

Urban Biodiversity: Patterns, Processes and Implications for Conservation

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As the world becomes increasingly urbanised, more and more species either reside in cities, suburbs and exurbs or are influenced by their growth. On the bases of our literature survey, species richness and diversity of animals, especially vertebrate animals, and plants usually declines in cities. However, contrary to the prevailing notion that bird abundances usually increase in cities, studies reporting increases or decreases of bird abundances are about equal. The mechanisms underlying patterns of urban biodiversity are complex and not well-understood. Explanations for the observed changes in species diversity and composition in cities focus on local processes involving species responses to local abiotic environmental factors and interactions with other species and regional processes, such as dispersal. Recently, metacommunity theory has been applied to urban habitats to explore the relative importance of local and regional processes. This theory also provides insights into how biodiversity can be maintained and promoted in urban areas.

use as croplands, old fields, forests, deserts and grasslands give way to cities, exurbs, suburbs and their accompanying buildings, roads, drainage systems, airports, gardens and parks (McDonnell and Pickett, 1990; Faeth *et al.*, 2005). These changes often have dramatic repercussions on individuals, populations and communities not only within city boundaries (e.g. Faeth *et al.*, 2011) but also regionally and globally because cities are drivers of regional and global land transformation, climate change and alterations to biogeochemical cycles (e.g. Paul and Meyer, 2001; Grimm *et al.*, 2008). The urban, suburban and exurban habitat is the fastest growing habitat worldwide in both areal extent and external influences (the ‘urban ecological footprint’; Grimm *et al.*, 2008). Thus, urban areas will harbour an increasing fraction of the world’s biota and will increasingly affect species that reside far outside the city boundaries. The heightened awareness of the tremendous effects of cities on local, regional and global biodiversity has stimulated an explosion in studies examining biodiversity in urban environments. This review explores the patterns, causes and consequences of urbanisation on abundance and diversity of species. **See also:** [Urban Ecology: Patterns of Population Growth and Ecological Effects](#)

Introduction

We live in a rapidly urbanising world. As of 2008, more than half of the world’s population lives in urban areas. In the next 25 years, almost two billion more people are projected to move to cities. Approximately 3% of the world’s land area is urbanised but the effects of urbanisation on climate, resources, pollution and biodiversity extend far beyond the official boundaries of cities (Grimm *et al.*, 2008). Urbanisation brings about dramatic shifts in land

Urban Environment

Urban areas are characterised by highly fragmented and heterogeneous habitats that may select for colonisation and persistence of certain plant, animal and microbe species (e.g. McKinney, 2008; Faeth *et al.*, 2011). The urban matrix consists of a patchwork of various land use types such as industrial, urban, suburban and exurban residential, common green spaces such as remnants and parks, abandoned lots and transportation corridors (roads and highways) of varying size, age and isolation from other patches. Usually, available habitats for organisms are also reduced in area relative to pre-existing wildland or agricultural habitats due to increases in impervious surfaces and built structures. Often urban core areas have few green spaces and are mostly impervious surfaces. In some cities, however, supplemented water, nutrients and intense management may increase areal

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extent of specialised habitats, such as mesic urban forests in cities in semi-arid climates and extensive 'grasslands' in the form of lawns in temperate and semi-arid cities, than existed before urbanisation.

Coupled with extensive impervious surfaces and built structures in cities is radically altered hydrology, with increases in runoff and reduced groundwater percolation and recharge (e.g. Paul and Meyer, 2001). Urban streams are often highly modified and channelised, accompanied by increased flooding, higher temperatures, reduced riparian zones and a highly altered biota (Paul and Meyer, 2001). Impervious surfaces are also the main factor underlying local climatic changes in cities, notably reduced wind speed (Bang *et al.*, 2010) and higher temperatures (the urban heat island effect, e.g. Kuttler, 2008). These factors, coupled with human inputs of nutrients and water, contribute to another common feature of urban ecosystems – changes in overall net primary productivity (NPP) and increasing variation at the local scale. Individual patches in cities may vary from having zero NPP (impervious surfaces) to very high NPP (green patches, such as gardens, with human inputs of nutrients and water). More moderate winter temperatures and extended growing seasons in temperate and cold region cities and decreased wind speed in cities also may contribute to higher net primary productivity in cities (Imhoff *et al.*, 2004). Cities usually have overall lower NPP than surrounding wildlands or rural areas (Imhoff *et al.*, 2004) at the regional scale because the processes of land use transformations overwhelm these local effects (Imhoff *et al.*, 2004; Walker *et al.*, 2009), especially when urbanising areas replace highly productive agricultural or forested land (Imhoff *et al.*, 2004). However, cities in arid or semi-arid environments and cities with low-density development may have higher NPP overall than surrounding wildlands (Imhoff *et al.*, 2004).

The abiotic urban environment creates other selective filters on urban organisms and populations. Urban soils are usually highly modified, disturbed and heterogeneous. They may harbour toxic levels of heavy metals, acids, radionuclides, solvents and other pollutants (e.g. Sauerwein, 2011). Owing to inputs of nutrients and water and higher urban temperatures, urban soils may have higher respiration rates, especially in arid and semi-arid ecosystems. The enhanced nutrients may come from run-off from impervious surfaces, from nutrient-enriched lawns, gardens and landscapes and from the air in the form of NO_x compounds (e.g. Hall *et al.*, 2011). The urban atmosphere can also harbour other pollutants such as sulfur oxides, carbon monoxide, heavy metals, volatiles organics and particulates from emissions from cars and factories, all of which may affect growth, survival and reproduction of organisms. In addition to water, soil and air pollutants, urban organisms must contend with artificial and elevated levels of noise (Warren *et al.*, 2006) and polarised light pollution (Horváth *et al.*, 2009) both of which may disrupt physiology, mating behaviours, circadian rhythms, migration, phenologies and thus, ultimately, fitness.

