CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Hierarchical filters determine community assembly of urban species pools

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Abstract. The majority of humanity now lives in cities or towns, with this proportion expected to continue increasing for the foreseeable future. As novel ecosystems, urban areas offer an ideal opportunity to examine multi-scalar processes involved in community assembly as well as the role of human activities in modulating environmental drivers of biodiversity. Although ecologists have made great strides in recent decades at documenting ecological relationships in urban areas, much remains unknown, and we still need to identify the major ecological factors, aside from habitat loss, behind the persistence or extinction of species and guilds of species in cities. Given this paucity of knowledge, there is an immediate need to facilitate collaborative, interdisciplinary research on the patterns and drivers of biodiversity in cities at multiple spatial scales. In this review, we introduce a new conceptual framework for understanding the filtering processes that mold diversity of urban floras and faunas. We hypothesize that the following hierarchical series of filters influence species distributions in cities: (1) regional climatic and biogeographical factors; (2) human facilitation; (3) urban form and development history; (4) socioeconomic and cultural factors; and (5) species interactions. In addition to these filters, life history and functional traits of species are important in determining community assembly and act at multiple spatial scales. Using these filters as a conceptual framework can help frame future research needed to elucidate processes of community assembly in urban areas. Understanding how humans influence community structure and processes will aid in the management, design, and planning of our cities to best support biodiversity.

Key words: biodiversity; city; community assembly; filters; human-dominated landscapes; urban ecology; UrBioNet.

Introduction

Today over 50% of the human population lives in urban areas, which has resulted in the rapid expansion of urban landscapes around the world (Martine 2007). Because the majority of the world's cities are in areas of high biodiversity (Kühn et al. 2004, Pautasso 2007, Rebelo et al. 2011), the rapid urbanization of the world has a profound effect on global biodiversity. Despite recognition of the importance of urban biodiversity by the Convention of Biological Diversity through the

Curitiba Declaration of Cities and Biodiversity (United Nations Environment Programme 2007) and a growing body of science investigating the biodiversity of urban areas (Pickett et al. 2001), a general synthesis on urban biodiversity remains in a fledgling state (McDonnell and Hahs 2013). Only a broader comparative approach addressing biodiversity at multiple spatial and sociopolitical scales across different kinds of cities will allow for an understanding of the patterns and processes structuring biotic communities in urban areas (Grimm et al. 2008, Warren et al. 2010, McDonnell and Hahs 2013). Cities are novel ecosystems that provide natural laboratories for examining processes of colonization, primary succession, and community assembly. Evaluating such processes in cities is critical as much of ecological knowledge and theory has been derived from pristine or non-urban systems which may function quite differently (Hahs and Evans 2015).

In a recent analysis of 110 cities with complete floras and 55 cities with complete bird lists across six biogeographic realms, the examined cities were shown to support 20% of the world's bird species and ~5% of the world's plant species. The majority of urban bird (94%) and plant (70%) species in cities are native, and cities do support populations of rare and endangered plant and bird species (Aronson et al. 2014). However, on average, cities have lost 74% of the predicted pre-urban density of plant species and 92% of predicted pre-urban bird species density. The species remaining in these cities were found to be primarily driven by anthropogenic features of the cities, such as land cover and city age, rather than biogeographic and climatic features of the cities. These analyses utilized the largest urban biodiversity database to date, showing that large, globally comparative studies can inform management and practice within cities, but also that we still have a limited understanding of how humans influence community assembly processes, particularly at finer scales.

It may seem tautological to assert that humans have an influence on urban biotic communities, because humans by definition are the dominant species in urban settings. However, the bioregional context, climatic conditions, and local biophysical variables remain important factors in determining species distributions, even in cities (Aronson et al. 2014). Quantitative evaluation is needed of the relative influences of anthropogenic factors, such as historical settlement patterns, urban growth forms, management, and human culture and socioeconomics vs. the usual biophysical drivers of biodiversity. Understanding the relative roles of abiotic, biotic, and anthropogenic filters that shape local communities will provide a deeper understanding of community assembly theory and lead to practices that ensure the future of sustainable and biodiverse cities. In this paper, we introduce a new conceptual framework for understanding the filtering processes that mold diversity of urban floras and faunas, briefly discuss these filters, and provide new directions for future research.

