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A research agenda for urban biodiversity in the global extinction crisis

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Abstract

Rapid urbanization and the global loss of biodiversity necessitate the development of a research agenda that addresses knowledge gaps in urban ecology that will inform policy, management, and conservation. To advance this goal, we present six topics to pursue in urban biodiversity research: (i) the socioeconomic and social-ecological drivers of biodiversity loss vs. gain of biodiversity, (ii) the response of biodiversity to technological change, (iii) biodiversity-ecosystem service relationships, (iv) urban areas as refugia for biodiversity, (v) spatiotemporal dynamics of species, community changes, and underlying processes, and (vi) ecological networks. We discuss overarching considerations and offer a set of questions to inspire and support urban biodiversity research. In parallel, we advocate for communication and collaboration across many fields and disciplines in order to build capacity for urban biodiversity research, education, and practice. Taken together we note that urban areas will play an important role in addressing the global extinction crisis.

Keywords

Biodiversity loss, Ecosystem services, Extinction crisis, Social-ecological systems, Urban conservation

Biodiversity is declining worldwide, driven foremost by the intensification in land management and the transformation of natural areas for agriculture, production forestry, and settlements (IPBES 2019). Urban areas have doubled since 1992 (IPBES 2019), and in comparison to 2020 are projected to expand between 30% and 180% until 2100, depending on the scenario applied (Chen et al. 2020). Notably, though, urban growth is often located in regions of high biodiversity (Miller & Hobbs 2002, McDonald et al. 2008, Seto et al. 2012) and impacts ecosystems far beyond urban areas, through resource demands, pollution, and climate impacts (McDonald et al. 2019). Therefore, biodiversity conservation in urban areas needs to be shaped in a way that supports global conservation efforts.

Urbanization affects biodiversity at various inter- and intra-specific levels, from taxonomic (Beninde et al. 2015) and functional (Lososová et al. 2016, La Sorte et al. 2018) to phylogenetic (Ricotta et al. 2009, Sol et al. 2017), and genetic diversity (Miles et al. 2019) and to the composition of species communities and assemblages (see e.g., Williams et al. 2015 for functional trait composition of urban floras). Relative to natural areas, urban areas often contain depleted ecological communities (Aronson et al. 2014, Sol et al. 2017, Fournier et al. 2020, but see Sattler et al. 2011) but for vascular plants support exceptionally high numbers of both native and non-native species, including a range of rare and threatened native species (Kowarik 2011, Ives et al. 2016, Planchuelo et al. 2020). Across taxa, urbanization filters regional biotas with differences among native and non-native species and species of different residence time, creating a novel arrangement of assemblages (e.g., Williams et al. 2009, Merckx and Van Dyck 2019). Since the early 2000s there has been a marked increase in evaluating how ecological (Kowarik 2011) and socioeconomic factors (Hope et al. 2003) drive urban biodiversity patterns in species abundance, richness, and distribution. However, much of this increase focused on local/regional description of patterns leading McDonnell and Hahs (2013) to call for a research agenda that identified generally valid relationships between urban environments and biodiversity, set local results into global context, integrated potential social predictors of biodiversity, reached mechanistic understanding of urban biodiversity, and translated practitioner questions into actionable science. Likewise, other urban ecology publications advocated for cross-region, multi-scale, and transdisciplinary studies that considered the complexity of urban environments (Niemelä 2014, Pataki 2015, McPhearson et al. 2016, Barot et al. 2019). Since then, the number of cross-region comparisons has increased (Aronson et al. 2014, Pataki 2015) and the focus of urban biodiversity research expanded to include urban evolutionary ecology and the rapid adaptation of species to urban settings (Marzluff 2012, Alberti 2015, Rivkin et al. 2019), how urban biodiversity influences ecosystem functions and underlying services that affect human wellbeing (Ziter 2016, Schwarz et al. 2017), and whether urban habitats are hotspots or ecological traps (or neither) for biodiversity (Noreika et al. 2015, Lepczyk et al. 2017).