Although the urban abiotic environment has often been termed 'unique' or 'novel', Richardson *et al.* (2010) argued that there are analogues of urban selective pressures in more natural or wildland habitats. For example, the characteristic impervious surfaces and built structure of cities have analogues in rock beaches and cliff faces (Richardson *et al.*, 2010). Although cities may not present unique selective pressures to organisms, they may be distinctive in the intensity, scale and combination of these selective pressures (Faeth *et al.*, 2011) and select for species based on functional traits such as dispersal abilities, lifespan, reproductive modes and behaviour (e.g. Sattler *et al.*, 2010; Fokidis *et al.*, 2011).

Whereas these abiotic selective pressures may act as a filter for some species in urban areas, vegetation composition and structure dictate the presence or absence of most urban species. Most consumer species and other associated plant (e.g. epiphytic) species depend on the plant communities for food, shelter and breeding sites. Indeed, the use of 'habitat' in urban areas generally refers to vegetation in terms of type (e.g. mesic or xeric), species diversity and composition (e.g. trees, shrubs and grasses), cover (percent area occupied by plants) and structure (e.g. mono-layered lawns or multilayered forests). We have argued elsewhere (Faeth *et al.*, 2011) that vegetation is the only urban biological component where species composition, relative abundances, structure and successional stage are intentionally controlled by individuals, neighbourhoods and institutions. When this control lapses, plant communities become more spontaneous with the colonisation of vacant lots, brown fields and roadsides or successional changes within existing vegetation patches. The intensely managed, human modified and reconstructed terrestrial plant communities of cities, many harbouring non-native species, act as templates for ecological and evolutionary interactions with their herbivores, carnivores and detritivores. Species richness, evenness, composition and structure of the human-controlled plant communities affect diversity of the associated animal and microbial communities (e.g. Faeth *et al.*, 2011). Aquatic primary producers are usually less modified by human activities (e.g. humans generally do not intentionally select and introduce algal or cyanobacterial species in urban streams and ponds). However, abundances and species composition may still be intentionally altered via control measures (e.g. algaecides) or unintentionally by nutrient inputs and water flow controls. In contrast to direct human control of plant communities, humans only indirectly modify animal and microbial communities. Other than some domesticated pets, which often do not fully interact with the biotic urban community, relatively few animal or microbe species are intentionally introduced or entirely eliminated in urban ecosystems (Faeth *et al.*, 2011). For example, elimination of most vertebrate species from cities is an unintentional consequence of habitat alteration. Humans are not particularly successful at eradicating targeted pest species (e.g. mosquitoes, rats and cockroaches) despite continuous and enormously costly efforts to do so.

Patterns of Biodiversity in Cities

Studies of urban effects on biodiversity have rapidly accumulated in the past two decades. The majority of these studies have documented changes in diversity and abundances of specific taxa in urban or suburban areas compared to wildlands, rural (usually a mixture of wildlands and agricultural lands) or to agricultural areas. Some studies use an urban to rural gradient (e.g. McDonnell and Pickett, 1990) approach where diversity is documented along a gradient of increasing urbanisation (e.g. wildland – exurban – suburban – city core) while others compare diversity in two or more land use types (e.g. wildland versus urban) (e.g. Faeth *et al.*, 2011). To understand the patterns of biodiversity changes in cities, we reviewed studies on urbanisation effects on abundance, diversity and species richness of terrestrial animals, bacteria, fungi and plants. We asked if there is a general pattern of the effects of urbanisation on abundance and species richness and if the effects vary among animal taxa (mammals, birds, arthropods, bacteria and plants). Based on published review articles, we expected the abundances of terrestrial animals to increase and species richness to decrease in urbanised areas. For plants, we expected abundances to decrease but species richness and diversity to increase. Web of Science was used to identify 1644 articles with abstracts containing words 'urban', 'ecology' and 'biodiversity'. Each article was examined to see if they contained information about changes in diversity, abundance and species richness related to urbanisation. Data involving the following taxa were collected from the articles: Amphibia, Arthropoda, Aves, Mammalia, Nematoda, Reptilia, Fungi, Bacteria, Lichens and Plantae. We found 154 articles that reported diversity measures (e.g. Shannon–Weiner index), species richness (number of species), and/or abundance (number of individuals) data along some gradient of urbanisation (Table 1). These studies span a wide temporal, spatial and geographic spectrum including urban environments of Asia, North and South America, Europe and Australia. Some individual articles included multiple studies on different response variables, taxa or geographic regions and these multiple studies within articles were treated independently. We acknowledge that individual studies used different sampling methods that may also render comparisons among studies as tenuous.

The results of our literature survey demonstrate that patterns of biodiversity are relatively well documented for plants, birds and arthropods, but less is known about patterns of biodiversity for other taxonomic groups. The majority of studies indicate that urbanisation reduces species richness, abundance and diversity of terrestrial vertebrates (Table 2 and Figure 1). Likewise, most arthropod studies show declines in richness or diversity with urbanisation.

For plants, studies showing gains and losses in species richness in cities are nearly equal. Fifteen studies included in our review separated the effects of urbanisation on native and introduced plant species, with the following

results: five studies found decreased richness of native species, nine studies found increased richness of exotic species and one study reported increases richness of native species with urbanisation. The remaining studies did not distinguish between native and exotic species. Our result that urbanisation is not associated with increased plant species richness and, at least for native plant species, is often associated with richness declines, is at odds with conventional wisdom. Cities have been often viewed as hotspots for plant species richness, although phylogenetic diversity may be reduced (Knapp *et al.*, 2008) because (1) cities often develop in geologically and structurally diverse landscapes (Kühn *et al.*, 2004; Pautasso, 2007), (2) humans import many alien species and increase evenness in urban landscapes (e.g. Walker *et al.*, 2009), (3) cities harbour highly structured and heterogeneous habitats (e.g. Faeth *et al.*, 2011) and (4) altered temperatures and increased resources in cities may promote persistence of certain plant species (Knapp *et al.*, 2008). However, plant richness may also vary within cities depending on the degree and extent of urbanisation. On the bases of reviews of existing studies, McKinney (2002, 2008) concluded that plant richness decreases in the urban core while increasing in suburbs and exurbs. Nonetheless, based on our results, we conclude that cities do not generally harbour greater plant species richness than nonurbanised habitats.