Hierarchical Filters Determine Species Composition

We employ a commonly used framework in community assembly theory, that of hierarchically imposed filters through which species must have the appropriate traits to pass in order to colonize or persist in a community (Poff 1997, Ackerly and Cornwell 2007, Williams et al. 2009, Morin 2011). A key difference between urban biotic communities and non-urban ones, however, is that urban communities are shaped in complex ways by human values, preferences, and activities (Williams et al. 2009, Warren et al. 2010, Swan et al. 2011). Consequently, we hypothesize that the biota of cities are shaped by a hierarchical series of environmental, biotic, and anthropogenic filters that determine species composition at different spatial scales (Fig. 1), and that the strength and direction of the influence of these filters is different across taxonomic groups. We hypothesize that the following hierarchical series of filters (Fig. 1) influence species distributions in cities: (1) regional climate, biogeography, and land use; (2) human mediated biotic interchange; (3) urban form and development history; (4) socioeconomic and cultural influences; (5) local human facilitation; and, (6) species interactions. Aside from these filters, life history and functional traits of species are important in determining community assembly (Morin 2011) and act at multiple spatial scales. We build upon a framework designed for analyzing the filtering effects of urbanization on emergent floras (Williams et al. 2009) by including additional scales of analysis, taxonomic groups, and anthropogenic processes. Comparing the differential influence of these filters among cities and geographic regions will help identify global patterns and processes as well as the relative contributions of environmental and anthropogenic filters to species composition. Use of this framework will provide new insights into the ways that humans modulate community assembly in urban areas as well as identifying key points of entry for managing urban biodiversity.

Species pools

All communities are assembled based upon the species pools available. In our model, we have identified three main species pools that are affected by urbanization: regional, city, and local. The regional pool consists of the species that exist within the bioregion and represents all potential species that could have the opportunity to exist in a city, including both native and non-native species. The city pool represents the pool of species that have been filtered from the regional pool and other species that have been introduced via human activities, either intentionally or unintentionally, and exist within the city. Finally, the local pool are those species that are filtered from within the city pool and exist at a discrete location within the city, such as a park, roadside, or residential yard. The local pool is primarily where species interactions occur.
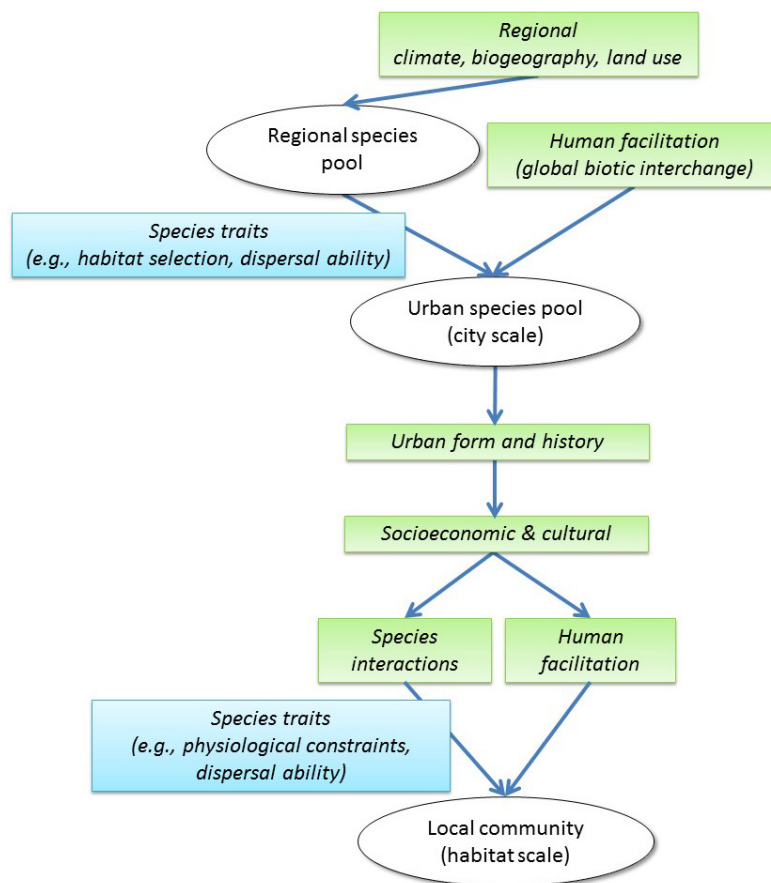
Fig. 1.   Community assembly of urban species pools is determined by a series of hierarchical filters (modified from Morin 2011). Green boxes represent the filters hypothesized to be important determinants of species distributions at different scales. White circles represent species pools. Species life history and functional trait filters are represented in blue boxes.

