3 Wildlife in the City: Human Drivers and Human Consequences

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Abstract

The urban development process results in the removal, alteration and fragmentation of natural vegetation and environmental features, which have negatively impacted many wildlife species. With the loss of large tracts of intact wildlands (e.g. forests, deserts and grasslands), and the demise of specific habitat features (e.g. early successional habitat or native plants), many specialist species are filtered out from urban ecosystems. As a result, some argue that urbanization has a homogenizing effect on wildlife communities. However, these general patterns belie a high degree of variability in urban biodiversity patterns. In this chapter, we focus on vertebrate and invertebrate species that contribute to urban fauna (hereafter 'wildlife'). We review how wildlife species have responded to altered conditions of the urban environment, with a focus on the environmental features and species traits that filter wildlife communities from the regional scale to the city scale. We also focus on how built structures, species interactions and socio-cultural factors further influence the local species pool. Within this context, we assess the ecosystem services and disservices provided by urban wildlife, how management decisions are shaped by attitudes and exposure to wildlife, and how these decisions then feed back to the local species pool. By understanding why some animals are better able to persist in human modified landscapes than others, land managers, city planners, private homeowners and other stakeholders can make better-informed decisions when managing properties in ways that also conserve and promote wildlife.

Introduction

More than half the world's population lives in cities and suburbs (Grimm *et al*., 2008), and an estimated 80% of the world's population will live in urbanized areas by 2050 (United Nations Department of Economic and Social Affairs,

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Population Division, 2019). A consequence of this migration to and expansion of cities includes the degradation of wildlife habitat, with implications for local and regional biodiversity (Grimm *et al.*, 2008; Seto *et al.*, 2012). The urban development process results in the removal, alteration and fragmentation of natural vegetation and environmental features, which have negatively impacted many wildlife species (McKinney, 2002; Grimm *et al.*, 2008). Natural habitats transform into human-dominated environments, which include residential developments, public parks, commercial/industrial districts, transportation corridors and impervious surfaces (e.g. buildings and roads), and become a prominent feature that supports a growing urban population. Urban wildlife studies commonly document a depauperate fauna in cities compared to their non-urban habitats, resulting in lower species diversity (Emlen, 1974; Beissinger and Osborne, 1982; Mills *et al.*, 1989; Blair, 1996; Marzluff, 2001; Donnelly and Marzluff, 2004; Chace and Walsh, 2006; Croci *et al.*, 2008). With the loss of large tracts of intact wildlands (e.g. forests, deserts and grasslands), and the demise of specific habitat features such as early successional habitat or native plants, many specialist species are filtered out from urban ecosystems (Blair, 1996; Aronson *et al.*, 2016; Evans *et al.*, 2018). As a result, some argue that urbanization has a homogenizing effect on wildlife communities (McKinney, 2006; Sol *et al.*, 2014; Knop, 2016; Morelli *et al.*, 2016; Murthy *et al.*, 2016; Salomão *et al.*, 2019), wherein invasive species (e.g. pigeons, Norway rats and cockroaches) dominate. However, these general patterns belie a high degree of variability in urban biodiversity patterns.

Negative effects of urbanization on biodiversity are not ubiquitous across taxa. Indeed, some urban areas can support high levels of biodiversity, and for some taxa, like birds, native species largely dominate urban communities (Aronson *et al.*, 2014). Some invertebrates and mammals also respond positively to urban areas. For example, in two separate studies, one from Phoenix, Arizona, and the other a meta-analysis that included various cities in Europe, Japan and Canada, investigators found that ground arthropod diversity did not differ between natural areas and various urban land areas, owing to the turnover of communities from habitat-specialist to non-specialist species (McIntyre *et al.*, 2001; Magura *et al.*, 2010). In addition, some taxonomic groups, like pollinators, may also thrive in urban landscapes due to increased resources. For example, a high diversity of bees can occur in urban areas (see Chapter 6, Protecting Pollinators in the Urban Environment), likely due to abundant flowers (Baldock *et al.*, 2015; Hall *et al.*, 2017; but see McIntyre and Hostetler, 2001), which are available in untreated lawns (Lerman and Milam, 2016) and in cultivated gardens (Levé *et al.*, 2019). Herbivorous and predatory insects also may be abundant in certain urban habitats when resources are available, such as appropriate host plants and vegetative complexity (Raupp *et al.*, 2010). However, despite high diversity, the species that colonize urban areas tend to consist of distinctly different suites of species from those that remain in natural habitats (e.g. Bang and Faeth, 2011; LaSorte *et al.*, 2018; Collado *et al.*, 2019). For mammals, generalist species such as raccoons (*Procyon lotor*) may thrive at high densities and occupancies in some types of urban green space, but not in others (Crooks and Soulé, 1999; Parker and Nilon, 2008; Gallo *et al.*, 2017). Thus, both the degree of urbanization and the quality of habitat within urban systems can have complementary forces driving the particular animal species that is able to occupy and thrive in urban systems.

In this chapter, we focus on vertebrate and invertebrate species that contribute to urban fauna (hereafter referred to as 'wildlife'). We review how wildlife species have responded to altered conditions of the urban environment, with a focus on the environmental features and species traits that filter wildlife communities from the regional scale to the city scale (Fig. 3.1). We also focus on how built structures, species interactions and socio-cultural factors further influence the local species pool. Within this context, we assess the ecosystem services and disservices provided by urban wildlife, how management decisions are shaped by attitudes and exposure to wildlife, and how these decisions then feed back to the local species pool (Fig. 3.1). Our taxonomic focus includes birds, bees, lepidopterans, ground arthropods and mammals, as the majority of research focuses on these groups (Pickett *et al.*, 2011; Beninde *et al.*, 2015). We provide a global perspective when data and examples are available, though much of the available

