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Cities Shape the Diversity and Spread of Nonnative Species

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Abstract

The globalization of trade and increased human mobility have facilitated the introduction and spread of nonnative species, posing significant threats to biodiversity and human well-being. As centers of global trade and human populations, cities are foci for the introduction, establishment, and spread of nonnative species. We present a global synthesis of urban characteristics that drive biological invasions within and across cities, focusing on four axes: (a) connectivity, (b) physical properties, (c) culture and socioeconomics, and (d) biogeography and climate. Urban characteristics such as increased connectivity within and among cities, city size and age, and wealth emerged as important drivers of nonnative species diversity and spread, while the relative importance of biogeographic and climate drivers varied considerably. Elaborating how these characteristics shape biological invasions in cities is crucial for designing and implementing strategies to mitigate the impacts of invasions on ecological systems and human well-being.

INTRODUCTION

A defining feature of the Anthropocene is the predominance of anthropogenic drivers of diversity patterns over naturally occurring ecological and evolutionary processes (Aronson et al. 2014, Helmus et al. 2014, McKinney 2006). Cities, as complex and dynamic environments, exert a profound influence on biodiversity and ecosystems worldwide (Grimm et al. 2008), often acting as centers for the introduction, establishment, and spread of nonnative species (Kühn et al. 2017, Pyšek 1998). This phenomenon has garnered increasing attention from ecologists, conservationists, and policymakers alike, as the consequences of urban-induced changes in species composition extend far beyond city boundaries (Grimm et al. 2008, McKinney 2006).

The heightened human-mediated transportation of goods and organisms, coupled with the modified environmental conditions within and around urban areas, has led to an unprecedented acceleration in the rate of nonnative species introductions. As a result, urban areas harbor a larger proportion of nonnative species than nonurban areas. The unique characteristics of urban ecosystems, including altered species interactions, increased human-mediated disturbances, and global connectivity, contribute to the creation of novel environmental conditions that facilitate the establishment of nonnative species (Potgieter & Cadotte 2020). Once introduced, those nonnative species can spread to natural areas within and surrounding towns and cities (Cadotte et al. 2017, McLean et al. 2017). The consequences are multifaceted, ranging from disruptions in ecosystem functioning to economic and public health implications (Potgieter et al. 2017). As urbanization continues to expand globally, the degree to which cities act as initial and/or ongoing sources of widespread biological invasions will intensify (Perrings et al. 2010). Understanding the underlying processes that govern invasion success is essential for devising effective strategies to mitigate the ecological, economic, and social impacts associated with biological invasions in urban areas.

Socioeconomic and ecological characteristics of cities such as connections with other cities (e.g., travel, shipping, geography), human population size and density, colonization history, cultural background, economic differences, and environmental conditions likely filter nonnative species based on their form and function (Celesti-Grapow et al. 2006, Pyšek 1998). These features can help us understand nonnative species' success in cities across the world. While ecologists have made great strides in recent years toward understanding the patterns and processes of urban biological

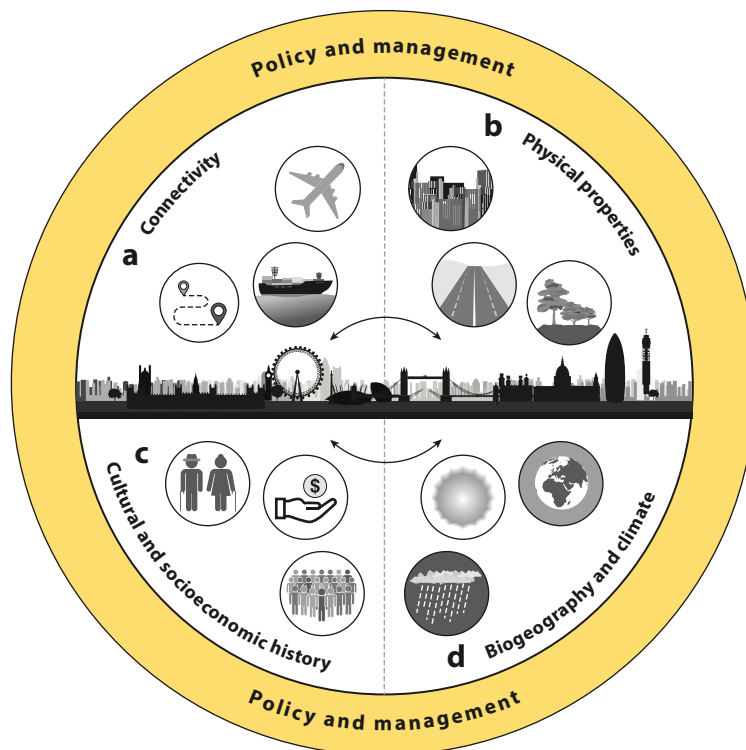


Figure 1

A conceptualization of urban characteristics across four axes that shape the diversity, abundance, and spread of nonnative species: (a) connectivity (e.g., travel and trade, distance to urban centers), (b) physical properties (e.g., city size, urbanization intensity, and proportion of green space), (c) culture and socioeconomic history (e.g., human population density, wealth, and age of inhabitants), and (d) biogeography and climate (e.g., precipitation, temperature, and latitude). These interact to drive nonnative species invasions in cities, and their relative magnitudes can vary with differing historical and environmental contexts. Policy and management aimed at preventing and mitigating the impacts of invasive species must consider these facilitating mechanisms.

invasions, a global synthesis of the factors influencing nonnative species success within cities is still lacking. For this article, we review the extent to which urban areas are sources of biological invasions and evaluate which factors make urban areas vulnerable to biological invasions and shape the diversity and spread of nonnative species.

We conceptualize urban characteristics that are potentially important for biological invasions across four axes (**Figure 1**): (a) connectivity (e.g., geographic distance, trade and travel, corridors), (b) physical properties (e.g., city area, urbanization intensity, proportion of green space), (c) culture and socioeconomic history (e.g., age of the city, wealth and ethnicity of the inhabitants, colonization history), and (d) biogeography and climate (e.g., regional pool species richness, precipitation, temperature). We ask a fundamental question across these four axes: To what degree do the anthropogenic drivers associated with urbanization override the natural ecological and evolutionary processes that underpin global diversity patterns? Specifically, we review how these four axes are linked to biological invasions in urban areas. We also briefly review how policy and management can help control biological invasions within cities. To conclude, we summarize current knowledge gaps and make recommendations for future research.