Filters of Community Assembly in Cities

Regional climate, geography, and land use

At the global scale, spatial variation in species richness correlates with a number of interrelated geographic and climatic factors, such as climate, latitudinal gradients, energy, and water availability (Gaston 2000, Hawkins et al. 2003). Within this framework, species-energy theory suggests that local to global climate patterns result in the spatial distribution of energy availability, which in turn influences the potential capacity of ecosystems to support the number of individuals and their variety. Although relationships between energy availability and species richness are often complex (Mittelbach et al. 2007), the consensus indicates that potential energy is the main driver of species richness (Hansen et al. 2011).

However, this current framework of understanding species distributions and abundances may be overly simplistic and based on system potential and average effects that neglect anthropogenic drivers and urban ecosystems. In fact, these relationships may be modified by global climate change and land cover, particularly fragmentation of natural habitats and built land covers. For example, cities are well known to be urban heat islands, affecting species distributions and biotic interactions (Parris and Hazell 2005, Youngsteadt et al. 2014), and many plant and animal species have been documented in cities outside of their natural climatic range. By expanding the current species-energy framework to evaluate how human influences on the landscape affect geographic and climatic drivers of regional biodiversity, we can refine a core concept in ecology and provide needed information for conservation.

At the regional scale, human history and land use practices have a strong influence on modern species composition (Foster et al. 2003). Throughout history, people have manipulated disturbances and altered land cover, influencing not only the species present, but also ecosystem structure and function for subsequent decades or centuries (Foster et al. 2003). Both past and present land use practices within the region therefore influences the regional species pool, and in turn the pool of possible species that can be found in the city. For example, past agricultural practices in the region influences archaeophyte distribution in cities (La Sorte et al. 2014).

Regional species pools are also the product of contemporary landscape change and global climate change. These two sources of change are expected to drastically alter regional species pools into no-analog communities, as suggested with models of future North American bird distributions (Stralberg et al. 2009). Thus, while some birds may be more resilient to climate change, particularly warming, in fragmented and built areas than those communities found in contiguous habitats (Jarzyna et al. 2015), others may not be as resilient. On the other hand, biodiversity in cities may be more vulnerable to climate change with interacting effects of the urban heat island and reductions in air quality (urban forests; Ordóñez and Duinker 2014). Cities can act as natural laboratories for examining the effects of global climate change on ecological, ecosystem (Youngsteadt et al. 2014), and evolutionary processes.

Global scale human facilitation filter

City species pools are not only affected by human mediated biotic interchange operating regionally but also across broad geographic extents. Global human mediated dispersal of species has resulted in the introduction and establishment of non-native species (La Sorte et al. 2007). In cities, this process has led to the assembly of novel communities consisting of native and non-native species. As such, we need to understand historic and current global connectivity via global trade of cities as driving factors in the biotic interchange of species. Although connectivity among cities, particularly trade routes, has been well studied in the human geography literature (Guimera et al. 2005, Woolley-Meza et al. 2011), it has not been widely incorporated into analyses of urban biodiversity. Previous analyses have suggested that human facilitated movement of plants has been primarily unidirectional from Eurasia to the rest of the world (with few exceptions) and that species introduced from Europe, in particular, act as homogenizing source among cities, indicating the importance of European settlement and commerce on patterns of global biodiversity (La Sorte et al. 2007, 2014). However, these homogenizing forces have yet to be studied across taxonomic groups. Determining the importance of human-mediated biotic interchange on biodiversity within and among cities is important for biological conservation as well as natural resources management.

