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Incorporating human behaviors into theories of urban community assembly and species coexistence

Editor's OIKOS Choice

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In cities, humans directly and indirectly affect plant and wildlife communities. These human–species interactions are not included in traditional ecological approaches used to understand why and how organisms are distributed. Here, we incorporate human behaviors into urban community assembly theories and detail all the complex ways humans affect the dispersal, selection and persistence of species in cities. To do this, we integrate human behaviors and actions into traditional filter frameworks used to study community assembly. We use our framework to develop testable hypotheses to predict patterns of urban diversity as well as pose key considerations for future research. In order to have a predictive understanding of how urban biodiversity responds to environmental, social and land use change, it is necessary to better understand interactions between humans and other organisms.

Keywords: cities, dispersal, management, selection, urbanization

Introduction

Although cities were once thought of as virtually devoid of biodiversity, by the late 1990s it was well established that many species live in cities (Sukopp 1998). In fact, species diversity of plants (Pautasso and McKinney 2007, Müller 2011, Pearse et al. 2018, Avolio et al. 2020), arthropods (McIntyre 2000) and birds (Callaghan et al. 2019) can be higher in cities than surrounding less urbanized areas. Given the wealth

> **Synthesis**
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> Human behaviors impact how ecological communities assemble in cities in a myriad of way, which makes studying urban community composition both challenging and exciting. Here, we develop a filters framework to understand urban community assembly that focuses on how human behaviors affect dispersal and selection of plant, animal, and microbial species in cities. We differentiate between naturally versus human dispersed species pools and include commercial viability and manager species selection as filters in addition to dispersal ability, environmental conditions, and biotic interactions.

of biodiversity found in cities, and the continuing growth of cities (Grimm et al. 2008), it is important to understand what controls patterns of urban biodiversity within and among cities. We broadly define urban biodiversity as the types and distributions of species in cities. It is well established that species in cities are directly and indirectly affected by humans (Müller et al. 2013). Consequently, applying theories of community assembly developed for areas with minimal human impact overlook key processes in urban areas because they do not consider human behaviors – broadly defined here as the ultimate actions of humans that are influenced by a suite of internal and external factors. In fact, there is a recognized need for better understanding the mechanistic processes of community assembly in urban areas, beyond just describing patterns (McDonnell and Hahs 2013), by directly incorporating human actions, behaviors and agency into ecological theory (Groffman et al. 2017, Sagoff 2017, Pataki 2019).

Theories of community assembly aim to understand the mechanisms of species coexistence in space and time. In natural ecosystems, a series of filters have been proposed that determine community assembly and narrow the range of possible species that can occur at a given location through the influence of biotic and environmental effects on growth, reproduction and mortality (Diamond 1975, Weiher et al. 2011, HilleRisLambers et al. 2012). Vellend (2010) and his subsequent book (Vellend 2016) organize the contemporary theory of community ecology into four processes: dispersal, selection, drift and speciation. Dispersal is the movement of individuals among local assemblages in space, predominantly, and time, in the case of diapause. Urbanization can affect the ability of species to disperse across the landscape. For example, densely urban areas can impede arthropod dispersal (Egerer et al. 2017). Selection refers to whether species can tolerate local conditions, typically called 'environmental filtering', and any subsequent biotic interactions. Selection processes are influenced by urbanization, such as similar yard management may be selecting for unmanaged species with similar traits (Knapp et al. 2012). Ecological drift is the random change in species abundances, and alone can explain significant variation in species diversity patterns (Leibold and McPeek 2006). For example, drift explained earthworms community composition in urban lawns (Tiho and Josens 2007). Lastly, speciation is the evolution of new species, and there is evidence that species are evolving in cities (Lambert et al. 2021). Here we focus on dispersal and selection, which we hypothesize are most strongly influenced by human behaviors in ways that existing ecological theory does not yet fully encompass. Nonetheless, urban communities may also be affected by drift, and increasing evidence suggests rapid evolution in cities may also alter patterns of biodiversity.

In order to translate community assembly theory to cities, human behaviors need to be incorporated into such theoretical frameworks. We focus on behavior to encompass actions that are the outcomes of decisions, which can be influenced and limited by a range of factors, including preferences, economic constraints and institutional rules and norms. We suggest that drivers of people's behaviors are complex and highly variable over space and time, a result, predicting patterns of biodiversity at local, regional and inter-habitat scales is difficult, but not impossible. We suggest predictions can be improved by incorporating human behaviors into expanded theories of urban community assembly and species coexistence. In this paper we review drivers and patterns of urban biodiversity and summarize current frameworks to explain urban biodiversity. We then integrate this knowledge into a synthetic framework for understanding urban biodiversity patterns that is explicit about the role of human behaviors. Finally, we utilize this framework to address the complexity of land uses across urban ecosystems and propose hypotheses about patterns of urban biodiversity that should be tested across a wide range of urban ecosystems to gain a fully mechanistic understanding of urban community assembly.

Urban biota and diversity patterns are related to management actions

From microbes to mammals (Fig. 1), recent studies show that cities are teeming with diverse taxa. There is increasing evidence that urban microbial communities cover nearly every surface, including animals, plants and engineered materials, and are ubiquitous in the atmosphere, soil and water (Cáliz et al. 2018, Gilbert and Stephens 2018). Plants are found growing in diverse human-dominated habitats ranging from roof tops to crevices in walls (Cervelli et al. 2013) to planted gardens and street trees (Avolio et al. 2020). Invertebrate species are abundant and diverse both aboveground – on the soil surface, in the litter and on plants (Smith et al. 2006) – and belowground (Joimel et al. 2017, Szlavecz et al. 2018). Pets, particularly cats and dogs, are very abundant (Matheson 1944) and their effects on communities (van Heezik et al. 2010) and ecosystem processes (Hobbie et al. 2017) may be underappreciated. Other vertebrates, such as rodents and birds, tend to live in more vegetated areas (Beninde et al. 2015), and green areas tend to support abundant (Gallo et al. 2017) and diverse (Alvarez Guevara and Ball 2018) vertebrates communities. Given the abundance and diversity of non-human taxa, there is a need for testable theories of spatiotemporal variability in observed urban biodiversity patterns.

