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The patterns of biodiversity changes in cities are now fairly well established, although diversity changes in temperate cities are much better studied than cities in other climate zones. Generally, plant species richness often increases in cities due to importation of exotic species, whereas animal species richness declines. Abundances of some groups, especially birds and arthropods, often increase in urban areas despite declines in species richness. Although several models have been proposed for biodiversity change, the processes underlying the patterns of biodiversity in cities are poorly understood. We argue that humans directly control plants but relatively few animals and microbes—the remaining biological community is determined by this plant “template” upon which natural ecological and evolutionary processes act. As a result, conserving or reconstructing natural habitats defined by vegetation within urban areas is no guarantee that other components of the biological community will follow suit. Understanding the human-controlled and natural processes that alter biodiversity is essential for conserving urban biodiversity. This urban biodiversity will comprise a growing fraction of the world’s repository of biodiversity in the future.

Keywords: urbanization; biodiversity; species interactions

Introduction

As the world’s population increasingly inhabits cities, urbanized areas have become the most rapidly expanding habitat type worldwide.¹ Cities currently represent about 3% of the world’s land usage, but their effects on climate, resources, pollution, and biodiversity extend far beyond their municipal borders.¹ Within cities, biological communities are usually radically altered in terms of species composition, abundances, richness (number of species and a component of diversity), and evenness (how individuals are distributed among species and another component of diversity).^{2,3} We first explore how patterns of biodiversity of various groups of animals vary across cities that vary in general climate. We then examine the causes for these patterns.

Patterns of animal biodiversity in cities

To understand the patterns of biodiversity changes in cities, we reviewed studies on urbanization (the ecological forcing functions created by the growth

of cities and associated human activities⁴) effects on abundance, diversity, and species richness of terrestrial animals. We asked if there is a general pattern of the effects of urbanization on diversity and abundances and if urbanization effects vary with different climatic zone and among animal taxa (birds, arthropods, reptiles, mammals, nematodes, and amphibians). Web of Science was used to identify 1,509 articles with abstracts containing the words *urban*, *ecology*, and *biodiversity*. Each paper was examined to see if they contained information about changes in diversity, abundance, and species richness related to urbanization. Analysis was limited to only terrestrial animals because there are few studies of the effects of urbanization on microbial diversity (however, see Refs. 5 and 6), and effects on aquatic animal diversity have been reviewed elsewhere.⁷ We found 92 articles that reported diversity measures, species richness, and abundance (number of individuals) data of terrestrial animals along some gradient of urbanization. These studies span a wide geographic spectrum and include urban environments of all

major climatic zones. Climatic zones were either self-identified in the papers or were obvious from the city location. However, most of the studies were conducted in temperate regions (54 of a total 92), and most involved arthropods (44) and birds (39). We recognize that *urbanization* has varying meanings among researchers. Definitions may be based on human population density, economics, dwelling density, or amount of paved surfaces,^{8,9} and may vary by spatial scale.¹⁰ Thus, urbanization as an independent variable differs among these biodiversity studies.

As expected, the majority of studies indicate that urbanization decreases overall diversity, abundance, and species richness of terrestrial animals (Table 1). These results are comparable to recent reviews by McKinney¹¹ and Luck and Smallbone.¹⁰ However, there is a surprisingly high amount of variation among taxonomic animal groups. As has been noted in previous studies,^{3,11} bird abundances often increase in cities relative to rural or natural habitats, while bird richness and diversity decline. Increases in bird abundance are often due to increases in non-native species such as English sparrows and European starlings in North American studies and a subset of native species that are urban adapters and exploiters.^{3,12,13} In addition, subsets of bird species tend to increase (e.g., granivores) whereas others decrease (e.g., insectivores) in urban areas.¹⁰ Similarly, nearly all arthropod studies show either declines or no effects of urbanization on richness (49 of 52) and diversity (20 of 20). Similar to birds, a sizeable fraction (11 of 26) of studies show either that arthropod abundances increase or do not change in urban habitats. Studies involving other taxa are too few to draw any general conclusions. Nonetheless, the conclusion, at least for birds and arthropods, is that urbanization generally reduces richness and diversity but often increases abundances, especially for birds.

Most studies of the effects of urbanization have occurred in temperate cities (Table 1), which may distort our views on how urbanization affects diversity and abundances worldwide. This asymmetry, plus the difference in methods and study taxa, makes comparisons among cities with differing climates very tenuous. Nonetheless, a few trends emerge. First, most studies in temperate cities show general declines in species richness (27 of 46) but fewer reductions in abundances (19 of 38). In tropical

cities, the majority of studies also show declines in richness (6 of 11) and abundances (7 of 12). However, in cities with arid climates, the majority of studies (3 of 5) show increases in abundances and equal number of studies, where richness increases (5) or decreases (5). These trends suggest that the effects of urbanization vary among cities with different climates. The possible reasons for these differences are discussed.