Our results also do not support the conventional wisdom that human activities in urbanised areas increases overall abundance of birds despite declines in species richness (e.g. Shochat *et al.*, 2010). Instead, studies showing increase and decrease in avian abundances are about equal in number. Our results also emphasise that there is remarkable variability among studies for species richness and abundances of arthropods, birds and plants. This variability is likely related to the different research methods, time and spatial scales, and climatic regions in the various studies (e.g. Faeth *et al.*, 2011). For example, diversity and human activity may be scale-dependent (i.e. diversity may increase at larger spatial scales in cities but decrease at smaller scales, e.g. Pautasso, 2007) thus comparison among studies with different spatial scales probably contributes to this variability. Studies involving other taxa are too few to draw any general conclusions.

Another important component of biodiversity change associated with urbanisation is change in species composition (see the section on Metacommunity approach). There are often radical changes in the composition of communities, even when overall species richness is comparable or sometimes higher than in wildland communities (Faeth *et al.*, 2011; Bang *et al.*, 2012). Many urban communities are 'reshuffled' with non-native or synanthropic species replacing native ones (Bang and Faeth, 2011; Sattler *et al.*, 2011). We should expect that these reshuffled urban communities may function very differently in terms of ecosystem processes and services than their wildland or rural counterparts. **See also:** [Biotic Homogenization](#); [Ecosystem Services](#)

Table 1 Publications ($N = 154$) used in the analysis of the effects of urbanisation on diversity (as measured by a diversity index such as the Shannon–Weiner index), abundance (number of individuals) and species richness (number of species) of terrestrial animals, bacteria, fungi, lichens and plants

Taxon	Publications
Amphibia	Bickford <i>et al.</i> (2010), D'Amen and Bombi (2009), Hamer and McDonnell (2010), Lane and Burgin (2008), Tait <i>et al.</i> (2008)
Arthropoda	Ahrné <i>et al.</i> (2009), Andrew (2010), Bates <i>et al.</i> (2011), Bergerot <i>et al.</i> (2010, 2011), Bergh <i>et al.</i> (2009), Blair (1999), Centeno <i>et al.</i> (2004), Christite <i>et al.</i> (2010), Christian and Szeptycki (2004), Christie and Hochuli (2009), Clarke <i>et al.</i> (2008), Cook and Faeth (2006), Fattorini (2011), Ferreira and Tidon (2005), Fontanarrosa <i>et al.</i> (2009), Frankie <i>et al.</i> (2009), Friedrich and Philpott (2009), Gagné and Fahrig (2010), Hardy and Dennis (1999), Hornung <i>et al.</i> (2007), Iwata <i>et al.</i> (2005), Johnson <i>et al.</i> (2008), Kearns and Oliveras (2009), Knapp <i>et al.</i> (2008), Kocher <i>et al.</i> (2000), Kozlov and Zvereva (1997), Kumar and Mishra (2008), Lessard and Buddle (2005a, 2005b), Lubertazzi <i>et al.</i> (2010), Magura <i>et al.</i> (2010), Mauro <i>et al.</i> (2007), McIntyre <i>et al.</i> (2001), Menke <i>et al.</i> (2010), Mwabvu (2006), Niemelä <i>et al.</i> (2002), Nufio <i>et al.</i> (2009), Öckinger <i>et al.</i> (2009), Rango (2005), Sattler <i>et al.</i> (2010), Savitha <i>et al.</i> (2008), Sharma and Amritphale (2007), Shochat <i>et al.</i> (2010), Su <i>et al.</i> (2011), Sumoski <i>et al.</i> (2009), Tait <i>et al.</i> (2010), Tóthmérész <i>et al.</i> (2011), Uno <i>et al.</i> (2010), Venn <i>et al.</i> (2003), Vilisics <i>et al.</i> (2007), Watts and Larivière (2004), Winfree <i>et al.</i> (2007), Yamaguchi (2004), Zanette <i>et al.</i> (2005)
Aves	Aurora <i>et al.</i> (2009), Bhatt and Joshi (2011), Blair and Johnson (2008), Bock <i>et al.</i> (2008), Brambilla <i>et al.</i> (2010), Cappelatti and Barros (2010), Catterall <i>et al.</i> (2010), Caula <i>et al.</i> (2010), Chiari <i>et al.</i> (2010), Clergeau (1998), Conole and Kirkpatrick (2011), Devictor <i>et al.</i> (2007), Dures and Cumming (2010), Emlen (1974), Faggi and Perepelizin (2006), Filippi-Codaccioni (2008), González-Oreja (2011), Hanauer <i>et al.</i> (2010), Hedblom and Söderström (2010), Hennings and Edge (2003), Husté <i>et al.</i> (2006), Juri and Chani (2005), Knapp <i>et al.</i> (2008), Leveau and Leveau (2005), Luther <i>et al.</i> (2008), MacGregor-Fors (2010), MacGregor-Fors and Schondube (2011), MacGregor-Fors <i>et al.</i> (2010, 2011), Maestas <i>et al.</i> (2003), Mason (2006), McKinney and Paton (2009), McKinney <i>et al.</i> (2010, 2011), Merenlender <i>et al.</i> (2009), Møller (2011), Orteva-Álvarez (2009), Rensburg <i>et al.</i> (2009), Sandström <i>et al.</i> (2005), Smith and Chow-Fraser (2010), Sorace and Gustin (2010), Stratford and Robinson (2005), Strubbe and Matthysen (2009), Tait <i>et al.</i> (2007), Trammell <i>et al.</i> (2011), Vallejo <i>et al.</i> (2009), Villegas and Garitano-Zavala (2010), Walker and Shochat (2010)
Mammalia	Buckmaster <i>et al.</i> (2010), Cavia <i>et al.</i> (2009), Chernousova (2010), Dickman and Doncaster (1989), Duchamp and Swihart (2008), Fabianek <i>et al.</i> (2011), Loeb <i>et al.</i> (2009), Maestas <i>et al.</i> (2003), Mahan and O'Connell (2005), Møller (2011), Oprea <i>et al.</i> (2009), Ordenana <i>et al.</i> (2010), Tait <i>et al.</i> (2006)
Reptilia	Hamer and McDonnell (2010), Price <i>et al.</i> (2006), Tait <i>et al.</i> (2009)
Plantae	Ahrends <i>et al.</i> (2010), Benson and Picone (2009), Bernholt <i>et al.</i> (2009), Botham <i>et al.</i> (2009), Burton and Samuelson (2008), Burton <i>et al.</i> (2005), Cappelatti and Schmitt (2009), Celesti-Grapow <i>et al.</i> (2010), Deutschewitz <i>et al.</i> (2003), Dolan <i>et al.</i> (2011), Gavier-Pizarro <i>et al.</i> (2010), Guan and Chen (2003), Hall <i>et al.</i> (2002), Hedblom and Söderström (2007), Hope <i>et al.</i> (2006), Jim and Chen (2009), Kun <i>et al.</i> (2009), Landenberger <i>et al.</i> (2009), Manninen <i>et al.</i> (2010), Monge-Nájera and Pérez-Gómez (2010), Nagendra and Gopal (2010), Pautasso and McKinney (2007), Peng and Liu (2007), Pennington <i>et al.</i> (2010), Ranta and Viljanen (2011), Shaltout and El-Sheikh (2002), Turner and Freedman (2005), Ukhvatkina and Denisov (2010), Walker <i>et al.</i> (2009)
Fungi/bacteria/lichen	Cousins <i>et al.</i> (2003), Drinnan (2005), Ivanova <i>et al.</i> (2008), Kaltseis <i>et al.</i> (2009), Knapp <i>et al.</i> (2008), Lysak <i>et al.</i> (2000), Robles <i>et al.</i> (2011), Sipman (2009)

