

From patterns to emerging processes in mechanistic urban ecology

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Rapid urbanization has become an area of crucial concern in conservation owing to the radical changes in habitat structure and loss of species engendered by urban and suburban development. Here, we draw on recent mechanistic ecological studies to argue that, in addition to altered habitat structure, three major processes contribute to the patterns of reduced species diversity and elevated abundance of many species in urban environments. These activities, in turn, lead to changes in animal behavior, morphology and genetics, as well as in selection pressures on animals and plants. Thus, the key to understanding urban patterns is to balance studying processes at the individual level with an integrated examination of environmental forces at the ecosystem scale.

From descriptive to mechanistic urban ecology

More than 50% of humans will be concentrated in cities in <30 years [1] as a result of increased human population growth and migration from rural to urban areas (see Glossary). Because urbanization involves one of the most extreme forms of land-use alteration, generally leading to a complete restructuring of vegetation and species composition, it has become a major concern in conservation biology [2]. Urban ecology has become a multi-disciplinary field, in which biologists collaborate with anthropologists, sociologists and geographers to understand complex processes in these highly dynamic ecosystems [3].

Until recently, urban ecologists focused mainly on patterns of species abundance and diversity [4]. Only in recent years has research progressed into mechanistic urban ecology, with studies (mostly experimental) on behavioral ecology [5,6], species interactions [7,8], genetics [9,10] and evolution [11]. Although this mechanistic approach is still in its infancy, it already indicates that the urban environment is a unique setting, in which fundamental patterns and processes can be decoupled by human activities. For example, irrigation appears to weaken

seasonal rainfall effects on populations and community composition [12,13]. Thus, ecological 'rules' in urban environments might differ dramatically from those in less human-influenced habitats [11,14]. The tools used to understand these differences must also address the role of human behavior as a primary driving force of environmental change (Figure 1).

Here, we highlight recent findings in mechanistic urban ecology that implicate several human-mediated processes in the production of urban patterns: (i) elevation of habitat productivity and interspecific competition; (ii) buffering of temporal variability; and (iii) alterations of trophic dynamics. We suggest future directions for urban ecology and argue that understanding the relevant ecological processes operating in cities is essential to the practice of conservation in an urbanizing world.

Mechanisms underlying altered diversity and abundance

Animal diversity and abundance are altered radically in urban ecosystems relative to wildlands [4,15,16]. Most species that thrive in urban environments are remnant native species, some of which are synanthropic generalists. Others are less tolerant and could be on a slow march towards local extinction [16]. Thus, although high resource availability supports high animal density in

Glossary

Heat islands: metropolitan areas which, owing to increased cover of artificial surfaces (roof and paving materials) that reflect less of the sun's rays during the day and then trap more of that heat at night, have significantly (1–4°C) warmer air and surface temperatures than the surrounding countryside [50].

Productivity: the rate of biomass production per unit area by organisms.

Rural areas: residential areas not included in the urban definition.

Suburban areas: areas with relatively fewer built structures [2.5–10 ha⁻¹], less [20–50%] surface cover and located on the outer edges of urban areas [4].

Synanthropic generalist species: urban adapters that are tolerant of a wide variety of urban conditions

Urban adapters: species that can adapt to urban habitats but also utilize natural resources [26].

Urban areas: areas that are dominated by built structures [>10 buildings ha⁻¹] with more than a minimum density of human residents [typically >620 km⁻² or 10 ha⁻¹] and surface cover ($>50\%$) types [4].

Urban exploiters: species thriving as urban commensals to the point that they become dependent on urban resources [26].

cities [4], local (alpha) diversity (i.e. within-patch diversity) tends to decline with increasing urbanization [17–19]. These patterns indicate that, in contrast to wildlands, the number of individuals in urban areas is a poor predictor of species richness. Although urban descriptive ecology has traditionally emphasized the role of altered habitat structure in producing these patterns, mechanistic approaches to urban ecosystems have introduced two additional factors: habitat productivity and competition (Figure 1).

