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Adaptation and Adaptedness of Organisms to Urban Environments

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Abstract

Around the world the development and growth of cities and towns are having a significant impact on local and global biodiversity. There is growing interest in the adaptation of nonhuman organisms to urban environments, and we distinguish between the concepts of adaptation and adaptedness. Most of these studies have focused on animals, especially birds. Commonly recorded responses to urban environments include regulatory and acclimatory responses involving changes in behavior, communication, and physiology. Developmental responses tend to be morphological in nature but can also involve cultural learning. There is growing evidence of microevolutionary changes associated with adaptive responses to urban environments. This review also highlights the urgent need to refine the terminology currently used to describe the adaptation of organisms to urban environments in order to improve scientific understanding and more effectively identify and communicate the actions required to create biodiversity- and adaptation-friendly cities and towns for the future.

INTRODUCTION

Human-induced environmental changes to our planet are unprecedented in their rate, spatial scale, intensity, and magnitude. This is especially true regarding the evolution and adaptation of invasive organisms and poses a significant threat to global biodiversity (Millennium Ecosystem Assessment 2005, Secr. Conv. Biol. Div. 2012). In the past decade, the creation and growth of cities and towns have been identified as major threats to global biodiversity (Aronson et al. 2014, McDonald et al. 2008, Secr. Conv. Biol. Div. 2012). It is predicted that total global urban area will triple between 2000 and 2030 to accommodate a doubling in the urban human population, most of which will occur in undeveloped countries (Secr. Conv. Biol. Div. 2012). Seto et al. (2012) predicted that globally an additional 5.9 million km² of land will be converted to urban land use by 2030, and this increase will have significant impacts on global biodiversity hot spots.

Impacts of urbanization range from the relatively rapid destruction of habitats as a result of land clearing as cities are created and expanded to the slow, steady degradation of habitats due to increased exposure to edge effects, parasites and pests, invasive species, altered disturbance regimes, and reduced connectivity with other similar habitats. The introduction of noise, light, and vibrations creates additional impacts. There are also long-term chronic urban environmental changes affecting the ecology of cities associated with heat island effects, increased nutrient and pollution levels, and altered water availability and dynamics (Grimm et al. 2008, Paul & Meyer 2001, Pickett et al. 2001). In many cases these changes in urban environmental conditions have resulted in the creation of novel ecosystems that exhibit unique species compositions and ecosystem processes that may have little or no similarity to historic or existing ecosystems (Hobbs & Cramer 2008, Kowarik 2011). The creation of novel ecosystems may pose new survival and persistence challenges for many organisms specifically adapted to currently existing nonurban environmental conditions.

Since the emergence of the scientific discipline of ecology in the late 1800s, ecologists have directed much time, energy, and resources to elucidating the underlying factors that influence the distribution and abundance of organisms on our planet (McIntosh 1985). Inspired by Darwin's theory of evolution, early ecologists correctly believed that environmental conditions had a significant effect on the morphology, anatomy, physiology, and distribution of organisms via natural selection and adaptation processes (McIntosh 1985). One of the premiere ecologists of his day, Henry Cowles (1904) stated, "If ecology has a place at all in modern biology, certainly one of its great tasks is to unravel the mysteries of adaptation" (p. 880). The study of organism adaptation to urban environments builds on the rich and diverse ecological literature that already exists.

Ecologists primarily view adaptation as a dynamic evolutionary process that facilitates the survival and persistence of organisms under altered environmental conditions (Futuyma 2013). Thus, past environmental conditions impose selective pressures on organisms, and through the process of natural selection the organisms can adapt and persist (i.e., survival of the fittest) or go extinct. Although this process may have taken hundreds to millions of years, today most organisms appear to us to be well adapted to their native environmental conditions. Indeed, in many cases we only have fossil records of species that have gone extinct in the past due to their inability to adapt to changing environments (Futuyma 2013). The fast pace of human-accelerated environmental change in the nineteenth, twentieth, and twenty-first centuries has, for example, resulted in the global extinction of more than 160 species of animals, many of which were observed and collected before they were extirpated (for a list of the most recent animal extinctions, see The Sixth Extinction web site at <http://www.petermaas.nl/extinct>). Pimm et al. (2014) predicted that global extinction rates will continue to increase in the future primarily due to the increase in human population growth. There are also examples of local extinctions of plants (Hahs et al. 2009b), herpetofauna (Hamer & McDonnell 2010), and mammals (van der Ree & McCarthy 2005) within

urban areas. Thompson & Jones (1999) have found a direct correlation between human population density and local plant extinctions in Britain. However, an increasing number of examples of microevolutionary changes occurring in urban environments have been found (Alberti 2015, Gil & Brumm 2014, Kotze et al. 2011, Marzluff 2012). To maintain local urban and global biodiversity in urban landscapes, we need to understand how organisms have adapted to the altered environmental conditions and how we can create cities and towns that facilitate the persistence and adaptation of organisms to future urban environments (Alberti 2015, Donihue & Lambert 2014, Kowarik 2011, Marzluff 2012).

The aim of this review is to provide a synthesis of our current state of knowledge and understanding of the adaptedness and adaptation of organisms in an urbanizing world. The review is structured into the following sections: (a) spatial and temporal characteristics of urban environmental conditions and their relationship to selective pressures on organisms, (b) definitions of adaptedness and adaptations in urban environments, (c) pathways of species' adaptive responses to urbanization, (d) time frames of adaptive responses to urban environments, (e) a framework for considering the biological and cultural components of species' responses to urban environments within adaptive response time frames, (f) recommendations for creating cities and towns that facilitate adaptation of species to urban environments to reduce extinctions and conserve local and global biodiversity, (g) a discussion of how we might refine the terminology used to describe types of urban species, and (h) the identification of future research directions.