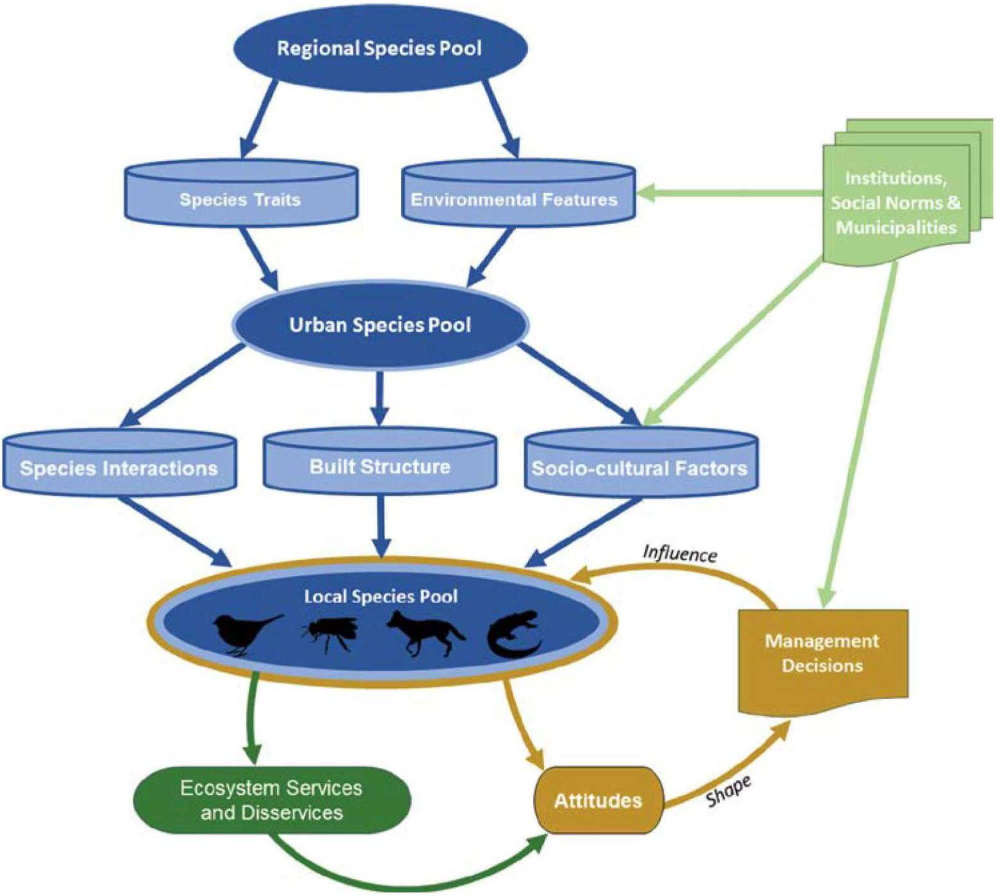

Fig. 3.1. A series of interacting ecological and social factors determine the local species pool in urban systems. The potential wildlife species that occupy a particular city is first determined from the regional species pool, which is primarily dictated by climate and latitude. Species traits (e.g. diet and body size) and specific environmental features (e.g. urban form and land use) filter the regional pool to the urban species pool. Species interactions (e.g. predator–prey dynamics), the built structure (e.g. roads and buildings), and socio-cultural factors (e.g. income and attitudes) further filter which species persist into the local species pool. Overarching each of these hierarchical layers are governance structures (i.e. institutions, social norms and municipalities) that interact at various levels and degrees with the factors shaping the urban and local species pool. It is at the local species pool level that people have regular contact with wildlife species and experience ecosystem services and disservices. These interactions further affect attitudes towards local wildlife, which subsequently shape management decisions to either encourage or discourage certain species, which ultimately feed back into influencing the local species pool. (Animal images by Creazilla.com are licensed under CC BY 4.0 and were recoloured.)

literature comes from North America, western Europe, Australia and New Zealand (Magle *et al.*, 2012; McDonnell and Hahs, 2013; Goddard *et al.*, 2017). We review the literature on habitat use of urban green spaces within the urban and suburban matrix itself rather than the response of animals to urban development compared to intact natural areas. A unique contribution of this chapter is that we integrate a description of the human drivers influencing urban wildlife communities with discussion of potential feedbacks to humans, particularly those at local scales, which can further alter management actions. By understanding why some animals are better able to persist in human modified landscapes than others, land managers, city planners, private homeowners and other stakeholders can make better-informed decisions when managing properties in ways that also conserve and promote wildlife.

Urbanization Shapes Species Pools

After the initial disturbance from urban development, novel habitats emerge in urban ecosystems (Kowarik, 2011; Swan *et al.*, 2011; Grimm *et al.*, 2017). The resulting altered landscape constitutes a complex mosaic of invasive (i.e. species that have a negative effect on the ecosystem), non-native (i.e. species that did not originate in a given habitat, but may have a neutral or even positive effect on the ecosystem) and native plants, large swaths of lawns, isolated trees and remnant habitat patches of varying sizes, all of which are interspersed with built structures, impervious surfaces and artificial sensory inputs (e.g. noise, light) that define urbanization for most observers. The green spaces in this mosaic frequently support the persistence of a number of wildlife species, populations and communities (Pickett *et al.*, 2011; Lepczyk *et al.*, 2017a). Since urban green space can encompass everything from residential yards, gardens, recreational parks, cemeteries, vacant lots and remnant patches of native vegetation, the quality and composition of habitat are tremendously variable among green space types (Lepczyk *et al.*, 2017a). In addition, within any type of green space there is considerable variation in management decision criteria (e.g. native plantings, having outdoor cats, and differences in mowing frequency; Loss *et al.*, 2013; Narango *et al.*, 2017; Lerman *et al.*, 2018) and management goals (i.e. regarding aesthetics, ease of maintenance and safety; Larson *et al.*, 2016) that can have far-reaching implications on habitat quality for wildlife. This results in heterogeneous patches of urban green space that support a range of both generalist and specialist native species, as well as non-native and invasive species (Shochat *et al.*, 2010; Aronson *et al.*, 2014; Lepczyk *et al.*, 2017b).

The communities of animals that inhabit urban landscapes are shaped by a series of interacting processes, often called filters, operating at scales from the regional to the local (Aronson *et al.*, 2016). Regional filters encompass eco-regional factors (e.g. climate and latitude) that dictate which species constitute the regional species pool and therefore have the potential to occur in a given city or metropolitan area (Aronson *et al.*, 2016). Urban form, urban land use, and species traits further filter species from the regional to the urban species pool. The built environment (e.g. roads and buildings), species interactions, and socio-cultural features (e.g. income and attitudes) act as further filters from the urban to the local species pool. Typically, it is these local species, encountered on a day-to-day basis by humans that deliver vital ecosystem services (Fig. 3.1). All of the filtering processes reflect human decisions and actions. However, the actors shaping broad-scale environmental filters are often institutions (e.g. municipal governments, regional planning boards, developers) rather than individual urban residents (Fig. 3.1; Warren *et al.*, 2010; Pickett *et al.*, 2011). Previous reviews have covered much of the literature on broader-scale regional and environmental filters (i.e. urban form and urban land use), as well as species traits filters (e.g. Aronson *et al.*, 2016; Evans *et al.*, 2018). Thus, we start by briefly summarizing the factors that lead to filtering at these broader scales, before delving into greater depth on species interactions and socio-cultural filters, which typically operate at smaller spatial scales. These finer-scale filters are therefore shaped strongly by individual human actions at the parcel level, e.g. in pocket parks, commercial parks and residential yards and gardens (Warren *et al.*, 2010; Swan *et al.*, 2011; Aronson *et al.*, 2017).

Environmental Features that Filter from the Regional to Urban Species Pool

At a coarse scale, wildlife communities frequently differentiate themselves among land-use types, largely due to differences in physical structure that shape habitat suitability (Ortega-Álvarez and MacGregor-Fors, 2009; Gallo *et al.*, 2017; Andrade *et al.*, 2018). For example, in Chicago, Illinois, coyotes, *Canis latrans*, have a higher detection rate in open golf courses, whereby white-tailed deer, *Odocoileus virginianus*, are more likely to persist in wooded cemeteries and natural areas embedded within the urban matrix (Gallo *et al.*, 2017). In the UK, allotment gardens (i.e. plots of land available for individual, non-commercial gardening or growing food plants) and private gardens support the highest pollinator (e.g. bees, hoverflies and non-syrphid *Diptera*) abundances when compared with cemeteries, nature reserves, parks, verges (green space associated with urban roads, typically 2–5 m wide, with trees sometimes being present) and other green spaces. Urban land uses that include habitat features and contribute to ecological function can also bolster connectivity in the urban landscape. For example, land uses with large proportions of vegetation, such as residential gardens, wooded streets and utility rights-of-way can link disparate habitat fragments into larger networks (Rudd *et al.*, 2002) and support movement, meta-community dynamics and increased genetic connectivity (Unfried *et al.*, 2013; Padilla and Rodewald, 2015; Gallo *et al.*, 2017).

Although different cities may have similar land-use categories, the particular urban form and structure of these land uses may differ. For instance, city age, amount of remnant vegetation and amount of impervious surfaces can vary dramatically both within and among cities, and wildlife communities respond to these differences (Ramalho and Hobbs, 2012). In Chicago, newer neighbourhoods supported higher bird richness (Loss *et al.*, 2009), contrasting with other studies that found higher bird richness in older neighbourhoods with more mature vegetation and extensive canopy cover (e.g. Palomino and Carrascal, 2005). However, context matters, and land-use legacies interact with urban development history. For instance, remnant vegetation in residential landscapes can differ based on former land use (e.g. cleared agricultural systems versus forests or woodlands; Hahs *et al.*, 2009), which can influence wildlife communities (DeGraaf and Wentworth, 1986; Loss *et al.*, 2009). Development patterns in cities often follow an urban-to-rural gradient, with more urban areas associated with higher percentages of impervious surface (McDonnell and Pickett, 1990; Blair, 1996; Pickett *et al.*, 2011). Wildlife communities respond to this gradient with a general pattern of lower species diversity; in particular, a lower representation of certain native species, but higher population densities of animals in the urban core versus more rural and wildland settings (Fortel *et al.*, 2014; Marzluff, 2017; Sol *et al.*, 2017). In some cases, maximum species richness occurs at intermediate levels of human development, i.e. suburban landscapes (Blair, 1996; Marzluff and Rodewald, 2008; Parsons *et al.*, 2018). High species richness in the suburbs may be due to the simultaneous local colonization of synanthropic species (i.e. species extremely tolerant of people) and the persistence of some habitat specialists as well as the high heterogeneity of habitat types in these systems (Marzluff and Rodewald, 2008).