Habitat productivity

Classic ecological understanding of diversity–productivity relationships states that species richness initially increases with increasing productivity, but declines again at the highest productivity levels [20]. Although now recognized as being far from universal, this ‘hump-shaped’ species richness–productivity relationship (SRPR) remains the dominant model at local scales and across community types [21]. We argue here that the hump-shaped SRPR provides a useful model for productivity as a key factor determining changes in urban population density, community structure and species diversity [4,12,13,16].

Highly developed areas with entirely impervious surface cover have a net primary production (NPP) of zero [22–24]. Thus, at the grossest scale, urbanization should decrease total NPP per area of coverage compared with wildlands. Along the hump-shaped SRPR curve, a decrease in NPP to near zero should lead to decreased species richness. Such a relationship was found in Taiwan, where development in the densely populated urban areas was associated with lower bird diversity [24]. However, at a slightly less extreme level of urbanization, landscape

management of green spaces (e.g. parks, gardens and golf courses) often elevates local productivity relative to surrounding wildland, with such green spaces lying close to the highest end of local productivity continua [22,25]. Altered rates of NPP in urban green spaces can partially mitigate losses in productivity caused by extensive impervious urban surface cover [22,25]. For example, a decadal increase of 1.9% in urban land-cover area in the southeastern USA led to only a 0.35% loss in total NPP [23]. Analysis of NPP for the contiguous USA (i.e. mainland US States, excluding Alaska) found elevated total NPP in urban areas relative to nearby wildlands, despite increased impervious surface cover, in two general cases: (i) cities in arid environments; and (ii) cities with lower-density development [22]. Direct measures of NPP in the arid grasslands of Colorado corroborate this finding: urban lawns exhibited four to five times the aboveground NPP relative to native grasslands [25]. In Phoenix, Arizona, a city that is in an arid environment and is largely developed as low-density housing, NPP in watered residential lawns is nearly as high as in agricultural lands, and spider diversity decreases with increasing productivity [12].

Several studies describe a hump-shaped relationship for species richness versus level of urbanization [15,16,18,26]. If NPP is highest in moderately urbanized areas owing to the combination of low-density development and high anthropogenic resource inputs in managed green spaces, these studies are likely to reflect the signature of a hump-shaped SRPR along urbanization gradients. However, effects of urbanization on productivity can be diverse, depending on the ecological region and the growth form of a city [22]. Future studies could account for some of the discrepancies among existing