This review is primarily focused on the ability of nonhuman organisms, as individuals, populations, and species, to adapt to urban environmental conditions. This includes mechanisms related to phenotypic plasticity, genotypic change, and cultural change in the sense of learned behaviors (Marzluff 2012). This review does not discuss adaptation by humans to urban environments (Smit & Wandel 2006) or coevolution between human and nonhuman species (Marzluff 2012). Nor will we be discussing adaptation in reference to resilience and ecosystem management (Nelson et al. 2007), although we recognize these topics may be indirectly related to the subject of this review.

URBAN ENVIRONMENTAL CHANGE IN SPACE AND TIME

Urban environmental forcing functions and corresponding biotic responses such as adaptation and extinction vary along spatial and temporal scales. In order to understand and assess the impacts of urban environments on organisms, we propose a simple operational scale paradigm similar to the one developed by Delcourt & Delcourt (1983) for the study of landscape ecology. Because the focus of this review is primarily on human-induced environmental change, our temporal operational scale ranges from seconds to centuries and the spatial scale ranges from meters to the entire planet (**Figure 1**). Our urban spatial operational scale represents a fine-grain scale that would sit within Delcourt & Delcourt's (1983) micro- and mesoscale domains.

Ecosystem changes associated with urbanization are considered to fall into four major categories: (a) creation of new land cover, (b) changes to the physical and chemical environment, (c) creation of new biotic assemblages and associated interactions, and (d) changes to the disturbance regime (Kinzig & Grove 2001, Sukopp 1998). The specific nature of these impacts has been well summarized in the literature (Gaston et al. 2012; Paul & Meyer 2001; Pickett et al. 2001, 2011; Williams et al. 2009). However, an alternative way to categorize these changes is in terms of their spatial and temporal footprints (**Figure 1**). To draw an analogy to the medical literature, acute impacts are relatively discrete in time and space, whereas chronic impacts accumulate over time and space. Examples of acute impacts are increased levels of artificial noise and light, novel biotic interactions (e.g., competition, predation, parasitism), altered food resource quality and quantity, acute disturbances, and the direct actions of humans. In all of these cases, the environmental

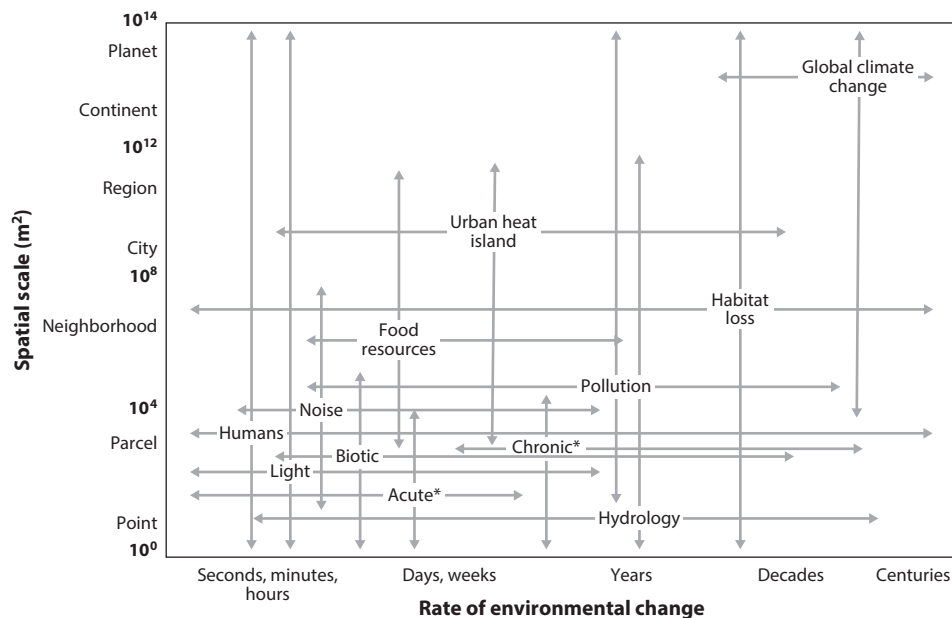


Figure 1

Urban environmental conditions viewed in the context of spatial scales and timescales. The location of the text indicates the most prevalent scale of impact. The horizontal arrows indicate the range of temporal scales and the vertical arrows indicate the range of spatial scales that may be impacted. Biotic interactions include competition, predation, parasitism, mutualisms, facilitation, etc. Physical disturbances have been divided into two broad categories (*asterisks*): Acute disturbances are generally individual events located within relatively discrete places in time and space (e.g., vandalism, storms), and chronic disturbances are generally more repetitive events that occur over longer timescales and possibly broader spatial scales (e.g., trampling).

changes have a major impact relatively quickly (minutes to weeks) at relatively small spatial scales (points to neighborhoods). At the other end of the spectrum, chronic environmental changes such as pollution, habitat loss, changes to the hydrological cycle, and the urban heat island all manifest as impacts over longer temporal scales (years to decades) and larger spatial scales (neighborhoods to regions). These two categories are not mutually exclusive: Chronic impacts can have acute effects at fine spatial and temporal scales, and acute impacts can have chronic effects that extend over larger spatial and temporal scales. However, the actions required to mitigate chronic or acute environmental impacts will differ, as we discuss later in this review.

ADAPTATION AND ADAPTEDNESS

Adaptedness

Organisms from a variety of environments possess traits that may confer fitness in urban environments without the need for adaptation. These species are considered preadapted to urban conditions due to their unique phenotypic traits and plasticity. This concept is related to Dobzhansky's (1970) term adaptedness, which refers to the degree to which phenotypes can tolerate and survive local environmental conditions. For example, cockroaches, pigeons, and rats are highly adapted to intensely altered urban environmental conditions; thus, we would say they

have a high level of adaptedness to living in cities and towns. However, for other organisms, exposure to urban environments may lead to a shift in traits that increases their fitness under these new environmental conditions. These adjustments can be considered to be an adaptive response to altered environmental selection pressures.