Beyond science, there has been an increase in public policies, programs, and science-policy discourse related to interactions of green infrastructure with human health and wellbeing, the development of livable urban areas, and the impacts of urbanization on biodiversity (Nilon et al. 2017, Barot et al. 2019). For instance, recent international agreements, such as the United Nations' (2015) Sustainable Development Goals seek to help towns and cities develop plans to protect biodiversity. However, even with the rapid gain in urban biodiversity knowledge and its increased inclusion in policy and planning, biodiversity loss continues. There are gaps in our understanding critical to improving biodiversity conservation policies and management in urban areas that need to be filled to improve global biodiversity outcomes.

To address these gaps, we identify six topics and three overarching considerations (Fig. 1) that capture trajectories of future urban biodiversity research. We then provide a set of emergent questions and examples on how to approach them (Box 1) that will be important to address if society is to accommodate biodiversity conservation within urban areas. Finally, we introduce local and international programs and highlight collaborative ways forward at the science-policy interface. Topics and overarching considerations were identified through an iterative process, similar to a Delphi approach, from mid-2018 to early-2020 amongst participants of a workshop held at Rutgers University, New Brunswick NJ, USA. Participants consisted of early-career and advanced researchers from Africa, the Americas, Australia, and Europe who represent a diversity of backgrounds, perspectives, and research foci. To select questions, each participant submitted their key question. The full list of questions was then revised by the group until consensus was reached (more topics and related questions exist, such as urban evolutionary ecology, which however, we do not present because they have only recently seen a strong increase in studies. We have deliberately focused on the six topics we felt were most relevant to the widest range of urban biodiversity studies). The topics and questions are offered to inspire and support future efforts in urban biodiversity research and to strengthen the role urban areas play in maintaining global biodiversity.

Future Topics in Urban Biodiversity Research

1. Gain a better understanding of social-ecological and socioeconomic drivers of urban biodiversity

A range of factors associated with people and our societies directly and indirectly influence urban biodiversity (McDonald et al. 2019). These factors include law (Mauerhofer and Essl 2018), policy (Meyer 2006), socioeconomic inequality (Hope et al. 2003, Cilliers et al. 2012), civic action such as that related to public enthusiasm about insect pollinators (Hall and Martins 2020), recent and past management (Boone et al. 2009, Johnson et al. 2015), and how people’s individual activities and choices, such as recycling habits, pet ownership, yard management, or vehicle use affect ecosystems and human-nature relationships (Lepczyk et al. 2004). Despite the meta-analysis of ecological and social factors driving urban biodiversity by Beninde et al. (2015) there is a need for greater clarity around which of these factors are more important for urban biodiversity and how their importance changes across spatial, temporal, or organization scales. For example, are the trends consistent between different levels of organization (e.g. individuals vs. species vs. communities) or different facets of biodiversity, such as rare vs. common, or native vs. non-native species; considerations of taxonomic vs. functional vs. phylogenetic representations; or even between habitats or along environmental gradients. Effects of legal systems on biodiversity can be indirect (e.g., subsidies to support commuting can promote urban sprawl, resulting in habitat loss; Meyer 2006), and laws for different goals (e.g., biodiversity conservation or climate change mitigation) are increasingly conflicting (Mauerhofer and Essl 2018). In order to inform policy and management, a thorough understanding of the factors that drive human behaviors that affect biodiversity in different places – e.g., in different regions, separate urban areas, or separate parts of an urban area – is needed. For example, the luxury effect (Hope et al. 2003) that has been identified in urban areas of the Global North does not necessarily hold in the Global South (Cilliers et al. 2012), or even Global North cities in the geographic South (Kendal et al. 2015). Identifying ways to promote behavioral change is critical for adjusting human actions to benefit urban biodiversity (Shwartz et al. 2014). For example, many property owners intentionally manage their yards for the benefit of wildlife (Lepczyk et al. 2004), through such activities as cultivating native plant species in an effort to support pollinators (Garbuzov and Ratnieks 2014). Specifically, we need to answer the following questions:

- Which factors modulate the strength of relationships between social-ecological, socioeconomic, and environmental drivers with biodiversity at different spatial scales?
- What tools (e.g., cultural, economic, political) can affect behavior change in people that will reduce their ecological impacts and promote biodiversity?
- Are laws and other protection mechanisms to support biodiversity adequate, enforced and effective (e.g., does management of urban protected areas support rare species)?
- Does a biodiversity-conscious urban public influence global conservation efforts?
- How do we operationalize our knowledge of social-ecological linkages into actions that promote biodiversity conservation in urban areas and beyond?