Human control of plant biodiversity

It is clear that urbanization greatly alters plant and animal species diversity and abundances in both negative and positive directions. Relative to other ecosystems, most think of urban ecosystems as tightly controlled, highly manipulated, and intensely managed by individuals, institutions, and governments.¹

Certainly, the development, infrastructure, maintenance, and operations of cities themselves are the result of human, governmental, or institutional decisions.^{14–16} However, humans, for the most part, only directly control plant diversity and abundances in urban biological communities (Fig. 1). Cities have historically developed in areas of high productivity (e.g., near lakeshores, coastlines, rivers, river deltas, and estuaries). Many of these urbanized areas also have a diverse geology, which also enhances plant diversity so that many areas occupied by cities are, or were, naturally species-rich in native plants.¹⁷ Humans sometimes actively preserve some of this native plant diversity in remnants of natural vegetation within cities or attempt to reconstruct habitats with native or mostly native plant species. More frequently, however, human activities completely deconstruct (via grading, burning, and herbicides) and then reconstruct plant communities with mostly nonnative grasses, herbs, forbs, trees, and shrubs to create lawns, recreational areas, urban forests, gardens, and landscapes.^{18,19} Diversity and abundances of plant species thus become influenced by legacies of land preservation and land usage and conversions,¹⁸ individual homeowner preferences,¹⁶ the cost and availability of plants from local nurseries, neighborhood CCRs (covenants, conditions, and restrictions), city and regional governmental regulations, and neighborhood socioeconomic levels.²⁰ For example, recent studies show that plant communities are more diverse in wealthier neighborhoods,²⁰ and, in the Phoenix

Table 1. Effects of urbanization on diversity, abundance, and species richness of terrestrial animals in 92 published articles. Many articles studied several taxa and included several climatic zones. Hence, the total number of taxa and climatic zones exceeds the number of articles. The number of studies involving each taxon or climate zone are in parentheses

Taxon	Diversity			Abundance			Species richness		
	Increased	Decreased	No effect	Increased	Decreased	No effect	Increased	Decreased	No effect
Amphibia (6)	1	0	0	1	2	0	0	1	1
Arthropoda (98)	0	11	9	6	15	5	3	25	24
Aves (77)	0	4	0	18	15	2	13	21	4
Mammalia (13)	0	3	0	1	3	0	0	5	1
Nematoda (3)	0	0	1	0	2	0	0	0	0
Reptilia (3)	0	0	0	0	2	0	0	0	1
Total (200)	1	18	10	26	39	7	16	52	31

Climate	Diversity			Abundance			Species richness		
	Increased	Decreased	No effect	Increased	Decreased	No effect	Increased	Decreased	No effect
Arid (18)	0	0	0	3	2	0	5	5	3
Mediterranean (35)	0	1	3	5	8	0	3	8	7
Mountain (6)	0	2	0	0	1	1	0	2	0
Polar (2)	0	1	0	1	0	0	0	0	0
Temperate (102)	1	10	7	14	19	5	4	27	15
Tropical (28)	0	5	0	3	7	2	1	6	4
Total (191)	1	19	10	26	37	8	13	48	29

metropolitan area, overall plant evenness is much higher, presumably because homeowners prefer “one of everything” in their yards.¹⁸ This “luxury effect” on plant diversity also appears to occur in southeastern Australian cities,¹⁰ but it is yet unclear if it is a general pattern across cities in different climatic areas.

Although some native plant species may become locally extinct and native plant species generally decline within cities,²¹ especially rare species, overall plant species richness and evenness generally increase in many cities, at least at large spatial scales.^{18,22} However, this pattern of increased diversity breaks down at smaller spatial scales. Cities consist of a matrix of highly heterogeneous patches, with patches that vary from no plants at all (e.g., impervious surfaces, such as parking lots) to those with high diversity (e.g., remnant patches of native habitat). Combined, these patches result in overall high plant diversity in cities, but any given patch may be devoid of species.¹⁸ This overall higher plant diversity, however, does not necessarily translate to increased diversity at higher trophic levels (see later).