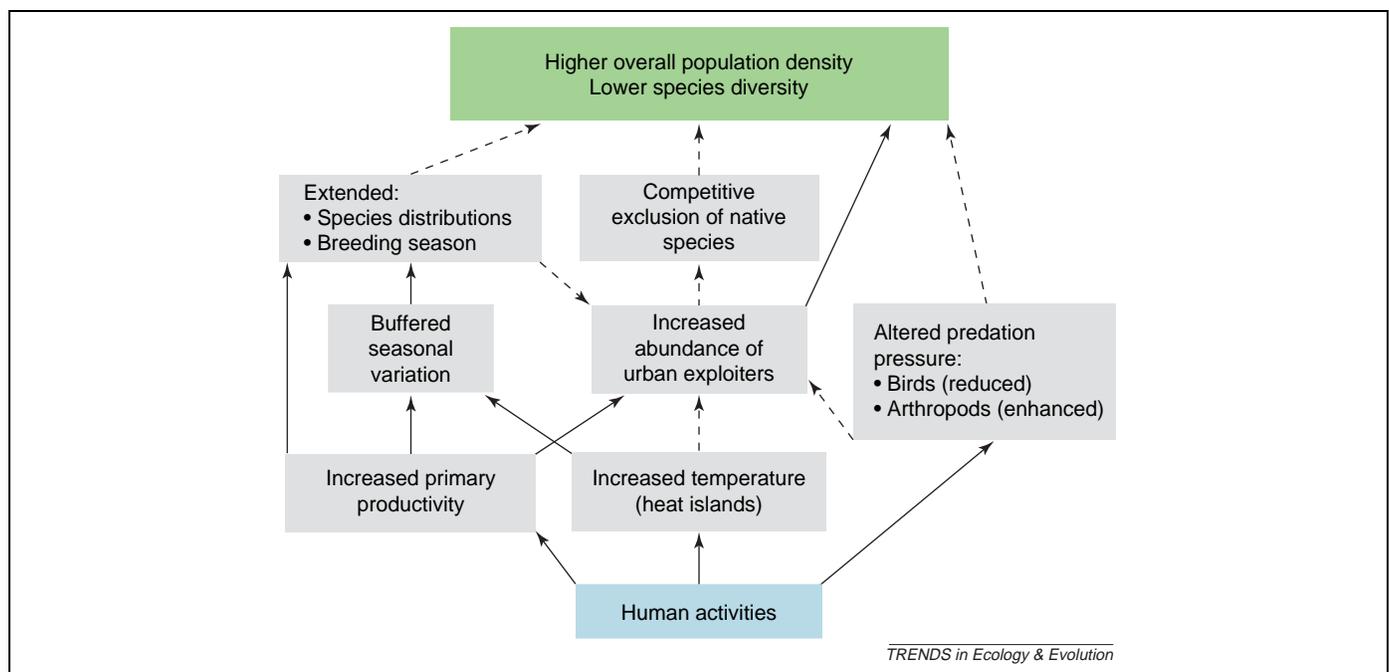


Figure 1. Pathways whereby human activities lead to altered biotic structure in urban settings. Previous studies have found general patterns of increased population densities and decreased species diversity in cities. Recent studies shed light on possible mechanisms underlying these patterns (given in grey boxes). Dashed line arrows indicate areas where more research is needed to address the mechanisms.

studies of urban biodiversity by incorporating more direct measures of NPP.

Thus, we hypothesize that, in managed green urban spaces, habitat productivity generally increases compared with surrounding wildlands. Although this might not be the case for heavily built urban districts, these are restricted to a small proportion of the greater urbanized area, with green patches representing a larger and increasing proportion owing to urban sprawl. The productivity–diversity relationship is, however, expected to vary across different regions and in cities with different growth forms. More empirical studies of diversity–productivity relationships in urban settings are needed, including manipulation of productivity [8], to understand the mechanisms affecting species diversity. Because productivity is associated with habitat structure in cities, future studies should separate these factors, perhaps by manipulation, to assess the role of productivity *per se* on species diversity and population density.

Species interactions

One possible mechanism causing decreases in diversity as productivity increases is competition (Figure 1). Good colonizers can find optimal conditions in cities within regions where they would not normally thrive. Examples include grey-headed flying foxes *Pteropus poliocephalus* in Melbourne, Australia [13] and the common house gecko *Hemidactylus frenatus* in Hawaii [7]. The abundance of such species might increase in response to productivity such that they come to dominate the community [4,12,17]. The increase in abundance of species that are highly efficient in exploiting food (i.e. can find and consume more food per time unit in a given patch) [6] can cause a local extinction of native urban adapter species, as described for *H. frenatus* in urban and suburban habitats in Hawaii [7].

Therefore, in addition to habitat loss, some species might fail to occupy urban habitats owing to increased competitive exclusion associated with the increase in habitat productivity [6]. In some cases, habitat management *per se* might not result in increases in urban species diversity. Understanding the key factors that should be controlled to reduce the density of urban exploiters might enable native species to tolerate urban conditions. Future studies on urban diversity should also pay attention to dominance. For example, it is likely that, for any given taxon, a few highly abundant species account for a much higher proportion of the whole community in urban environments than in surrounding wildlands.

Buffering effects of human activities on temporal variability

Change in habitat structure *per se* can explain the differences in community composition between cities and wildlands [4]. However, the functioning of urban ecosystems is characterized by two additional, more subtle features: thermal habitat and resource availability.

Thermal habitat

The heat island effect can buffer against cold winters [13] and extend growing seasons in temperate-zone cities [22], while adding thermal and drought stress in tropical,

desert and subtropical cities; for example, urban warming in Phoenix, Arizona, USA, has increased cotton *Gossypium hirsutum* plant stress, which has led to lower fiber quality [27]. Conversely, irrigated green spaces can buffer against high temperatures via evapotranspiration (e.g. Guadalajara, Mexico; Phoenix, Arizona, USA; and Gaborone, Botswana [28–30]). High water availability in managed green spaces further facilitates adaptation of some species to arid urban environments (e.g. Box 1).