Adaptation

There is a rich and extensive literature in ecology that examines adaptation as a process that occurs over periods of thousands of years during which organisms become adapted to the environments in which they live (Futuyma 2013). There is also increasing evidence of microevolutionary adaptations occurring at much shorter timescales (i.e., 1–100 years), particularly in response to human actions (Alberti 2015, Palumbi 2001, Stockwell et al. 2003, Thompson 1998). Organisms persist under certain environmental conditions because they possess unique genotypes that code for physiological, behavioral, and morphological features and attributes, yet the survival of organisms under specific environmental conditions is actually determined by the expressed phenotype (i.e., adaptive traits). Organisms that possess the ability to alter their phenotype within their lifetime in response to environmental conditions, referred to as phenotypic plasticity, have a higher probability of surviving in changing environments and adapting to the new conditions through a process of acclimatization. Such changes can remain temporary (plasticity) or they can result in an eventual shift in genotypes (microevolution). The existence of phenotypic or genotypic differences between populations is not in itself indicative of adaptation to urban environments. Adaptation implies an advantage to organisms that results in higher fitness or reproductive success (Donihue & Lambert 2014). Phenotypic and genetic differentiation between populations may also occur without necessarily involving adaptations (e.g., genetic drift and random selection; Donihue & Lambert 2014).

The ability of organisms to adapt to changes in urban environmental conditions will also be determined by the magnitude of the environmental change as well as the temporal and spatial scales the change is acting over (**Figure 1**). As the magnitude of change increases, the selection pressure grows and it becomes increasingly likely that the organism must adapt in order to persist. Selection pressures associated with chronic environmental changes operating over longer temporal scales and at wider spatial scales are also more likely to require adaptation in order for organisms to persist in the long term. However, the selection pressures are likely to be consistent over this period, enabling directional developmental responses over generations (Thompson 1998). Opportunities for adaptation are more limited with respect to acute environmental impacts, as the timescale available for an adaptive response is greatly reduced. The reduced timescale of these impacts may also be associated with changes in the direction and magnitude of the impact, suggesting that less consistent adaptive responses may be advantageous and more likely to be observed (Stockwell et al. 2003).

Urban ecologists during the past decade have begun exploring in more detail the adaptation of organisms to urban environments. There are several excellent reviews of the current state of knowledge in the field including those by Evans (2010), Marzluff (2012), Donihue & Lambert (2014), and Gil & Brumm (2014). There have also been a number of reviews on specific topics regarding the adaptation of animals to urban environments that include the following: behavioral responses (Garroway & Sheldon 2013, Lowry et al. 2013, Sol et al. 2013, Tuomainen & Candolin 2011), endocrine system responses (Bonier 2012, Bonier et al. 2006), hormonal responses (Atwell et al. 2012, Fokidis et al. 2009), stress (Partecke et al. 2006), avian productivity (Chamberlain et al. 2009), landscape genetics (Manel & Holderegger 2013), invasion and adaptation processes by birds (Evans et al. 2010, Möller 2009), responses to noise (Chan & Blumstein 2011), and responses to

light (Gaston et al. 2012, Rich & Longcore 2004). There are relatively few papers specifically about adaptation of plants to urban environments (Cheptou et al. 2008, Evans 2010, Williams et al. 2015).

Problematic Terminology

The urban ecology literature is replete with papers that classify organisms based on their ability to use urban environments (Grant et al. 2011, Marzluff 2012, McKinney 2002). One of the commonly applied classifications uses the terms urban avoiders, urban adapters, and urban exploiters (McKinney 2002). These terms roughly correspond to species that are sensitive to urban environments and avoid them, species that can use urban environmental resources but may not reside in them, and species that thrive in urban environments. Although this classification may be useful when conveying ecological information about organisms in cities to educators, planners, managers, and designers, there are multiple reasons why certain organisms occur in urban areas in different parts of the world at different times (Fischer et al. 2015).

This scheme is problematic when applied to the ecological study of urban ecosystems, primarily because the terms adapt and adaptation have different meanings for scientists and the general public. We encourage urban ecologists to use the traditional biological meaning of these terms where organisms are preadapted or can adapt to new environmental conditions through well-described nonevolutionary and evolutionary processes. The misapplication of the concept of adaptation could mislead students, scientists, and urban practitioners by obscuring the true biological and ecological factors determining the distribution of organisms in urban environments with implications for the efficacy of conservation and management actions (Fischer et al. 2015). We return to this concept again at the end of the review where we present recommendations for improving terminology.

PATHWAYS OF ADAPTIVE RESPONSES TO URBAN ENVIRONMENTS

Cities and towns have been and will continue to be built on existing natural ecosystems, such as forests, grasslands, savannas, and swamps, as well as on human-modified ecosystems previously used for agriculture, mining, and timber harvesting (McDonald et al. 2010). When any ecosystem or landscape is urbanized, the resident or native organisms can (*a*) migrate out of the area if they are capable of moving, (*b*) persist because they are preadapted to the new environmental conditions and possess a high level of adaptedness to urban environments, (*c*) adapt to the new urban environmental conditions and persist in the same geographic area, or (*d*) perish and become locally extinct (**Figure 2**). The magnitude, timing, and spatial extent of the changes will determine how many organisms are able to adapt and persist or will become locally extinct. The total and permanent destruction of existing habitats and a rapidly changing environment may make it virtually impossible for some organisms to adapt and survive locally (Grant et al. 2011). This rapid local extirpation of organisms is not unique to the process of urbanization, for it occurs in the development of other human-modified ecosystems, such as those used for agricultural development and resource extraction (Dobson et al. 1997). However, the magnitude and rate of subsequent changes to urban environmental conditions may increase pressure on organisms to adapt or become locally extinct. Similar magnitudes and rates of environmental change can also emerge following natural events, such as volcanic eruptions, catastrophic fires, tsunamis, and earthquakes, with similar consequences for the likelihood of species adapting and persisting or becoming locally extinct.