Once plant communities are preserved or constructed in cities, enormous energy and resources (e.g., fertilizers, herbicides, water, weeding, pruning, mulching, and replacement of annual plants or

perennial plants that die prematurely) are usually required for their maintenance. This is especially true of lawns, which are often the vegetation type of choice in yards of urban and suburban homeowners, by municipalities in public areas such as parks and golf courses, and in landscaped areas of industry and businesses, at least in temperate and some arid and semiarid climates. Lawns are typically composed of a monoculture or near monoculture of nonnative turf grass cultivars that are selectively bred for traits such as drought and disease resistance, fast growth, and good covering traits. The amount of fertilizer and water used to maintain lawns often greatly exceed that used in agro-ecosystems.²³ The conversion of native desert, woodland, or grassland habitats to lawns or park-like settings with trees and lawns but little understory vegetation has profound effects on species composition and abundances of vertebrates, invertebrates, and microbes.^{13,24} This transformation also dramatically alters ecosystem functions such as productivity, nitrogen cycling, water flow, and carbon balances.^{23,25,26}

Reconstructed native or seminative plant communities also typically require inputs of energy and resources. For example, Martin and Stabler²⁷ found that households use surprisingly large amounts of water to maintain desert-adapted plants in xeric

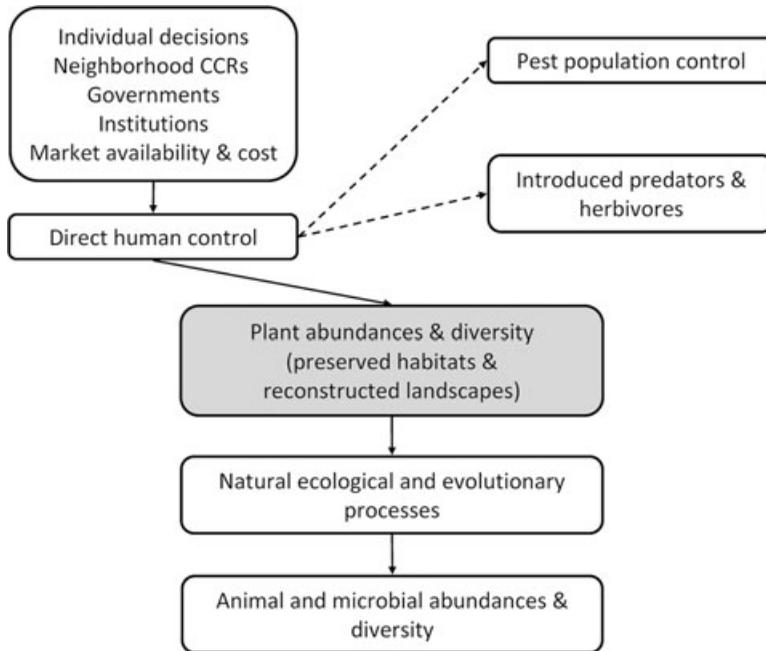


Figure 1. Conceptual model of the how plant abundance and diversity are directly controlled by individuals, institutions, and economics, whereas other biological components are only indirectly controlled by humans. Weaker controls are indicated by dashed arrows; stronger controls are indicated by solid arrows.

yards, mainly to keep them green and growing, even during periods when desert plants normally senesce. Failure to provide energy and materials typically results in rapid successional changes (e.g., vacant lots) and immigration and dominance of undesirable weeds (e.g., along right-of-ways) such that desired plant communities may rapidly disappear. When these inputs are maintained, natural processes such as plant immigration, herbivory, disease, competition, succession, local extinction, and natural selection are often short-circuited by human decisions and actions. For example, when a perennial shrub dies in a flower bed, it is usually replaced quickly by a homeowner or city maintenance crew. In that same flower bed, competing weeds may be removed manually or chemically. For urban plant communities, rapid human actions usually supersede slower ecological interactions and evolutionary processes.

Whereas humans establish and maintain urban plant communities and dictate their diversity in terms of richness and evenness,¹⁸ we propose here that humans have little direct control over the remaining urban biological community (Fig. 1). Humans, of course, introduce, either intentionally or unintentionally, some invertebrate and vertebrate

species, and probably some microbial species, but by and large they have little direct control over the abundances or diversity of most urban nonplant species, especially arthropod species. Even directed human attempts at control or eradication of specific vertebrate (e.g., rats, mice, pigeons, and deer) and invertebrate (e.g., mosquitoes and cockroaches) pest species have limited success, require large and frequent inputs of resources and time, and are often constrained by local and federal ordinances as well as public opinion and perception. For example, the city of Greensboro, NC, cannot control problem beavers that block waterways with dams and destroy landscape trees because state law allows only two methods for control: trap and relocate them or kill them.²⁸ The former is ineffective and the latter engenders public outcry.