Drivers of Biodiversity Patterns in Cities

The studies summarised above focused on establishing patterns of biodiversity change across urban–rural gradients or between different land use types. However, there have been far fewer attempts to determine the processes or mechanisms underlying these patterns (Shochat *et al.*,

2010; Faeth *et al.*, 2011). Explanations for changes in biodiversity as a consequence of urbanisation fall into broad categories – those focusing on responses to abiotic factors and species interactions at the local level and those that incorporate broader scale regional processes, notably dispersal and factors that influence dispersal (Sattler *et al.*, 2011; Swan *et al.*, 2011; Johnson *et al.*, personal

Table 2 Effects of urbanisation on diversity (as measured by a diversity index such as the Shannon–Weiner index), abundance (number of individuals) and species richness (number of species) of terrestrial animals, bacteria, fungi and plants based upon 154 published articles

Taxon	Diversity			Abundance			Species richness		
	Increased	Decreased	No effect	Increased	Decreased	No effect	Increased	Decreased	No effect
Amphibia (6)	1	0	0	1	2	0	0	1	1
Arthropoda (125)	1	14	11	8	19	5	5	36	26
Aves (139)	0	7	0	33	29	18	15	31	6
Mammalia (26)	0	3	0	4	11	2	0	5	1
Nematoda (3)	0	0	1	0	2	0	0	0	0
Reptilia (4)	0	0	0	0	2	0	0	1	1
Fungi (17)	2	4	0	2	1	1	3	4	0
Bacteria (2)	1	0	0	0	0	0	1	0	0
Plantae (50)	2	5	4	2	4	0	14	18	1
Total (372)	7	33	16	50	70	26	38	96	36

communication). **See also:** [Regional Influences on Local Species Composition](#)

Local processes affecting urban biodiversity

At the local or patch level, changes in species richness, evenness and composition of an urban community may result from species interactions and interactions of organisms with local abiotic factors (Shochat *et al.*, 2010). As discussed earlier, cities are characterised by highly fragmented and heterogeneous habitats, with altered abiotic and biotic environments that usually negatively affect local (alpha) or within-patch biodiversity. Traditionally, altered habitat structure associated with fragmentation has been proposed as the overriding factor in causing changes in biodiversity and abundances at the patch level (Donnelly and Marzluff, 2006; Shochat *et al.*, 2010). However, fragmentation per se is not the cause of the presence or absence of species in a patch. Rather, alterations in habitats lead to demographic and behavioural changes that dictate the presence or absence of species in a patch (e.g. Donnelly and Marzluff, 2006). For birds, absence in an urban patch may result from increased brood parasitism or nest predation or inadequate nesting sites, leading to local extinction (Donnelly and Marzluff, 2006). Other factors that may dictate presence or absence of species in an urban patch include behavioural preferences for certain habitats, changes in survival and reproduction due to interspecific interactions such as competition, predation or mutualism, or response to abiotic environmental factors, such as air pollutants or urban heat island effects (Faeth *et al.*, 2011). **See also:** [Ecological Consequences of Habitat Fragmentation](#)

Shochat *et al.* (2010) emphasised two interrelated factors that influence urban biodiversity at the local spatial scale – productivity and competition. They argued that the characteristic ‘hump-shaped’ relationship between species richness and net primary productivity (NPP), commonly found for ecological communities (e.g. Mittelbach *et al.*, 2001), is applicable to urban ones as well. In this scenario,

diversity is highest in areas with intermediate productivity, such as low-density suburbs, but declines when productivity is very low, such as the urban core, which is characterised by large fractions of area of impervious surfaces and built structures. In highly productive areas within cities (e.g. golf courses, gardens and lawns) where overall NPP is high and stable seasonally (due to moderated temperatures and continuous inputs of nutrients and water), urban exploiting species increase in abundance and become dominant, and the communities becomes less even. Increased abundances of competitively superior exploiters exclude native species and thus cause observed declines in species richness and increased overall abundances. This interaction of productivity gradients with competition that causes declines in urban species richness can be modified by another interspecific interaction, predation (e.g. Crooks and Soulé, 1999; Faeth *et al.*, 2005; Shochat *et al.*, 2010). If predators of urban exploiters are absent or reduced in cities, then the negative effects of interspecific competition by non-native, urban exploiters on native species may be exacerbated (Shochat *et al.*, 2010).