There are several well recognized drivers of patterns of species diversity (Gaston 2000, Field et al. 2009), many of which also apply in cities across a range of taxa (Kowarik 2011, Beninde et al. 2015; Table 1). For example, within a city, larger patches are home to more species (Table 1). In addition, within cities many species respond to quality of habitat, in particular to plant assemblages, as vegetation provides resources for wildlife either as food, shelter or cover (Table 1). However, cities have additional variables, such as income and education of residents, that are correlated with the diversity of plants and vertebrates in many locations (Table 1). In addition, vertebrates have been shown to respond to built infrastructure and human resource
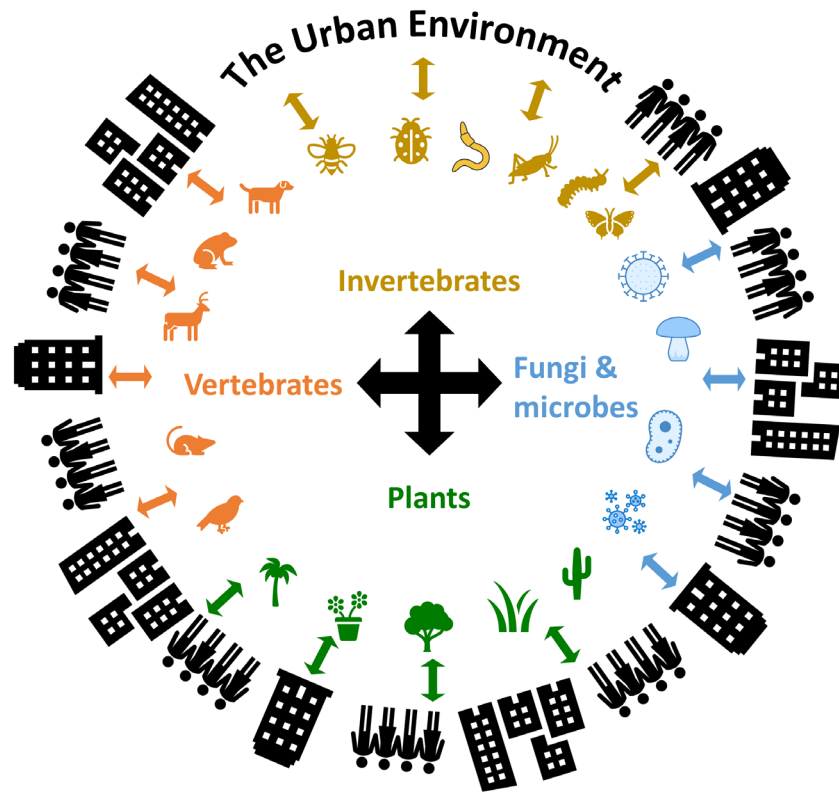
Figure 1. Cities are filled with species that interact with one another, humans, and built environment.

subsidies, such as bird feeders and refuse (Ditchkoff et al. 2006). These observations suggest that there are factors unique to cities that must be accounted for to understand and predict patterns of biodiversity within and across urbanized areas. Indeed, in a meta-analysis of intra-city biodiversity patterns, management intensity had a strong positive effect on overall diversity (Beninde et al. 2015).

The management, or control, of species in cities is both widespread and understudied (Groffman et al. 2017). Some populations of species can be under direct management by people. For example, commercially available soils are now amended with plant beneficial microbes (Deng et al. 2019). Plants are commonly affected by the active choice to maintain or eliminate species in managed spaces (Johnson and Swan 2014, Avolio et al. 2020), and by hybridization of new cultivars through horticulture (Trusty et al. 2009). In contrast to plants, invertebrates, typically insects, (Frankie and Ehler 1978, Robinson 1996) and vertebrates (Morzillo and Mertig 2011) are rarely under direct management unless they are considered pests, in which case they are managed to reduce population size. Most urban non-plant species are indirectly managed, often through planting practices. Intentionally designed butterfly and pollinator gardens are examples of indirect management of invertebrates through direct management of plants. To explain urban biodiversity patterns, it is therefore necessary to account for the complex ways in which humans manage organisms both directly and indirectly (Fig. 1).

Frameworks of community assembly in cities

Several frameworks have been developed that modify existing theories of community assembly to capture the complex interactions among humans, other organisms and the physical environment in urban areas. Most of these frameworks categorize assembly as a series of filtering processes, which despite critiques (Cadotte and Tucker 2017), remain a powerful approach for conceptualizing community assembly processes. For plants alone, Williams et al. (2009) suggested there are a series of filters in which species are successively lost during the process of urbanization, including habitat loss and fragmentation and ultimate degradation. Alongside these losses, preferred species are imported. There is some empirical support for these filters as drivers of urban diversity (Lopez et al. 2018), but few traits emerge as undergoing strong selection in cities, limiting the utility of such models to explain specific patterns and make predictions (Williams et al. 2015). Alternatively, Pearse et al. (2018) and Cavender-Bares et al. (2020) described a regional species pool that is the source of urban spontaneous species as well as a horticultural pool that is the source of urban cultivated species. Both pools can be subject to different types of management and are influenced by individual preferences.

Other frameworks for understanding urban patterns of biodiversity have not been limited to plants. Aronson et al. (2016) considered a series of hierarchical filters that affect assembly

Table 1. Studied drivers of urban biodiversity for different urban taxa. Please note this is not an exhaustive list of examples. An * denotes that this driver has also been established for non-urban systems.

Driver of biodiversity	Fungi and microbes	Plants	Invertebrates	Vertebrates
Area*		Nielson and Smith 2005, Beninde et al. 2015, Matthies et al. 2015	Insects: Smith et al. 2006, Beninde et al. 2015	Reptiles and amphibians: Dickman 1987; and birds: Beninde et al. 2015
Habitat connectivity*		Davis and Glick 1978, Beninde et al. 2015	Arthropods: Vergnes et al. 2012, Beninde et al. 2015	Mammals: FitzGibbon et al. 2007, Vergnes et al. 2013; and birds: Beninde et al. 2015
Landscape heterogeneity*		Dallimer et al. 2012	Butterflies: Dallimer et al. 2012	Birds: Dallimer et al. 2012
Time*		Martin et al. 2004, Boone et al. 2010, Clarke et al. 2013, Avolio et al. 2015b		
Income		Hope et al. 2003, Martin et al. 2004, Avolio et al. 2018, Chamberlain et al. 2020		Kinzig et al. 2005, Strohbach et al. 2009, Lerman and Warren 2011
Education		Kendal et al. 2012b, Avolio et al. 2015a		
Plant community*	Fungi: Newbound et al. 2010		Arthropods: Smith et al. 2006, Sattler et al. 2010, Vergnes et al. 2012, Burkman and Gardiner 2014, Philpott et al. 2014	Birds: Marzluff and Ewing 2001, White et al. 2005, Ortega-Álvarez and MacGregor-Fors 2009, Litteral and Wu 2012; and mammals: Gomes et al. 2011, Hale et al. 2012, Alvarez Guevara and Ball 2018
Native plants*	Fungi: Lothamer et al. 2014		Arthropods: Burghardt et al. 2009, Narango et al. 2018	