For the most part, only the species composition, abundances, and distribution of plant species in cities are intensely manipulated and managed. There are a few exceptions, such as municipalities and individual homeowners that manage fish species in urban lakes and backyard ponds, respectively, and the exclusion, either intentionally or coincidentally, of large vertebrate grazers and predators from many

cities. In comparison, the other human-dominated system, the agro-ecosystem, is much more manipulated and managed than urban ecosystems in terms of control of primary producers (planting, maintenance, and harvesting of crop monocultures), control of competitors (e.g., herbicidal control of weeds and genetically modified crops that are herbicide resistant), and control of consumers (chemical and biocontrol of pathogens and pests and manipulation of vertebrate grazers).

Humans do intentionally introduce pet species, especially dogs and cats, into the urban community. Free-roaming house cats may be substantial predators on native and nonnative birds, small mammals, and herpetofauna in urban areas, especially cats that are not fed by owners or have become completely feral.²⁹ However, it is unclear if predation by domestic cats increases the likelihood of local extinction of birds. Instead, cat predation may simply be compensatory mortality for birds that would die from other causes, or killed birds are quickly replaced by migration from rural source populations.³⁰ That urban bird abundances are generally higher in cities² suggests that urban cat predation does not reduce overall bird abundances. Cat predation may, however, selectively reduce abundances of some species, and thus contribute to the well-established pattern of reduced bird species richness.

Most other pet species in cities do not become full interacting members of the biological community. Many cats, dogs, and other pets, especially in urban core regions, are confined to residences. In urban and suburban areas, most dogs are restricted to fenced yards or on to leashes in public areas, and thus have limited interactions with urban wildlife. Furthermore, unlike vegetation communities, pets are not intentionally introduced to become a part of the biological community and food web as secondary producers and consumers. Indeed, domestic animals in agro-ecosystems are far more manipulated as part of the food web than in urban ecosystems. In agro-ecosystems, abundances and diversity of livestock are highly controlled, as are competing and predatory wildlife species.

We argue here that preserved and reconstructed plant communities in cities are the stages upon which natural ecological and evolutionary processes play out to largely determine biodiversity and abundances of most nonplant species. These urban plant communities provide the resource base and the

above- and below-ground habitat structure for the remaining biological community. For example, the species composition and spatial configuration of these plant communities dictate bird,^{31,32} mammal, reptile,³³ invertebrate,^{34,35} and soil microbial^{5,6} abundances and species diversity.

Thus, it is essential to understand the individual, neighborhood, governmental, and socioeconomic drivers that dictate the structure, diversity, and turnover of urban plant communities. However, we argue here that these socioeconomic and institutional factors have far less roles in determining the nonplant biological community. Instead, ecological and evolutionary forces (e.g., succession, species interactions, immigration, and natural selection) become more dominant than human drivers for consumer communities. This is not to say that human factors do not influence diversity and abundances of nonplant species. For example, built structures and fragmented urban habitats may alter dispersal and migration and thus diversity and abundances of birds.^{11,24} But these are inadvertent consequences of urbanization rather than directed attempts to reconfigure and restructure biological communities.

There have been repeated calls for integration of socioeconomic factors into urban ecology.^{36–39} However, many of these social factors (at least in terms of biodiversity) occur at the plant diversity and community stage—the only one that humans directly control. This is not to say that human decisions and socioeconomic factors are not important at higher trophic levels, only that they become less direct and more unintentional determinants of biodiversity beyond the primary producers. For example, humans introduce exotic (nonnative introduced) ornamental plants into cities because of their esthetic appeal, availability in nurseries, ease of maintenance, and sometimes lower costs. An additional benefit of exotic ornamental plants is that they may be more resistant to local herbivores⁴⁰ because herbivorous arthropods often locate and feed upon host plants with which they have coevolved, thus reducing arthropod diversity.⁴¹ However, these same ornamentals may harbor their own coevolved arthropod herbivores, either from nursery stocks or later importation. These nonnative herbivores may reach very high abundances and attack native plants because they are released from their own natural enemies

and native plants have not evolved resistance.^{42,43} Thus, the intentional introduction of ornamentals has inadvertently altered the diversity and abundances of the arthropod community that has played out on the stage of evolutionary relationships and ecological interactions.

Mechanisms for biodiversity changes in cities

Cities are highly fragmented environments composed of a mosaic of patches of various sizes and land-use types, which range from preserved “natural” remnants to paved transportation surfaces to managed lawns of homeowners. Fragmentation alters the quantity, quality, and pattern of habitats and is associated with changes in vertebrate,^{44,45} invertebrate,³² and microbial^{5,6} species richness. *Habitat* in urban biodiversity studies usually means plant community diversity and structure, either as living or nonliving (e.g., logs, snags, detritus) components.⁴⁶ Thus, urban habitat quality, quantity, and pattern, at least in terms of the plant components, are also generally under direct control by humans (Fig. 1), which in turn affects consumer components of the community.