Some studies show higher species richness in areas of moderate levels of urbanisation, such as suburban areas (e.g. McKinney, 2002, 2008; Faeth *et al.*, 2011), supporting the species richness productivity hypothesis. However, the same pattern of biodiversity can be explained by the intermediate disturbance hypothesis (Connell, 1978). This hypothesis describes the same hump-backed relationship of species richness but with gradients of disturbance instead of productivity. Species richness is thought to peak at intermediate disturbance levels because moderate levels of disturbance promotes coexistence by preventing competitive dominant species from excluding less competitive species. At low levels of disturbance, competitively superior species outcompete and exclude other species; at high levels of disturbance, many species do not persist because of the harsh physical environment and thus species richness declines. The intermediate disturbance hypothesis has been applied to urban ecosystems because urbanisation itself

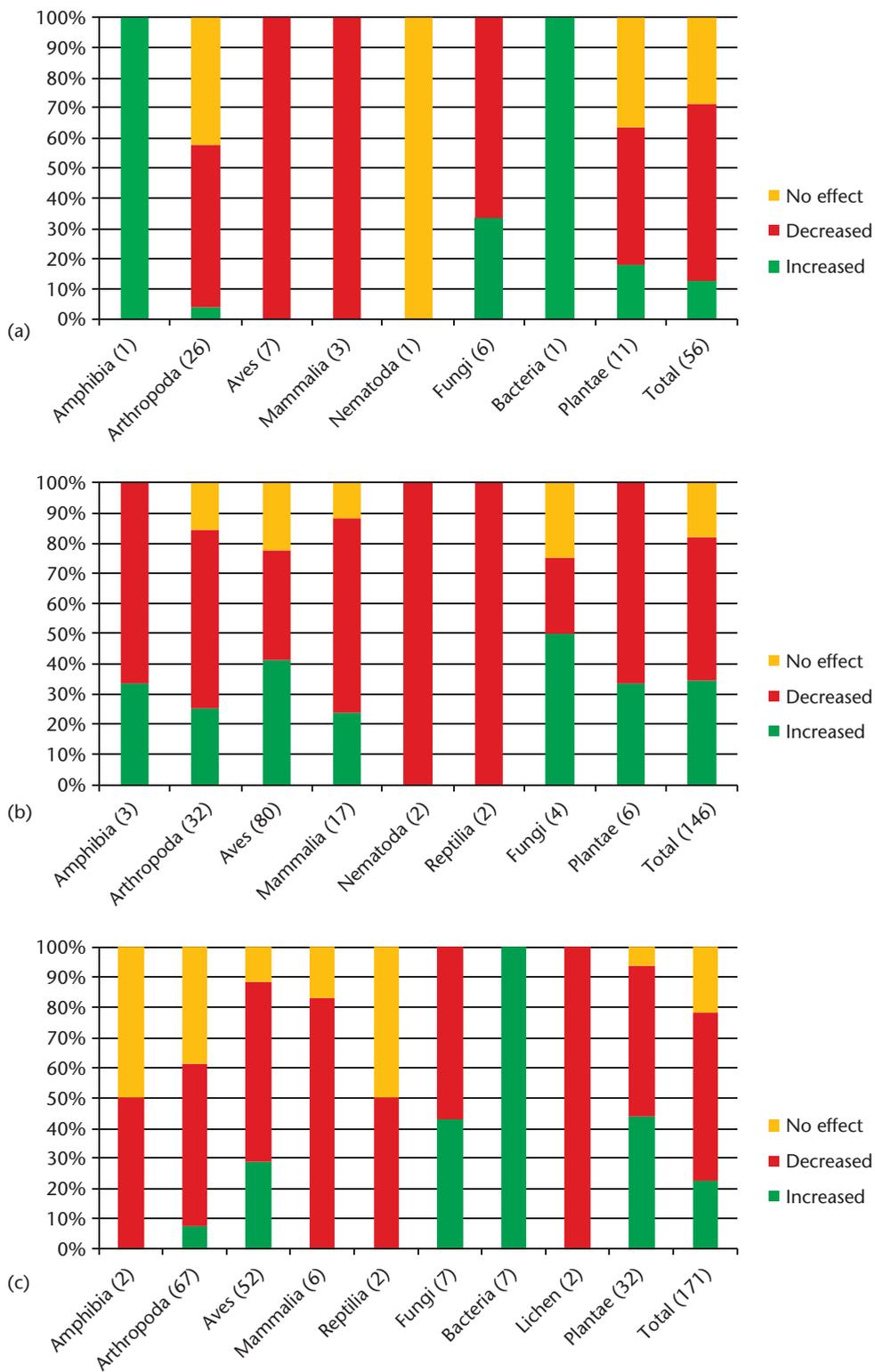


Figure 1 The effects of urbanisation on (a) diversity (as measured by a diversity index such as the Shannon–Weiner index), (b) abundance (number of individuals), (c) species richness of organisms separated by taxa. Number of studies is in parentheses.

can be viewed as disturbance, ranging from severe grading of landscapes to construction of buildings and reconstruction of plant communities to low-level, chronic disturbances such as weed and litter removal, lawn mowing, and replacing dead plants. Both the productivity-competition and intermediate disturbance hypothesis explain the sometimes-observed hump-shaped pattern of diversity with urbanisation and both incorporate local species interactions, notably competition and predation (Menge and Sutherland, 1987), as mechanisms determining species richness along urban to rural gradients. Because both productivity and disturbance may co-vary with the degree of urbanisation, it is not clear which gradient (or both) might underlie changes in biodiversity, and if this is consistent across cities in different regions and climates. Indeed, both productivity and disturbance may interact to influence species richness, and later models of the intermediate disturbance hypothesis (e.g. Menge and Sutherland, 1987) incorporate changes in productivity. In addition, other factors besides productivity and disturbance, such as habitat structure and heterogeneity, can co-vary along urban to rural gradients (e.g. McKinney, 2008). Future manipulative experiments will be necessary to determine the relative contribution of productivity, disturbance and other gradients that change with urbanisation on biodiversity.