Urban morphology and history filter

A recent global scale analysis found that species richness of birds and plants is predicted primarily by anthropogenic features related to city age and the percentage of urban and remnant vegetation land cover (Aronson et al. 2014). In this study, bird species loss was greater in cities with a greater proportion of urban land cover surrounding the city center. However, for plants, species loss is ameliorated in older cities with more remnant vegetation cover in the surrounding landscape (Aronson et al. 2014). Because the analysis in Aronson

et al. 2014 was applied primarily to developed cities in temperate realms, it is not known whether these patterns hold for developing cities in subtropical and tropical realms. Studies from cities in Latin America provide mixed evidence, with some patterns matching those in temperate regions and others being distinct (Ortega-Álvarez and MacGregor-Fors 2011).

Urban areas typically consist of a matrix of built surfaces with interspersed habitat patches of green (parks, gardens, remnant habitats) and blue (rivers, lakes, ponds) spaces. The amalgamation of these components gives each city its characteristic morphology and determine the space available for biodiversity (Sanders 1984). Literature on biotic homogenization suggests that the common features of cities—impervious surface, fragmentation of green space, high rates of disturbance from human activities, area dedicated to lawn—create conditions that promote the selection of species with similar traits and life histories. Yet, each city is unique because of its development history, demographics, cultural attributes, types and density of infrastructure, and the amount and connectedness of green space (McKinney 2006, Groffman et al. 2014, Parker 2015). While unique, comparative analyses of cities allow ecologists to discern the influence of each of these attributes on species assembly (e.g., Aronson et al. 2014). The interaction and spatial arrangement of these components leads to distinct urban biotic communities within sectors of a city with differing land use and land cover (Nilon et al. 2009). Additionally, the same land use/land cover type across the city may support different biotic communities. For example, low density residential areas typically contain a mixture of built structures, intensively managed green space, and unmanaged green space leading to distinct assemblages of plants and animals within each (Threlfall et al. 2015).

Species responses to habitats also differ based on the spatial arrangement of land use and cover (e.g., Pautasso et al. 2011, Harrison and Winfree 2015). For example, mammal diversity in urban areas is heavily influenced by the dispersal potential of the species and complexity of the urban landscape. Various species of ground-dwelling rodents, some species of sciurids, and lagomorphs have limited dispersal in urban areas. Populations of these species are often isolated in green space patches because they cannot inhabit or traverse the adjacent urban landscape (Munshi-South 2012). This renders small mammals with low dispersal potential especially sensitive to local extinction due to the intensity and type of human activities and poor connectivity because of structures and roads associated with urbanization (Baker and Harris 2007, Croci et al. 2008b). The dispersal limitation of small mammals is in contrast to larger species such as white-tailed deer (*Odocoileus virginianus*), coyote (*Canis latrans*), or red fox (*Vulpes vulpes*) that have a greater dispersal capacity due to their size and mobility (Baker and Timm 1998, Nielsen et al. 2003, Warren 2011). These species often reach elevated densities when compared to their non-urban conspecifics (Parker and Nilon 2008).

While certain species may thrive in individual patches, overall diversity within those patches can be greatly reduced because of competition, predation, and stochastic events such as disturbances and habitat degradation (Parker and Nilon 2012).

Many unanswered questions remain as to what are the finer scale patterns and drivers of urban biodiversity and how cities affect plant and animal community assembly (McDonnell and Hahs 2013, Chown and Duffy 2015, Isaksson 2015). Quantitative evaluation is needed of the relative influences of urban morphology and historical settlement patterns on species distributions, as there is some initial evidence that these factors may influence local plant species extirpation rates (Hahs et al. 2009) and the homogenization of tree cover (Bigsby et al. 2014). Global comparative analyses of urban morphology are essential not only to identify the urban forms that best support multiple elements of native biodiversity but also to inform decisions related to urban planning and the conservation of biological diversity.