It is also important to note that habitat fragmentation and alteration in cities usually also radically alter species composition and evenness—two other, but far less studied, components of biodiversity. Not only does number of species often decline in cities, but synanthropic species (species that are ecologically associated with humans) often replace native species in the community and communities are “reshuffled.”⁴⁷ In addition, evenness, at least of birds and arthropods,^{3,34} declines as synanthropic species increase in relative abundances and dominate communities.

Although fragmentation from urbanization is correlated, usually negatively, with changes in biodiversity, fragmentation of habitats is, in itself, not a mechanism of biodiversity change in cities, at least at the community level.³ Rather, fragmentation and altered habitats lead to changes in behavioral and ecological interactions and processes that dictate the presence and absence and relative abundance of species. Examples are shifts in habitat preference, immigration, and emigration, as well as changes in survival and reproduction due to interspecific interactions (e.g., competition, predation, and mutualism)⁴⁵ or abiotic environmental factors⁴⁸ (e.g., ur-

ban heat island effect¹). In the longer term, these ecological processes and interactions can lead to evolutionary changes such as genetic shifts in isolated urban populations and adaptation of some species to urban environments.^{49,50} Whereas the patterns of biodiversity change in cities have been increasingly well documented, our current knowledge of the ecological and evolutionary processes and mechanisms that underlie biodiversity changes is very rudimentary.

Fragmentation creates patches that isolate populations and hinder movements among patches. Therefore, island biogeography theory has been used to explain changes in biodiversity within cities by treating urban habitats as isolated patches of varying isolation, size, and complexity.^{8,51,52} Island biogeography theory predicts that species richness in isolated fragments depends on area of the island and its distance to source populations.⁵³ Small and distant patches support few species because distance or isolation limits migration and small patches provide fewer resources, thus supporting smaller, and more extinct-prone, local populations. Generally, bird⁴⁵ and arthropod⁵¹ species richness is lower in smaller urban fragments. For birds, the quantity and complexity of patches enhances breeding bird diversity.⁴⁵ In Seattle, immigration of earlier successional forest birds explained higher bird diversity in areas of intermediate levels of urbanization. However, diversity in more urbanized areas was reduced because loss of forest species outweighed immigration by early successional species and establishment of synanthropic species. Although the island biogeography approach provides mechanisms (e.g., immigration and extinction) at the species level for changes in urban biodiversity, it does not address the behavioral and ecological mechanisms to account for differences in immigration and extinction. For example, local extinctions in Seattle birds are likely caused by behavioral changes and increased brood parasitism and nest predation in highly urbanized patches.⁴⁵ Other hypotheses involving more explicit mechanisms, such as disturbance, productivity, species interactions, and abiotic factors, have also been proposed.

It has long been known that species diversity of various groups varies along urban–rural gradients, with species richness usually declining in the urban core (the intensely urbanized end of the gradient). However, sometimes species richness, especially

bird richness, peaks at intermediate levels of urbanization¹¹ in the suburbs or exurbs of cities. These regions represent the transitional zones from natural or rural habitats to urbanized ones. As we noted above, one explanation is based upon island biogeography theory. Another is based upon Connell's⁵⁴ intermediate disturbance hypothesis. This hypothesis states that species richness peaks at intermediate levels of disturbance because intermediate frequencies of disturbance promotes coexistence by preventing competitive dominants from excluding species. Urbanization can be viewed as a gradient of disturbance (after initial major disturbance, then frequent low-scale disturbance like litter removal, lawn mowing, removal of dead trees^{55,56}), and we may expect to find highest diversity at intermediate levels of development or disturbance.⁵⁴ The specific impacts of disturbance via urbanization on diversity may vary depending on the taxonomic group, geographic location of the city, historical and economical factors, and spatial scale.¹¹ Very frequent or severe disturbances (e.g., grading and then paving or erecting buildings) may prevent some species from occurring at all. For example, native arthropod populations in cities are restricted to patches of remnant vegetation in areas that are unsuitable for housing development.^{57,58} The intermediate disturbance hypothesis thus explains a pattern and also provides mechanisms—disturbance frequency combined with species interactions—for changes in species richness along the urban–rural gradient. Patterns of butterfly and bird richness in Palo Alto, CA,^{56,59} were explained by the intermediate disturbance hypothesis. The basic intermediate disturbance model was subsequently modified⁶⁰ to include not only disturbance, but also changes in predation, competition, and recruitment density over the disturbance gradient. However, other features affecting the presence or absence of species also change along urban–rural gradients, such as net primary productivity, in addition to disturbance.