We propose that when discussing biological adaptations it is uninformative to include examples of organisms that become locally extinct during the process of urbanization if the habitats in which

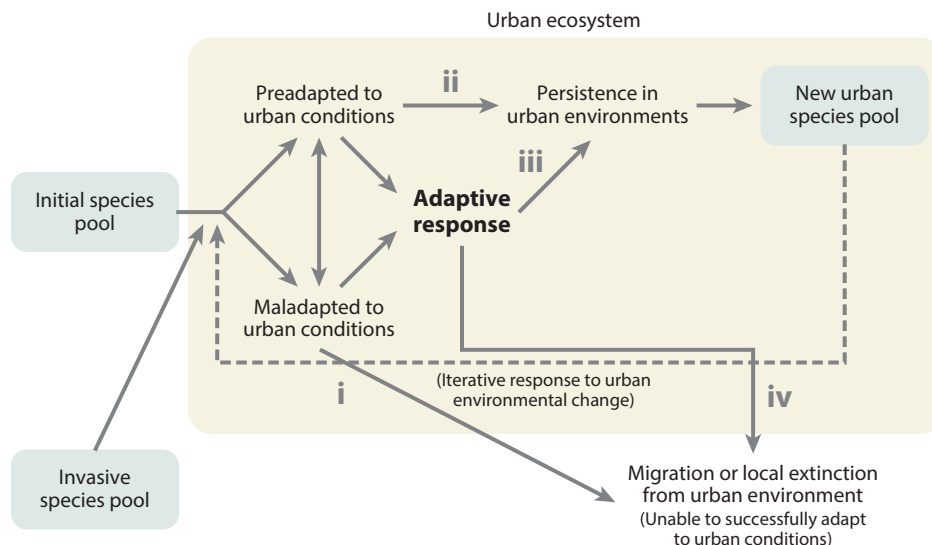


Figure 2

Pathways of organism responses to changes in urban environmental conditions related to either the initial urbanization event or to subsequent changes in the urban environment associated with increased densification, new technologies, or new environmental management practices. The numbers refer to potential pathways for organisms to (i) migrate, (ii and iii) adapt, or (iv) become locally extinct in urban environments.

they live (i.e., their niche) or the resources on which they depend (e.g., their food sources or nest sites) have been completely removed (Grant et al. 2011). For example, we would not expect wetland birds to be present in a landscape that did not contain an appropriate water body, although this may change following the construction of a wetland. If indigenous or native organisms are going to persist in newly created urban environments, they must first survive long enough to adapt to the new environmental conditions (Ashley et al. 2003). This means that during the process of urbanization some elements of the organism's niche need to be maintained and assimilated into the newly created or expanding city. These critical habitats can be preserved within cities (remnant patches) or they can be maintained in peri-urban and rural environments adjacent to cities (Kowarik 2011). In their study of plant extinction debt in 22 cities from around the world, Hahs et al. (2009b) found that urban areas with 30% or more native vegetation cover experienced fewer plant extinctions over the last century. Similarly, in their analysis of biodiversity in more than 100 cities around the globe, Aronson et al. (2014) found that the presence of intact vegetation cover was important for maintaining higher concentrations of birds and plants in urban areas.

In addition, the spatial extent of cities as well as the characteristics of the adjacent nonurban ecosystems can directly and indirectly influence which organisms can inhabit and survive in an urban environment (Luck & Smallbone 2010). The larger and older the city is, the greater the probability that populations of organisms become more isolated, which can reduce their ability to survive and persist in the future. It has been shown that larger cities are more likely to experience colonization events from adventive species, either due to the increased likelihood of the species encountering the city (Evans et al. 2010) or the greater diversity of habitat resources that may be found there (Fey et al. 2015). There is evidence that cities located close to coastal areas are more likely to be colonized by new species, as the coastline can act as a migration corridor (Fey et al.

2015). The close proximity of an urban area to intact or remnant ecosystems has also been shown to increase urban species richness, especially in regard to birds (Fernández-Juricic & Jokimäki 2001, Germaine et al. 1998).

TIME FRAMES FOR ADAPTIVE RESPONSES

Our analysis of the adaptive responses of organisms to urban environments begins with what we will refer to as classic textbook evolutionary adaptations. These typically occur over long time periods and involve the differential reproduction success of genetically based traits in response to selective pressures induced by urban environmental conditions. The most famous example of evolutionary adaptation to urban environments is the change in frequency of the melanistic form of the common light-colored peppered moth beginning in the late 1800s in England in response to the blackening of tree trunks due to severe air pollution (Kettlewell 1959). The selective pressure was the increased bird predation on the different colored forms of the moths depending on the color of the tree bark. In the 1950s, the newly adapted dark form of the moth was camouflaged against the dark tree trunks and thus suffered less predation, but as the air pollution subsided in the 1970s and the tree bark became lighter the dark forms had higher predation rates (Cook et al. 2012). Recently, there has been a growing recognition of other examples of rapid evolution involving changes due to human activities, referred to as microevolution (Alberti 2015, Palumbi 2001, Stockwell et al. 2003). Donihue & Lambert (2014), in their recent analysis of adaptive evolution in cities, found only a handful of classic evolutionary adaptations to urban environments described in the literature. They considered this a prime field for future research to inform evolutionary theory and broaden our understanding of the ability of species to adapt to rapidly changing urban environments.