Socioeconomic and cultural filter

Human activities, conditioned by socioeconomic status, institutional influences, and cultural preferences, act as a fine scale filter for species composition at neighborhood and parcel scales (Lepczyk et al. 2004a, Warren et al. 2010, Swan et al. 2011). Social scientists have generated rich, and sometimes conflicting, bodies of knowledge and theory related to human social dynamics and environmental quality in cities (reviewed in Warren et al. 2010). One key process, social stratification, links wealth and environmental quality, predicting the unequal distribution of resources in different regions of a city, partly due to differential access to power by residents of higher socioeconomic status (Warren et al. 2010). Direct tests in a handful of studies show evidence for the predicted pattern of environmental quality and ecological quality following economic wealth for a variety of taxa, including birds, mammals, herpetofauna, aquatic invertebrates, and plants (Whitney and Adams 1980, Nilon and Huckstep 1998, Hope et al. 2003, Kinzig et al. 2005, Overmyer et al. 2005, Lubbe et al. 2010, Smallbone et al. 2011, Lepczyk et al. 2012). While it is tempting to generalize the relationships between local scale biodiversity and wealth from this growing body of examples, we highlight here several challenges to this generalization. First, there are currently no quantitative comparisons of socioeconomic-biodiversity relationships across cities globally. Second, most studies to date have been conducted in temperate regions of the northern hemisphere with few studies in sub-tropical and tropical systems, the southern hemisphere, and developing countries (but see Lubbe et al. 2010, MacGregor-Fors et al. 2010, Cilliers et al. 2012, 2013, Gatesire et al. 2014). Finally, studies conducted to date are strongly biased taxonomically, with far more work on plants and passerine birds, compared to other taxonomic groups that are often represented by only a single study (Warren et al. 2010).

A number of examples exist that fail to demonstrate the predicted increase in biodiversity with increasing socioeconomic status (e.g., Loss et al. 2009, Kendal et al. 2012b, Matteson et al. 2013, Meléndez-Ackerman et al. 2014). These counter examples point to a need for a more sophisticated understanding of the interactions of time (i.e., lag effects), land use, and social and cultural attributes (Warren et al. 2010). For example, in South Africa, large residential house yards in poor areas on the urban fringes provide important ecosystem services due to the retention of many native plant species including medicinal and native food plants (Cilliers et al. 2012). Within more densely developed portions of South African cities, however, lower plant species richness is found in poorer areas (Lubbe et al. 2010), due to smaller yard sizes with lower vegetation cover and the legacy of racial segregation during apartheid (Cilliers et al. 2013). Similar legacy effects of racially driven policies can be found in U.S. cities, such as Baltimore, Maryland, New York, New York, and New Haven, Connecticut (Boone et al. 2009, Grove et al. 2014, Locke and Baine 2014), but these studies have only examined the relationships between neighborhood social conditions and woody plant cover. The legacy effects of social change, such as racial or ethnic segregation, and the time lag between social change and biotic compositional change remains greatly understudied in both developed and developing countries.

Methodological challenges have contributed to the lack of global comparative studies across cities that examine relationships between socioeconomics and biodiversity. Median household income is often used to characterize socioeconomic status (e.g., Hope et al. 2003, Loss et al. 2009, Lerman and Warren 2011). In developing countries, however, this information either does not exist or is not always reliable. Property value, increasingly available from commercial real estate databases and tracked at a finer temporal resolution than census data, may be an effective alternative measure that can shed light on how biodiversity is distributed in relation to socioeconomics (Reid 2011). Furthermore, aspects such as unemployment rate, schooling status (% individuals with no schooling), household size, and access to basic services to characterize the socioeconomic status of residents have been successfully used in South African cities (Lubbe et al. 2010). Thus, an important component of a global research agenda on biodiversity filters in cities is developing protocols and tools to reconcile socioeconomic data within and across different countries.

Local-scale human facilitation filter

People design and manage landscapes at the scale of individual land parcels (Lepczyk et al. 2004a, Gaston et al. 2005, Goddard et al. 2010), thereby controlling many characteristics of community assembly at finer scales. Signatures of individual human values can be

detected in some features of individual yards (Kendal et al. 2012*a*), such as more pro-environmentally oriented residents having more structurally complex gardens (Van Heezik et al. 2013) or reflecting the native landscape (Goddard et al. 2013), compared to simplistic gardens of large swaths of turf grass lawn with few trees and shrubs. However, a variety of social processes, interacting across scales, influence human decision-making at the parcel scale. Aesthetics, cultural traditions, and social norms are important drivers of yard and garden management decisions. City and neighborhood scale processes of governance (e.g., water-metering, city ordinances, Home Owner Association regulations) also shape or constrain the actions taken by individuals (Martin et al. 2003, Lerman et al. 2012). Likewise, broader scale economic conditions (recessions and/or growth periods) and market availability (plant species in nurseries; Pincetl et al. 2013, garden technology; herbicides/pesticides; Muratet and Fontaine 2015) also affect the options available to individuals (Ignatieva 2011). Thus, yard management decisions are driven by interactions among individual homeowners, communities, landscaping/gardening service providers, and local nurseries, and control the dominant features of urban habitats at finer scales (Lerman et al. 2012, Goddard et al. 2013).