of the species pools of urban organisms, including environmental, and social, human cultural drivers that successively remove species based on their traits. Martin et al. (2004) and Kinzig et al. (2005) suggested that there are anthropogenic top–down (government decisions and rules) versus bottom–up (individual and household-scale choices) controls on urban diversity. Kinzig et al. (2005) hypothesized that both top–down and bottom–up filters would be stronger for plants, which are under more direct human control, than birds. Swan et al. (2011, 2017) introduced theories of meta-communities and turnover to processes of assembly for both species that self-assemble (termed spontaneous or volunteer) and those that experience facilitated assembly, such as human dispersed species. Andrade et al. (2020) expand on how socio–environmental interactions affect metacommunities to explain community assembly. Finally, Lerman et al. (2020) proposed a framework for animals diversity that notes the services and disserves of city wildlife can affect resident perceptions of wildlife and their resulting management. These perspectives all advance urban community ecology by highlighting the utility of broadening traditional ecological theory to encompass the interrelationships among humans, non-human organisms, and the built and biophysical environment (Fig. 1). Further, they point to the potential for a predictive understanding of how urban communities assemble.

Despite advancements in understanding the ways that community assembly differs in urban versus non-urban areas, our theoretical understanding of how specific human behaviors structure human dispersed organisms is limited. Using plants as an easily conceptualized example, it is clear that human behaviors are important. Plants have probably been cultivated in cities since urbanization first began (Kelcey and Müller 2009, Wilson et al. 2016). Today, horticultural cultivars undergo artificial selection for traits that facilitate urban human–environment relationships such as aesthetics, food production, ease of maintenance, floral abundance and longevity, and physiological tolerance of urban environmental conditions, e.g. compacted soils and the presence of pollutants (Gessert 1993, Wilson et al. 2016). These interactions, along with a complex suite of economic and social drivers, structure the cultivated species pool that is commercially available in a given location (Pincetl et al. 2013). Within the pool of species available for purchase in commercial nurseries, individual actors make choices to add or remove species according to institutional factors such as rules and ordinances (Larson et al. 2020); economic factors such as affluence and cost/benefit tradeoffs (Kinzig et al. 2005); cultural norms and design standards for urban gardens (Locke et al. 2018); and/or individual preferences for particular landscapes and plant traits (Avolio et al. 2018, Padullés Cubino et al. 2020). The effects of human behaviors are not limited to plants, and extend to all urban organisms. Given the range of factors that influence human behaviors and in turn directly and indirectly impact biodiversity, urban ecology is at a relatively

early stage of developing generalizable and predictive theory for cultivated landscapes in which human behavior is a dominant driver of species community composition. Sagoff (2017) calls for ecologists to expand their purview to include species whose dispersal and population is dominated by human actions. In cities, this is essential as the interrelationships between human actions and eco-evolutionary processes are driving forces that structure urban biodiversity.

Incorporating human behavior into an urban biodiversity framework

The application of filter frameworks to urban systems

Here we integrate disparate frameworks for urban community assembly to advance an integrated framework aimed at broadly explaining the composition of urban communities and making predictions about the distribution of species within a city. Our framework was developed based on literature largely from Euro-American cities, reflecting that Euro-American cities are the focus on most urban research. However, although fewer in number, similar findings are also found around the world. For example, Kendal et al. (2011), demonstrate that deliberately cultivated species planted for ornamental purposes are found in cites around the world, and Zhang and Jim (2014) suggest studying traits that deliver 'ecological amenities' desired by people are key to understanding urban tree biodiversity in Hong Kong. Further, studies in India (Jaganmohan et al. 2012), Burundi (Bigirimana et al. 2012), Turkey (Acar et al. 2007), China (Wang et al. 2015), and Tasmania (Kirkpatrick et al. 2007) all demonstrate the importance of human behaviors on patterns of urban biodiversity. Thus, we expect our framework would apply to any city, globally.

We start by recognizing two species pools: naturally dispersed and human dispersed (Fig. 2). Naturally dispersed species, which have also been called spontaneous, volunteer and self-assembled, are drawn from a regional species pool. Our term human dispersed is used in the same sense as in Bullock et al. (2018) – dispersal that is directly or indirectly impacted by anthropogenic activities – but also encompasses human-vectored dispersal (Bullock et al. 2018) – dispersal as the result of humans physically moving species. As noted in Bullock and Pufal (2020), while human dispersed species are often non-native, the term also includes native species. There are two types of human dispersed species: those that are intentionally dispersed, which have also been called cultivated and facilitated-assembled species, and those that are unintentionally dispersed and become a naturally dispersed species (see the below section 'Naturally dispersed versus human dispersed species' for details). Human dispersed species can be drawn from a much larger species pool, where species may be sourced locally or potentially even globally, given the extent of exotic species and the global horticultural trade (Pemberton and Liu 2009, Ignatieva 2011).

We hypothesize that dispersal processes will differ for naturally and human dispersed species (Fig. 2). Naturally dispersed species disperse according to their dispersal traits, and it is important to note that in the altered landscape of cities, the dispersal of all species are at least indirectly affected by humans (Bullock et al. 2018). Once brought to a region, unintentionally human dispersed species also disperse according to their dispersal traits. Intentionally human dispersed species will be brought to a region depending on their commercial viability, which reflects whether there are market incentives to bring a species to a region to try to sell it. Ideally, commercial viability is limited to whether it is legal to bring the species to market (although we recognize illegal importation of species occurs). Commercial viability will also depend on how easy it is to bring to market and sell in nurseries, pet stores, agricultural supply stores and other places of commerce, and whether there is a demand for the species. Next, selection filters narrow these species into local species pools (Fig. 2). We hypothesize there are three selection filters that affect all species to varying degrees: manager species selections, local environmental conditions and biotic interactions (Fig. 2). We broadly define managers as anyone making decisions about a given landscape such as choosing plants species to add or remove, and determining overall management of mowing, watering, fertilizing, herbicide and pesticide practices. Central to this hypothesis is the importance of human behavior. While not a direct filter, human behavior affects commercial viability, manager species selections, local environmental conditions and biotic interactions (Fig. 2). Importantly, there are feedbacks between commercial viability, manager species selection and environmental conditions, where, for example, what is offered for sale is affected by what managers want, and what managers want is affected by environmental conditions. We also note that manager species selections may be affected by the local biotic conditions, where people's experiences with their local species might affect their species selections (Engebretson et al. 2020). Together, we propose these filters account for the primary processes of how species at a given location arrive and coexist.