In general, greater availability of limiting resources (such as water in desert cities and nutrients in temperate cities) increases and stabilizes primary productivity within cities, at least in patches with comparable vegetative cover and structure as outlying areas.^{2,61} Additionally, extreme climate events are buffered and seasonal fluctuations are dampened so that plant flowering and animal breeding seasons are prolonged in “pseudo-tropical bubbles”

in desert and temperate cities.² In addition, reduction in ozone⁶² and wind⁶³ and increases in temperature,⁵⁵ especially in the winter, in cities may also lead to higher productivity.⁶⁴ Species richness–productivity models² predict richness of plants and animals initially increases with higher productivity, but declines at high productivity levels,⁶⁵ in a hump-backed relationship similar to that based upon the intermediate disturbance hypothesis.

Shochat *et al.*^{2,3} proposed a comprehensive model combining gradients in productivity, abiotic factors, and altered species interactions to explain higher overall population densities but lower species diversity in cities relative to wildlands. They proposed that increased primary productivity from human activities (e.g., increased temperatures, water, and nutrients) increased abundances of urban exploiters, species with superior competitive abilities for urban resources. These urban exploiters competitively exclude many native species, thereby reducing richness and decreasing evenness. Increasing habitat productivity in cities appears to explain observed losses of spider⁴⁸ and bird diversity.³ Another reason that urban exploiters may become dominant both competitively and in terms of numbers is that their natural enemies are often reduced in cities. This model is similar to that of Menge and Sutherland,⁶⁰ except that the gradient of interest is productivity rather than disturbance. Both models emphasize abiotic factors (see “Are cities unique biological habitats?” later) and species interactions that play out on the “stage” set by gradients in primary productivity or by disturbance.

More recently, the emphasis on species interactions as mechanisms that affect urban biodiversity has led to extensions and tests of ecological food web theory in urban areas.⁶¹ All species interact with other species via competition, predation, parasitism, or mutualism. Determining whether structure and diversity in biological communities is dictated by bottom-up (resources and competition) or by top-down (predation, disease, parasitism) forces has long been a goal for ecologists.⁶¹ By Shochat *et al.*'s^{2,3} model, bottom-up forces via interspecific competition for resources mainly control urban communities. Competition is further intensified because predators of synanthropic species that would reduce densities, and thus competition, are absent or greatly diminished. However, there have been few studies of top-down

forces (predation, parasitism, and disease) and their effects on diversity in cities. Density of large predators may decrease with fragmentation, but this may lead to increased density of smaller predators.⁶⁶ For arthropods, top-down control increased in urban areas compared to wildlands due to increased predation by birds in one experimental study in Phoenix, AZ.⁶⁷ In turn, greater predation pressure on arthropods in cities may reduce consumption of plants by herbivorous arthropods, thus also enhancing productivity.^{61,66} It is unclear, however, whether enhanced predation pressure by birds increases across urban areas because often the observed increase in density in cities are due to granivorous (seed-eating) birds with little or no direct effect on arthropods.¹³ Nonetheless, we would expect that increased density of granivorous birds in cities may cascade downwards to plants because granivores have direct effects on plant reproduction and dispersal. Understanding how urbanization alters food web and trophic dynamics is the key to unraveling how urbanization alters biodiversity. Yet there have been very few studies that have addressed this important question.

Studies of the patterns of biodiversity along rural/wildland to urban gradients or among land-use types within cities have increased rapidly over the past two decades (Table 1). Yet there are still very few studies that test the mechanisms underlying these patterns or that test alternative hypotheses for biodiversity differences in cities relative to wildlands or rural areas.² Furthermore, these hypotheses may not be mutually exclusive. For example, both disturbance and productivity may covary in similar ways along wildland–urban gradients. An additional challenge is that neither the pattern nor underlying mechanisms affecting biodiversity in cities are static in time. Urban ecosystems go through successional stages like other ecosystems,^{37,68} and thus it is important to monitor long-term patterns and understand shifting mechanisms. For example, predatory birds, which are largely absent in young cities, may establish in cities as prey populations stabilize, providing a more predictable food source.¹³

Complicating the picture is that fragmentation and differences in urbanization within cities lead to an urban matrix consisting of widely heterogeneous habitats of different age and successional stages, as well as different vegetation, surrounding buildings, ground surfaces, and soil legacies.^{69,70} This het-

erogeneity may result in changes in overall diversity in cities, but highly patch- or habitat-specific mechanisms. Urban ecological field experiments are currently rare, but are indispensable to understand these mechanisms at different spatial and temporal scales. Two recent manipulative urban field experiments that test mechanisms underlying changes in urban abundances and biodiversity involve arthropods.^{40,67} We are unaware of any that do likewise for vertebrates.

