (upward arrows) and responder to (downward and horizontal arrows) environmental change. Land change to build cities and support their populations drives local to global alterations of biogeochemical cycles, climate, hydrosystems, and biodiversity. Large local environmental changes are greater than those that filter down from global environmental change (horizontal black arrow). Not all possible interactions and drivers are shown.

summertime of cooler regions), urban warming greatly increases energy consumption for cooling. For example, about 3 to 8% of electricity demand in the United States was estimated to be used to compensate for UHI effects (42), representing another indirect feedback to global climate change. One way to mitigate the UHI effect is by increasing vegetation cover and albedo (39), but this strategy is a trade-off requiring greater water use, especially in arid regions.

unmodified. Within cities, water is intricately linked to not only domestic use but also industrial processes, adequate sanitation, and protection from natural disasters (floods, hurricanes, and tsunamis). Thus, humans have modified hydro-systems to meet a large array of oft-conflicting goals. Designed or altered streams, rivers, flood channels, canals and other hydrosystems serving urban areas neither replicate the aquatic ecosystems they replace nor preserve the ecosystem services lost (except for those, like flood convey-

ance or water delivery, for which they are designed). Consequently, there are few model systems with which to compare these highly altered environments [e.g., (44)]. Some have called for restoration of streams in urban areas (45), while others advocate study and management of such designed ecosystems as unique ecosystems, with a view to optimizing services to urban populations (46). Among such services we would include flood protection, habitat for a diverse aquatic biota, nutrient retention, and a sense of place.

Among the most important modifications that affect streams in urban areas is increased impervious cover, which changes hydrology and funnels accumulated pollutants from buildings, roadways, and parking lots into streams. Point-source pollution has been dramatically reduced by regulation in the United States, but remains a serious issue in many developing countries (47). Industrial discharges, as well as sewage, contaminate rivers and lakes. Stormwater infrastructure systems in newer cities are separate from wastewater discharges, but the two streams are mixed in older European and American cities, creating acute pollution events in recipient systems. Both storms and low flow-discharge from cities contribute to localized or even regional pollution downstream, especially from pesticides and persistent organic pollutants.

The changes in chemical environment, exposure to pollutants, simplified geomorphic structure, and altered hydrographs of urban streams combine to create an urban stream “syndrome” of low biotic diversity, high nutrient concentrations, reduced nutrient retention efficiency, and often elevated primary production (48, 49). Other ecosystem functional attributes respond less consistently to urbanization, perhaps because the extent and form of hydrologic alteration vary tremendously among urban areas. Countering the urban stream syndrome may require abandonment of the ideal of a “restored” stream in favor of a designed ecosystem. Successful, ecologically based designs of novel urban aquatic ecosystems are becoming more common and exemplify stream-floodplain protection, retrofitting of neighborhood stormwater flowpaths, and use of low-impact stormwater/water capture systems as creative solutions to urban stormwater management (figs. S3 to S5).

Biodiversity Changes in Cities

Within cities, urbanization and suburbanization usually reduce both species richness and evenness for most biotic communities [e.g., (48, 50)], despite increases in abundance and biomass of birds (51) and arthropods (52). Because the urban footprint extends far beyond municipal boundaries, urbanization may also reduce native species diversity at regional and global scales (Fig. 2). For example, urban sprawl in northern latitudes appears related to declines in abundances in some migratory birds in southern latitudes (53). Two

exceptions to this pattern are notable: (i) Plant species richness and evenness both often increase in cities relative to wildlands (54–56), probably owing to the highly heterogeneous patchwork of habitats, coupled with human introductions of exotic species and preferences for species with few individuals of each in landscaped yards. (ii) Bird species richness may peak at intermediate levels of urbanization because of increased heterogeneity of edge habitats (57).