Regional processes altering biodiversity

Cities are characterised by heterogeneous and fragmented patches that isolate populations and inhibit movement among patches. Therefore, island biogeography theory (IBT) (MacArthur and Wilson, 1967) has been used as one conceptual framework to explain patterns of biodiversity within urban areas by treating patches as insular-like habitats of varying size, complexity and degree of isolation (Faeth and Kane, 1978; Davis and Glick, 1978; Marzluff, 2005). IBT predicts that species richness in insular habitats is a function of immigration from a regional species pool and extinction of local populations. Generally, distance or isolation from the species pool dictates immigration or colonisation rates and size and complexity of the patch determines population size and hence probability of local persistence or extinction (MacArthur and Wilson, 1967). Small and isolated patches support fewer species than larger and less isolated patches because colonisation and extinction rates are lower and higher, respectively. Thus, IBT combines regional processes of dispersal (immigration) with local processes (extinction within patches). Changes in population size, and hence in probability of extinction, are related to the same local processes discussed earlier, namely differences in the abiotic and biotic environment among patches that causes niche-based differences in individual behaviour, survival and reproduction. There is support for IBT in that bird and arthropod species richness tends to be greater in larger and more complex urban fragments (e.g. Faeth and Kane, 1978; Davis and Glick, 1978; Donnelly and Marzluff, 2006). However, it

becomes difficult to disentangle the relative contribution of the myriad local biotic and abiotic filters and regional processes such as dispersal that affects urban biodiversity.

Metacommunity approach

Recently, researchers have employed a metacommunity approach to ascertain the relative importance of regional and local processes in determining species richness, evenness and composition across spatial scales in communities. Metacommunity theory is an outgrowth of metapopulation theory and IBT (e.g. Leibold *et al.*, 2004). Metacommunity theory views local communities in a landscape as connected, rather than isolated, through dispersal of many potentially interacting species from a regional pool. The metacommunity approach is a compilation of four ecological paradigms that differentially emphasise regional processes such as dispersal (immigration/emigration) and local processes such as niche-based species sorting through environmental filters among patches and species interactions that determine community diversity and composition. These four paradigms or perspectives (Leibold *et al.*, 2004) include: (1) patch dynamics, where local diversity is limited by dispersal and local extinction, patches are assumed identical (habitat is not important), (2) species-sorting, that emphasises local resource gradients and species interactions in addition to spatial dynamics, (3) mass-effect, where immigration and emigration and spatial dynamics may override local species interactions and are independent of resource gradients and (4) the neutral perspective, where all species are equal in competitive ability, dispersal and fitness and biodiversity is a function of the probabilities of species loss from emigration and extinction and species gain via immigration and speciation. Whereas there is not yet a 'metacommunity' theory that synthesises these four perspectives (Leibold *et al.*, 2004), the metacommunity approach can provide insights into forces structuring ecological communities in general, and urban ones in particular (Swan *et al.*, 2011). The main advantages of a metacommunity approach is that it focuses not only on explaining species richness and evenness but also on species turnover and compositional changes across spatial and temporal scales, key features of urban communities (e.g. Faeth *et al.*, 2011; Bang *et al.*, 2012) and provides tools for distinguishing the relative roles of niche- and dispersal-based mechanisms. For example, local processes may be more important in structuring communities that are composed mainly of passively dispersed species whereas regional processes may be more influential in communities where active dispersers dominate (P. Johnson, personal communication). Because human activities in cities have large effects on both local (Faeth *et al.*, 2005; McKinney, 2008) and regional (e.g. Gade, 2010) processes, metacommunity theory should be particularly applicable to understand how urban communities are structured. Moreover, understanding the relative influence of niche- and dispersal-based mechanisms provides a sound conceptual framework for conservation of existing

biodiversity and re-constructing habitats and communities to encourage future biodiversity in cities (see the section on Implications for conservation). **See also:** [Metacommunities: Spatial Community Ecology](#)

To date, despite numerous applications of meta-community to natural communities, there have been few attempts to apply metacommunity theory to urban ecosystems. Parris (2006) tested the basic premises of metacommunity theory for pond-breeding amphibian communities in the greater Melbourne, Australia urban area. She found that both pond size, degree of isolation (by roads) and quality of the patch (vertical versus sloped bank) explained changes in species richness among ponds. Parris (2006) concluded that these results best supported the species-sorting and/or mass effects perspectives of the metacommunity theory because not only patch area and isolation but also quality of the patch acted as an environmental filter. In a more recent study, P. Johnson (personal communication) recently examined wetland communities in the rapidly urbanising Front Range area of Colorado. They found that richness of amphibians, and aquatic reptiles and arthropods declined in urban ponds relative to those in surrounding grasslands. This decline was associated with biotic (the presence of introduced fishes and bullfrogs) and abiotic factors (nutrients and vegetation structure) and landscape features (road density and surrounding wetland areas). However, changes in urban species richness were mediated largely by changes in regional processes that affect migration, particularly road density. In addition, discrete urban communities formed along the urbanisation gradient, with passively dispersed species more likely to be found in the more urbanised communities. They concluded that both local (biotic and abiotic environments) and regional (dispersal) processes were important in structuring urban communities. In an urban metapopulation study, Buczkowski (2011) found that spatiotemporal dynamics of black carpenter ant colonies across gradients of urban development was best explained by habitat quality, colonisation and spatial structure of trees. Sattler *et al.* (2011) found that the composition of spider, bee and bird communities in three Swiss cities showed weak spatial structuring and was mostly explained by local environmental variables, and thus largely niche-based processes. Results from these urban studies are consistent with those from other metacommunity analyses (e.g. Ficetola and De Bernardi, 2004) – both regional spatial and local environmental processes are important in determining species richness and community composition.