Species Traits that Filter from the Regional to Urban Species Pool

Species assemblages that colonize urban habitats are also filtered according to their traits, which ultimately determine their success as well as their relationships with people (Aronson *et al.*, 2016). For some taxa, functional diversity tends to homogenize with increasing urbanization (Devictor *et al.*, 2008; Deguines *et al.*, 2016). For example, observations of plant–pollinator interactions across France showed that urbanization promoted a functional homogenization toward more generalist foraging insects (Deguines *et al.*, 2016), but increasing garden space generally positively benefitted pollinator diversity (Normandin *et al.*, 2017; Levé *et al.*, 2019). However, the identification of a common set of species traits associated with urbanization has proved elusive with conflicting findings in different studies (Croci *et al.*, 2008; Evans *et al.*, 2011; Reif *et al.*, 2011; Francis and Chadwick, 2012; Leveau, 2013).

One general trend, however, is a broad distinction between responses of generalists versus specialists. Urban areas have higher diversity and abundance of generalist and synanthropic species, whereas habitat specialists tend to decline (McIntyre *et al.*, 2001; Martinson and Raupp, 2013, p. 2013; Deguines *et al.*, 2016; Evans *et al.*, 2018; Callaghan *et al.*, 2019). Non-native and invasive species often become common in urban areas because of their synanthropic nature (e.g. house sparrows, *Passer domesticus*, nesting in buildings) or their introduction via global trade routes (Aronson *et al.*, 2016). For example, an invasive insect pest, the emerald ash borer, *Agrilus planipennis*, was introduced via the horticultural industry and has decimated urban *Fraxinus* trees (Cregg and Dix, 2001). Over-abundant invasive species, such as the Argentine ant (*Linepithema humile*) thrive in urban areas and reduce species richness and turnover by exclusion of native ant species (Holway and Suarez, 2006). Although urban areas support diverse communities of bees (Lerman and Milam, 2016; Hall *et al.*, 2017; Baldock *et al.*, 2019), insects of other functional groups like predators and parasites decline with increasing urbanization (Guenat *et al.*, 2019). Bat responses to urbanization are highly species-specific; some species strongly associate with human habitation, whereas others are absent from urban areas (Jung and Kalko, 2011), possibly due to species partitioning into different diet and foraging guilds. Thus the responses of different taxonomic groups to urbanization are complex and often taxon-specific due in part to differences in ecological function and linked to mechanisms that either enhance or limit population growth.

The availability of specific food items and nesting substrates vary within and among urban systems, and contribute to the filtering of species by their traits. For example, urban bird communities lose species with specialist dietary niches, like insectivores (Chace and Walsh, 2006; Rodewald and Bakermans, 2006; Evans *et al.*, 2018). The increase in generalist species may be due to complementary responses of animals that have the flexibility to utilize limited resources, as well as animals that respond positively to human resource supplements such as bird-feeding or refuse (Galbraith *et al.*, 2014). Specialist species such as herbivorous insects rely on native host plants, which are often uncommon in urban and suburban areas (Burghardt and Tallamy, 2013). Specialists are also more sensitive to introduced competitors or predators (Shochat *et al.*, 2010). Likewise, because of abundant nesting substrates, cavity-nesting species of birds (Chace and Walsh, 2006; Evans *et al.*, 2011) and bees (Matteson *et al.*, 2008) are abundant in urban areas, whereas ground-nesting birds (Evans *et al.*, 2018) and ground-nesting bees (Matteson *et al.*, 2008) lack nesting opportunities due to the loss of snags and deadwood, and bare, permeable ground. However, when nesting resources are present, some urban areas (e.g. suburban gardens) can support high densities of ground-nesting bees (Fetridge *et al.*, 2008; Lerman and Milam, 2016). Further, wildlife species with life-history characteristics that promote reproduction, e.g. large clutch sizes (Callaghan *et al.*, 2019) and/or dispersal, e.g. large wing morphology (Piano *et al.*, 2017), also thrive in urban areas. Although larger body size is often negatively associated with urbanization, the interaction between urban heat islands and habitat fragmentation might negate clear patterns. For example, in an investigation of ten taxonomic groups of aquatic and terrestrial invertebrates that persist in urban environments, ground spiders and ground beetles were found to decrease in size, following Atkinson's temperature-size rule (Atkinson, 1994), whereas species with a positive size-dispersal link increased in size, including orthopterans, macromoths and rotifers (Merckx *et al.*, 2018). Additional examples of large-bodied organisms persisting in urban areas can be found in mammals (Murray and St. Clair, 2017), beetles (Martinson and Raupp, 2013, p. 2013) and birds (Callaghan *et al.*, 2019). In addition to declines in taxonomic diversity, some urban wildlife communities have reduced evolutionary and phylogenetic diversity (Morelli *et al.*, 2016; Ibáñez-Álamo *et al.*, 2017; Sol *et al.*, 2017). These losses in key components of ecological processes could result in reduced ecosystem function.

Built Structural Features Shape Local Species Composition

A defining feature of urbanization is the built structure (e.g. buildings, roads and other transportation infrastructure). Collectively, these features yield a landscape with large swaths of impervious surfaces and fragmented natural areas (McDonnell and Pickett, 1990). Roads cross the landscape, rendering the remaining habitat unsuitable for species that require large tracts of unfragmented habitat (Forman and Alexander, 1998; Crooks, 2002) and create a barrier to movement or dispersal for many species (Orłowski, 2008; Beebee, 2013; Grilo *et al.*, 2014; Murray and St. Clair, 2015; Keilsohn *et al.*, 2018). Roads also alter local scale processes through mortality or behavioural changes for a variety of taxa, ranging from highly mobile animals, such as birds, insects and coyotes, to those with more restrictive movement, such as amphibians (Shepard *et al.*, 2008; Beebee, 2013; Loss *et al.*, 2014a; Murray and St. Clair, 2015; Keilsohn *et al.*, 2018). In terms of scale, an estimated 89–340 million birds (Loss *et al.*, 2014a) and billions of insects (Baxter-Gilbert *et al.*, 2015) collide with vehicles each year, a significant source of mortality in wildlife populations. Roads also have sublethal effects by altering animal behaviour and movement. In the northern city of Edmonton, Canada, urban coyotes changed their behaviour by avoiding roads or shifting the timing of their peak activity to times when road traffic had higher survival rates (Murray and St. Clair, 2015).

Vehicles travelling on roads also contribute to a significant source of noise. The peak amplitudes of highway or roadside noise have been shown to overlap in frequency with bird, frog and insect vocal signals, causing some individuals to shift their communication frequency in order to be heard by rivals or potential mates (Warren *et al.*, 2006; Barber *et al.*, 2010; Narango and Rodewald, 2016). Road noise also reduces detectability of important signals, such as anti-predator alarm calls (Grade and Sieving, 2016) or nestling begging (Leonard *et al.*, 2015). In addition to effects on communication, road noise also has detrimental impacts to individuals, populations and communities. For example, to experimentally isolate the effects of road noise from the physical effects of noise, McClure *et al.* (2013) created a 'phantom highway' by placing speakers across an intact forest and played the sounds of a busy highway. Migrating birds that experienced the noise treatment had lower body conditions and stop-over efficiencies compared to birds who experienced the 'road-less' control (Ware *et al.*, 2015). In addition, the abundance of birds significantly decreased when the speakers were on, and some species demonstrated high sensitivity to noise by avoiding the area completely during playback (McClure *et al.*, 2013). Noise effects from roads and highways extend one kilometre, or beyond the footprint of the road itself, amplifying their impacts even in areas with intact natural habitat (Grade and Sieving, 2016). Anthropogenic noise originates from a variety of sources, not just roadways. Construction, airplane engines and drilling, all predominantly located in urban environments, also interrupt settlement, animal communication, predator detection and breeding success (Shannon *et al.*, 2016; Swaddle *et al.*, 2016).