The lack of examples of classic macroevolutionary adaptations (i.e., speciation) to urban environments is not unexpected in light of the short time humans have been building cities and the speed and magnitude of human-induced urban environmental change. We propose that the probability of organisms undergoing classic evolutionary adaptations or becoming extinct in urban environments is related to the generation time of the organism and the rate of environmental change (**Figure 3**). Organisms with generation times measured in days, months, and years, such as microbes, insects, and small mammals, have a higher probability of adapting and surviving in rapidly changing urban environments, whereas organisms with slow generation times of tens to hundreds of years, such as large mammals and trees, have much lower probabilities of adapting to urban environments and higher rates of local extinction over extended time frames. A worthwhile future research question could explore the rates of environmental change that would facilitate adaptation in organisms with fast versus slow generation times (i.e., quantify X_1 and X_2 in **Figure 3**). One question worth pursuing is whether we would find different rates in older versus younger cities. If we had a better understanding of these relationships, we could potentially reduce local extinctions and facilitate adaptations.

In addition to evolutionary adaptations to urban environmental change, ecologists have recognized that organisms are capable of nonevolutionary adjustments to their physiology, morphology, and behavior in response to environmental change. Ricklefs (1990) identified three basic nonevolutionary adaptive responses that occur over different timescales: regulatory, acclimatory, and developmental. Regulatory responses occur over short time periods of seconds, minutes, and hours; these responses commonly involve changes in physiology and behavior. Examples of regulatory responses to urban environments include alterations of bird calls (Hu & Cardoso 2010) and avoidance behavior by urban mammals (Lowry et al. 2013). Acclimation can occur over days and

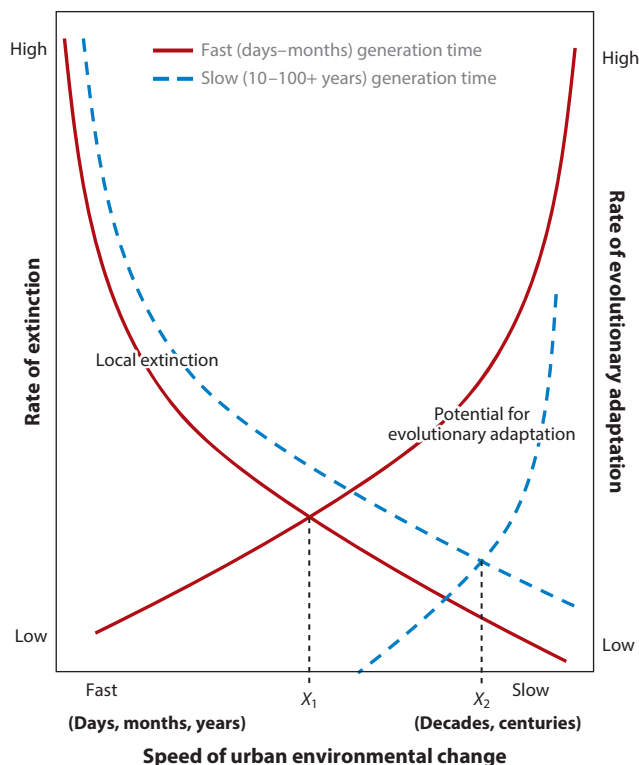


Figure 3

A heuristic model of the relationship between the speed of urban environmental change, generation time of organisms, and rates of local extinction and evolutionary adaptation. X_1 and X_2 are the speeds of urban environmental change at which organisms with fast and slow generation times, respectively, would have lower probabilities of undergoing adaptive evolution in order to survive and persist in cities.

weeks and typically involves physiological and morphological changes. Examples of acclimatory responses to urban environments include diet switching (Jiménez et al. 2013) and niche shifts in insects (Kamdem et al. 2012). Both regulatory and acclimatory responses are reversible by an individual organism within its lifetime. Developmental responses occur over longer time periods (e.g., years) and commonly involve the growth and development of organisms; they are typically not reversible within a single individual or lifetime. Examples of developmental responses to urban environments include changes in root investment in plants (Ferguson et al. 2015) and changes in bill size and shape in birds (Badyaev et al. 2008). All of these adaptive responses to urban environmental change can involve microevolutionary processes that through time may lead to changes in gene frequency (i.e., adaptive evolution) or they may simply reflect phenotypic and behavioral plasticity. Marzluff (2012) presented a good summary of contemporary evolution (i.e., microevolution) in urban ecosystems involving both genetic and cultural traits. Adaptive responses may also be temporally interrelated. For example, an acclimatory response to prolonged traffic noise may initially manifest as a regulatory behavior (e.g., change in calling pitch), but it may subsequently emerge as a developmental adaptation (e.g., reduced body size) with an accompanying genetic component (Parris et al. 2009).

BIOLOGICAL AND CULTURAL COMPONENTS OF ADAPTIVE RESPONSES

When thinking about the types of responses an organism can display [e.g., changes to song characteristics (Slabbekoorn 2013) or changes to beak morphology (Badyaev et al. 2008)], seven general strategies of response emerge: communication, behavior, autecology, demographics, phenology, physiology, and morphology. The cultural evolution and adaptation referred to by Marzluff (2012) would manifest as changes to communication, behavior, and autecology when the transmission between individuals is based on learning rather than genetics. When these response strategies are combined with the time frame of response presented in the previous section (regulatory, acclimatory, developmental, evolutionary), several useful trends can be identified (**Table 1**).

A regulatory response is the real-time response of an organism to an environmental condition or stimulus. Within the current urban ecology literature, the majority of research related to regulatory responses has been in the areas of acoustic communication (Slabbekoorn 2013), behaviors such as flight initiation distance of birds in response to approaches by humans (Carrete & Tella 2010), and physiological responses such as those related to levels of stress hormones (Partecke et al. 2006). Most of this research has been focused on birds and other mobile organisms such as reptiles and invertebrates. Regulatory responses of plants have been less intensively studied (Evans 2010) even though they do have the capacity to respond in this time frame through physiological strategies such as altering respiration and transpiration rates, adjusting leaf orientation or seed release, and regulating stomatal apertures.