2. Identify the response of biodiversity to technological change

New and existing forms of technology are being used within urban areas that are likely having unintended consequences on species and ecosystems. For instance, artificial lights, anthropogenic noise, new forms of transportation, and novel building materials have no natural analogues but are prevalent in urban areas (Gaston et al. 2015). Notably, both light and noise pollution are a growing focus of urban biodiversity research. In the case of lighting, changes from incandescent and fluorescent to light-emitting diodes (LED) have resulted in light that is both brighter and cheaper. Urban administrations have thus embarked on a trend towards building brighter and denser networks of streetlights (Hölker et al. 2010). But, artificial lighting has been demonstrated to cause changes in functional traits such as circadian and circannual rhythms (Dominoni et al. 2014, Robert et al. 2015), disrupt courtship behaviors and mating success in fireflies and moths (Van Geffen et al. 2014, Firebaugh and Haynes 2019), and led to shifts and declines in invertebrate and vertebrate diversity (Hale et al. 2015, Knop et al. 2017). Consequently, artificial lighting may have large effects across species and trophic levels. As such, important questions that need to be addressed are:

- Whether and to what extent do changes to LED – in relation to other lights sources – contribute to decreasing biodiversity, altered behavior of organisms, and shifts in the taxonomic and functional composition of communities?
- How does artificial lighting affect migratory species' pathways?
- How does artificial lighting interact with climate change to create larger trophic mis-matches than expected with just climate change?

Anthropogenic noise arises from a variety of sources, including vehicles, planes, construction, tools, and human interactions. It impacts biodiversity through the behavioral traits of a range of taxa dependent on acoustic communication in a variety of ways, including habitat choice and mating, which has evolutionary implications (Parris et al. 2009, Nordt and Klenke 2013, Lampe et al. 2014). While urban transportation is moving towards more electric vehicles (Ortar and Ryghaug 2019), which may decrease noise, this may increase the number of vehicle-wildlife collisions as vehicle collisions are correlated with the human footprint on the landscape (Hill et al. 2019). Air traffic has received less urban biodiversity research attention than road or railway traffic, although its noise emissions and collisions can affect birds, bats, flying insects and even wind dispersed plant seeds. Unmanned aerial vehicles will increase the frequency of these interactions (Davy et al. 2017). Given these changes in noise and transportation it is important to connect transport planning and policy with urban biodiversity knowledge to decrease current and potential future threats. As such, the following questions are important to address:

- How do technological advances, such as changes in vehicle types and related noise, select for novel adaptations in animal physiology and behavior, and what does this mean for population dynamics and species fitness?
- What are the implications of noise-induced selection pressure on biodiversity and ecosystem functioning?
- How are animals affected by new transport options (e.g., unmanned aerial vehicles) and which protection measures can be taken to mitigate negative effects?

Another form of technological change is the shift in building materials and technologies that can lead to both problems and opportunities for urban biodiversity. For instance, glass façades are sources of collision for birds (Hager et al. 2017), and new insulating materials hinder birds, bats, and insects from nesting within buildings. Gaps in walls and roofs can provide habitat for a range of plants and small animals (Yalcinalp and Meral 2017), but new walls are often made from different materials and are seamless, while roofs are made animal proof. In addition, new architectural fashions or building technologies might lead to novel challenges for biodiversity. Even green façades, roofs, and walls that can support a range of taxa (Filazzola et al. 2019) cannot fully substitute for the loss of habitat on the ground (Williams et al. 2014). Still, design solutions exist that better integrate buildings and species conservation, such as window decals and fenestration or well-connected ground-, façade- and roof vegetation that could decrease fragmentation (Apfelbeck et al. 2020). New building trends and materials require that architects, planners and practitioners work with ecologists to learn from action and to mitigate negative effects. Such negative effects can be reduced through answering the following questions:

- Which materials provide the best synergies for construction suitability, longevity, and embodied energy that also minimize impacts to biodiversity?
- How can buildings be designed to promote human health and wellbeing, sustainability, and biodiversity?
- Which synergies or tradeoffs can arise from reconciling ecological and engineering solutions that aim to provide a suite of benefits for different types of built infrastructure?