Buildings (e.g. residential and business structures) serve as another hazardous feature for wildlife to navigate, with direct and indirect consequences. It is estimated that 365–988 million birds collide with buildings each year in the USA, and roughly 99% of these collisions occur on low-rise buildings and residences (Loss *et al.*, 2014b). The reflections of vegetation on window surfaces disorientate birds, and they fly into the window as if they were simply moving from tree to tree. Although window strikes present a large source of mortality, particularly for migratory species (Loss *et al.*, 2015), buildings also provide nesting cavities or roosts for birds and bats (e.g. Tomasevic and Marzluff, 2017).

Because roads and buildings often replace vegetation in urban and suburban environments, the built environment influences the local and regional climate (Hondula *et al.*, 2017). As a result, factors such as the urban heat island (UHI) have the potential to affect wildlife and other urban organisms. The effect of the built environment on climate is partly due to the reduced evapotranspiration and shading by trees, in combination with the use of building materials that retain heat (Oke, 1995). Subsequently, urban heat can drive phenological patterns, behaviour, population cycles and species distributions of wildlife (Aronson *et al.*, 2014; Dale and Frank, 2018). For instance, when the effects of the UHI were isolated from habitat features and species interactions, the warmer conditions were responsible for driving pest insect outbreaks in Raleigh, North Carolina (Meineke *et al.*, 2013). Additionally, changes in local microclimates and the effect of the UHI can potentially influence activity time of thermo-sensitive wildlife such as herpetofauna (Ackley *et al.*, 2015a).

One of the most iconic images depicting the extent of urbanization is the satellite imagery of the earth at night. Artificial light has become ubiquitous with the urbanization of the planet (see Chapter 10). Light pollution can influence the phenology of plant (Škvareninová *et al.*, 2017) and animal life history events, and change foraging (Stone *et al.*, 2015), reproduction (Silva *et al.*, 2017), migration (Van Doren *et al.*, 2017; McLaren *et al.*, 2018) and sleep behaviours (Raap *et al.*, 2015; Ouyang *et al.*, 2017) across taxa (Gaston *et al.*, 2017). Artificial light pollution can also influence navigation, as seen in the case of the 'Tribute in Light' in New York City, which researchers estimate disorientate over a million birds during migration (Van Doren *et al.*, 2017). Artificial light at night can also influence predator–prey dynamics, in that some insectivorous bat species take advantage of artificial light and congregate around lit areas for foraging (Minnaar *et al.*, 2015; Stone *et al.*, 2015). In contrast, frugivorous bats avoid lit areas while foraging (Lewanzik and Voigt, 2014). This in turn has negative consequences for ecosystem services, particularly in tropical cities, since frugivorous bat avoidance interrupts the dispersal of fruiting plant seeds.

Solutions have been proposed to address many of these challenges imposed on wildlife by roads, buildings and fragmentation (Yanes *et al.*, 1995; Glista *et al.*, 2009). For example, wildlife crossings, bridges and culverts can minimize roadway collisions and wildlife mortality (Dodd *et al.*, 2004; Mata *et al.*, 2008). Policies that incentivize compact development (Farr *et al.*, 2018), reduction of sensory pollution (e.g. Audubon's Lights Out campaign; https://www.audubon.org/conservation/project/lights-out) or broad adoption of bird-safe glass in combination with altering vegetation and bird-feeder placement (Kummer *et al.*, 2016) provide other potential mechanisms to increase the capacity of urban areas to support wildlife species. But it is likely that the physical structure of cities will remain a barrier to colonization by many species.

Species Interactions Shape Local Species Composition

As described, thus far urban systems differ in their structural components and abiotic factors from non-urbanized systems. This affects biotic factors such as the quality and quantity of resources, as well as biotic interactions such as predator–prey dynamics, competition and host–parasite relationships. Predator–prey dynamics and urban food webs influence the success or failure of urban wildlife. Successful urban mesopredators (i.e. species that occupy the middle trophic level and serve as both predator and prey), such as raccoons (*Procyon lotor*), foxes (*Vulpes* spp.) and striped skunks (*Mephitis mephitis*), increase in abundance and occupancy relative to apex predators (i.e. predators at the top of a food chain, with no natural predators) (Crooks and Soulé, 1999; Prange *et al.*, 2003; Ellington and Gehrt, 2019; Santini *et al.*, 2019). Their success is partly due to the extirpation of apex predators through direct culling by humans or through the loss of habitat (Gompper, 2002; Gehrt, 2004; Estes *et al.*, 2011; Ellington and Gehrt, 2019). This extirpation 'releases' mesopredators from predation pressure (Crooks and Soulé, 1999) and has consequences that ripple throughout entire urban food webs (Newsome *et al.*, 2015; Santini *et al.*, 2019).

Sometimes, the interaction between 'bottom-up' (resources) and 'top-down' (predation) trophic dynamics in urban habitats results in counterintuitive patterns (Shochat *et al.*, 2006). One such example is the 'predation paradox', in which urban habitats have higher densities of potential generalist predators, yet lower per capita predation rates (Shochat, 2004; Stracey, 2011; Fischer *et al.*, 2012). Specifically, the input of alternative food resources for avian and mammalian mesopredators may dampen nest predation pressure (Shochat *et al.*, 2004; Rodewald *et al.*, 2011; Newsome *et al.*, 2015; Malpass *et al.*, 2017). Still, elevated populations of potential predators present a serious threat to songbirds and small mammals, and may alter wildlife behaviour, foraging and long-term reproductive success through non-lethal or fear effects (Creel and Christianson, 2008; Martin, 2011; Lerman *et al.*, 2012; LaManna and Martin, 2016). In natural systems, mesopredator populations that are not regulated by higher trophic levels tend to suppress populations of their prey. In some cases, this leads to local extinction of species, and therefore reduced biodiversity (Ritchie and Johnson, 2009; Estes *et al.*, 2011). Despite this tendency in natural systems, urban ecologists have found a different dynamic in urban systems. Few studies have attempted to understand the interactions between trophic levels in urban environments, particularly those related to direct human-directed management.

These interactions are complex and dynamic. For example, private gardens landscaped with non-native ornamental plants can have negative impacts on insect populations which, in turn, have cascading consequences for birds that rely on insect prey (Narango *et al.*, 2018). Alternatively, artificial light, which promotes accelerated plant growth, can both promote herbivorous insect abundance via bottom-up effects and reduce abundance via top-down predation by visual predators (Bennie *et al.*, 2016).

Although the overall effect of increased mesopredator populations in urban habitats is still unclear, the introduction of domesticated mammals, especially domestic cats (*Felis catus*), has had a significant impact on urban wildlife. It has been estimated that cats kill 1.4–3.7 billion birds and 6.9–20.7 billion mammals annually in the USA alone (Loss *et al.*, 2013). Cats also induce fear and alter behaviour, causing sublethal effects. For example, the fear instilled by the mere presence of a cat reduces bird fecundity by one offspring per year, resulting in up to a 95% reduction in bird abundances (Bonnington *et al.*, 2013). Outdoor cats, whether pets or feral, often receive supplemental food, potentially decoupling cats from predator–prey relationships, and allowing them to kill prey *ad libitum* without corresponding feedback to outdoor cat populations (Sims *et al.*, 2008). Yet, unlike native mesopredators, cats are beloved household companions, which makes the control of feral and outdoor cats in urban areas a particularly complex conservation challenge.