It is likely that the degree to which human behavior affects community assembly varies across three broad categories of human management: 1) minimal management, which include remnant patches and nature preserves; 2) low management, where there is little to no control of species composition, including park lawns, road medians, transportation right of ways and vacant land; and 3) intensive management, where more attention is paid to species composition, which generally include private yards, street and road right-of-way plantings, commercial and industrial landscapes, and highly maintained, or planted, park spaces. These different management approaches may lead to vastly different community assembly processes in intensively managed areas, where humans make decisions about habitat structure and species inclusion, versus minimally managed areas that are largely independent of human actions. Across this heterogenous landscape, all groups of organisms undergo community assembly, but the specific controls depend on coupled biophysical and human facilitated factors. Below, we explain
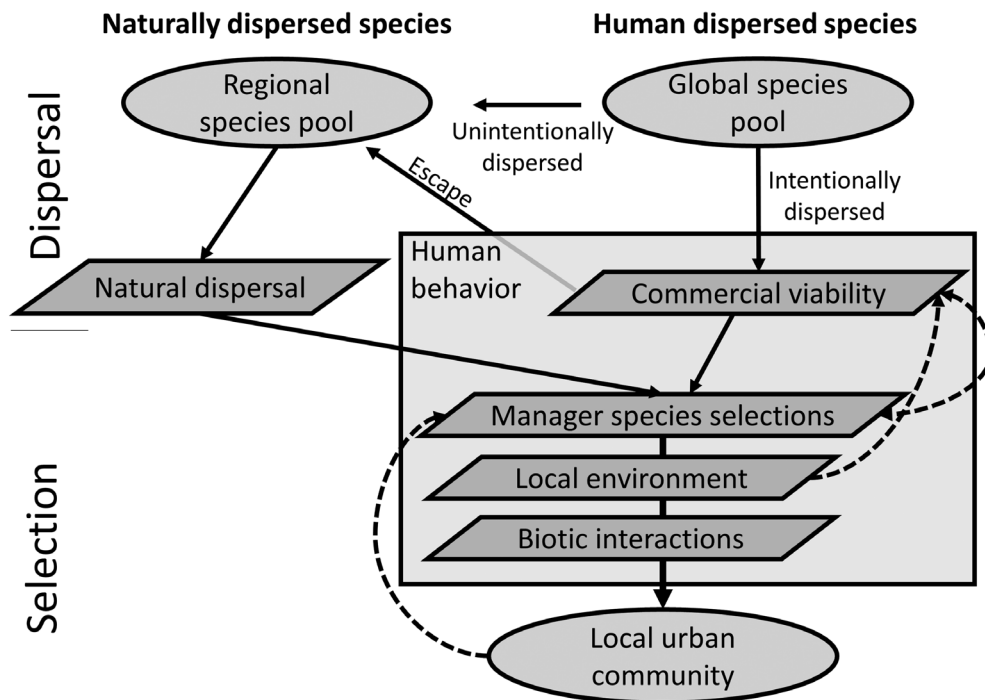
Figure 2. Overall conceptual figure of the filters in urban systems. There are two pools of species, naturally dispersed and human dispersed. Unintentionally human dispersed species and escaped intentionally human dispersed species become a part of the regional species pool. For naturally dispersed species, dispersal is limited by their dispersal mode. For intentionally human dispersed species, dispersal is limited by their viability in industry (ease to import and sell). Manager species selections determine which species are either brought into or removed from the landscape. Following these filters, are two traditional community assembly filters, local environmental conditions and biotic interactions, both of which are affected by human management in cities. Finally, human behavior can affect and is affected by commercial viability (store owners deciding what to sell), manager species sections, local environmental conditions and biotic interactions. Dashed arrows show feedbacks. Commercial viability is affected by manager species selections and the local environment, and what species managers select can change depending upon their experience with the local community.

these aspects of our filter framework in more detail, with associated hypotheses.

Naturally dispersed versus human dispersed species

There are both naturally dispersed and human dispersed species for virtually all organism types in cities (Table 2). Naturally dispersed species are sourced from the regional species pool, and successfully reproduce and maintain a population without direct human intervention. Naturally dispersed species are typically either urban exploiters that exist almost solely in urban environments (e.g. pigeons and

the brown rat) or adapters that thrive in urban environments (e.g. raccoons and dandelions; McKinney 2006), and can be native (e.g. present in a region pre-urbanization) or non-native. Human dispersed species can be sourced from anywhere in the world, either local or distant, and can become a source of non-native species in the regional species pool in two ways. First, when unintentionally human dispersed species can survive in local growing conditions, they disperse and become part of the regional species pool. Second, intentionally human dispersed species can escape and establish local populations. These are examples of vertebrates that have escaped the pet trade (Kraus 2003, Carrete and Tella 2008)

Table 2. Hypotheses of how the species pools and filters apply to different taxa in cities.

| Organism type	Species types: naturally or human dispersed	Commercial viability	Manager species selections
Fungi and microbes	Mostly naturally dispersed, including unintentionally human dispersed species	Weak filter: affected by horticultural and agricultural industries	Weak filter
Plants	High numbers of naturally and intentionally and unintentionally human dispersed species	Strong filter: cultivated plants are strongly affected by horticultural industry	Strong filter
Invertebrates	Mostly naturally dispersed, including unintentionally human dispersed species	Weak filter: affected by agricultural industry and horticultural industry	Strong filter
Vertebrates	Mostly naturally dispersed	Weak filter: affected by pet trade industry	Strong or weak depending on the species
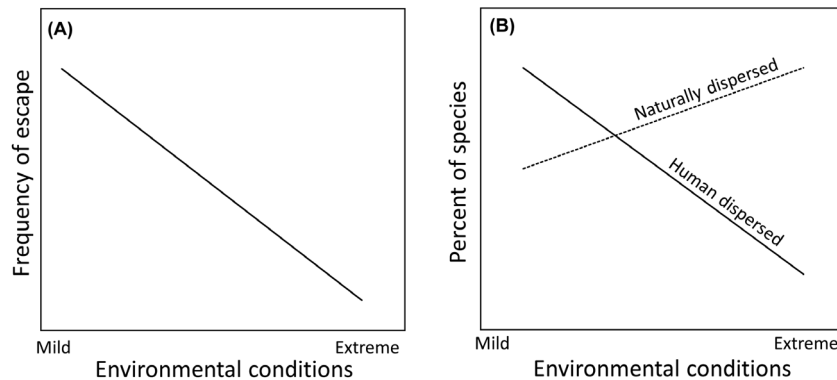
Figure 3. Hypotheses on how local environmental conditions affect frequency of human dispersed species escaping to the region species pool (A) and the proportion of species that are naturally or human dispersed (B).

and escaped horticultural plants (Reichard and White 2001, Kowarik 2005, Dehnen-Schmutz et al. 2007). We hypothesize that more human dispersed species will become part of the regional species pool in mild climates compared with more extreme climates because fewer species can physiologically withstand extreme climates such as deserts and temperate or boreal regions with cold winters (Fig. 3A). However, the degree to which human dispersed species will become a part of the regional species pool will also depend on local socio-environmental feedbacks.