3. Better understand how urban biodiversity links to ecosystem services

Urban development and climate change amplify health and wellbeing risks to the public such as heat waves, pollution, pest occurrence, and their interactions. As a result, the scientific and political interest in urban ecosystem services (Haase et al. 2014) is growing. Policies increasingly promote the enhancement of ecosystem service delivery in urban areas. For example, a European Union report on “the multifunctionality of green infrastructure” emphasizes that the role of green infrastructure “in protecting biodiversity is highly dependent on its role in promoting ecosystem services and vice versa” (European Commission’s Directorate-General Environment 2012: 2). While a positive biodiversity-ecosystem service relationship is often assumed (Schwarz et al. 2017), biodiversity can cause disservices as well (Lyytimäki and Sipilä 2009), and biodiversity-ecosystem service relationships can be positive, negative, or neutral (Ziter 2016, Schwarz et al. 2017). Moreover, taxonomic diversity has mainly been tested as an indicator of urban ecosystem services, but a more complete and nuanced understanding will only come from testing these relationships across different levels of biodiversity, such as different functional groups, rare vs. common or native vs. non-native species (Ziter 2016, Schwarz et al. 2017). Managing urban habitats for the delivery of ecosystem services will not automatically benefit biodiversity. On the contrary, it might impose an additional anthropogenic filter on top of the existing environmental, social-ecological, and socioeconomic filters that affect species in urban habitats (Aronson et al. 2016) – such as by cultivating non-native species for the sake of ecosystem service delivery, raising the risk of biological invasions. Similarly, benefits or impacts from the terrestrial realm may be offset by gains or repercussions in freshwater or aquatic environments (Bugnot et al. 2019). Understanding whether and how biodiversity supports ecosystem services better than single species is imperative for urban planning as well as for understanding how it may provide resilience to the impacts of climate change and other stressors that are deteriorating urban biodiversity (Kabisch et al. 2016). Moreover, we cannot assume that biodiversity-ecosystem service relationships are the same across urban areas, cultures, and regions. For example, poorer households tend to rely more on cultivating crop species in their gardens than households of higher economic status (Lubbe et al. 2010), thus promoting different species. This is particularly pronounced in cities of developing nations (du Toit et al. 2018). We need to identify generalities and particularities, and communicate successes and failures across science, policy, and practice. In particular, it is important to address the following questions:

- How do environmental, social-ecological, and socioeconomic factors affect biodiversity-ecosystem service relationships, and how do these compare between the Global North and the Global South?
- What is the role of different types of biodiversity (habitat, taxonomic, genetic, and phylogenetic diversity) as well as inter- and intra-specific functional diversity, and of different groups of species (e.g., non-native and invasive, rare species, functional groups) in relation to ecosystem services?
- Which synergies and tradeoffs among biodiversity and ecosystem services exist in urban environments (e.g., if in the light of climate change, cities increasingly cultivate non-native species, what implications will this have on biodiversity)?