Human landscaping decisions thus create and maintain the basic elements of most urban habitats both in terms of physical structure and composition of vegetation. Horticultural plantings are the primary means of introducing non-native species into urban environments (Reichard and White 2001). Spontaneous growth of plant species occurs in the interstices of these managed landscapes depending on the degree of control exercised by human management. The gradient in intensity of human control produces a highly heterogeneous urban landscape with individual parcels varying between highly manicured lawn-gardens (with heavy watering, frequent mowing, fertilization and trimming, removal of leaf litter, and more non-native horticultural species) to "wild" gardens (less lawn, more native plantings, wildflowers, and water-wise gardens). Species composition is further influenced by the use of herbicides and physical removal of unwanted ("weed") species. This fine-scale filter therefore has a marked influence on the assembly of plant communities across urban scales.

The occurrence of native animal species depends on available, juxtaposition, and configuration of habitat resources, human tolerance of animals, competition and predation from non-native species, and individual species' tolerances. Humans deliberately remove undesirable animal species (e.g., rodents, insect "pest" species), and also deliberately attract desirable species (e.g., birds, butterflies) by supplementing resources, such as water, shelter, and food. For example, supplementary bird feeding in yards is widespread in many countries and can restructure urban bird communities (Galbraith et al. 2015) and influence bird abundance at regional scales (Fuller et al. 2008, 2012, Zuckerberg et al. 2011). Bird feeding may also relate to socioeconomic status, although the degree to which has shown mixed results as feeding has been related to socioeconomic status in some cases (Fuller et al. 2008), but not others (Davies et al. 2012, Lepczyk et al. 2012, Goddard et al. 2013). Understanding the relationship between wildlife-oriented activities in gardens and yards and socioeconomic, demographic, and cultural factors is vital for understanding both basic ecological phenomena, such as altered trophic dynamics (Faeth et al. 2005, Fischer et al. 2012), as well as for enhancing human-wildlife interactions in cities.

The local-scale human facilitation filter is also dynamic, reflecting potentially sudden changes in aesthetic preferences, policies, economic conditions, and markets. As such, this filter can change the suitability of habitat for particular species over very short time scales, altering both the distribution and abundance of species at the local habitat scale. For example, in Phoenix, Arizona, plant communities reflect the dynamic nature of human decisions. Ancient plant communities at archeological sites in Phoenix show distinct spatial variation in species composition in relation to human settlement patterns hundreds of years ago (Hall et al. 2013). More recent human decisions, such as regulations on water usage, caused a radical transformation of the urban residential landscape whereby lawns across the city disappeared and were replaced by xeric plant species in both Phoenix and Tucson, Arizona (Zube et al. 1986, Hope et al. 2006). Sudden changes in human landscaping or management can have profound and lasting effects on the success or failure of different species in the urban landscape.

Species interactions filter

At the local scale, species interactions are an important filter on the composition of species. However, in urban areas, novel associations of introduced and native plants, herbivores, pollinators, insectivores, detritivores, and carnivores change how these species interact and therefore what species will be found in any given local habitat. Cities are epicenters of species introductions (Pyšek 1998) and have been shown to support higher non-native species richness than surrounding rural areas (McKinney 2008, Aronson et al. 2015). Interactions among invasive and native species plays a strong role in filtering species and their distributions. Competitive effects of invasive plant species often result in reduced growth of co-occurring native plant species and reductions in local plant species diversity (Vilà et al. 2011). Non-native species plantings cause changes in insect community composition (Burghardt and Tallamy 2013), which may affect higher trophic levels. New interactions between introduced and native animal dispersers and plants also influence the composition of plant communities. For example in southeastern Australian cities, native (Pied Currawong—*Strepa graculina*) and introduced (Blackbird—*Turdus merula*) bird species disperse the fleshy-fruited invasive native shrub *Pittosporum undulatum,* which changes urban

bushland soil nutrient levels and plant composition to be dominated by more mesic, shade-tolerant and introduced species, particularly at patch edges (Gleadow and Ashton 1981, Gleadow 1982, Rose and Fairweather 1997).