CONNECTIVITY

Connectivity plays an important role in maintaining populations and communities in ecological systems (Taylor et al. 1993). Geographic distance, barriers (e.g., mountains, oceans, lakes), and conduits (e.g., rivers, ocean currents) have implications for species dispersal and distributions across scales from local metacommunities to global biogeographic patterns (Nekola & White 1999). In invasion ecology, connectivity is important for both the transport and spread stages of invasion, allowing species to overcome geographic dispersal barriers (Pyšek et al. 2020). In particular, cities act as hubs for the transport of nonnative species across the globe during the transport phase (Pyšek et al. 2010, 2020), and features of cities that connect them to suburban, agricultural, and natural areas facilitate the spread of nonnatives from initial points of introduction (Von der Lippe & Kowarik 2008).

Here, we consider connectivity in relation to urban biological invasions from three perspectives. First, we explore the role of connectivity between and among multiple cities in the transport stage of biological invasions. Second, we focus on connectivity in or out of a focal city where the city acts as a hub for immigration and emigration during the spread stage of invasion. Finally, we consider connectivity within a focal city. From these three perspectives, we review the most common predictors of, response variables for, and biodiversity responses to the connectivity of nonnative species.

Connectivity Among Cities

Linking metrics and attributes of connectivity to invasions among and within cities is done in a variety of ways. For studies that compared biodiversity or species composition among multiple cities, the most common connectivity metric used was geographic distance, as measured by geodesic distance for global comparative studies (e.g., La Sorte et al. 2014, Yang et al. 2015) and Euclidean or straight-line distance for regional and local studies (e.g., Sobrinho Soares et al. 2021). Other forms of connectivity among cities include trade and travel connections (Banks et al. 2015, Olden et al. 2021). When investigating the role of connectivity among cities in species invasions, one of the most common approaches is to assess the compositional similarity of nonnative assemblages in relation to the connectivity between two or more cities. The most frequently used diversity metric is beta diversity, including different aspects (e.g., dissimilarity in species composition, functional composition, and genetic composition) and different measurements (e.g., Simpson multisite dissimilarity, Sørensen dissimilarity, Bray–Curtis dissimilarity, and zeta diversity).

In general, the compositional similarity of urban nonnative assemblages increases with shorter geographic distance and, therefore, increased connectivity among cities. For example, Sobrinho Soares et al. (2021) found that floristic similarity among urban forests in Brazil was higher for those that are geographically closer. Yang et al. (2015) found that urban forest composition similarity among 38 cities across the world decreased with geodesic distance. As human-mediated transport between cities (e.g., travel, trade) allows for nonnative species to overcome geographical barriers (Banks et al. 2015) (**Figure 2**), the compositional similarity of nonnative species likely increases more with shorter geographic distance than that of native species. For example, across 11 cities in China's Yangtze River region, assemblages of nonnative species were more similar than their native counterparts (Jin et al. 2020), suggesting that transport of nonnative species was homogenizing these urban floras. Similarly, La Sorte et al. (2014) found that invasive species had lower beta diversity among cities than native species, suggesting connectivity among cities had a worldwide effect on the beta diversity of urban plant assemblages specifically through the exchange of nonnative species.

At the species level, genetic differentiation among populations across cities is used to assess the role of connectivity in connecting conspecific populations. For example, genetic differentiation of

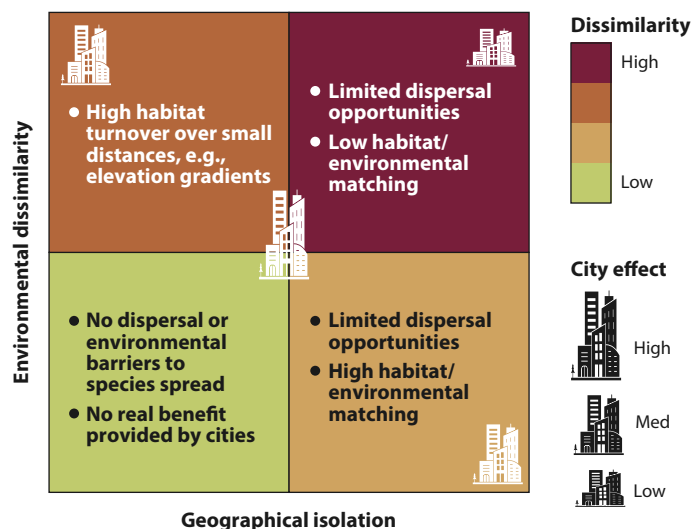


Figure 2

Whether nonnative species homogenize urban biota depends on species overcoming dispersal and environmental barriers. Cities that are isolated (either through remoteness or economic isolation) or in extreme environments are unlikely to experience the homogenizing effect of species introductions. The effect of cities on homogenization should be greatest at intermediate levels of isolation and environmental difference because cities can provide opportunities for introduction and establishment.

the German cockroach (*Blattella germanica*) was weakly positively correlated with distance across nine cities in China (Tang et al. 2016). However, the relationships differed across spatial scales with positive relationships at close geographic distances and negative relationships at greater distances. At the global scale, there was little global genetic structure to German cockroach populations, which is likely due to a centuries-long history of human transport genetically homogenizing urban populations (Vargo et al. 2014). This is not the case for other nonnative species, though. For example, the feral pigeon (*Columba livia*) has a significantly higher level of genetic differentiation with larger geographic distances (Jacob et al. 2015). Across nine harbors on the Mediterranean coast of the Iberian Peninsula, strong genetic differentiation among populations was found for the introduced ascidian *Styela plicata*. Nonetheless, a weak correlation between geographic distance and gene differentiation indicates that ship traffic is not a major driver of genetic structure (Pineda et al. 2016).

Trade between cities can also give insight into how connectivity between cities drives the spread of nonnative species. Olden et al. (2021) quantified the geographic routes of live aquatic organisms over a 7-year period and found that buyer and seller locations ranged across 39 countries but were mostly concentrated in major cities of the United States and several European and southeast Asian countries. López-Legentil et al. (2015) found that closely located harbors shared more ascidian nonnative species among them than those that were further apart.

Connectivity of a Focal City

While connectivity between cities is important in the transport stage of invasion, once a species arrives, a city can act as a hub during the spread stage (Banks et al. 2015). Conduits into and out of cities determine the effectiveness of a city as a hub for biological invasions. Therefore, studies that focus on connectivity in or out of a focal city often link linear features to invasive species movement. These linear features include road and railway length, direction, and density as well as

river length and flow direction as proxies for travel and trade (Aronson et al. 2017). Roads, rivers, and railways coming into a city and those connecting city centers to outlying suburbs, rural, and natural areas can play a role in the spread of invasive species (Aronson et al. 2017, Kühn et al. 2017, Von der Lippe & Kowarik 2008). Additionally, port size, distance to ports, and distance to urban centers are important correlates of invasive species introductions (Kalwij et al. 2008, Yemshanov et al. 2012). The most studied response variable for assessing the connectivity of a focal city is the alpha diversity of nonnative species, mostly in terms of species richness and to a lesser degree genetic diversity. Other common response variables include the presence or detection probability, the abundance of nonnative species, and the proportion of nonnative species within communities.