Are cities unique biological habitats?

Abiotic factors play an important role in determining biodiversity, in addition to species interactions, in the hypotheses and models described earlier in explaining changes in urban biodiversity. Indeed, abiotic factors often drive or modify species interactions. For example, additional nutrients, an abiotic factor, increase plant productivity, which in turn changes competitive interactions among plant species and the herbivore species consuming the plants, and then the predator species that feed upon the herbivore species.⁴⁸ Some abiotic factors associated with cities would seem unique, such as concrete surfaces of roadways, noise from human activities, air pollution from automobiles and industry, large amounts of artificial and polarized light, and severe and frequent disturbances, such as grading surfaces and excavations.

Thus, urban habitats are often viewed as novel habitats that differ radically from more natural habitats^{55,71–73} because they are intensively modified by human activities and because of these novel environmental features. However, Richardson *et al.*⁷⁴ argue that there are natural equivalents of most, if not all, urban habitat and environmental features. High levels of fragmentation, one of the key features of urban habitats, of course occurs in most natural habitats at varying spatial scales.⁴⁴ Frequent and severe disturbances in cities⁵⁵ have analogs in habitats that suffer seasonal storms and hurricanes or intertidal communities with frequent wave and tidal action. Other seemingly unique features of cities, such as impervious paved surfaces and buildings,⁵⁵ also have natural habitat analogs in rock beaches and outcrops and cliff faces, respectively.⁷⁴ Consequently, species inhabiting urban habitats are often the same or functionally equivalent species from natural habitat analogs.⁷⁴ For example, peregrine falcons roost and nest on tall buildings, and cliff swallows nest

under eaves and bridges.¹³ Similarly, environmental factors affecting biodiversity that seem unique to cities such as the heat island effect,⁷⁵ polarized light pollution from glass surfaces,⁷⁶ and air, water, light, and noise pollution^{22,77} also occur in more natural habitats. For example, heat island–like effects occur on heat-absorbing rock surfaces, polarized light reflects from water surfaces and natural asphalt pits,⁷⁶ and volatile organic compounds and carbon dioxide are released by plants and decaying materials. Thus, we contend that cities do not present novel features or environmental factors to organisms. Rather, cities differ from more natural environments by the intensity, scale, extent, and combination of these selective pressures, which can lead to urban populations that are behaviorally, physiologically, and genetically distinct from their wildland counterparts.^{49,78,79}

This distinction is important because, as we noted earlier, once vegetation is established and maintained via human control, ecological and evolutionary processes dominate, just like in any other ecosystem. Even the resetting of vegetation locally by human activities (grading, removal, pruning, and replanting) occurs in other habitats (e.g., hurricanes, volcanic eruptions, herbivore defoliation). Thus, we argue that urban ecosystems, beyond the human processes that establish vegetation/landscape, should be dominated by ecological and, to a lesser extent, evolutionary (because of shorter time frames) processes.

Prescriptions for conserving and managing urban biodiversity

With the broad-scale alterations to biodiversity, usually in the negative direction, conservation biology in urban landscapes may seem like fighting an already lost battle. It is, however, rarely the intention of conservation biologists to restore urbanized areas back to a natural and pristine state, mainly because this is not feasible for a variety of reasons. Instead, the goal of conserving and reconstructing habitats within cities is often to minimize loss of species; however, for this to work, environments must be preserved and created where wildlife and humans can coexist.⁸⁰ In urban environments, this usually involves the coexistence of native and nonnative species in the same environment. Motivations for conserving urban biodiversity were recently reviewed by Dearborn and Kark,⁸¹ who concluded that urban biodiversity conservation is

important, but faces many challenges to be successful. Some motivations for conserving biodiversity in cities are purely anthropogenic, such as ethical responsibilities rooted in religion and moral beliefs.⁸¹ Others involve provisioning of ecosystem services⁸² such as carbon sequestration,⁸³ improved hydrology, and temperature regulation.^{84,85} Richer biodiversity may also directly improve human mental well-being,⁸⁶ but this may vary greatly among neighborhoods. In some high crime areas, increased vegetation structure instead inspires fear,⁸⁷ showing that socioeconomic factors need to be considered when evaluating the rationale for preserving biodiversity. Thus, motivations and considerations for conserving and enhancing urban biodiversity extend far beyond saving native species from local extinction.