Resource availability

Urban management strategies often make spatially and temporally patchy resources more continuously available (Figure 1). Temporal changes in habitat structure and the availability of food and water are dampened in several cities [11–13]. For example, in temperate cities, growing seasons are extended [22], altering opportunities for breeding. Feeding animals, whether directly (e.g. bird feeders [31]) or indirectly (e.g. fruit and seeds of exotic vegetation, or refuse [32–34]), can also buffer seasonal variation [35]. In tropical, desert and subtropical cities, one of the most noticeable effects is that managed ‘grasslands’ are perennial, as a result of the year-round irrigation of lawns and parks [22,25].

Therefore, we suggest that, in terms of contrast between hot–cold or rainy–dry seasons, cities can be viewed as ‘pseudo-tropical bubbles’ regardless of their latitude. Consequently, some native species thrive under this dampened temporal variability, contributing to elevated urban population densities (Figure 1). For example, the grey-headed flying fox became established in Melbourne, Australia following long-term climatic changes stemming from a heat island effect in the city. Elevated winter minimum temperatures and productivity made the urban habitat similar to the more northerly wildland occupied by this species [13]. Dampened seasonality also enabled the establishment of the dark-eyed junco *Junco hyemalis* in San Diego, California (Box 1). A weak contrast between seasons owing to irrigation or continuous food input enables birds to extend their breeding season compared with conspecifics in adjacent wildlands [36–38]. Furthermore, in many cities, including those in temperate zones, invasive bird species are tropical (e.g. parrots in Valencia, Spain) [39,40]. That these species do not spread into wildlands suggests that urban environments maintain essential factors that facilitate their persistence.

Future research should address the role of altered local climates and buffered seasonality in supporting species invasions in urban areas, and to what extent these factors can be controlled through management of irrigation practices or impervious surface cover. Such information might also be useful for conservation of native species in urban settings.

Alteration of trophic dynamics and foraging behavior

Urban areas are often characterized by: (i) increased and stabilized productivity, at least in planted areas such as parks and yards [22,25]; (ii) reduced native vertebrate predators [16]; (iii) increased abundance of some urban-adapted vertebrate and invertebrate consumers, at the

Box 1. How do species become urban dwellers?

The low risk of predation and high food abundance associated with urban areas might sound like paradise for wildlife populations, but new settlers in the city must overcome stressors such as noise [5], toxins [47] and diseases [48] to become successfully established. Although adaptations to novel environments require plasticity in heritable characteristics, populations might decline rapidly and vanish over a relatively short period of ecological time before such genetic change can occur. This is where urban environments differ from wildlands. Resource availability and dampened seasonality in cities might serve as facilitating factors (i.e. factors that slow the rate of population decline), enabling persistence until genetic change occurs. Although establishments are rarely documented, a recent study of dark-eyed juncos *Junco hyemalis* [11,49] reveals how this species became urban-dwelling in southern California (Figure 1).

The example of dark-eyed juncos

Juncos established in coastal southern California during the early 1980s. The breeding season of mountain populations in southern California is restricted owing to climatic conditions, whereas the juncos that established in San Diego enjoy much milder climatic conditions. Consequently, the length of their breeding season, which is correlated with reproductive output, is extended compared with that of the mountain populations [49]. It is adaptive plasticity in behavior, rather than the immigration of new individuals, that enables the population to persist in the urban environment. Although the climatic conditions in coastal southern California are milder than in inland mountain ranges regardless of habitat type, the newly established population is restricted to a small part of the urban area where the proximity and availability of irrigation systems are facilitating factors for late-season breeding. Without these factors, it is likely that the established population would not have persisted [49].

During the two decades since establishment, the urban population has evolved rapidly, losing 22% of the white in their tails [11]. The change in this socially selected signaling trait was the result of selection rather than of either plasticity or genetic drift. Selection on this trait reveals the differences between the wildlands, where there is strong competition for mates (and, hence, socially selected signals are important), and cities, where increased parental care and strong competition for food prevail and so there is less need for such signals [49].