Overall, cities that were larger and had more incoming connections tended to have greater nonnative species richness. For cities in the US and Canada situated along the Great Lakes, those with more commercial vessel trips and larger marinas had a greater richness of nonnative aquatic species (O'Malia et al. 2018). Across 11 cities in Serbia, those with a higher urbanization level, based on roads, rails, and population size, had the highest richness of neophytes (i.e., nonnative species introduced after 1500 AD) (Rat et al. 2017). In Germany, rivers, roads, and railroads contributed to the increase in neophyte species diversity, but the effect was disproportionately lower in more urbanized areas, possibly due to the denser network of traffic routes and the already higher number of neophytes in cities (Kühn et al. 2017). Across 54 central European river-port cities, those that were larger harbored more nonnative plant species (Jehlík et al. 2019). Further, aircraft were identified as the main pathway by which invading mosquitoes arrive in New Zealand ports, with a temporal shift in recent times to increasing introduction through ships. Auckland, the largest city in New Zealand, has experienced the largest number of nonnative mosquito intercepts (Derraik 2004). Connectivity to hotspots of human activity or major vectors had strong positive effects on the invasion of aquatic ecosystems (Chapman et al. 2020, Ulman et al. 2019).

The distance from city centers and the number of transport connections affect the spread of nonnative species and the resultant communities. The Port of Savannah in Georgia served as a conduit for ant invasions, with 13 nonnative species found adjacent to the port, including a county record and the northernmost record of the invasive ant *Nylanderia fulva* (Gochnour et al. 2019). In this case, having a hub city facilitated range expansion. Vakhlamova et al. (2016) found a higher richness and percentage of nonnative species along larger roads and at closer distances to Pavlodar, Western Siberia, Kazakhstan. Similarly, Brunzel et al. (2009) found that neophytes were more abundant closer to the city and that the species richness of neophytes was influenced by connectivity. Spread of a nonnative bird, the Javan myna (*Acridotheres javanicus*) occurred along an urban–suburban gradient in the cities of Kuala Lumpur and Johor in peninsular Malaysia through the escape and release of captive individuals over a 40-year period (Arazmi et al. 2022). Further, the spread of zebra mussels (*Dreissena polymorpha*) from their ports of origin in the eastern United States was linked to trailered boats along main roads where they were found to have a higher prevalence (Britton & McMahon 2005).

Spread from cities can also influence the genetic differentiation among populations of invasive species. If populations are highly connected, they are likely to show little genetic differentiation, while infrequent connections could promote it. Heavy boat traffic between the Peruvian port city of Iquitos and six Amazonian River communities promoted population mixing of the invasive mosquito *Aedes aegypti* and resulted in no correlation between population genetic structure and geographic distance (Guagliardo et al. 2019). On the other hand, in Paris, France, 15 populations of the invasive plant *Senecio inaequidens* showed a genetic gradient along a railway line from Paris to the surrounding suburbs (Blanchet et al. 2015).

Connectivity Within a Focal City

Compared with the above two categories, studies that examine connectivity within a focal city are less frequent. Such studies often link invasion patterns within a city with the connectivity of roads, rivers, or habitat patches such as green spaces (e.g., by measuring distance between green spaces within a city). In general, within-city connectivity can facilitate the spread of nonnative species. For example, although river corridors serve as important connections among habitat patches for native plants and animals, they also increase the spread of invasive plants within a city (Aronson et al. 2017). Similarly, in the Hungarian city of Debrecen, over 65% of the functional green space was connected by corridors, facilitating the dispersal of both native and neophyte species (Hüse et al. 2016). The invasive Argentine ant (*Linepithema humile*) while colonizing green spaces in the city of Madrid, Spain (López-Collar & Cabrero-Sañudo 2021), has established isolated and apparently unrelated new colonies, indicating that it is dispersed mainly through human-mediated transport of goods, plants, and gardening tools (López-Collar & Cabrero-Sañudo 2021). However, the importance of connectivity for biological invasions within cities might be context dependent. For example, Caughlin et al. (2023) found a negative relationship between connectivity and the abundance of puncturevine (*Tribulus terrestris*) an invasive plant species, in the city of Boise, Idaho. This negative relationship occurred because more affluent, connected areas of the city had lower availability of bare ground cover, the microhabitat required for puncturevine to establish (Caughlin et al. 2023).

Generally, higher connectivity among cities increases the compositional similarity of nonnative assemblages and, to a lesser extent, the population genetic similarity of nonnative species. Higher connectivity of a focal city also tends to increase the diversity of nonnative species. Importantly, within-city connectivity can facilitate the spread of nonnative species.

PHYSICAL PROPERTIES

The physical properties of cities play crucial roles in shaping the diversity and spread of nonnative species within urban environments. Biodiversity changes along major urbanization gradients through features like city size and species–area relationships, the level of urbanization, and the density and diversity of urban habitats, which have been frequently studied. Other variables, such as urban geology, vegetation structure, and the effect of riverbanks, have also been addressed but less frequently.

Area

City size has long been considered a predictor of the species richness of nonnative urban floras (but much less so for taxa other than plants) because of the general species–area relationship. In one of the first comprehensive studies, based on 54 cities in Czechia, Poland, and Germany, Pyšek (1998) showed that both the number of neophyte species and their proportion in the total urban flora significantly increased as the size of a city increased. This relationship explained 26% and 59% of the variation in these variables, respectively. The patterns found for archaeophytes (i.e., nonnative species introduced before 1500 AD) differed; their species richness increased, but the proportion decreased with city size, reflecting their affinity for rural rather than industrial settings and that their species pool was more limited than that of neophytes (Pyšek 1998). Recently, another study using 45 towns and cities of different sizes within a broader area of Central Europe confirmed a significant increase in the richness of neophytes with area, while once again archaeophytes, a homogeneous group of species with similar traits and a limited species pool, were equally widespread through settlements of all sizes (Čeplová et al. 2017). These patterns have also been found globally, with higher nonnative richness found in larger cities (Aronson et al. 2014).