Humans as Producers and Providers of Resources

Environmental and biotic factors partially explain why some species successfully colonize urban habitats. However, one key factor that sets the urban environment apart from the surrounding wildlands is the introduction of anthropogenic (i.e. human-provided) resource subsidies (Shochat *et al.*, 2006; Tryjanowski *et al.*, 2015; Ciach and Fröhlich, 2017). People and their land management activities in urban green spaces have manipulated urban resources, primarily for their benefit. Thus, humans have had a heavy hand in determining habitat characteristics, and consequently have controlled patterns of urban wildlife biodiversity (Shochat *et al.*, 2006; Aronson *et al.*, 2017; Reed and Bonter, 2018). Though many land management decisions have been made without regard to wildlife, some of these management decisions have been made intentionally to enhance perceived habitat value for wildlife. Examples include the addition or retention of specific vegetation features (e.g. trees, shrubs, grasses and flowering plants), supplemental feeding, avoiding the use of pesticides, adding structural features such as ponds, and erecting nestboxes (Belaire *et al.*, 2014). Despite considerable guidance to householders, we lack consensus regarding the effectiveness of wildlife-friendly gardening strategies (but see Gaston *et al.*, 2005) since wildlife populations and communities have responded to these human subsidies in both positive and negative ways, depending on the specific action (Prange *et al.*, 2003; Newsome *et al.*, 2015; Santini *et al.*, 2019). These actions, which have a social and cultural context (Fig. 3.1), help shape local species pools. The composition of local species pools has the most direct influence on human–wildlife interactions. Further, it is at the local level where the delivery of ecosystem services is the most direct.

Local Landscaping Decisions

Perhaps the largest structural change in urban systems is the shift in vegetation composition. Not only is vegetation less abundant, but it is also often comprised of invasive, non-native and ornamental plant species (Burghardt *et al.*, 2009; Goddard *et al.*, 2017). Non-native plants may differ in the timing of leaf-out (McEwan *et al.*, 2009; Shustack *et al.*, 2009; Wolkovich and Cleland, 2011), in their fruit or flower production (Corlett, 2005), and in the abundance and diversity of arthropods that they host, compared to native plants (Burghardt and Tallamy, 2013; Litt *et al.*, 2014; Narango *et al.*, 2017). Consequently, the dominance of non-native plant species can have an impact on wildlife communities and resource availability for higher trophic levels that use these plants for foraging and reproduction (Narango *et al.*, 2018). For example, Phoenix, Arizona, and Chicago, Illinois, neighbourhoods have strong and positive relationships between abundances of native plants and native birds (Lerman and Warren, 2011; Belaire *et al.*, 2014). Further, native plants support more foraging activity by both insectivorous (Narango *et al.*, 2017) and nectivorous bird species (French *et al.*, 2005).

Native plants may also increase pollinator diversity by supporting species with host-specific specialized diets (Pardee and Philpott, 2014), though several naturalized non-native species appear to be highly attractive to many pollinators (Lerman and Milam, 2016; Baldock *et al.*, 2019). However, even when a preferred foraging plant is present, novel non-native species can disrupt natural processes because of differences in resources or phenology. For example, migratory monarch butterflies (*Danaus plexippus*) exposed to blooming non-native milkweed (*Asclepias*) species, found in southern-US gardens, may forgo southward movements in favour of breeding, with the unintentional consequence of increasing pathogen prevalence in the population (Satterfield *et al.*, 2015). Many ornamental plants introduced via the horticultural trade produce fruits used extensively by generalist omnivorous and frugivorous birds, despite low nutritional values. Further, dispersal of non-native seeds from birds can facilitate invasion throughout both urban and natural systems that can have cascading impacts on plant communities, succession, and trophic interactions with consumers (Gosper *et al.*, 2005). Fruit and vegetable gardens also directly provide important food sources to many animals, from pollinators to large mammals (Contesse *et al.*, 2004; Daniels and Kirkpatrick, 2006; Baldock *et al.*, 2019), although the wildlife resources that result from these gardens may or may not be intentionally planted to attract wildlife (Goddard *et al.*, 2013; Mumaw and Bekessy, 2017).

Landscaping requires laborious upkeep, which, often, is driven by aesthetics (Cook *et al.*, 2012; Larson *et al.*, 2016). Humans provide inputs that are important and often naturally limited such as water, carbon, nitrogen and phosphorus (Kaye *et al.*, 2005; Trammell *et al.*, 2016; Palta *et al.*, 2017; Souto *et al.*, 2019), while some inputs such as the application of herbicides and pesticides can significantly degrade habitat (Aronson *et al.*, 2017; Sievers *et al.*, 2019). Humans also eliminate certain resources such as standing deadwood, spontaneous lawn flowers and leaf litter (Blewett and Marzluff, 2005; Templer *et al.*, 2015; Aronson *et al.*, 2017; Lerman *et al.*, 2018), which can further degrade the potential habitat. For example, frequent lawn mowing results in an aesthetically pleasing garden (Robbins, 2007), but removes floral resources, which in turn has a negative influence on bee abundance in suburban gardens due to their role as potential nectar sources (Lerman *et al.*, 2018). Regardless of the particular landscaping decision, the resulting landscapes have profound influence on wildlife communities (Goddard *et al.*, 2010).

Feeding Wildlife

Another distinguishing characteristic of urban habitats is the artificially inflated abundance of food resources (Prange *et al.*, 2003; Shochat *et al.*, 2006; Newsome *et al.*, 2015). Humans provide these resources directly or indirectly, and intentionally as well as unintentionally. Actively feeding wildlife, in particular birds, has become the most popular and widespread intentional resource-provisioning activity, which influences wildlife populations at multiple spatial scales (Reynolds *et al.*, 2017; Cox and Gaston, 2018; Baverstock *et al.*, 2019). Typically, resource (i.e. food) provision includes sugar water, commercial seed, meat, suet or bread (Rollinson *et al.*, 2003; Lepczyk *et al.*, 2012). In the UK, nearly 50% of householders feed birds, equating to approximately one bird feeder for every nine UK birds (Davies *et al.*, 2009). A similar percentage of households feed birds in the USA (approximately 50 million people; U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, US. Census Bureau, 2014) as well as in Australia (Rollinson *et al.*, 2003; Jones *et al.*, 2008) and New Zealand (Galbraith *et al.*, 2014). Households in New Zealand put out a staggering estimated 5.1 million loaves of bread per year, which has caused a shift in the bird community, towards species tolerant of this food source (Galbraith *et al.*, 2014).

The benefits of feeding birds and other wildlife are more often articulated in terms of their benefits to humans, through increased well-being, which typically reflects a state characterized by health, happiness and prosperity (Fuller *et al.*, 2007; Goddard *et al.*, 2013), the opportunities to interact with nature (Lepczyk *et al.*, 2012) and/or ecosystem services (Orros and Fellowes, 2012). Many people feed birds and other wildlife to enjoy wildlife viewing as well as for a personal sense of stewardship for their local fauna (Jones *et al.*, 2008; Cox and Gaston, 2018). Birds also benefit from the increased resources, as evidenced by higher species richness and abundance in areas with resource provisioning (Fuller *et al.*, 2008). Supplementary feeding in the city of Reading, UK, provided food for up to 320 red kites (*Milvus milvus*), contributing to their high abundance (Orros and Fellowes, 2015). Subsidizing food resources can increase winter survival or augment resources when food is scarce (Jones *et al.*, 2008), and can increase breeding success (Schoech and Bowman, 2001). Providing supplemental food for wildlife can improve survival and reproductive output (Brittingham and Temple, 1988; Robb *et al.*, 2008; Cox and Gaston, 2018; Santini *et al.*, 2019) as well as facilitate northward expansion of species distributions (Robb *et al.*, 2008; Greig *et al.*, 2017). However, negative effects might counteract some of the benefits. Frequent feeding or providing an unreliable food source might lead to dependence on human resources, and can also have detrimental effects on survival and productivity (Robb *et al.*, 2008). For example, food items with lower nutritional value might decrease individual fitness (Rollinson *et al.*, 2003), or high-fat and high-protein food items might cause earlier egg-laying. In the latter case, this might lead to a phenological mismatch whereby, for example, insect food required for nestlings is unavailable (Renner and Zohner, 2018). Feeding stations might elevate competition among the species attracted to feeders, leading to novel interspecific interactions. For example, when squirrels were present at feeders in Sheffield, UK, bird visitation and the amount of food consumed by birds decreased by more than 90% (Bonnington *et al.*, 2014). Human subsidies also attract higher densities of non-native and invasive wildlife species (Daniels and Kirkpatrick, 2006; Galbraith *et al.*, 2014) that could out-compete native species (Galbraith *et al.*, 2015). Increased aggregations of birds around feeding stations can facilitate the spread of disease and parasites, increase exposure to predation (Adelman *et al.*, 2015; Becker *et al.*, 2015; Galbraith *et al.*, 2017; Civitello *et al.*, 2018) and disease transmission (Robb *et al.*, 2008). If the negative implications of intentionally or unintentionally feeding wildlife outweigh positive aspects, then feeding wildlife might create an ecological trap (Schlaepfer *et al.*, 2002; Robb *et al.*, 2008; Plummer *et al.*, 2013). This is particularly true when supplementary food leads to false cues that the green spaces consist of high-quality habitat, but lack sufficient resources for breeding, or have increased stressors that lead to decreased fitness (Plummer *et al.*, 2013). It is still unclear whether wildlife feeding has a net benefit or a cost to urban wildlife populations, but what is clear is that it has a cultural and personal benefit to people around the world (Cox and Gaston, 2018).