Acclimatory responses are the responses an organism displays over days to weeks; they generally indicate a response to some general conditions within the urban environment, such as changes in food quality or abundance (Shochat et al. 2014) or changes in photoperiod exposure (Partecke et al. 2004). In some cases, the regulatory response that an organism displays may be the manifestation of an acclimatory response. For example, the consistent exposure to road noise over time may prompt an organism to call earlier in the day (acclimatory response) or during breaks in traffic (regulatory response) (Fuller et al. 2007). Within the urban ecology literature, acclimatory responses show the greatest diversity and cover all seven types of response strategies. Examples of acclimatory responses include reduced migratory behavior in blackbird populations in Europe (Partecke & Gwinner 2004), switched diet in response to food availability (Dorn et al. 2011), reduced clutch sizes (Chamberlain et al. 2009), changed emergence dates (e.g., common brown butterflies in Melbourne, Australia; Kearney et al. 2010), altered plant phenology (Neil & Wu 2006), changed immunity (Martin & Boruta 2014), and altered leaf dimensions, cuticle thickness, and stomatal density in plants (Evans 2010).

Developmental responses accumulate over a longer time frame of years to decades and are therefore most likely to occur in response to chronic alterations to urban environmental conditions (**Figure 1**). Although there are examples of developmental changes associated with more acute disturbances—for example, changes in song learning of birds exposed to artificial noise (Mockford & Marshall 2009) or behavior syndromes in birds due to accumulated maternal effects in mothers experiencing higher levels of stress (Atwell et al. 2012)—these developmental responses tend to be predominantly morphological (**Table 1**) due to the number of generations required for the response to manifest. Developmental changes in plants include shifts in seed dispersal modes, such as those documented in *Crepis sancta* (Cheptou et al. 2008), whereas developmental changes in animals may relate to altered brain size (Sol et al. 2008), body size (Kotze et al. 2011), wing morphology (Venn 2007), or beak morphology and bite strength (Badyaev et al. 2008). Some of these developmental responses may be manifest through phenotypic or behavioral plasticity, but examples of microevolution, where the different phenotypes are accompanied by changes in the associated genes, have also been found (Partecke & Gwinner 2004).

Table 1 Examples of the types of responses recorded for organisms in urban environments

	Regulatory	Acclimatory	Developmental	Evolutionary
Communication				
Birds	Call frequency, amplitude, duration, content, type (alarm, territorial), location (e.g., perch height), and timing	Call memes	Song learning (dialects)	
Frogs	Call pitch and timing			
Bats	Call pitch			
Reptiles		Visual display		
Behavior				
Birds	Harm avoidance Fear response (tonic immobility, feather loss, fear scream, wriggle) Disturbance response (flight initiation distance) Human cues	Dispersal Defense strategy (nest, territory, offspring) Habituation Surveillance time Exploratory behavior Extrapair paternity Flight distance/variance Parental roles (e.g., nest building) Nest location Innovation Diet switching Flocking Colonial nesting Territoriality	Altered migration Behavior syndromes (aggression, boldness, exploration) Individual susceptibility Visual cues Neophilia and neophobia	
Reptiles	Heat avoidance			
Demographics				
Birds		Annual fecundity Incubation period Clutch size Number of clutches/year Number of fledglings/year	Population density and size Reproductive rate Mortality rate Adult survival Age ratio Number of subspecies	
Plants			Longevity (seed, adult)	
Autecology				
Birds		Breeding range Environmental tolerance Habitat use Resource use	Nest type Dietary guild	
Plants			Pollination mode Seed dispersal mode	
Phenology				
Birds	Reproductive hormones	Onset of breeding Initiation of nest building Initiation of mating Lay date Hatching date	Reproductive age	
Insects		Emergence		

(Continued)

Table 1 (Continued)

	Regulatory	Acclimatory	Developmental	Evolutionary
Plants		Germination Leaf emergence and fall Bud burst Flowering onset, length, and volume		
Physiology				
Birds	Stress hormones Feeding rates	Stress hormones Maternal effects Disease prevalence Parasite prevalence Anxiety regulation Harm avoidance		
Mammals		Genetic variability Immune response Metabolic rate		
Reptiles		Stress physiology Antioxidant defenses		
Insects	Heat tolerance	Thermal tolerance Niche shifts	Thermal tolerance Desiccation tolerance	
Fish		Pollution tolerance		
Plants	Leaf moisture content Respiration rates Transpiration rates Photosynthesis rates	Nectar quality and quantity Ellenberg niche indicators Chlorophyll concentrations	Hybridization Photosynthetic pathways Heavy metal tolerance	
Morphology				
Birds			Brain mass size, variance, and skewness Body mass Bill size and shape Asymmetric growth Sexual dimorphism Feather coloration Altricial young Song production (higher vocal center nucleus)	
Bats			Wing span and shape	
Insects			Wing size and fragments Anatomical deformities	Color
Plants	Stomatal aperture Leaf orientation	Stomatal density Leaf dimensions Specific leaf area Cuticle thickness Wood density	Height Plant life form Clonality Seed mass Root investment	

Evolutionary responses typically occur over timescales of centuries. Many cities and towns around the world have existed for centuries and may have experienced rapid environmental changes accompanying the industrial revolution and the technological developments in the twentieth century. However, there are no clear examples in the urban ecology scientific literature of an evolutionary response to urban environmental change that has resulted in the loss of breeding compatibility between populations. If we were to be bold, we would hypothesize that the most favorable conditions for evolutionary adaptations have occurred within cities that were established 300–400 years ago (Type II cities from Hahs et al. 2009b) and that have continued to experience rapid urbanization and highly altered environments where strong selection pressures have been in effect for relatively long timescales (e.g., New York City and Singapore).

CREATING BIODIVERSITY-FRIENDLY ADAPTATION ENVELOPES WITHIN CITIES AND TOWNS

In this review we have presented two conceptual frameworks. The first addresses the environmental changes that act as selection pressures on organisms in urban environments over different spatial and temporal scales (**Figure 1**). The second has multiple elements (**Figures 2 and 3, Table 1**) related to the responses of organisms to urban environments. This section will address the interplay between these two frameworks and the implications for how we might alter the design and management of our urban areas to facilitate adaptation in a wider range of organisms and creation of more biodiversity-friendly cities and towns in the future.