The effect of area has also been documented at a smaller scale within cities. In Hanover, Germany, patches of urban green space affected the diversity of nonnative plants, whose proportion was driven by a combination of patch size, shape, and distance to the urban edge (Matthies et al. 2015). A similar pattern was found by Crowe (1979), who demonstrated that vacant urban lots have similar immigration and extinction rates to those of true islands. In a study that focused on nonnative plant species richness on university campuses in over 130 Chinese cities, campus area was a significant determinant of the number of nonnative species, alongside mean annual temperature, precipitation seasonality, and campus age (Wang et al. 2021). This area effect is not ubiquitous; for example, Figueroa et al. (2018) showed that urban park area and age affected native plant richness in Santiago, Chile, while nonnative plant richness was determined only by park age (see the section titled Culture and Socioeconomics).

Level of Urbanization

Many studies exploring the effects of physical properties on nonnative diversity use the level of urbanization as an explanatory variable. The two major mechanisms that are highly relevant when considering urbanization in the context of biological invasions are perturbations associated with fluctuations in resource availability (Davis et al. 2000) and nonnative propagule pressure. Urban habitats were shown to be exposed to high propagule pressure from nonnative plants, including cultivated species spreading from gardens (Cubino et al. 2015). Different proxies are used to quantify levels of urbanization, including the position on an urban–rural gradient (Kühn et al. 2017), the proportion of impervious areas or green spaces, the distance to the city center (Štajerová et al. 2017), and the density of human population (Pyšek 1998). Urban habitats are also compared and quantified according to the frequency and severity of disturbances. Most of these proxies reflecting urbanization are usually applied within a single city, probably due to difficulties associated with collecting standardized data quantifying urban–rural gradients or distance to the city center for multiple cities differing in their size, character, or structure of the surrounding landscapes.

Despite the different approaches to defining levels of urbanization, some kind of urban effect on the diversity of nonnative species is consistent across different taxa and regions. Urbanization generally increases the richness and abundance of nonnative species in cities, as documented for plants and land snails, and is regarded among the main underlying factors of invasion processes (e.g., Celesti-Grapo et al. 2006, Horsák et al. 2013). High levels of urbanization with frequent and intense disturbances in cities with a high proportion of impervious or built-up areas support mostly species-poor communities with high percentages of nonnative species (Horsák et al. 2013, Lima et al. 2013, Lososová et al. 2012a, Zerbe et al. 2003).

At local (city) scales, the highest proportion of nonnative species is usually found in the middle of the urbanization gradient, whereas less urbanized areas harbor greater richness and diversity of native species. A study on plant species richness in vacant lots in Montreal and Quebec City, Canada, found that nonnative species richness was highest at moderate urbanization intensities (Blouin et al. 2019). This is likely because the wealth of the population is greater along the intermediate urbanization gradient, leading to a higher proportion of green spaces and more resources dedicated to gardening and the importation of nonnative species (which enhances propagule pressure). For plants, examples supporting the positive effect of urbanization on nonnative species richness include detection of a significantly higher number of nonnatives in urban areas than in near-natural ecosystems in Berlin (Kowarik et al. 2013) and the highest proportion of nonnatives in high-density developments within the same city (Zerbe et al. 2003). An analysis of 69 sites in Bengaluru, India, found that nonnative species richness was higher in intermediate density housing quarters, which also had the highest socioeconomic status (Gopal et al. 2019). This pattern is

consistent for plants, birds, land snails, and fish in different parts of the world. In a study of cities in Central Europe, both the number of neophyte species and their proportion of the total urban flora significantly increased with the density of the human population, which can also be regarded as a proxy for the intensity of anthropogenic pressure and level of urbanization (Pyšek 1998). Still, there are indications that the factors driving species richness in cities are not fundamentally different from those outside cities but differ in their magnitude (Kühn et al. 2017).

Similar effects of urbanization have been observed for other taxa as well. Using community science data from the United States, Callaghan et al. (2019) found that the richness and diversity of nonnative bird species was positively related to the level of urbanization; it was distinctly higher in urban green areas compared to natural green areas due to an increase in habitat heterogeneity in cities. Studies focused on ants (Vonshak & Gordon 2015), bees (Gruver & CaraDonna 2021), beetles (Grez et al. 2019), and fruit flies (Gottschalk et al. 2007) have all demonstrated that urbanization, with accompanying land-use change and high propagule pressure, increases the proportion of nonnative species. An opposite effect of urbanization was reported in Beijing, China, where the relative abundance of nonnative fish in lotic waters increased linearly with the distance from the city center because urban pollution reduced nonnative fish diversity (Zhang et al. 2022).

Habitats

Urban habitats, such as vacant lots, road verges, and city parks, are unique components of physical urban properties, shaped by most of the features mentioned above. As such, they are important determinants of the presence of nonnative species, as documented for plants (Pyšek & Chytrý 2014). In the city of Rome, Italy, habitat type explained the greatest variation (12%) in the proportion of neophytes among all species recorded; this proportion was highest in the habitats of urban parks, residential areas, and the historical center, and at the scale of the city, it decreased as the area available to vegetation increased (Celesti-Grapow et al. 2006). The differences in richness and proportion of nonnative plant species among urban habitats of 32 Central European cities were associated with increasing similarity of species composition in urban floras (see the section titled Connectivity) (Lososová et al. 2012b). These authors found that archaeophytes contributed to homogenization and neophytes to the differentiation of floras among cities. This reflects the main mechanisms by which nonnative species cause differentiation. Low differentiation was observed in highly disturbed urban habitats, such as city squares, boulevards, and early successional sites. In contrast, the highest differentiation was evident in moderately disturbed habitats, including city parks and residential areas characterized by an open building pattern.

Vegetation and Substrate

Vegetation structure such as shrub or tree cover in gardens was shown to be an important driver of bird diversity in a study in Dunedin, New Zealand. Increasing vegetation cover and reduced garden complexity, together with housing density, reduced the densities of native and, to a lesser extent, nonnative birds, except for the house sparrow, which responded positively to increased housing density (van Heezik & Adams 2016). In Germany, geology affected the richness of urban nonnative plant species indirectly, as this factor was associated with the position of the city, i.e., where the cities were developed (Kühn et al. 2004). Overall, city size and degree of urbanization (with associated land-use change and propagule pressure) increase the richness and diversity of nonnative species. Moreover, the network of roads, railways, and water streams is an important driver of propagules of nonnative species, contributing to the richness and diversity of nonnative species in cities.