Human Variation

Social and demographic differences in urban planning, landscaping and human values also correlate with wildlife communities, resulting in unequal exposure to urban biodiversity by people. For example, in some cities, affluent neighbourhoods have higher diversity of birds, mammals, reptiles and arthropods (Leong *et al.*, 2018). This may be due to closer proximities to green space, a positive correlation between income and tree canopy (Grove *et al.*, 2014) and/or the capacity to provide more wildlife-friendly features such as plants that provide resources in garden landscaping, or that provide bird seed (Lepczyk *et al.*, 2012; Goddard *et al.*, 2013; Belaire *et al.*, 2015; Baldock *et al.*, 2019). The biodiversity disparity is especially apparent in arid cities, where fewer species and fewer habitat specialists are found in low-income and minority neighbourhoods for both birds (Lerman and Warren, 2011; Warren *et al.*, 2019) and lizards (Ackley *et al.*, 2015b). In temperate systems, high-income neighbourhoods may also harbour high numbers of mammals (Magle *et al.*, 2016) and frog species (Smallbone *et al.*, 2011), in part related to these neighbourhoods being less densely developed with lower human population densities, and located on the outskirts of the urban core. In four UK cities, higher pollinator abundance was associated with higher-income neighbourhoods, a pattern primarily driven by higher quality of floral resources (Baldock *et al.*, 2019). However, in Chicago, Illinois, lower-income neighbourhoods had higher native and migratory bird diversity due to the higher presence of non-developed patches (i.e. >40% in a non-urban land-use class) of habitat (Loss *et al.*, 2009). Thus, generalizable relationships between income and biodiversity may not exist across cities but, rather, are driven by the specific context of an individual city's development pattern.

Humans are the primary drivers of environmental change in cities, and at times wildlife populations and communities benefit from these management decisions. However, management decisions are often facilitated or constrained by attitudinal, geographical and structural factors (Cook *et al.*, 2012), and must be considered in order to fully understand urban wildlife patterns and processes. In the remainder of the chapter, we describe how personal experiences shape attitudes, how attitudes shape management actions (with a focus on garden management), their feedbacks on wildlife species and people, and the ecosystem services, as well as disservices, associated with directly and indirectly interacting with urban wildlife.

Attitudinal Factors Associated with Urban Wildlife

Attitudinal factors are defined as the positive or negative evaluations of an object and are underpinned by values, beliefs and affect/emotion (Thurstone, 1928; Stern, 2000). The attitudinal literature on urban wildlife encompasses a variety of taxa, including birds, herpetofauna, arthropods and mammals. Attitudes are commonly used as both dependent variables (driven by personal characteristics and experiences with nature/wildlife) as well as explanatory variables (used to help explain behaviour, such as garden management decisions and support of conservation initiatives), and thus can be considered as a construct with dynamic feedback loops. For example, attitudes about the local bird community in Chicago neighbourhoods are correlated with a key determinant of ecological resource provisioning in residential back gardens (Belaire *et al.*, 2016). The resulting ecological resources, such as gardens with fruit- and berry-producing trees, were, in turn, important for determining actual bird species richness in the same residential neighbourhoods (Belaire *et al.*, 2014). This iterative feedback loop, in which people both affect and are affected by local wildlife, underscores that people and wildlife are connected through attitudinal factors (Fig. 3.1).

Negative attitudes are driven by perceptions of wildlife as threatening. For example, people often kill snakes indiscriminately due to their perception that they are 'dangerous', despite the fact that most laypeople are unable to distinguish venomous from non-venomous snakes (Alves *et al.*, 2012, 2014; Pandey *et al.*, 2016). Gender and personal vulnerability are important factors in the case of attitudes toward snakes. For instance, in Brazil, women were more likely to hold negative attitudes toward snakes, largely due to gender differences in risk perceptions (Alves *et al.*, 2014). A person's belief that West Nile virus would harm a family member can be directly related to the management practices used to decrease mosquito abundance in their residential garden (Tuiten *et al.*, 2009). Risk perceptions also influence the likelihood that a person will formally complain about alligators in Florida, despite positive attitudes toward alligators more generally (Hayman *et al.*, 2014). Concerns about coyote encounters being dangerous negatively influences support for the presence of coyotes in the urban areas of Washington, DC (Draheim *et al.*, 2013). Conversely, reptiles that are not perceived as dangerous, such as turtles, are more likeable (Tisdell, 2010).

The likeability (or popularity) of species or taxa is one of the most common measures of positive attitudes for urban wildlife (Schuetz and Johnston, 2019), with much of the literature focusing on garden and urban birds. These studies have found support for the connection between likeability and positive attitudes towards a species, such as songbirds being more likeable compared with other bird species (Cox and Gaston, 2015; Belaire *et al.*, 2015). In general, iconic species (e.g. sports mascots), readily encountered species and species with distinguishing physical characteristics represent traits related to positive attitudes (Ainsworth *et al.*, 2018; Schuetz and Johnston, 2019). Biodiversity and species richness are also associated with positive attitudes

(Lerman and Warren, 2011; Cox and Gaston, 2015; Warren *et al.*, 2019). For example, people would rather see ten individual birds of different species than ten similar looking individuals of the same species (Cox and Gaston, 2015), and higher satisfaction with the desert bird community in Phoenix, Arizona, neighbourhoods aligned with actual desert bird species richness (Lerman and Warren, 2011). However, the mechanisms driving the attitudinal–wildlife biodiversity relationship remain unclear, as people often do a poor job of assessing actual biodiversity levels (Dallimer *et al.*, 2012).

Tolerance Threshold

Contrasts in positive versus negative attitudes towards wildlife, and how these attitudes translate to human–wildlife interactions, emerge as one of the most interesting themes from the wildlife attitudinal literature. For example, residents in Bakersfield, California, had positive attitudes toward endangered San Joaquin kit foxes (*Vulpes macrotis mutica*) and supported their protection in urbanized areas (Bjurlin and Cypher, 2005). In contrast, the residents in a suburb of Munich, Germany, did not want red foxes in their residential gardens and neighbourhoods, largely due to concerns about the health risks, despite the fact that they agreed foxes were ‘useful’, ‘beautiful’ and ‘had the right to live’ (König, 2008). People living in the Munich suburbs held positive attitudes toward foxes in general, until it came to foxes being present in their own neighbourhoods. In contrast, the majority of people in Bakersfield, California, did not associate kit foxes in their neighbourhood with any potential risk. As a result, people in Bakersfield supported the presence of foxes whereas Munich residents did not, though people in both cities held generally positive attitudes towards foxes. Similarly, for arthropods, people are tolerant and even have positive attitudes about arthropods present in outdoor areas of their property, but are simultaneously intolerant of arthropods indoors (Hahn and Ascerno, 1991).