Humans often directly control plant richness, evenness, and density. Individual human and institutional choice do not directly control most other functional groups of species (herbivores, predators, parasites, omnivores, detritivores) or their trophic interactions (52), except for select pest species and intentionally introduced, domesticated herbivores and predators (e.g., cats). Human-dictated urban plant communities, often based on socioeconomic status, form the template for these other functional groups of species. Proposed mechanisms for changes in richness and evenness include increased rate and seasonal variability in productivity (58), relaxed predation on the dominant species (59), increased competitive abilities of some urban species (60), or increased parasite pressure on less successful urban species (61). These hypotheses are not mutually exclusive. Certain species may become better urban competitors because they are released from natural enemies.

Urbanization also alters the species composition of communities. Within cities, biological communities are often dissimilar to surrounding communities as urban species become reshuffled into novel communities (56). For example, bird communities often shift to more granivorous species at the expense of insectivorous species (51), and arthropod communities may shift from more specialized to more generalist species (62). Soil nematode diversity does not vary between rural and urban riparian soils, but functional composition changes to fewer predaceous and omnivorous species in urban than in rural soils (63). At the global scale of diversity, McKinney (64) argued that cities are great homogenizing forces, where some “urban-adapted” species become common in cities worldwide, and a subset of native species, usually species adapted to edges, become locally and regionally abundant at the expense of indigenous species. This homogenization of terrestrial and aquatic communities via urbanization proceeds at different rates in different geographic areas depending on human population growth and species composition (65).

The urban environment is a powerful selective force that alters behaviors, physiologies, and morphologies of city-dwelling organisms (66). Anthropogenic changes that are both direct (e.g., built structures, habitat modification and fragmentation, wildlife feeding) and indirect (e.g., altered temperatures, productivity, and light; noise and air pollution) (67) may cause short-

term changes in phenotypes of urban-dwelling organisms [e.g., (68)]. In the longer term, urban environments act as a potent evolutionary force on population genetics and life-history traits of urban species (68). Human organisms are not immune to selective action of the urban environment. Social structure and interactions, physiology and health, morphology (e.g., increased obesity), and even long-term changes in genetics of human urban residents may be associated with urban living [e.g., (67)].

Given that urban land use and its footprint will continue to expand worldwide, the prognosis for maintaining diversity and function of biological communities and their associated ecosystem services within and near cities seems dire. However, intensified conservation efforts to preserve existing natural or semi-natural habitats or to reconstruct habitats within or near cities may ameliorate these biological changes (69). Introduction of nonnative species combined with the UHI may in some cities actually enhance ecosystem services, such as soil mineralization (70). Furthermore, reconciliation ecology (69), where habitats greatly altered for human use are designed, spatially arranged, and managed to maximize biodiversity while providing economic benefits (57, 69, 70) and ecosystem services (64, 71), offers great promise that ecologists will be increasingly called upon to help design and manage new cities and reconstruct older ones (fig. S6). Cities offer real-world laboratories for ecologists to understand these fundamental patterns and processes and to work with city planners, engineers, and architects to implement policies that maximize and sustain biodiversity and ecosystem function. With an ever-increasing fraction of humans living in or near cities, these are the biological communities that humans experience—human connections and encounters with urban nature have supplanted experiences with natural biodiversity (64). Paradoxically, these human experiences with nonnative, global “homogenizers” (72), such as pigeons, may be essential for conserving global biodiversity in complex, human-modified environments.

Prospects

Cities are concentrated centers of production, consumption, and waste disposal that drive land change and a host of global environmental problems. Locally, they represent microcosms of that global environmental change and offer opportunities for enriching both ecology and global-change science. We know that the totality of human activity occurs on a biophysically constrained planet, and urban ecology can elucidate the connections between city dwellers and the biogeophysical environment in which they reside. As our ecological footprint expands, so should our perception of issues of the greater scales beyond us, and of the broader impacts of our individual and collective life-styles, choices,

and actions. Thus, our hope is that cities also concentrate the industry and creativity that have resided in urban centers throughout much of human history, making them hot spots for solutions as well as problems. Urban ecology has a pivotal role to play in finding those solutions and navigating a sustainable urban future.

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Supporting Online Material

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