Culture and Socioeconomics

The most common socioeconomic drivers of biological invasions in urban areas explored in the literature are wealth of the owners and neighborhood (household income); age of the buildings, neighborhood, and city; cultivation; age of the inhabitants; and ethnicity of the inhabitants (although this was often associated with wealth). Socioeconomic factors affecting nonnative species richness and abundance are frequently studied, yet none evaluated how socioeconomic factors affect or mediate the impacts or spread of nonnative species. Many studies highlighted factors that influence the richness of all species, including both natives and nonnatives. Although socioeconomic drivers are deeply intertwined, in the absence of systematic comparative analyses assessing them, they are individually described below.

Wealth and Household Income

Wealth and household income was the most frequently reported socioeconomic driver of biological invasions in urban areas, often with a positive correlation (Hope et al. 2003, Yücedağ & Aşık 2023). Larger, wealthier houses and neighborhoods; higher incomes (both individually and nationally); and higher educational levels were positively associated with the richness and abundance of nonnative species. This is probably because greater wealth is associated with more green spaces and more resources allocated to gardening (Nguyen et al. 2021). For instance, a study across 23 urban areas in Spain analyzed 46 urban parks and found that the proportion of nonnative species increased in towns with older human populations and larger homes (Bayón et al. 2021). One literature review explored the luxury effect [a positive relationship between biodiversity measures and socioeconomic status (Hope et al. 2003)] in urban areas globally and found that the luxury effect was stronger for nonnative than native plant species, as many nonnative plant species are ornamental, and wealthier households were more likely to buy, grow, and manage them (Chamberlain et al. 2020). These empirical results were also confirmed by theoretical study. Using a simulated reference species, Hui et al. (2017) investigated the correlation between invasive plant species' spread in green areas and socioeconomic indicators in the 100 most populous cities globally. They found that smaller urban populations and higher gross domestic product per capita were key predictors of greater invasive spread potential, indicating that wealthier, less densely populated cities might face higher invasion risks. The luxury effect, however, was not always observed for animal taxa. A study of three nonnative birds across 120 sampling sites in Santiago, Chile, located in residential areas with different socioeconomic status found that the nonnatives domestic pigeon (*Columba livia forma domestica*) and house sparrow (*Passer domesticus*), were more abundant in low-income neighborhoods, whereas monk parakeet (*Myiopsitta monachus*) was most abundant in high-income ones (Silva-Ortega et al. 2023). This difference could be explained by the pathways of introduction of these species, as *C. livia* and *P. domesticus* are synanthropic species often classified as urban pests and *M. monachus* is a pet bird commonly sold in pet shops. Reported bird escapes occur more frequently in areas with higher incomes (Vall-Llosera & Cassey 2017).

Cultivation of Plant Species and Animals in Captivity

Cultivation of plant species and animals in captivity can increase nonnative species richness and the abundances and homogenization of local floras and faunas. Cultivation in urban areas often results in a shift from predominantly native to predominantly nonnative species. Besides residential gardens, urban parks can also be important sources of nonnative species. Nonnative taxa classified as established or invasive in the Czech Republic were recorded as escaping from cultivation in 69% of the parks sampled, showing that parks play a similar role in invasions to other sites in urbanized landscapes (Vojtk et al. 2020). Like residential gardens and urban parks, cultural heritage sites can

also provide opportunities for the spread of invasive plants, whose impact on monuments (biodegradation) could threaten their conservation (Celesti-Gradow & Ricotta 2021). Cultivation increases propagule pressure and lowers the environmental barriers for the survival and reproduction of nonnative species, hence facilitating biological invasions (Cadotte et al. 2017, Potgieter & Cadotte 2020). The role of botanical gardens as sources of plant invasion has long been recognized (Hulme 2011), yet we have not found specific quantitative studies on this topic in urban settings.

Age of Buildings, Neighborhoods, and Cities

Buildings, neighborhoods, and cities accumulate nonnative floras and faunas over time and increase the colonization pressure of invasive species. In Canada, for instance, the presence of older buildings near urban forests was positively correlated with nonnative species richness (Duchesneau et al. 2021). The same effect was observed in China where the richness of nonnative flora (cultivated and established) on 253 university campuses across 130 cities was positively correlated with campus age (Wang et al. 2021). In a study on plant species diversity in urban parks along an urban–rural gradient in Santiago, Chile, the age of the parks emerged as the main determinant of nonnative plant species richness, with older parks containing more nonnative species than newer ones (Figueroa et al. 2018).

This age effect could be the legacy of colonialist practices where human settlers commonly introduced species to their new settlements. In South Africa, for instance, past policies led to a predominance of nonnative species in older, wealthier neighborhoods, and colonial introductions and inequalities in the distribution of green spaces left a burdensome legacy of species that have become invasive (Shackleton & Gwedla 2021).

Age and Ethnicity of the Inhabitants

Age of the inhabitants was found to positively affect nonnative species richness in urban areas but not always. In Dunedin, New Zealand, older people with smaller, lower-value properties tended to have greater diversity of nonnative plants in their gardens (van Heezik et al. 2013). A similar pattern was observed in five urban areas in the region of Costa Brava, Spain, where the proportion of retired residents was related to nonnative and invasive plant composition in suburban gardens (Cubino et al. 2015). However, few studies have evaluated age of inhabitants as a driver of biological invasions in urban areas, and no general conclusions can be drawn on the topic yet.

Ethnicity of inhabitants was also identified as a social driver of nonnative species richness, although ethnicity was often associated with wealth. In 58 urban residential neighborhood blocks in and around Chicago, nonnative species richness was correlated with the percentage of residents identifying as Hispanic (Lowenstein & Minor 2016). Similarly, in Phoenix, Arizona, invasive bird species were more abundant in neighborhoods with a higher percent of Hispanic residents, but these neighborhoods had higher human population densities and lower income levels (Warren et al. 2019). In South Africa, where ethnicity and socioeconomic class are strongly correlated, much of the nonnative species' diversity in urban areas was concentrated in white-dominated suburbs (Lubbe et al. 2010).

In summary, the socioeconomic drivers most positively associated with urban nonnative species richness and abundance include wealth and household income, cultivation of plant and animal taxa in captivity, age of buildings, human and housing densities, and ethnicity of the inhabitants (Table 1). However, these drivers cannot be considered independent as there are deep cultural, economic, and historical connections among them.