Tolerance of urban wildlife can easily turn to intolerance when personal welfare and property come into play (Clergeau *et al.*, 2001). Although attitudes toward urban birds are generally positive, attitudes toward specific species, such as house sparrows (*Passer domesticus*) and rock pigeons (*Columba livia*) are more negative, since many people perceive these birds as a ‘nuisance’ (Cox and Gaston, 2015). Species with abundant local populations are more likely to cross the ‘threshold of tolerance’, and are often considered as ‘pests’ (Clergeau *et al.*, 2001). In general, pest control at the household level is largely targeted at abundant species such as rats and arthropods, which can quickly cause noticeable property damage when overly abundant (Morzillo and Mertig, 2011; Schoelitsz *et al.*, 2019).

Individual and Household Structure

Given that attitudes have a strong tie to people’s identity, it is important to consider how individual and household structure, or socio-cultural factors, influence attitudes (Heberlein, 2012). These variables associated with attitudes include income, age, education, cultural identity and gender. For example, older and wealthier individuals tend to hold more positive attitudes about the birds present in residential neighbourhoods and gardens (Clergeau *et al.*, 2001; Clucas *et al.*, 2011; Belaire *et al.*, 2015; Cox and Gaston, 2015). For attitudes towards species that carry a greater perceived risk, a person’s social vulnerability measured by factors such as socioeconomic status and being a cultural or racial minority become important attitudinal drivers. For instance, a person’s identity and position within society influences attitudes toward tigers (*Panthera tigris*) in Nepal more than past experiences with tigers (Carter *et al.*, 2014). Variables related to individual and household structure also influence management decisions along with attitudinal judgements, which ultimately affect wildlife biodiversity.

Overall, attitudes have an important but complex relationship with behaviour. A better understanding of attitudes will improve our understanding of how people affect and are affected by urban wildlife. The benefits or negative impacts on well-being associated with interacting with urban wildlife occur in both indirect and direct ways and may be driven by how these services play out in an urban landscape. Ultimately, understanding the interaction between attitudinal and structural factors can inform our understanding of the interactions between people and wildlife in cities, and how these interactions help drive urban wildlife patterns and process.

Ecosystem Services and Disservices

Broadly speaking, biodiversity is imperative for functioning ecosystems, and the wildlife found in urban areas provides essential ecosystem services. Here we define ecosystem services as those services that provide benefits for people, including supporting, provisioning, regulating, and cultural and social services (Millennium Ecosystems Assessment, 2005; Larson *et al.*, 2019). We define disservices as the health and other hazards associated with interacting with 'nuisance' or 'pest' animals (e.g. mosquitoes; Lyytimäki *et al.*, 2008). In general, biodiversity correlates positively with ecosystem services, provided that as plants and animals increase in richness, so does the efficiency and efficacy of the ecological service (Schwarz *et al.*, 2017). However, urban areas, which are composed of novel ecological features, and animal and plant communities, may have different relationships between biodiversity and ecosystem services compared to natural areas (Ziter, 2016). Increased services may be driven by higher functional diversity within animal communities, or the presence of particular species that contribute disproportionately to services (Schwarz *et al.*, 2017). In either case, intentional and unintentional management activities can either promote or discourage a wide breadth of taxa that perform ecosystem services, as well as promote disservices in urban ecosystems. Conversely, the reception of wildlife-derived services may be a mechanism of encouragement to promote urban habitat restoration. Thus, managing urban green spaces in a manner that aims to maximize ecosystem services while minimizing disservices has gained considerable traction (Goddard *et al.*, 2013; Larson *et al.*, 2016). Here we describe the variety of ecological and cultural services that are derived from urban wildlife, and describe how feedback loops between public attitudes may contribute to the management of urban green space (Fig. 3.1).

Ecological Services (Regulating and Supporting)

The presence of wildlife can provide ecosystem services that both support and regulate ecosystems and provide provisions and goods. Pollinators (e.g. bees) and seed dispersers (e.g. birds) provide supporting services, which ultimately increase economic yields in urban agriculture and promote vegetation growth more generally (Sekercioğlu *et al.*, 2004; Luck *et al.*, 2009; Cardinale *et al.*, 2012). The role of pollinators and seed dispersers further supports other ecosystem functions, due to the role vegetation plays in mitigating the urban heat island, providing flood control and purifying water (Bolund and Hunhammar, 1999). In addition, agricultural opportunities in urban areas have increased in recent years as more derelict lands have been restored into functional food-producing spaces (Lin *et al.*, 2015; Ferreira *et al.*, 2018, but see Badami and Ramankutty, 2015).

With increased floral resources in certain urban green spaces (e.g. gardens and allotments; Baldock *et al.*, 2019) comes increased pollen deposition (Werrell *et al.*, 2009), which further enhances a positive feedback loop that increases the floral resources and abundances in urban green spaces. Urban areas also contain small fragments of retained natural lands, which serve as support networks for surrounding intact natural areas. These small fragments can act as sources of pollinators to the surrounding matrix of natural lands (Hall *et al.*, 2017). Thus, ensuring management of urban green space and cultivated floral resources can have cascading effects that benefit both people and wildlife. And finally, birds and mammals provide long-distance dispersal of seeds, aiding in restoration and forest growth (Corlett, 2005; Whelan *et al.*, 2015), though sometimes contributing to non-native plant invasions, which further degrades habitat quality (Gosper *et al.*, 2005; Minor and Gardner, 2011). Species that disperse long distances (e.g. migratory birds) or have expansive home ranges (e.g. large mammals) can be important transporters of nutrients such as nitrogen across space and in between habitat boundaries (Whelan *et al.*, 2008). Though not directly derived from animals themselves, the provision of habitat for wildlife by way of planting trees or conserving natural green space can also provide additive service by sequestering carbon, preventing erosion, reducing urban heat and improving air quality (Livesley *et al.*, 2016).

Wildlife species that scavenge carrion (e.g. crows, *Corvus* spp.) and consume vertebrate and invertebrate pests provide regulating services (Sekercioğlu *et al.*, 2004; Luck *et al.*, 2009; Cardinale *et al.*, 2012). These regulating services, in turn, provide pest control of insect and rodent outbreaks, and dispose of waste (Luck *et al.*, 2009). For example, insectivorous birds consume billions of insects, which improves the health of the urban forest, plant growth and survival, and increases crop production in urban gardens (Wenny *et al.*, 2011; Whelan *et al.*, 2015). Pest consumption by birds, along with other biocontrol agents, may also contribute to reducing populations of disease vectors, such as ticks and mosquitoes (Samish and Rehacek, 1999). Vertebrates are not the only taxa that provide regulating services. Although 'urban entomology' may invoke thoughts of pests and disease vectors, urban areas also harbour immense diversity of beneficial taxa and species of conservation importance. Urban arthropods perform important ecosystem services such as pest consumption and parasitization (Shrewsbury and Raupp, 2006) and decomposition and consumption of refuse (e.g. Youngsteadt *et al.*, 2015). Insects also serve as the crucial food resources for diverse taxonomic groups that provide other ecological and social values, such as insectivorous songbirds (Narango *et al.*, 2017). Predatory and parasitic arthropods reduce the impact of herbivorous consumers, like caterpillars, by reducing herbivory, stymieing disease vectors (i.e. presenting such difficulties as to discourage or defeat the effectiveness of the vector) and improving plant health (McIntyre, 2000).