Linking metacommunities and socioecology

Swan *et al.* (2011) recently reviewed how a metacommunity approach could be applied to urban communities and linked to socioecological factors. They also provided specific predictions regarding regional and local effects on urban biodiversity. Swan *et al.* (2011) distinguished between self- and facilitated assembly urban communities.

Self-assembled communities are urban communities indirectly influenced by human activities and actions but not directly manipulated for species composition. Examples include vacant lots, roadsides, retention ponds and modification of streams and rivers that result from human actions. Swan *et al.* (2011) argued that these habitats have a strong environmental filter, excluding species that cannot tolerate highly disturbed and polluted conditions. Because of spatial dynamics, species in self-assembled communities should have high dispersal and reproductive rates but are poor competitors, classical r-selected species. At the other end of the human-influenced gradient are facilitated assembly communities, where human actions and decisions directly alter richness and composition. Obvious examples are gardens, where human actions choose and manipulate species for aesthetic (flowering plants) or productivity (vegetable and fruits) reasons. They also include preserved parks and green-spaces as facilitated communities because they argue that without human action they would not persist. However, one could argue that preserved remnants composed largely of native species are fundamentally different than human-constructed gardens and lawns. Likewise, although Swan *et al.* (2011) claim that nonplant species are also manipulated by humans, we have argued elsewhere (Grimm *et al.*, 2008; Faeth *et al.*, 2011) that usually only plant community composition is directly controlled by human actions and other interacting species assemble on this template. Nonetheless, in their conceptual model, they link the amount of social investment, local urban community composition based on a gradient of self-assembled versus facilitated communities and local (niche-based) and regional (dispersal-based) factors from metacommunity theory (Figure 3.5.1 in Swan *et al.*, 2011). They provide testable predictions about biodiversity, community composition and turnover in urban communities. For example, they predict that species turnover between self-assembled and facilitated communities (beta diversity) should be determined by a combination of the distance between them and the configuration of patches and environmental filters, similar to the species-sorting perspective of metacommunity theory.

Implications for Conservation

Dearborn and Kark (2010) reviewed motivations for conserving urban biodiversity and concluded that urban biodiversity conservation is important, but faces many challenges to be successful. Some motivations for conserving biodiversity in cities are purely cultural and aesthetic, such as ethical responsibilities rooted in religion and moral beliefs (Dearborn and Kark, 2010). Others are motivated by economic and health value, and involve provisioning of ecosystem services, such as carbon sequestration, improved hydrology and temperature regulation (e.g. McGranahan *et al.*, 2005). Richer biodiversity may also directly improve human physical and

mental well-being (e.g. Tzoulas and Greening, 2011), but this may vary greatly among neighbourhoods. In some high crime areas, for example, increased vegetation structure inspires fear rather than mental well-being (Kuo and Sullivan, 2001). Thus, socioeconomic factors are important in understanding the motivation to preserve existing, and encourage additional, urban biodiversity just like socioecological factors are essential in understanding the processes by which urban biodiversity arises and is maintained (Swan *et al.*, 2011).

Conservation biology in cities may be daunting because we must understand and accommodate the individual, neighbourhood, governmental and socioeconomic drivers that dictate the structure, diversity and turnover of urban communities (Gordon *et al.*, 2009). Thus, the metacommunity approach provides a framework on which conservation efforts can build upon. The goal of conserving and reconstructing habitats within cities is usually to minimise loss of species, but for this to work, environments must be preserved and created where wildlife and humans can coexist. In urban environments, this usually involves coexistence of native and non-native species in the same patch type.

Understanding the different types of communities, and how they are influenced by metacommunity processes (local versus regional) and their socioecological factors, is vital to conserving biodiversity in urban environments. Composition of urban plant communities are influenced by natural substrate, legacies of land preservation, land usage and conversions (e.g. Walker *et al.*, 2009), individual homeowner preferences (e.g. Larson *et al.*, 2009), the cost and availability of plants from local nurseries, neighbourhood covenants, conditions and restrictions (CCRs), city and regional governmental regulations and neighbourhood socioeconomic levels (e.g. Hope *et al.*, 2003). Thus, plant communities in cities can be quite diverse, but typically contain 30–50% non-native plants in terms of composition (e.g. Walker *et al.*, 2009).

Once plant communities are preserved or constructed in cities, substantial and continuous inputs of energy and resources (e.g. fertilisers, herbicides, water, weeding, pruning, mulching and replacement of annual plants or perennial plants that die prematurely) are usually required to maintain them at the desired compositional and successional stage (e.g. Faeth *et al.*, 2011). These inputs are similar to those in agroecosystems and silvacultures, but urban systems are managed mainly for aesthetics and recreation rather than for food, fuel or fibre. When these inputs are maintained, natural processes such as plant immigration, herbivory, disease, competition, succession, local extinction and natural selection are often short-circuited by human decisions and actions. For example, when a perennial shrub dies in a flower bed, it is usually replaced quickly before it is decomposed by natural processes and organisms (e.g. insects, mites, fungi and microbes). In that same flower bed, competing weeds may be removed manually or chemically. Failure to maintain inputs typically results in rapid successional and

compositional changes with dominance of undesirable weeds (e.g. in vacant lots, brownfield sites and along right-of-ways) such that preferred plant communities may rapidly disappear. Exotic ornamental plants may be more resistant to local herbivores (Tallamy, 2010) because herbivorous arthropods often locate and feed on host plants with which they have coevolved, thus reducing arthropod diversity. However, these same ornamentals may harbour their own coevolved arthropod herbivores, either from nursery stock or imported later. These non-native herbivores may reach very high abundances and attack native plants because they are released from their own natural enemies and native plants have not evolved resistance (e.g. Raupp *et al.*, 2010). In addition, pest outbreaks may be greater in non-native plant communities because generalist natural enemies, usually supported by a suite of native herbivores, are reduced or absent (Tallamy, 2010). These altered vegetation regimes may thus support higher abundances of generalist herbivores species, or urban adapters (Bang and Faeth, 2011; Bang *et al.*, 2012).