Ecological network studies, such as plant-pollinators networks, have demonstrated shifts in network structure with urbanization for a range of taxa. For instance, a comparison of plant-pollinator networks across the United Kingdom habitats found that pollinator communities in urban areas had higher generality (i.e., they visited a greater number of plant species) but also higher specialization (i.e., they visited a lower proportion of available plant species) compared to pollinator communities in non-urban habitats, due to the higher species richness of non-native plants in cities (Baldock et al. 2015). The higher generality of pollinators in urban habitats could reduce pollinator efficiency with negative consequences for plant fitness (Geslin et al. 2013, Irwin et al. 2014, but see Verboven et al. 2014). Other trophic interactions can also break down in urban habitats, such as between hosts, parasitoids, and parasites (Nelson and Forbes 2014, Calegaro-Marques and Amato 2015), between songbirds and nest predators (Rodewald et al. 2011, Fischer et al. 2012), and between birds and their arthropod prey (Faeth et al. 2005, but see Bang et al. 2012). Human activities for encouraging wildlife can also have indirect effects on non-target species. For instance, supplementary bird feeding has been associated with decreased population size and survivorship of arthropods in gardens via increased predation (Orros and Fellowes 2012).

Interactions between domestic and wild species, such as those between predator and prey, are also important determinants of mammalian and avian diversity in urban settings. The domesticated cat (*Felis catus*) has been identified as a major contributor to the decline of biodiversity in urban areas throughout North America (Lepczyk et al. 2004b, Loss et al. 2013), South Africa (Tennent and Downs 2008), Europe (Hilton and Cuthbert 2010), islands of the Pacific Ocean (Medina et al. 2011, Duffy and Capece 2012), and Australia (Calver et al. 2011). In all regions, domestic cats, whether pets let out to roam at night or free living and feral, pose serious threats to the diversity of various groups of urban fauna (Loss et al. 2013, Lepczyk et al. 2015). Globally comparative studies are needed to understand how these species interactions are affected by higher-level filters and influence community assembly.

Species traits

Species traits govern how these aforementioned filters determine species pools. Elucidation of the traits of species that succeed in cities enables us to understand how cities filter species at the regional, city (i.e., urban species vs. non-urban species), and local scales, which govern community assembly and composition in different urban land use types and intensities. A better understanding of life history and functional traits and

their underlying adaptedness or adaptive potential improves process-based understanding on how species and communities respond to strong environmental gradients and high disturbance frequencies—both of which are prevalent in urban landscapes (McDonnell and Hahs 2015). While the evolutionary responses of species in cities is a new area of research, studies suggest that some species are capable of rapidly adapting over only a few generations to the resources, stressors, and habitats in cities (Cheptou et al. 2008, Harris et al. 2013). Cities share common features such as fragmented natural habitats and a high proportion of impervious surfaces. Consequently, cities may be expected to harbor assemblages of species that share common traits or life history characteristics that increase their fitness in urban areas. Life history and functional traits determine how species response to the unique abiotic conditions present in cities such as air, water and soil pollution, soil compaction, and the urban heat island.

Plant survival, growth, reproduction, and dispersal within specific environments are largely determined by their life history and functional traits (Shipley et al. 2006). Many plant traits show inconsistent responses to urbanization. Traits associated with plants growing in human settlements include being biennial or perennial, C-strategists (competitors), wind-pollinated, flowering in mid-summer, reproducing by seed and vegetatively, dispersing by wind or humans, and having a high demand for light and nutrients (Lososová et al. 2006). Other studies have found that urban plants exhibit traits such as non-native origin, tolerance of fertile, dry and alkaline soils, heavier seed mass, endozoochory, greater plant height, and annual lifespan (Aronson et al. 2007, Thompson and McCarthy 2008, Duncan et al. 2011). Few clear patterns have emerged from existing individual city or urban habitat plant trait studies due to the complexity of plant-environment interactions in urban systems and limitations of existing data and methods (Williams et al. 2015). Others, including those commonly reported in plant functional trait ecology studies, such as specific leaf area (SLA), have not been examined frequently enough in urban areas to permit generalization. There is evidence that there is no single urban syndrome (i.e., combination of traits) that accounts for all the kinds of species that thrive in cities, but rather a suite of related syndromes (Williams et al. 2015). Natural history and basic ecology of urban species is needed to identify and understand these syndromes.