Social and Cultural Services

Urban wildlife provides social and cultural ecosystem services that improve the quality of life for urban dwellers. Arguably, out of all ecosystem services, these social and cultural services have the broadest and most tangible impact on people's lives. For example, bird diversity is linked to the well-being of city residents through affective (emotional) mechanisms such as experiencing the restorative properties of hearing bird song (Ratcliffe *et al.*, 2016; Hedblom *et al.*, 2017). Further, songbirds provide value by their beauty, their song and as objects of educational study, connecting people with nearby nature (Belaire *et al.*, 2015). Likewise, park visitors reported 'feeling better' in environments that support greater species richness for trees, birds and butterflies (Fuller *et al.*, 2007). Bird feeding and birdwatching best exemplify cultural activities, which are both multi-million-dollar industries. These activities are structured so that people can have intimate and personal experiences with birds (Reynolds *et al.*, 2017). At the other end of the experiential spectrum with nature, feelings of disconnect from nature have been linked to negative environmental attitudes (Soga *et al.*, 2016) and the reduction of personal subjective well-being (Nisbet *et al.*, 2011). Ultimately, positive interactions with wildlife can mediate pro-environmental behaviours and people's support for public environmental initiatives, which hold important conservation implications (Soga and Gaston, 2016). Therefore, one of the most critical ecosystem services that urban wildlife provides is the ability to galvanize urban residents' support for conservation of the natural world (Hughes *et al.*, 2018).

Disservices

In addition to services, urban wildlife can also provide disservices, since not all wildlife is a desirable component of the landscape from the perspective of the public (Belaire *et al.*, 2015). Thus, by inviting wildlife to share our living and working spaces in cities and suburbs, there may be unintentional consequences. Despite tremendous ecological and economic importance, insects are often either overlooked or despised by the public (Kellert, 1993). For example, urban areas harbour increased abundance of insects that perform disservices, such as disease vectors (e.g. West Nile virus; LaDeau *et al.*, 2007), tree pests (e.g. insects such as the gloomy scale, *Melanaspis tenebricosa*; Frank *et al.*, 2013), or species that are generally despised due to aesthetic or cultural revulsion (e.g. cockroaches; Kellert, 1993). Invasive insects alter forest health and are particularly detrimental to urban forests, which are often planted in monocultures, or experience frequent drought-induced stress. For example, in 2007 it was estimated that the emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) killed more than 53 million native ash trees (*Fraxinus* sp.) in Ohio, Michigan and Indiana, with the majority of mortality occurring in urban environments (Kovacs *et al.*, 2010). Given the importance of urban trees for regulating climate, stormwater mitigation, well-being and habitat (Bolund and Hunhammar, 1999), the impact from EAB and other invasive insects is far-reaching.

Urban generalist mammals and birds can also invoke negative reactions from the public when interactions with private land become more apparent or detrimental to human well-being. For example, predatory carnivores (e.g. coyotes, and mountain lions, *Puma concolor*) are seen as threats to children and pets (Soulsbury and White, 2015) and vectors of disease (e.g. rabies; Riley *et al.*, 1998). Generalist omnivores (e.g. black bears, *Ursus americanus*, raccoons, gulls (*Larridae* spp.)) often scavenge in human refuse and garbage, and are therefore considered a nuisance (Newsome and Van Eeden, 2017). Large flocks of birds (e.g. starlings (*Sturnus vulgaris*), crows (*Corvus brachyrhynchos*) and geese (various species in the family *Anatidae*)) also can be seen as problems because of the noise and mess they create *en masse* when congregating in forage or roosting locations (Whelan *et al.*, 2015). Surprisingly, although white-tailed deer (*Odocoileus virginianus*) populations were once threatened due to over-hunting, deer populations have rebounded and enjoy some of the highest densities around urban metropolitan areas where hunting opportunities may be limited and their natural predators have long since been extirpated (Indiana Division of Fish & Wildlife, 2019). Consequently, deer populations perform disservices by over-browsing managed gardens and natural plant communities, degrading habitat quality for songbirds and other wildlife, disrupting forest succession, causing car accidents and serving as a long-distance dispersal agent for Lyme disease (Conover, 1997; McShea and Rappole, 2000; Kilpatrick *et al.*, 2007; Indiana Division of Fish & Wildlife, 2019). Yet deer are also a well-recognized representation of 'nature,' creating a conundrum for managers who need to appease public stakeholders, which may have conflicting attitudes towards deer (Rutberg, 1997). It is clear that urban wildlife provides both ecosystem services and disservices, sometimes simultaneously. As urbanization continues to encroach on natural areas, urban managers and residents will have to cope with the trade-offs associated with the management of urban green spaces for wildlife.

Directions for Future Research in Urban Wildlife Ecology

In this chapter, some of the ecological and social filtering factors that affect wildlife patterns in urban environments have been highlighted (Fig. 3.1). Although we attempted to include examples from a range of taxa, a few groups have received the majority of research interest. In addition to advancing our understanding of species with broad public appeal, like songbirds (Marzluff, 2017), bees and butterflies (Ramírez-Restrepo and MacGregor-Fors, 2017), we suggest that future studies continue the recent trend of investigating less 'charismatic' taxa such as ground arthropods, flies, moths, reptiles, amphibians and small mammals (e.g. Merckx *et al.*, 2018; McCary *et al.*, 2018). Similarly, expanding research in neo-, Afro- and Indo-tropical regions can expand our level of inference of urban wildlife patterns (McDonnell and Hahs, 2013), particularly with regard to social and cultural contexts. These understudied tropical regions are also critical for future investigations since they contain both the most rapidly growing metropolitan regions in the world and high overlap with biodiversity hotspots (Seto *et al.*, 2012). Recent reviews of urban biodiversity in urban green spaces have highlighted avenues ripe for future research (Beninde *et al.*, 2015). For example, a deeper understanding of the thresholds of green space size, and whether green spaces serve as population sources or sinks, can help inform managers who require detailed information for a variety of different species (Aronson *et al.*, 2017; Lepczyk *et al.*, 2017a).

There has been an increased interest in how management can enhance the conservation value of urban green spaces (e.g. Goddard *et al.*, 2013; Lerman *et al.*, 2014; Aronson *et al.*, 2017). Thus, additional detailed studies that identify particular recommendations and actions that managers, urban planners and the public can take to restore ecological integrity and improve biodiversity in urban green spaces can further advance biodiversity goals. Experimental manipulative studies are necessary to isolate potential mechanistic drivers, but are curiously absent in this field (Felson *et al.*, 2013; Marzluff, 2017). Recent research that has assessed specific mechanisms includes identifying simple solutions for promoting pollinators via less frequent lawn mowing (Lerman *et al.*, 2018) and how to manage urban green spaces to reduce ticks and Lyme disease by planting native plants (Adalsteinsson *et al.*, 2016). In addition, identifying specific thresholds, such as the amount of native plants necessary to support stable insectivorous bird populations (Narango *et al.*, 2018), can help guide restoration efforts and provide empirical support for planning goals. These and future studies will help homeowners, developers, urban green space managers and designers make informed decisions that may simultaneously promote biodiversity and improve human health and ecosystem services (Aronson *et al.*, 2017).

We also encourage further exploration of the links between wildlife and ecosystem services that are particular to novel urban systems. Increasing our understanding of the interactions and feedback loops between management decisions, their impact on a variety of different species, and how interactions and subsequent attitudes, in turn, further shape decisions, can assist with future management recommendations that aim to enhance urban habitats for wildlife and people. With this information, we could begin to uncover the answers to ultimate questions in the field, such as how does the taxonomic and functional homogenization of some taxa impact ecosystem services? Do people recognize the value of biodiverse animal communities, and how can we highlight opportunities for enhancing communication strategies that affect management decisions? Finally, what are the primary drivers of personal conservation stewardship, and what scale is necessary to support sustainable and biodiverse urban wildlife communities?

Conclusion

Urban areas represent a fascinating and novel mixture of human-provided resource inputs, altered ecological communities and human–wildlife interactions. We have highlighted some key differences between vertebrate and invertebrate responses to the urban landscape, the unique barriers associated with filtering urban communities, and the dynamism within this coupled social and ecological system. Urban settings also present unique opportunities for conservation, education and stewardship. In particular, recommendations for managing urban green spaces can empower local communities to promote features that enhance habitat, improve biodiversity and ensure beneficial services for people.

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