As identified above, the magnitude as well as the spatial and temporal scales of the environmental impact determine the likelihood that an adaptive response is required for an organism to persist under the new conditions as well as the likelihood of the organism persisting long enough for an adaptive response to emerge. There are five characteristics of species that may influence their capacity to adapt to changes in urban environmental conditions: generation time, mobility, isolation, adaptedness, and population size. By designing and building biodiversity-friendly urban environments that reduce the magnitude and spatiotemporal extent of urbanization impacts, we create environments that may allow adaptation in organisms with a wider range of values for each of those characteristics, thereby increasing the biodiversity of our urban areas (**Figure 4**).

The biodiversity of future cities and towns will be composed of the resident and transitory facilitative organisms that currently exist in urban landscapes as well as the adventive organisms that colonize from the adjacent landscapes [e.g., blackbirds (Evans et al. 2009) and wood pigeons (Fey et al. 2015) in Europe]. In the face of the rapid urbanization required to accommodate the 1.6 billion additional people predicted to live in urban areas over the next 20 years (Fragkias et al. 2013), there is an urgent need to identify actions that can assist in the creation of biodiversity- and adaptation-friendly cities and towns. These actions not only need to provide the resources and environmental conditions that allow the current and future assemblages of organisms to persist, they also need to provide a favorable envelope in which a wide range of organisms have the opportunity to adapt to the acute and chronic disturbances associated with urban environments.

Due to the relatively short timescales and small spatial scales in which acute impacts manifest, there is an enormous opportunity to implement site-specific, short-term technological and management actions that can have broad-ranging benefits. The best current examples of cost-effective direct action include several technological solutions that alter the local impact of artificial night lighting. These solutions shift the spectral profile of the light using different light sources, direct and restrict the light impact to the target area through lighting designs, and adjust the duration of the light impact through the use of sensors and timers (Gaston et al. 2012).

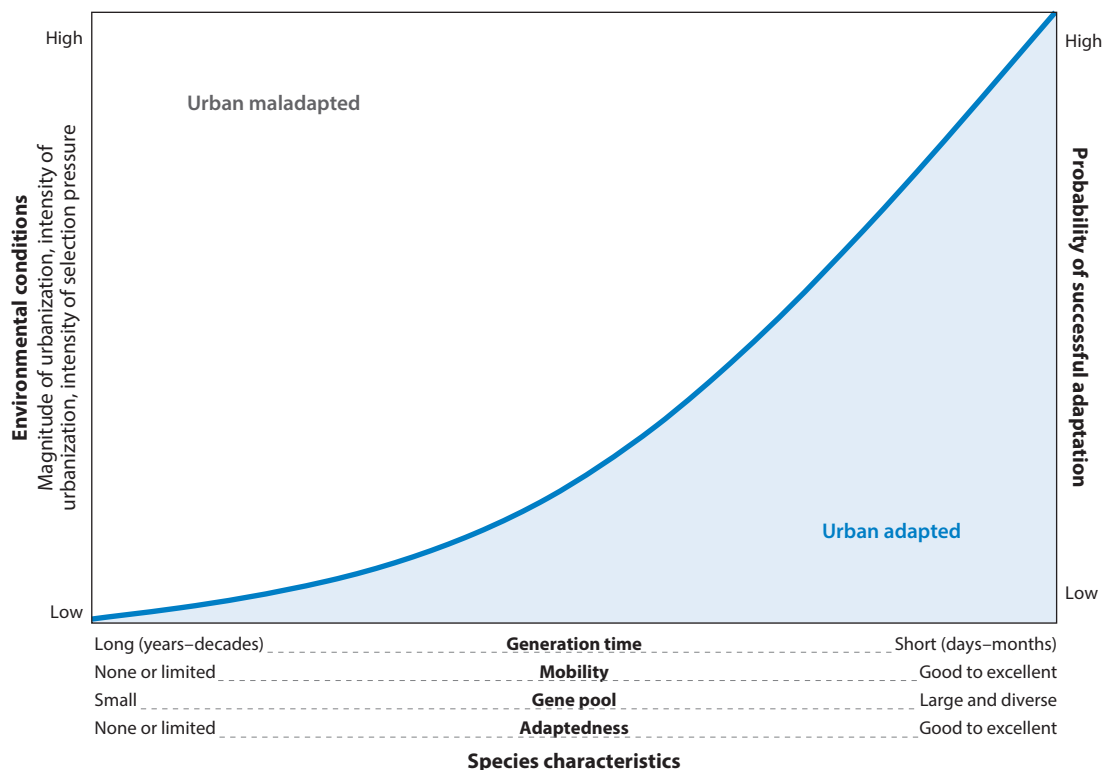


Figure 4

Predictions for the proportion of adapted and maladapted species in urban environments based on the characteristics of the organisms and the environmental conditions in which they live.

Actions that address acute impacts can often be implemented at the site and are therefore under the control of individuals during the course of their decision-making process. Therefore, there is an enormous opportunity to address these acute impacts through small-scale, site-specific designs, technologies, and management practices.

Although chronic environmental changes in urban landscapes act over long timescales and broad spatial scales, there are still key actions that can be used to reduce the magnitude of these impacts. However, these actions will generally rely upon coordinated solutions that are most likely to be implemented through legislation, policy, planning, and systematic changes that manifest as changes to the design of urban landscapes at the city scale. For example, addressing changes to the hydrological cycle across cities due to the extensive covering of impervious surfaces and the engineering infrastructure will require a shift toward managing our cities as catchment areas. This is achieved through large-scale implementation of water-sensitive urban design and changes to our water-use systems and practices in urban landscapes (Walsh et al. 2007). These are large-scale, long-term changes that are costly to retrofit to existing urban landscapes; therefore, they will rely on political and governance mechanisms for implementation. However, it is critical that these actions are implemented, as they are complementary to and essential for the success of the small-scale actions addressing acute environmental impacts. Implementing changes to create biodiversity- and

adaptation-friendly cities and towns will allow our future urban landscapes to support a higher diversity of plants, animals, birds, reptiles, invertebrates, fungi, algae, and microorganisms than would otherwise be possible.