Omnivory, sedentariness, and a broad geographic range are important for urban birds (Croci et al. 2008a, Evans et al. 2011). A number of studies have supported broad separation between bird species that persist in urban landscapes and those which decline, generally through the use of multiple trait groups or correlations (Croci et al. 2008a, Conole and Kirkpatrick 2011). Importantly, single traits have rarely been found that offer consistent separation between species that are well adapted to urban environments, and those which perform poorly (Kark et al. 2007,

Croci et al. 2008*a*). For instance, large birds with low frequency vocalizations may be excluded from noisy urban areas whereas smaller birds with high frequency vocalizations may persist (Francis et al. 2011). Furthermore, some birds fall into neither category but differ from both groups based on traits (Lepczyk et al. 2008). Whether consistent trait based relationships extend across multiple urban areas in different biomes remains unknown.

Particular life history and functional traits govern species response to filters across multiple spatial scales. For example, dispersal traits enable species to pass from the regional species pool to the city pool to habitat units. Many bird dispersed plants move successfully across urban landscapes and within cities (Robinson and Handel 1993, Aronson et al. 2007). On the other hand, at the local scale, lower dispersal ability in plants may be highly selected for (Cheptou et al. 2008). But for carabid beetles, flightless species are more common in rural environments and species capable of flight are found more commonly in urban environments (Niemelä and Klotze 2009). Similar results have been found for other ground dwelling arthropods (Vergnes et al. 2014), indicating that the urban environment may select for species with greater dispersal ability. Dispersal traits ultimately determine the ability of a species to arrive within a habitat and therefore deserve more attention to understand community assembly rules in urban landscapes.

To understand how traits govern filters, globally comparative trait databases are needed. Global databases of life history traits currently do not exist for most taxa and there is currently only a global trait database available for plants (e.g., TRY; Kattge et al. 2011). Regional databases also exist for plants, fish, birds, bees, and bats, but not all are in the public domain. Initiatives and funding to compile these existing trait databases are necessary.

Conclusions

Humanity is poised at a critical window for defining the form of future urban environments (Seto et al. 2012). Cities are surprisingly biodiverse (Aronson et al. 2014, Ives et al. 2016), but with continuing rapid urbanization, we need a better understanding of the processes assembling the biotic communities we find in cities. Understanding whether community assembly is similar across taxa and among cities is critical for both ecological theory and successful science-based planning and management decisions. However, there is a strong taxonomic bias in the published literature on species communities in cities. Further studies on underrepresented groups may elucidate how these filters act and interact to determine urban communities.

To understand the role of environmental and anthropogenic filtering in urban biotic communities, comparative, global collaborations are necessary. For instance, UrBioNet: A global network for urban biodiversity research and practice (http://urbionet.weebly.com/), funded by the U.S. National Science Foundation, has been established to develop a network that brings together researchers, practitioners, and students with an interest in biodiversity in cities. The network provides a forum for discussion, data sharing, and collaboration on topics relevant to urban biodiversity research, management, design, and planning. These collaborations provide opportunities to build global datasets on: (1) key variables for each filter; (2) regional, citywide, and local species pools; and (3) life history and functional traits for species in these databases. Furthermore, most of our understanding of urban biodiversity comes from cities in the northern hemisphere. There is an immediate need for better compilation and monitoring of urban biota in areas of high regional biodiversity, such as tropical cities. The majority of new urban areas will be in developing countries, many of which are in tropical regions (Müller and Werner 2010, Seto et al. 2012).

Our conceptual framework proposes that community assembly in urban ecosystems is affected by a series of filters, each of which has a substantial human-driven component. Cities are unusual in the degree to which human facilitation has a strong influence on what species make up local communities and are ideal for studying contemporary ecological patterns and processes. Understanding how humans influence community structure and processes will aid in the management, design, and planning of our cities to best support biodiversity.

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CONCEPTS & SYNTHESIS