Human dispersed species are typically cultivated plants, and in some cases are even human created species such as cultivars and hybrids (Gessert 1993, Wilson et al. 2016); however, human dispersed species are not limited to plants. For example, insects may be human dispersed to alleviate pest problems (e.g. ladybugs to eat aphids) or because they are prized (e.g. butterflies). Soil microorganisms and fungi are added to soils and dispersed to increase plant growth. Some intentionally human dispersed species cannot successfully reproduce and maintain populations without human intervention and are dependent on humans for their persistence, especially in more extreme environments. Intentionally dispersed species are most commonly bought from nurseries, agricultural supply stores or pet stores. The number of naturally versus human dispersed species differs depending on organism type (Table 2). We hypothesize that there will be more naturally dispersed species than human dispersed in extreme environments (Fig. 3B). In mild environments such as cities with non-freezing temperatures, more species may be human dispersed because many species from a wide range of habitats will be able to withstand the environmental conditions, as was observed for trees (Jenerette et al. 2016).

It is important to note that at a given location, a species could be both naturally dispersed and human dispersed. For example, some individuals may have been intentionally brought to a given location, while others are either progeny and naturally disperse or exist in the regional species pool and disperse. This highlights the difficulty in using the native/non-native status to determine the processes by which a species arrived at a given location. For example, in Salt Lake City,

the third most common tree species sold at mass merchandisers stores was native (Avolio et al. 2018). Local knowledge is needed to consider all the ways a species may have dispersed to a given location.

Dispersal

Factors affecting dispersal of naturally dispersed species are well studied and will not be reviewed here. However, dispersal mechanisms of intentionally human dispersed species remain uncertain. The horticultural industry disperses plants, fungi, soil microorganisms and invertebrates, of which we currently have the best understanding of plants (Ignatieva 2011). Both the horticultural and pet industries are important and understudied agents of global dispersal of organisms and contribute to what we term commercial viability (Table 2). Most people get their plants from nurseries (Hu and Gill 2015), and studies have shown that the plant species found in residential yards are similar to what is offered in local nurseries (Avolio et al. 2018, Cavender-Bares et al. 2020). Commercial viability in nurseries is affected by numerous factors, such as hardiness zone (temperature) in the United States and many market-driven parameters (Safley and Wohlgenant 1995), including novelty and susceptibility to disease and pests, cost, ease of propagation, aesthetic value and other physical attributes (Townsley-Brascamp and Marr 1995, Pincetl et al. 2013). Presumably, local climate is less of a concern for importation of vertebrates through the pet trade industry, as most pets are imported for indoor environments. However, commercial viability should be as important in the pet trade industry as is in the horticultural industry and detailed studies of the local nursery and pet industries are necessary to understand how managed species are dispersed to a given region.

Selection

Once a species has arrived to a given city, there are selection filters that determine whether it will arrive or persist at a location. Here, we broadly classify urban areas into one of three management-types that are arrayed along a gradient
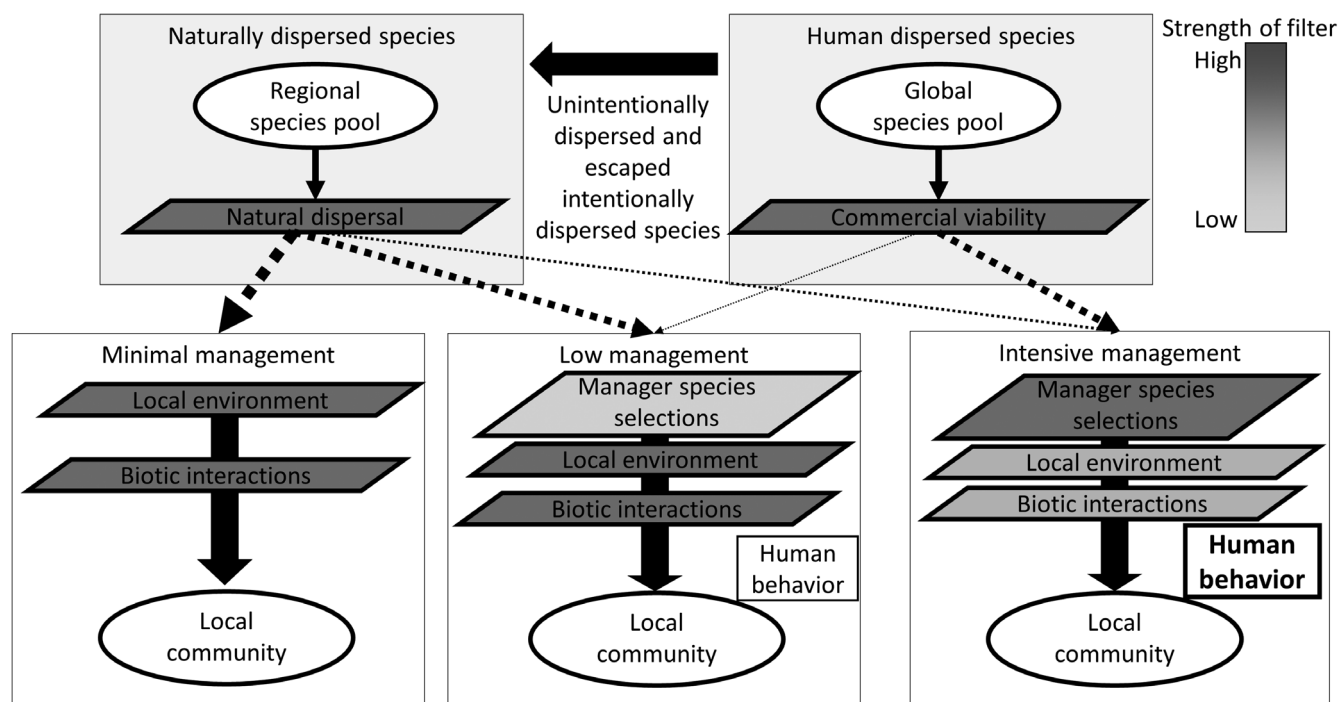
Figure 4. Expanding our filter framework across a heterogenous urban landscape of different management intensities. In minimally managed areas (e.g. abandoned areas) there are only naturally dispersed species, which after dispersal need to be able to withstand the local environment and compete with other species for resources. In low management areas (e.g. medians, park lawns), both naturally and human dispersed species will be found. Manager species selections mostly determine the plant community, typically turf grass species. The local environment is still an important determinant of which species will be there, followed by biotic interactions. Human behavior affects community assemblages but to a lesser extent. In intensive management areas most species will be human dispersed, but there will also be naturally dispersed species. Here, the manager species selections are very strong compared with the local environment and biotic interactions. Human behavior is an important consideration of local community assemblages.