REFINING TERMINOLOGY

We encourage urban ecologists to use the terminology, principles, and methods that ecologists have developed over the last 100 years in their study of the distribution and abundance of organisms in nonurban environments in order to better compare and contrast the structure and function of urban and nonurban ecosystems in the future. For example, the ecological study of a newly created artificial wetland presents the same terminological, conceptual, and methodological challenge as that faced by ecologists studying a newly built city. There will be organisms from the pre-wetland ecosystem that have high adaptedness to the new wetland ecosystem, and there will be other organisms with traits that will make them unable to tolerate and survive the new, wetter environmental conditions. There will also be organisms in the surrounding landscape adjacent to the wetland with the ability to use the resources or invade these newly created ecosystems. There is no evidence in the ecology literature of the classification of organisms in relation to their residency in a wetland ecosystem as wetland adapters, avoiders, or exploiters (*sensu lato* McKinney 2002).

Traditionally, organisms present in any ecosystem have been described as residents, short- and long-distant migrants, nomads, or invaders. Indeed, there are numerous examples of organisms changing their residency status on the basis of changes in climate (Hoffmann & Sgrò 2011), resource availability (Dorn et al. 2011), and disturbance regimes (Dwire & Kauffman 2003). A future productive approach to studying adaptations in urban environments involves identifying organisms that are residents, short- and long-distant migrants, and nomads in cities around the world. It may also be useful to recognize that because most organisms have habitat-specific requirements, their distribution patterns are likely to reflect resource gradients as well as gradients of selection pressure. Therefore, trends in the composition of assemblages will most accurately be captured by these factors, rather than land use per se (McDonnell & Hahs 2013). The ability of organisms to alter their residency status in urban environments may reduce selection pressures for some species but may also increase selective pressures and result in new adaptations in other species.

CONCLUSION

Although many urban ecology studies have investigated the responses of organisms to urban environments, very few of them have placed their findings within the framework of adaptedness or adaptation as presented in this review. We believe this distinction is highly informative, as it provides important information about which characteristics translate to fitness within urban environments (i.e., adaptedness) and identifies those characteristics that have the capacity to confer a fitness advantage following adaptation. There are a few notable exceptions largely related to urban birds, as this is the one taxonomic group that has consistently received concentrated research attention throughout the past 20 years (Lepczyk & Warren 2012, McDonnell & Hahs 2008). Therefore, investigations into adaptedness and adaptations by organisms to urban environments offer a rich and untapped area for future urban ecology research and have enormous potential to increase our mechanistic understanding and predictive capacity related to biodiversity in urban environments (Alberti 2015, Donihue & Lambert 2014, Fischer et al. 2015, Marzluff 2012).

FUTURE ISSUES

1. Organisms can respond to many different aspects of the urban environments, such that phenotypic and genotypic differences do not necessarily imply adaptation. Research that disentangles adaptedness, phenotypic or behavioral plasticity, environmental responses, genetic drift, neutral genetic variation, and other types of response from confirmed adaptive evolution (*sensu* Donihue & Lambert 2014, Evans 2010, Marzluff 2012) will be a critical first step in elucidating the myriad ways in which urban environmental impacts can affect organisms.
2. Adaptive responses may involve multiple characteristics, which may have different implications in terms of fitness for the organism. Understanding the interactions and trade-offs that occur when there are multiple traits (Evans 2010) and the phylogenetic constraints these adaptive responses emerge within (Thompson 1998), as well as capturing potential nonlinear responses, will also enhance our understanding of how organisms are affected by urbanization.
3. Future research should identify options for prescriptive interventions that can deliver specific, goal-driven outcomes for biodiversity conservation in cities and towns. This research should focus on understanding the causes (*i.e.*, environmental drivers) and effects (*i.e.*, associated changes in related traits and overall implications for fitness) for different types of adaptive responses (**Table 1**) as well as the rates of adaptive change (Donihue & Lambert 2014, Evans 2010) under different urbanization scenarios, such as city spatial extent, human population size and density, geographic location, urban form, and green space network structure (Evans 2010).
4. The environmental changes in cities and towns and their subsequent role in contributing to an organism's response are notoriously difficult to disentangle and may have independent as well as interactive effects. Quantifying the selective pressure attributable to the different environmental impacts is imperative if we are to identify successful options for interventions. The opportunities for incorporating designed experiments (Felson et al. 2013) into adaptation research will contribute critical knowledge about the relative influence of various environmental pressures as well as practical solutions for retrofitting urban areas to make them more biodiversity- and adaptation-friendly landscapes.
5. Consistent and informative terminology is imperative for scientific advancement. Over the past 20 years, urban ecologists have repeatedly refined their use of terms as their level of understanding has become more refined (Fischer et al. 2015, Hahs et al. 2009a, MacGregor-Fors 2011, McIntyre et al. 2000, Theobald 2004). The time has now come to revisit the use of terms related to adaptation and confine their use to the well-established definitions provided in the broader ecology and evolution literature (*e.g.*, Futuyma 2013). We strongly urge the spatial distributions of species in urban landscapes to be described in terms of gradients of resources or environmental conditions and their temporal distributions characterized in terms of their status as residents, short- and long-distant migrants, nomads, or invaders. This terminology is not only more accurate but also important for refining research questions, conveying the complexity of biological assemblages, and informing the necessary actions required to create more biodiversity- and adaptation-friendly cities and towns.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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