Clearly, human values, perceptions, and limited city budgets often cause dilemmas for urban conservation biology. It is sometimes difficult for the general public to fathom what lies behind “the intrinsic value of biotic diversity.”⁸⁸ As half of the people in the world now live and grow up in cities, the connection with nature becomes weaker and may create future generations with little understanding of the importance of conserving biodiversity.⁸⁹ If future politicians and voters have little firsthand experience with nature, global conservation strategies may be imperiled.⁹⁰ The “pigeon paradox”⁹⁰ illustrates the importance of involving citizens in conservation, in particular in poorer socioeconomic areas. Global conservation action relies on direct experiences with wildlife, yet an increasing fraction of people only experience urban wildlife. Hence, nonurban worldwide conservation efforts may be inextricably linked to experiences with urban wildlife, such as pigeons. One strategy is to educate, with urban biodiversity at hand, the synanthropic species such as the abundant rock doves, pigeons, and starlings. One example from the city of Phoenix, AZ, is the Rio Salado Project, where a previous dump in a relatively poor neighborhood in downtown Phoenix was converted into a diverse riparian area, with associated educational “urban wildlife” programs for children in the area (Fig. 2). Although adult residents may question the economic costs of this project, school children may reap the benefits as they actively participate in bird surveys and observations (e.g., 250 bird species and counting). Urban green areas, despite their reduced



Figure 2. The Rio Salado Project in Phoenix, AZ (<http://phoenix.gov/riosalado>). A former dump along the Salt River in downtown Phoenix was turned into a riparian habitat restoration project that now supports a high diversity of birds, arthropods, reptiles, and mammals. School children and citizens are actively involved.

biodiversity and altered species composition, can effectively be used to educate both school-age children and adults while providing recreational, health, and well-being benefits.⁹¹

The main strategies to preserve biodiversity are to protect remnant habitats that are threatened by further developments and to restore or reconstruct habitats that have already been converted for other land uses. As in traditional conservation biology, size,⁹² structure,⁴⁵ and connectivity⁹³ should be considered to maintain species interactions, resist species invasions and disease, and maintain sufficient population sizes. However, preservation and reconstruction is really limited to the control of plant structure and diversity “templates” with the hopes that certain desirable species will follow. We argue here that better and deeper knowledge of the mechanisms that determine animal and microbial diversity in these plant “templates” is necessary for viable and long-term conservation efforts in cities. We now know that simply because an urban habitat resembles a wildland habitat in terms of vegetation cover and structure does not mean that biodiversity and function of the urban and wildland communities are equivalent.⁴ Many wildlife

species, especially herbivorous¹⁹ and pollinating⁹⁴ invertebrates, are associated with specific host plant species. Thus, constructing new landscapes with native plants or replacing nonnative plant species in existing landscapes can greatly enhance wildlife biodiversity in urban and suburban areas.^{19,61} Systematic land-use planning,⁹⁵ educational programs that increase knowledge and appreciation of diversity, and encouragement of backyard ecosystems that support diversity can enhance overall biodiversity in cities^{96–99} and engender support for nonurban conservation efforts.⁹⁰

Summary and conclusions

Patterns of biodiversity for some taxonomic groups are well documented at least for plants, birds, and arthropods in temperate cities, but less is known about the patterns of biodiversity for other taxonomic groups and cities in other climatic zones. Humans directly control urban vegetation, and, consequently, also urban habitat quality and quantity, because habitats are defined in terms of vegetation. The rest of the biological community, however, is largely determined by this vegetation template and interactions with other species and the environment.

Therefore, whereas understanding the origins and maintenance of this vegetation template requires the input of social scientists, ecologist/evolutionary biologists can contribute greatly to understanding the structure, diversity, and function of the remaining biological community.

Fragmentation is inherent in cities and is given as a cause of biodiversity losses. However, fragmentation does not provide demographic or trophic mechanisms for how biodiversity is lost (or how abundances increase and evenness decreases for some taxonomic groups). Therefore, several hypotheses involving abiotic factors and species interactions have been extended to test the mechanisms of biodiversity in cities.

Specific abiotic factors thought to be novel to cities also have analogs in wildland environments. However, the intensity, duration, periodicity, and combination of these factors in cities present potent selective forces on urban organisms.

Urban areas are repositories of current and future biodiversity. Therefore, understanding the socioeconomic, ecological, and evolutionary processes that determine this biodiversity is critical to preserving and increasing urban biodiversity.

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Conflicts of interest

The authors declare no conflicts of interest.

Supporting information

Additional supporting information may be found in the online version of this article:

Supplement I. References used for Table 1.

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