of management intensity (minimal, low and intensive). We expect that management intensity affects the types of species found in a given area, where minimally managed areas are dominated by naturally dispersed species, and low and intensive management areas contain both naturally and human dispersed species, with more human dispersed species in intensively managed areas (Fig. 4 – dashed arrows). Across this heterogeneous landscape, we break down assembly processes into three filters that select for species: 1) manager species selections, 2) the local physical environment, and 3) biotic interactions. Manager species selections determine whether a species is intentionally brought to or removed from a location – for example, planting trees and killing rodents and undesirable insects. All three filters are affected by human behaviors.

We hypothesize that the strength and applicability of each filter varies across the three land-use types (Fig. 4, Table 2). In minimally managed areas, we hypothesize that the environment and biotic interaction filters are dominant, as naturally dispersed species need to withstand the local environment and compete with other species for resources (Fig. 4). In low management areas, we hypothesize that manager species selections will be a weaker filter than the local environment and biotic interactions (Fig. 4). In intensely managed areas, the majority of plant species are generally intentionally

human dispersed but most animal species are still largely naturally dispersed species. Hence, in intensively managed areas, we hypothesize that managers species selections will be the most important filter, and that management (e.g. watering and pruning) will also overwhelm local environmental conditions and biotic interactions (Fig. 4).

Human behavior

It was noted in the 1970s that human actions influence urban biodiversity (Kowarik 2020), with human behaviors noted as important drivers of urban ecosystems (Alberti et al. 2003, Shochat et al. 2006). Given that the addition of *human behavior* to community assembly theory is a relatively recent development in the study of biodiversity and community composition, we explore how behaviors are influenced by preferences and values and how they are limited by institutional rules, norms and socio-economic standing.

Behaviors are influenced by individual landscape preferences and values
Landowners and managers make choices about purchasing or removing existing species from private and public parcels. These choices are influenced by a variety of personal experiences, values, attitudes and worldviews, and act through

the manager species selections filter. One example is a particularly robust literature on the value orientations associated with 'pro-environmental behaviors'. These behaviors include reducing fertilizer, water and pesticide use, landscaping with native species, and intentionally attracting wildlife (Schultz and Zelezny 1998, Stern 2000, Nordlund and Garvill 2003, Yabiku et al. 2008, Larson 2010, Cook et al. 2012), which act through the local environment, and biotic interactions filters. The value–belief–norm theory (Stern et al. 1999) draws on the typology of human values (Schwartz 1994), and suggests that degrees of self-interest, altruism toward other people, and altruism toward other species form the core values that lead to an environmental worldview encompassing 'a person's belief about humanity's relationship with nature' (Schultz et al. 2005, p. 458). Dunlap et al. (2000) offered a survey to measure orientations toward a worldview concerned about humanity's influence on nature. The resulting new environmental paradigm (NEP) scale has been utilized in a number of studies of urban landscaping preferences, choices and behaviors that were linked to personal values (Schultz 2000, Balram and Dragićević 2005, Yabiku et al. 2008, Kurz and Baudains 2012, van Heezik et al. 2012).

In parallel to studies of the values that motivate landscaping behaviors, there has been a growing literature addressing city resident preferences and linkages to urban biodiversity. For example, specific plant traits, such as color, lead to human selection for cultivation (Gessert 1993), and selection to plant in an area (Goodness 2018). Plant traits can lead to cultural ecosystem services (Goodness et al. 2016). Head and Atchison (2009) suggested that 'a certain sort of plant charisma draws in human attention and care' (p. 239). Pataki et al. (2013) used a functional trait approach to develop a suite of 'ecosystem services-based traits' aimed at capturing aspects of plant form and function that urban residents recognize as beneficial, such as the presence of showy flowers, specific water requirements and rates of growth. And resident's preferences for plant traits have been correlated with the predominance of plants with those traits in the urban areas (Kendal et al. 2012b, Avolio et al. 2015a, 2018). Similar work has been done for bees, and residents who have positive feelings towards bees are more likely to plant vegetation to attract bees (Larson et al. 2021). At the level of the landscape, in Phoenix, AZ, Larsen and Harlan (2006) found that landscape preferences often matched landscape behaviors (e.g. residents that reported wanting an oasis landscape typically had landscaped their yard in an oasis style). This suggests that a trait-based approach that considers resident preferences for species selections can contribute to a better understanding of community assembly. However, there are notable geographic, demographic and individual differences in stated preferences for species, their traits, and landscape attributes (Ho et al. 2005, Sevenant and Antrop 2010, Jim and Shan 2013, Kalivoda et al. 2014, Avolio et al. 2015b, Lin et al. 2017, Wang and Zhao 2017). A general understanding of why individual species are preferred or undesirable for a given sociodemographic group or location has yet to emerge.

Behaviors are affected by institutional rules, landscape norms and racism

Political ecology (Robbins 2007) has demonstrated that the role of equity, power, and social capital in structuring human choices about urban landscapes points to larger political, social and institutional dynamics. Among these are institutional rules and cultural norms about allowable species that limit the species pool through the commercial viability and manager species selections filters. Public rules include municipal ordinances, public agency planting lists and invasive species eradication programs (Cook et al. 2012, Larson and Brumand 2014, Larson et al. 2020). Private institutions can also have rules such as homeowner associations (Roy Chowdhury et al. 2011, Cook et al. 2012, Larson and Brumand 2014). Each of these institutional drivers is influenced by particular organizations, knowledge, and stakeholders that have access to the decision-making process. Informal rules and cultural norms around landscaping aesthetics also strongly influence the relationship between human behaviors and community composition. In the U.S. and Europe, lawns, hedges, flower gardens, and other landscape structural features of 'neatness' and 'orderliness' are the dominant norm for urban yards, parks and gardens (Nassauer 1988, Lyytimäki et al. 2008). Nassauer et al. (2009), who referred to these norms as internalized social rules, found that conformity to social rules was more influential in decision-making about the front yards of residential parcels than individual homeowner preferences. In fact, several studies have quantified differences in the community composition and diversity of front yards versus backyards (Richards et al. 1984, Daniels and Kirkpatrick 2006, Larsen and Harlan 2006, Locke et al. 2018), which can be partially attributed to social pressures, or what Grove et al. (2006) has called 'the ecology of prestige.' Front yard landscaping, in particular, may convey cues about values, status, social obligations, or membership in a particular lifestyle group (Grove et al. 2006, Larson 2010, Larson and Brumand 2014, Locke et al. 2018).