Table 1 A summary of the effects of urban characteristics across four axes that shape the diversity, abundance, and spread of nonnative species

Axis	Main findings
Connectivity	Higher connectivity among cities generally increases the compositional similarity of nonnative assemblages and, to a lesser extent, the population genetic similarity of nonnative species.
	Higher connectivity of a focal city tends to increase the diversity of nonnative species.
	In general, within-city connectivity can facilitate the spread of nonnative species.
Physical properties	City size is the main predictor of increasing richness of nonnative species.
	Urbanization, with associated land-use change and propagule pressure, generally increases the richness and diversity of nonnative species.
	The network of roads, railways, and water streams is an important driver of propagules of nonnative species, thereby contributing to the richness and diversity of nonnative species.
Culture and socioeconomics	Wealth and household income are the main socioeconomic drivers of biological invasions in cities and are positively correlated with an increase in green spaces and the richness of nonnative species.
	The age and ethnicity of inhabitants and housing density are also related to nonnative species richness, although they are often also associated with wealth.
	The age of the cities and the cultivation of plants and animals in captivity increase the available propagules over time and the nonnative species richness.
Biogeography and climate	Generally, the distribution of urban nonnative species is governed by biogeographical and climatic drivers, such as tropical and warmer cities having higher nonnative diversity.
	There is evidence that cities can expand nonnative species distribution, as some species are restricted to cities in climatically unfavorable regions.
	How urbanization affects the importance of biogeographical drivers governing urban nonnative species strongly varied between studies, with some studies findings that biogeographical drivers showed the highest importance and others showing other drivers, such as socioeconomic variables, were more important.

Biogeography and Climate

Biogeography and climate are primary determinants of the abundance and distribution of species over large spatial scales (Whittaker 1956). Species range limits reflect large-scale environmental gradients (Sexton et al. 2009) and respond to shifts in climate, sometimes quite rapidly (Clark 1998). Biogeography and climate do not only provide important insights into large-scale diversity patterns, but they are also important for investigations into the factors influencing nonnative species spread and ecosystem invasibility (Hulme 2017). Due to the value of environmental variables for explaining species distributions, the use of niche modeling has become widespread for understanding and predicting nonnative species distributions (Thuiller et al. 2005) and for determining potential invasion hotspots (O'Donnell et al. 2012). Further, on biogeographic spatial scales, the environmental conditions that support a higher diversity of native species also appear to sustain greater numbers of nonnative species (Fridley et al. 2007). While we might have a robust understanding and set of tools for elucidating and predicting invasions across regions based on environmental conditions, cities, as pointed out earlier in this review, are novel habitats with novel environments that could provide opportunities for species establishment and spread. In this section, we discuss the influence of biogeographical and climatic conditions on whether nonnative species expand their range, increase diversity, or increase compositional similarity in cities and whether there is evidence that cities weaken the influence of environmental milieus (for details on the specific drivers assessed, see **Supplemental Appendix 1**).

Range Size

Cities include unique environmental and ecological spaces where some limiting climatic conditions might be relaxed (e.g., in dry or cold systems) or where negative trophic or competitive interactions are reduced (Pickett et al. 2001). Thus, cities might provide new beachheads for species to establish outside of both their climatic and geographical ranges, and where they are unlikely to establish in intact habitats (Borden & Flory 2021, Cadotte et al. 2017, Pyšek et al. 2010, Sukopp & Wurzel 2003). We found mixed support for the role of cities in expanding nonnative species ranges. In an examination of landscaping plants used in 36 cities across China, Jin et al. (2021) found that species of tropical origin were largely restricted to tropical and subtropical cities, while species that originated from cold regions were largely restricted to colder cities. Only temperate species were found in temperate and tropical cities, revealing that there was limited evidence that cities were expanding species ranges beyond what the climatic conditions would permit. Indeed, variation in occurrence probability or abundance of nonnative species along several biogeographic gradients often followed similar trends in cities as in natural habitats, including decreasing colonization probability as the elevation of cities increased (e.g., Kulfan et al. 2020) and more successful colonization of island cities compared to mainland cities [e.g., for nonnative urban birds in the Iberian peninsula (Palomino & Carrascal 2005)], calling into question whether cities expand the biogeographic ranges of species (Lososová et al. 2012a).

Conversely, in a study of the spread of the invasive ant *Tetramorium immigrans*, Cordonnier et al. (2020) show that it can maintain populations in harsh climates only in heavily urbanized habitats. Similarly, Polidori et al. (2021) concluded that urbanization favors the spread of the nonnative mud-dauber wasp (*Sceliphron curvatum*) into climatically nonoptimal latitudes in Europe, as the tendency of the wasp to occupy preferentially urban areas increases toward the north. The notion that cities can expand the ranges of nonnative species (Sukopp & Wurzel 2003) is also supported by Geron et al. (2021), who demonstrated that nonnative plant species originating from warm or dry climates are more restricted to urban areas in Oceanic Europe. Physiology-based models also predicted that overwintering emerald ash borer (*Agrilus planipennis*) can experience more severe and frequent mortality due to cold stress in northern Canadian cities compared with other cities in North America (Cuddington et al. 2018).

While cities might provide establishment opportunities for range-expanding species, subsequent spread is still likely to be under the control of climate (Abellán et al. 2017), though such species could emerge as future threats as climate changes continue (Borden & Flory 2021). Alternatively, climate changes could also reduce the success of nonnative species, especially those established in cities located in warm regions (Seebens et al. 2015). Overall, this could result in a zero-sum game for invasive species in some regions, as suggested by Stephens et al. (2016) for fruit flies in Australia and New Zealand, where southern and cooler cities are predicted to become more prone to invasion due to increasing temperatures, while the suitability for fruit-fly invasion is expected to largely decrease in northern cities. The above literature indicates that there is a complex interaction between climate and urbanization, and urbanization can provide range-expanding opportunities if environmental aspects that limit species spread are ameliorated in cities, but globally, this is not the case.

Diversity

Urbanization is well known to cause declines in native species' abundances and diversity (Aronson et al. 2014) while at the same time increasing the relative abundance and diversity of nonnative species (Cadotte et al. 2017). There are conflicting findings for biome comparisons; studies found that cities harbored a high diversity of nonnative species regardless of the floristic zone in



which the cities were found (Panitsa et al. 2020), while another study found that cities in Mediterranean ecoregions maintained lower nonnative diversity compared to cities in other regions in Italy (Celesti-Grapow & Blasi 1998). Some ecoregions might just be more susceptible to invasion or better connected than others (see the section titled Connectivity), and this is reflected in the urban biota (Celesti-Grapow & Blasi 1998). For example, a study of urban nonnative diversity in Yunnan Province in China showed that cities in subtropical ecoregions harbored more nonnative species than cities in other ecoregions (Gao et al. 2023).