Figure 1. Nest of a dark-eyed junco *Junco hyemalis* in a styrofoam bike helmet at San Diego, California. Reproduced with permission from Pamela Yeh.

expense of other species [20]; and (iv) altered behavior and phenology [34]. These changes set the stage for altered trophic dynamics [8] (Figure 1).

Top-down versus bottom-up control

Control of food-web structure in urban communities is likely to differ greatly from that in wildlands, but few studies have experimentally addressed urban trophic dynamics. Recent experimental research in Phoenix, Arizona, finds that classic resource-based (bottom-up) and consumer-based (top-down) factors operate in urban communities, but their relative importance is altered compared with surrounding wildlands. The control of arthropod abundance shifts from almost exclusively bottom up in Sonoran desert habitats to a combination of bottom-up and top-down forces in Phoenix [8]. The study indicates that, in urban environments, complex trophic dynamics occur that are not predictable based only on knowledge of species composition. We need more research on urban trophic dynamics from other cities, especially from non-desert areas, to determine how general such phenomena are in urban ecosystems (Figure 1).

It has been suggested that predation risk for birds is higher in urban habitats, owing to the high density of domestic and feral predators, such as cats and dogs [41]. However, the high abundance of birds in spite of high predator abundance in urban environments sets a paradox [14]. Experiments with artificial nests have produced conflicting results regarding the intensity of

nest predation rates in urban habitats [42,43], although the high reproductive output of the rufous-banded honeyeater *Conopophila albogularis* in Darwin, Australia, has been explained by the scarcity of predators in this city compared with its natural environment [36].

The solution to the predation paradox might be that contemporary urban bird communities represent the 'ghost of predation past', where those species unaffected by predation from cats and corvids thrive and potential adapter species that are sensitive to predation have disappeared. The inflated densities and tame behavior of urban birds suggest that there is little empirical support for the hypothesis that predation pressure in the urban environment is high and that estimating predation risk based on predator density alone can be misleading. Further support comes from studies of the foraging behavior of birds [6] and squirrels [44], indicating that competition for food is stronger in urban environments, whereas the risk of predation is higher in wildlands.

Evolutionary responses to novel environments

Natural selection is short-circuited in many circumstances in urban environments. Selective pressures, such as temporal variation in food, water and predation, are often relaxed [4,34,36,44]. Simultaneously, the novel environments constructed by humans in cities set new selective forces in motion, altering the behavior [5], morphology [9,11] and genetic structure of populations [9–11]. Behavioral flexibility might facilitate adaptation to

these novel environments by some species. For example, species occurring in urban habitats in their native range can be more successful at establishing themselves in novel regions, although behavioral flexibility on its own does not appear to distinguish urban dwellers from other species [45].

The changes in ecological processes illustrated in Figure 1 should alter selective forces in cities, leading to the genetic differentiation of urban and wildlands populations or genetic changes associated with the fragmentation and isolation of wild populations [10,46]. Morphological changes in urban areas can be rapid, as in the case of the dark-eyed junco in San Diego, California (Box 1). Alternatively, continuous migration to and from wildland habitats, as well as anthropogenic activities that construct and deconstruct entire biological communities, might prevent the genetic differentiation of urban populations and dampen evolutionary responses to these novel selective forces. Greater attention should be paid to urban evolutionary aspects because the type and direction of physiological, behavioral and morphological changes can indicate how selection forces in urban environments differ from those in habitats that are less influenced by humans [11].

Conclusions

Results of recent mechanistic studies indicate that urbanization changes animal behavior [5,6], morphology [11], population dynamics [33], and community structure [6]. Yet, these studies only begin to identify the missing links between human activities and patterns of population densities and species diversity (Figure 1). Future insights from urban ecology depend on balancing more carefully between descriptive and experimental ecology to recognize explicitly the role of human activities in altering ecological and evolutionary processes. Mechanistic research should focus on manipulations of food and predation pressure. Linking the processes of establishment, population fluctuations and the extinction of introduced species with long-term changes in human society might shed light on how human activities affect urban populations and communities. Control of invasive species in favor of native species depends on a greater understanding of ecological and evolutionary processes operating in urban and other human-dominated areas.

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