Informal social rules are also influenced by the predominance of particular landscape designs within a neighborhood, as adoption of new landscaping types (e.g. native landscapes or xeriscapes) has been shown to accelerate as neighbors emulate each other. Hunter and Brown (2012) called this phenomenon 'spatial contagion', which they defined 'as a form of social facilitation that yields a spatially clustered outcome' (p. 408). Consequently, social networks and other social dynamics may result in a non-random clustering of landscape types across urban residential parcels. Studies have found that geographically proximal plant communities are more similar than those that are further apart (Avolio et al. 2018). The extent to which these spatial dynamics are analogous to or conform to theories and models in landscape ecology remains to be determined.

Racist behaviors can also have lasting effects on urban ecosystems (Grove et al. 2018, Schell et al. 2020), but the effect of racism and segregation on ecological processes is understudied (Pickett and Grove 2020). For example, in the United States, redlining was a formal policy of the U.S. Home

Owner Loan Corporation to deny residents home loans in neighborhoods that were deemed hazardous based largely on racism towards black Americans (Schell et al. 2020). Today, former red-lined neighborhoods have much higher summer temperatures due to greater impervious surfaces and a lack of trees (Hoffman et al. 2020, Locke et al. 2021). In the US and in cities around the world, the effects of all forms of racism and segregation on community assembly processes and species co-existence has rarely been formally studied. This needs further investigation.

Behaviors are limited by socioeconomic factors

Economic constraints can limit behavior at various scales. At the city scale, economic activity and available resources and budgets for landscaping can vary dramatically among cities and are often too small to implement desired landscapes (Baur et al. 2013, Kabisch 2015). Within U.S. and European cities, socioeconomic status is an important determinant of biodiversity given commonly observed patterns of higher plant (Hope et al. 2003, Clarke et al. 2013, Avolio et al. 2018) and bird (Kinzig et al. 2005, Strohbach et al. 2009) species richness in higher income neighborhoods. While many urban residents appear to have aesthetic preferences for visually diverse landscapes (Lindemann-Matthies and Marty 2013, Hoyle et al. 2017), more plants are found in higher income areas (Leong et al. 2018). This disparity has many causes, including unequal distribution of public resources in city street trees and public parks (Pham et al. 2012), and from residents and communities lacking the economic resources and land ownership to invest in biodiversity in private areas (Leong et al. 2018). Education can also affect patterns of biodiversity, where there is higher tree cover (Kendal et al. 2012a) and tree richness (Avolio et al. 2015a) in neighborhoods where residents have more education. Additionally, residents with a higher socioeconomic status may choose a greater variety of plants or more unique plants as a means of complying with neighborhood norms or displaying status or wealth (Grove et al. 2006, 2014).

Hypotheses about human behaviors

We have several hypotheses about how human behaviors shape urban biotic communities. Our framework suggests the impact of human behavior is relatively weak in areas where there is low management and is highest in intensively managed areas (Fig. 4). In addition, we hypothesize that neighborhoods are an important scale of urban ecological variation. Different neighborhoods will have different biotic communities due to rules, norms and segregation that scale from individually owned parcels and yards to neighborhood processes. Additionally, we hypothesize that factors that influence environmental values, such as cultural background and education, will affect people's preferences for landscape and organismal types and will be important determinants of communities. Lastly, we hypothesize that socioeconomic status increases the ability of people to realize their preferences and interacts with all aspects of our framework. For example, with plants, residents with a higher socioeconomic status can invest more money in securing, removing and planting species, and therefore have access to a larger range of sources of cultivated organisms, e.g. plant nurseries (Turner and Dorfman 1990), affecting dispersal processes. Through manager species selections, more residents with a higher socioeconomic status may prefer a greater variety or more novel species to signify wealth. Affluent residents can also spend more on yard maintenance (Zhou et al. 2009) and can afford to regularly fertilize, irrigate, or otherwise intensively manage their yards, affecting the environmental filter and supporting a larger number of species through increased resource availability. Additionally, yard maintenance such as intensive pruning, mowing, weeding, pest control and disease prevention – all different forms of removals – will reduce competitive interactions and remove biotic constraints on assembly processes, affecting the biotic interactions filter. Finally, more affluent residents will be able to realize their preferences or predominant aesthetic and cultural norms in their yards to a greater extent than less affluent residents or managers. These hypotheses together combine drivers of preferences with the capacity to manage communities to achieve intentions.

Predicting patterns of alpha and beta diversity

In our framework, filters and processes interact and give rise to local biotic communities, which can be characterized in
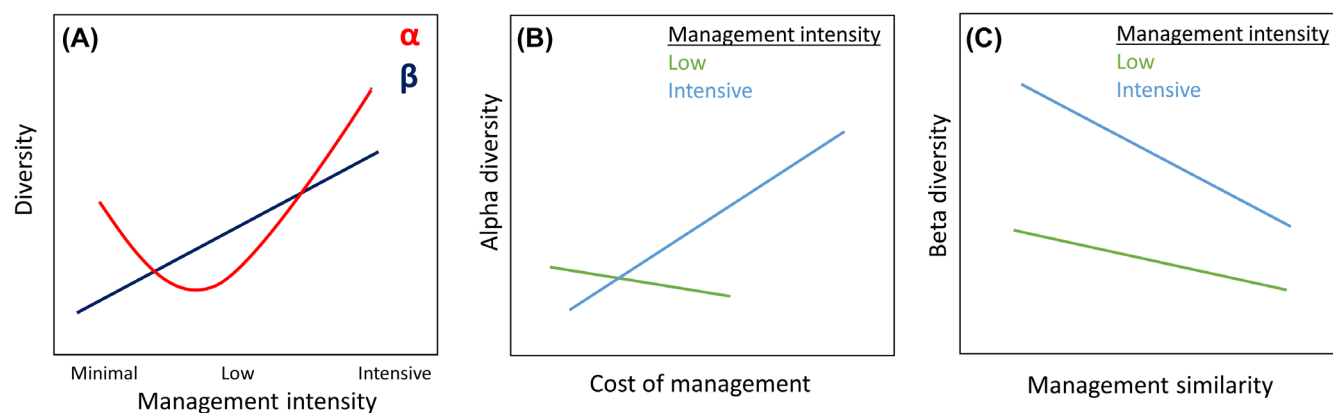