Other biogeographic drivers often significantly affected the diversity of nonnative species in cities, despite the effect of urbanization. For example, Pyšek (1998) showed that European cities at higher elevations and at higher latitudes tend to harbor fewer nonnative plant species, which is in line with general latitudinal and elevational gradients of biodiversity. Similarly, Reyes-López & Carpintero (2014) showed that urban green areas in inland Spanish cities tend to harbor disproportionately fewer nonnative ant species compared to cities on the coast and on islands, both of which are typically highly prone to invasion even outside of cities.

Studies have also reported that nonnative plant richness is higher in warmer cities across Europe (Pyšek 1998) and China (Wang et al. 2021), although other studies have reported weak relationships between nonnative richness and temperature in urban snail and plant communities (Horsák et al. 2013, Zhu et al. 2019). Another frequently tested driver is precipitation, with results ranging from significantly higher nonnative species richness in wetter cities (Wheeler et al. 2017) to weak relationships (Pyšek 1998, Zhu et al. 2019). Compared with temperature and precipitation, other climatic drivers (**Table 1**), such as wind speed and the variability of temperature and precipitation, are rarely tested. While these results demonstrate how nonnative species richness varies along climatic gradients, a stronger test of how climate and urbanization interact would require controlling for introduction efforts, which have been shown to strongly vary for nonnative birds across regions (Dyer et al. 2017) and possibly obscure or even confound the effects of climatic gradients (Blackburn et al. 2020). Controlling for the number of birds introduced to different regions globally, Tsang et al. (2019) found no interaction between climatic conditions and urbanization extent in regulating the number of nonnative urban bird species.

Compositional Similarity

Globally, nonnative species have been observed to replace native species in urban habitats, which can be one of the mechanisms driving increased compositional similarity across cities (i.e., biotic homogenization) (McKinney 2006).

The effect of urbanization on compositional dissimilarity among cities appears to be influenced by both environmental dissimilarity and geographical distance (**Figure 2**; see also the section titled Connectivity). There is evidence that urban habitats such as roadsides and recreation areas in different ecoregions are more similar in their nonnative biota than are other environments including forests and agricultural fields (Ahrens et al. 2011). However, several studies found that nonnative dissimilarity was lower across cities within ecoregions than between ecoregions (Garcillán et al. 2014, Ramage et al. 2013), though other studies found that geographical distance was more important than ecoregion (see the section titled Connectivity). Generally, studies found that climatic conditions can shape species composition in cities (Horsák et al. 2013, Ramage et al. 2013, Yang et al. 2015), although their importance can strongly vary across studies. For example, the independent effects of climatic conditions are less important than spatial processes in shaping nonnative plant composition in Europe, although both processes have a shared effect (Lososová et al. 2012a). Detailed analyses showed that the importance of climatic conditions relative to geographical distances in shaping compositional similarity strongly varied across plants with different life forms,

regions, and spatial scales (Wang et al. 2021, Yang et al. 2015). Interestingly, studies showed that climate was a stronger predictor of compositional similarity between urban communities than other drivers such as socioeconomic variables (Ramage et al. 2013), campus areas (Wang et al. 2021), and geographic distance (La Sorte et al. 2014), although the opposite results have been reported when comparing their importance with predictors such as land uses (Lososová et al. 2012a).

Given the high level of inconsistency in the compositional similarity patterns of urban biotas across studies, we propose a theoretical framework addressing potential interactions between environmental dissimilarity and geographical distance, with high nonnative dissimilarity when cities are environmentally dissimilar or far apart (**Figure 2**). However, cities increase the nonnative compositional similarity not only by ameliorating environmental conditions but also by serving as nodes in transportation networks, allowing species to overcome geographical barriers (see the section titled Connectivity). This increased nonnative compositional similarity should be strongest at intermediate environmental and geographical distances or when only one is a factor, but compositional dissimilarity should still be high for environmentally very dissimilar cities that are very far apart (**Figure 2**).

Overall, while there are reasons to expect the roles of cities in driving invasion across geographical and climatic gradients to vary, their exact roles could also be complicated by introduction histories, which can affect observed patterns of nonnative richness, among other factors. There is some evidence of an interaction between biogeographic drivers and urbanization affecting nonnative diversity. The evidence is inconclusive as to whether the influence of large-scale biogeographic drivers on nonnative species diversity is weaker than its effect on native species diversity.

POLICY AND MANAGEMENT

Effective management of urban biological invasions is crucial for mitigating their negative impacts on biodiversity, ecosystem services, and human well-being. This is remarkably challenging due to the complex interactions of multiple ecological, economic, and social factors. Urban conservation managers must balance the imperative to conserve biodiversity, the demands of economic development, and the diverse needs and preferences of urban inhabitants.

Urban Biodiversity

Although most urban ecosystems still support many native species, nonnative species have been introduced to provide diverse ecosystem services. This necessitates careful consideration of the native versus nonnative dichotomy and the inherent trade-offs between native biodiversity conservation and the services provided by nonnative (and invasive) species. Several studies promote the introduction of nonnative species to enhance native biodiversity and ecosystem services. For example, de Andrade (2022) recommends planting more *Terminalia catappa* (a nonnative tree) to improve the long-term persistence of native marmosets in João Pessoa, Brazil.

Practical Management Recommendations

While most publications concerning urban biological invasions lack explicit management and policy recommendations (Potgieter et al. 2022a), several studies do offer precise management guidance. For example, Grimalt et al. (2011) shows that azadirachtins (secondary metabolites present in *Azadirachta indica* seeds) are an environmentally acceptable systemic insecticide for the control of the emerald ash borer (*A. planipennis*) in Canada. Buczkowski (2017) demonstrates that prey baiting using live, fipronil-treated termites is effective against Asian needle ants (*Brachyponera chinensis*) near Liberty, Washington. Some studies also provide useful management frameworks such as decision support tools (e.g., Gaertner et al. 2016); site-, species-, or pathway/vector-specific

prioritization frameworks (e.g., Padayachee et al. 2017, Potgieter & Cadotte 2020, Potgieter et al. 2022b); or novel modeling approaches for invasive species surveillance (e.g., Epanchin-Niell et al. 2014).

Stakeholder Perceptions

Invasive species that are both beneficial (e.g., providing aesthetic value) and detrimental (e.g., displacing native biodiversity) usually generate conflicts around their use and management (Woodford et al. 2017). Such conflicts often arise due to differences in value systems and less often due to divergent perceptions of risk among stakeholders (Estévez et al. 2015). These differences can be pronounced in urban areas, which typically have a greater number and diversity of stakeholders than rural and natural areas (Potgieter et al. 2019). Value-based conflicts are inherently difficult to resolve, and the management of urban biological invasions is increasingly viewed as a wicked problem (*sensu* Rittel & Webber 1973), as straightforward win-win solutions seldom exist.