From a metacommunity perspective, if these local scale processes largely determine the presence of desirable species, then conservation efforts should focus on these niche-based interactions. For example, if exotic plants bring non-native herbivores that become pests on native plants or out compete native herbivores, then elimination of exotic plants and their herbivores, or increased planting of native plants that support a background of generalist natural enemies (Tallamy, 2010) would be a viable conservation intervention. In aquatic environments, if non-native fish outcompete or prey upon native fish in urban ponds, then elimination of non-natives by draining ponds or selective elimination is a conservation measure that increases urban diversity (P. Johnson, personal communication).

At the smallest scale, homeowners' backyards create small ecosystems that support diversity (Sperling and Lortie, 2010). Private gardens cover substantial areas of the urban landscape. For example 23% of Sheffield, UK, is residential backyards (Smith *et al.*, 2006). Together with parks and urban greenspace, such facilitated assembly of urban communities is usually the only process that humans directly manipulate (Faeth *et al.*, 2011; Swan *et al.*, 2011). During construction processes, a range of mitigation techniques can be used to avoid loss of diversity, such as providing nests for birds and bees, bat roosts and hedgehog boxes (Sadler *et al.*, 2011).

Although some insect taxa may benefit from active garden management (e.g. Tallamy, 2010), most urban gardens can be considered 'Potemkin' gardens (pretty on the outside, but lacking substance) because of their lack of connectivity, function and self-sustainability (Quigley, 2011). Similar patterns can be seen at larger scales, where we actively preserve some of the native plant diversity in remnants of natural vegetation within cities, but fail to maintain associated, native arthropod communities (Bang and Faeth, 2011; Bang *et al.*, 2012). Simply because an urban habitat resembles a wildland habitat in terms of vegetation cover and structure, does not mean that the

associated biodiversity, composition and function of the urban and wildland communities are equivalent (Faeth *et al.*, 2005). Urban arthropod communities may in fact represent distinct communities different from surrounding natural areas. Whereas this may add value in terms of biodiversity (e.g. Sattler *et al.*, 2011), it may also change ecosystem services once provided by native communities, but not always in a negative fashion (e.g. McDonald and Marcotullio, 2011). For example, proliferation of non-native plants in the Phoenix, Arizona, USA urban area has reduced native pollinating species and their services (McIntyre and Hostetler, 2001), but non-native earthworms in urban New York, USA forests increase nitrogen mineralisation rates in soils (Steinberg *et al.*, 1997).

From a metacommunity perspective that focuses on regional scale processes, increased connectivity between patches may enhance the persistence of communities. This is in line with traditional conservation biology, where size (Donnelly and Marzluff, 2004), structure (Donnelly and Marzluff, 2006) and connectivity of fragmented habitats are considered to maintain species interactions, resist species invasions and disease, and maintain sufficient population sizes. Humans indirectly influence the self-assembly of communities by providing the environmental template (Swan *et al.*, 2011), particularly in terms of plant communities (Faeth *et al.*, 2011). Urban biodiversity loss can be minimised by building dispersal corridors for wildlife (including arthropods, reptiles and amphibians), reducing road density and keeping a range of patches at different successional stages, including brownfields, green roofs, retention ponds and roadside vegetation. Corridors represent a challenge because they require space that may be limiting and because they may also encourage migration of unwanted species and spread diseases (e.g. Hess, 1996). Thus, it is important to understand niche-based environmental factors and modes of dispersal to filter undesirable organisms from desirable ones.

Connectivity between green spaces can not only provide dispersal corridors for wildlife, but also provide health benefits for residents (e.g. Tszoulas and Greening, 2011). Green infrastructure should link green spaces and habitats at a variety of scales, from gardens to parks to rural areas (Douglas and Ravetz, 2011). Green roofs can mitigate habitat loss, whereas brown roofs (roofs with brownfield habitat) can provide habitats at different successional stages (Sadler *et al.*, 2011). Ideally, green infrastructure should be planned before development (Douglas and Ravetz, 2011), but already urbanised areas can be rethought and redesigned, especially when opportunities such as urban renewal, present themselves.

Unfortunately, the metacommunity approach does not provide any 'short cuts' for urban biodiversity conservation. Instead, it emphasises that both local and regional scale processes are important and vary by habitat, individual species, climatic zone and will require detailed knowledge of individual species traits and interactions with other species. This is something many conservation biologists already know and advocate, but challenging to

effectuate. **See also:** Conservation Biology and Biodiversity; Restoration Ecology: Principles; Restoration of Terrestrial Communities

The key to successful conservation measures is that they are accepted and appreciated by the public. Clearly, human values, perceptions and limited city budgets often cause dilemmas for urban conservation biology. It is sometimes difficult for the general public to fathom what lies behind 'the intrinsic value of biotic diversity' (Soulé, 1985). As half of the people in the world now live in cities, the connection with nature becomes weaker and may create future generations with little understanding of the importance of conserving biodiversity (Dunn *et al.*, 2006). If future politicians and voters have little firsthand experience with nature, global conservation strategies may be imperiled (Dunn *et al.*, 2006). The 'pigeon paradox' (Dunn *et al.*, 2006) illustrates the importance of involving citizens in conservation, in particular in poorer socioeconomic areas. One strategy is to educate with the urban biodiversity at hand, using the complex urban communities that are composed of native and non-native species, including the synanthropic species such as the abundant house sparrows, pigeons and starlings. Urban green areas, despite their reduced biodiversity and altered species composition, are complex communities and can effectively be used to educate both school age children and adults (e.g. Faeth *et al.*, 2011), while providing recreational, health and well-being benefits (e.g. Miller and Hobbs, 2002). As such, systematic land use planning, educational programmes that increase knowledge and appreciation of diversity, and encouragement of backyard ecosystems that support diversity, can enhance overall biodiversity in cities (e.g. Gaston *et al.*, 2005; Goddard *et al.*, 2010). These efforts may then engender support for a much larger conservation 'footprint' beyond the urban boundaries (Dunn *et al.*, 2006).

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