Figure 5. Predictions on patterns of alpha and beta diversity based on management intensity (A), cost (B) and similarity (C).

terms of alpha diversity – the number and abundances of species at a location – and beta diversity – the shift in community composition among locations. We hypothesize that management intensity will affect alpha and beta diversity (Fig. 5A). In minimally managed areas, such as forest patches, there will be moderate alpha diversity and low beta diversity because the environment is a strong determinant, making patches more like one another. We predict that similarity of manager preferences and practices in the low management areas, such as road medians, will enhance beta diversity to moderatelevels but keep alpha diversity low. In contrast, we predict the highest alpha and beta diversity in intensively managed areas, to which managers import many species and have different preferences and practices, making patches more different from one another, particularly across neighborhoods. We also predict that alpha diversity will change along a gradient of how much money is spent on management. We predict particularly high alpha diversity in highly managed areas, for example neighborhoods with a high socioeconomic status where affluence imparts more direct control over yard biodiversity (Fig. 5B). In contrast, we predict less alpha diversity in low managed areas that spend more on management. For example, in park lawns where the goal is typically to create a clean aesthetic and reduce weeds, spending more money will reduce the number of species. Finally, we hypothesize that similarity of management practices will affect beta diversity (Fig. 5C), as suggested by Kendal et al. (2010). Areas that are more similarly managed will have more similar plant communities, reducing beta diversity and low managed areas will be more similar than intensively managed areas. Patterns of beta-diversity will also strongly depend on the mobility of a particular organism or population. For example, we expect lower beta-diversity for bird species, which can easily disperse, compared with plants and small flightless insects.

Interactions among trophic levels

City residents have the most direct control over plants; however, many plant choices of residents are based on trophic interactions. When a resident creates a butterfly garden, they choose certain plants to attract desirable insects. Conversely, when grazing pressures from deer are high, residents will usually limit the types of plants they import into their yards to choose those that are resistant to grazing (Sayre et al. 1992). This phenomenon is not limited to aboveground trophic interactions. Many soil substrates that are commercially sold are now supplemented with soil microorganisms including bacteria and mycorrhizal fungi, which are presumed to be beneficial for plant growth. Even in the absence of deliberate choices for other trophic levels, plant composition affects other types of urban organisms. For example, yard vegetation can affect insect composition, which scales to affect bird populations (Narango et al. 2018), and removing leaf litter and dead wood from a yard or park limits food resource for the detritivore community (Sayer 2006). Thus, trophic interactions are an important and understudied driver of urban biodiversity, especially for animals and microbial communities.

Further considerations: drift and speciation

Two ecological processes that are poorly understood in cities and not directly addressed in our framework is ecological drift and speciation. Drift, the stochastic variation in species abundance, is not well studied in urban systems. Vellend (2010) argues that in areas where selection pressures are low and a community is small, drift may be the dominant process shaping ecological communities. Drift might be an important process in lightly managed lawns, as random processes drove lawn earthworm community composition in Belgium (Tiho and Josens 2007). Speciation has received more attention in cities (Alberti 2014, Johnson et al. 2015, Des Roches et al. 2021), and there is evidence of genetic differentiation and evolutionary processes occurring in animals, including the famous example of moths in industrial Britain (Kettlewell 1953), mice in New York City (Munshi-South and Kharchenko 2010) and ground beetles in Berlin (Keinath et al. 2020). There are also examples of adaptation in plants, for example, Crepis in tree pits (Cheptou et al. 2008) and white clover along an urban heat island gradient (Thompson et al. 2016). Another form of speciation occurs through artificial selection in the ornamental plant industry. New cultivars are chosen for human aesthetic values, such as color and floral petal complexity (Gessert 1993). These are all examples of genetic differentiation and adaptation to urban environments, but most fall short of speciation. However, population differentiation and genetic separation of populations are precursors to evolution of new species.

Future directions

The two-way interactions between nature and people's values and experiences of nature, and how these shape behaviors, are some of the fundamental uncertainties in predicting urban biodiversity. As such, many of the forward-looking questions in urban biodiversity research will require a deliberate incorporation of human behaviors. Although not directly addressed in our framework, we expect all filters to be dynamic over time and we stress the need to study temporal dynamics of urban biodiversity and human experiences, actions, and behaviors in general. In addition to temporal dynamics, how social–environmental dynamics of neighborhoods, cities and continents affect urban biodiversity is not understood and we need more integrated urban biodiversity research in cities worldwide. Building on our framework, we offer some lines of inquiry to guide such endeavors:

1. How do phylogenetic relationships among species affect manager species selections for functional characteristics, and then in turn affect local community composition?
2. How do commercial viability and manager species selections vary over time and affect local community composition?
3. How do the controls on urban biodiversity differ in cities with histories, climatic and economic conditions different

from Euro-American cities where our framework was developed?

4. What are the consequences of commercial viability and manager species selections for responses of urban ecosystem services to climate change?
5. To what extent does human behaviors create resilience or vulnerability in communities and ecosystem functions and at what scale from parcel to city?
6. Are the effects of segregation on urban biodiversity manifested most strongly through lack of economic investment or manager species selections and land management decisions?

Addressing these questions will help advance a theory of urban biodiversity within and among cities and in response to rapidly changing environmental and social conditions.

Conclusions

We still have relatively little understanding of the role of human behavior in shaping non-human urban biota relative to the longer history of advanced frameworks for studying non-urban biodiversity. Therefore, we hope the framework presented here helps urban ecologists advance research about the roles of humans in dispersing, removing and selecting species, as well as how the environment and species composition may influence human choices. Understanding and predicting urban biodiversity is an area of convergent research because a wide range of disciplines are necessary to understand the relationships between people, plants and animal diversity in cities. With advances in theoretical frameworks that help understand how and to what degree human actions shapes urban biodiversity, we can better support societal goals for advancing sustainability, improving resilience and promoting wellbeing (McPhearson et al. 2016). Instead of waiting to see how climate change harms populations, communities and ecosystems and associated ecosystem services, the role of humans in shaping urban biodiversity signifies the potential to design and build more resilient cities that are better adapted to future climates. To achieve such broad societal goals, we need to better understand the complex interrelationships between humans and other taxa.

Author contributions

Meghan L. Avolio: Conceptualization (lead); Writing – original draft (lead). **Christopher Swan**: Conceptualization (supporting); Writing – review and editing (supporting). **Diane E. Pataki**: Conceptualization (supporting); Writing – review and editing (supporting). **G. Jenerette**: Conceptualization (supporting); Writing – review and editing (supporting).

Data availability statement

This paper contains no original data.

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