Management decisions should explicitly and transparently consider divergent stakeholder perspectives (Shackleton et al. 2019). Few studies with policy and management implications for urban biological invasions include stakeholder views in their assessments. Active engagement with stakeholders from the onset of any decision-making process is essential for understanding the factors that inform their perceptions, integrating valuable local knowledge and practices, promoting awareness, fostering collaboration and trust, reaching consensus, and facilitating cooperative management programs (Sharp et al. 2011). For example, Mumaw & Bekessy (2017) discussed how collaborative wildlife gardening programs can engage with urban residents to garner support for conservation efforts. Potgieter et al. (2022a) combined published evidence and local stakeholder knowledge in developing an objective and systematic invasive species prioritization tool that can assist urban conservation practitioners.

Policy

The earliest and most sustained policy and governance initiatives for regulating invasive species were primarily developed at the state or national level, with an initial emphasis on safeguarding agriculture but recently extending to biodiversity (protected areas), ecosystem services, and human well-being (e.g., the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services).

Few studies either directly assessed policies relevant to urban biological invasions or explicitly mentioned the policy implications of their work. Most of these studies originated from Australia, Canada, South Africa, and the United States, all of which have robust legislative and policy frameworks guiding invasive-species management. Several studies provide evidence linking biodiversity loss to urbanization and outline detailed policy recommendations to mitigate further impact. For example, Drayton & Primack (1996) showed that native biodiversity loss in a conservation area in Metropolitan Boston coincided with an increase in human activity (e.g., increased fire frequency, thinning of the forest, and trampling of the vegetation). They recommended policies such as preventing new trails from being developed, excluding people from sensitive areas, and reintroducing some of the native species lost. Other studies highlight the failings of existing policies and propose ways to resolve challenges. For example, Maceda-Veiga et al. (2019) lament a lack of enforcement of new legislation to curb the release of nonnative pets in Spain. They propose a four-tier approach to deal more effectively with pet-abandonment issues. Addressing policy development and implementation challenges often requires a combination of public awareness, scientific research, collaboration, and political will. Advocacy efforts; education; and highlighting the ecological, economic, and social benefits of addressing biological invasions can contribute to the development and implementation of effective policies.

As cities grapple with the complex interplay of ecological, economic, and social factors, decisions regarding the control of invasive species necessitate a nuanced understanding of the trade-offs inherent in these management strategies. Decisions to manage urban biological invasions are often prompted by immediate external factors such as funding availability, public pressure, and emergencies (Potgieter et al. 2022a). These decisions are seldom informed by objective and transparent criteria and rarely involve consideration of local perspectives. Invasive species management, governance, and policy development in urban areas need to be evidence based and facilitated by comprehensive stakeholder engagement. Despite growing concerns about invasive species, given the many perceived and realized benefits they provide, we might have to accept them as permanent features of some urban landscapes.

KNOWLEDGE GAPS AND RECOMMENDATIONS FOR FUTURE RESEARCH

While substantial progress has been made in understanding the factors driving urban biological invasions, several critical knowledge gaps persist. Below we briefly highlight these and propose recommendations for future research.

One major obstacle involves the geographic and taxonomic biases in invasion ecology (Pyšek et al. 2020), which limit the inferences we can draw and preclude a global picture of the role of cities in biological invasions. Historically, most studies were conducted in Western European and North American countries, with China, Australia, and South Africa appearing as recent hotspots of studies on urban biological invasions. Also, most studies focus largely on plants and birds (e.g., Aronson et al. 2014, Callaghan et al. 2019), with other animal groups, such as fish (Zhang et al. 2022), insects (Gottschalk et al. 2007, Grez et al. 2019, Gruver & CaraDonna 2021, Vonshak & Gordon 2015), and snails (Horsák et al. 2013), being less represented (see **Supplemental Appendix 2**).

Compounding this issue are the scarcity and inconsistency of measurements of drivers of urban nonnative species abundance and diversity, as various methods are employed and systematic sampling is often overlooked. For example, the most common measure of connectivity, geographic distance, can serve as a proxy for many aspects of connectivity and is easy to measure, but specific anthropogenic measures of connectivity such as air traffic, shipping, and economic networks are likely to provide additional information about the role of cities in the spread of biological invasions. An important question worth pursuing is whether selected habitats, systematically sampled in a standardized manner, can serve as representative samples across other cities. The predominant focus on individual cities in research exacerbates the lack of systematic analyses of socioeconomic drivers of biological invasions across multiple urban areas. There is also a lack of clarity in terminology (specifically regarding the classification of species as native, naturalized, nonnative, or invasive) and, as a result, in defining what is being measured.

What is also not well understood is how biogeographical differences limit urban biological invasions or alternatively are overridden by the potentially homogenizing influence of urbanization on biota (McKinney 2006). The main reason for this knowledge gap is the dearth of global analyses that replicate sampling of cities within and among biomes or ecoregions, while accounting for the influences of spatial distances, environmental covariates, and the socioeconomic history of cities. Furthermore, the interactions between cities and their surrounding habitats need to be investigated systematically to understand the role of cities in the invasion of nonurban habitats. This research requires the use of meta-population and meta-community concepts to examine the dynamics between cities and their surrounding habitats.

Addressing these challenges and fostering greater standardization in research methods are imperative steps toward a more comprehensive and globally applicable understanding of urban biological invasions.



GENERAL CONCLUSIONS

The myriad anthropogenic effects on species distributions and biodiversity that are hallmarks of the Anthropocene are undoubtedly accentuated in cities. Urbanization results in the breakdown of geographical and environmental barriers to the introduction, establishment, and spread of species, and local physical and ecological modifications that are influenced by city history, growth, and socioeconomic realities can provide ecological opportunities that further facilitate species establishment and spread. Evidence has emerged showing that anthropogenic activities override natural processes (e.g., Helmus et al. 2014), and urbanization embodies many of these anthropogenic drivers. Our review shows how the connectivity, physical, and environmental changes associated with urbanization are restructuring species distributions and biodiversity patterns globally. Some of the natural processes that limit species distributions, like extreme environmental conditions (**Figure 2**), appear to remain strong despite urbanization, while others are easily overridden (**Table 1**). Yet, despite the knowledge outlined in this review, it is clear that our understanding of the role of cities in reshaping biodiversity is still limited.

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