4. Identify how cities act as refugia for biodiversity

Urban areas may serve as refugia for biodiversity, particularly when the surrounding non-urban landscape is heavily altered by agriculture, forestry, and other human land uses (Baldock et al. 2015). In fact, urban areas have become refugia for an increasing number of animal species, from those that have shared human settlements for centuries such as rats, to foxes or coyotes that have migrated to settlements only within the past decades (Gloor et al. 2001, Rashleigh et al. 2008). Urban areas can have positive impacts on regional biodiversity in five main ways. First, urban habitats can support populations that are threatened or extirpated from the regional landscape (Ives et al. 2016). For example, novel urban ecosystems such as wasteland sites support considerable numbers of rare plant and insect species (Kattwinkel et al. 2011, Kowarik & von der Lippe 2018). Second, the habitats and activities supported by people may buffer populations during periods of stress. For example, supplemental bird feeding can contribute to increased diversity of birds in urban landscapes (Plummer et al. 2019). Third, species may be released from negative interspecific interactions, such as herbivory, predation, or parasitism, allowing populations of species to persist in the urban landscape that could not persist in the regional landscape (Murray et al. 2019). These mechanisms might be similar to those driving biological invasions (e.g., enemy release hypothesis; see Jeschke (2014) for an overview). Fourth, populations adapted to urban environments may in part be precursors for adaptation to climate change, particularly to temperature increases (Ziska et al. 2003). Finally, nature in urban areas allows for opportunities to involve the public in biodiversity engagement and stewardship (Ramalho and Hobbs 2012). Open questions about cities as refugia for biodiversity include:

- Under which circumstances can urban populations be sources for repopulating non-urban areas?
- How do species that migrate into and through urban areas affect existing urban biodiversity and ecosystem functioning?
- How do we balance conserving urban biodiversity with human-wildlife conflicts?
- To which extent are species living in urban areas or species used for urban green infrastructure able to adapt to climate change?
- Are adaptations to urban environments precursors for adaptation to climate change or to habitat loss and fragmentation outside urban areas?

5. Beyond static snapshots – identify spatiotemporal dynamics of species, community changes, and underlying processes

Ramalho and Hobbs (2012) called for urban ecology to take the spatiotemporal dynamics of urban development into account. But few studies combine spatial and temporal patterns when analyzing the response of biodiversity to urbanization. Most urban biodiversity research has been conducted either at small and detailed spatial scales or at a large spatial extent but with low resolution (i.e. large grain; Magle et al. 2019). What we need to resolve this tradeoff in grain size and extent is more spatially explicit data that compares different land use/cover types across multiple urban areas (e.g., Kalusová et al. 2019). Studies that utilize these approaches are becoming more common but for a range of questions, no general answer has been found, such as whether there are common trait responses to urbanization across regions (Williams et al. 2015), what limits the establishment of self-sustaining populations within urban areas (Kowarik & von der Lippe 2018), and how this differs among groups of species (taxa, native vs. non-native, rare vs. common, etc.). Combined with long term data as well as (global) socioeconomic data, spatially-explicit approaches will let us elucidate how and why species are distributed across urban areas and thus derive management measures at the local scale (e.g., green space management adapted to biodiversity needs) –where management usually happens. Ultimately, urban ecology faces the same issue as all of ecology in that we need long-term monitoring, observations, and experiments. While studies based on long-term observations exist (e.g., Chocholoušková & Pyšek 2003, Salinitro et al. 2019), these usually neither consider urban spatial heterogeneity nor differences among urban areas. Long-term spatiotemporal research will enable us to better disentangle shifts in trajectories, such as those that highlight the extinction crisis, compared to natural fluctuations within the system (Onuferko et al. 2018). This knowledge will ensure that we can more reliably predict future trends in urban biodiversity and determine where our response may be short term (e.g. a change in supplemental watering practices) and where a more concerted, coordinated and longer-term response may be required (e.g., banning the use of neonicotinoid pesticides in garden plants; Lentola et al. 2017). Unanswered questions on spatiotemporal urban biodiversity dynamics include:

- Can urban areas harbor self-sustaining populations of species of conservation concern and in which habitats or under which conditions is this possible?
- What are the drivers and mechanisms shaping metapopulation and metacommunity dynamics across urban areas and beyond urban boundaries?
- How do connections beyond urban boundaries – e.g., due to resource demand – affect biodiversity within an urban area?

6. Gain an understanding of the effects of urbanization on multi-trophic interactions and ecological networks

Ecological networks are being simplified and disrupted by various global change stressors (Heleno et al. 2020), with the consequences only partially understood, particularly in regards to urbanization effects on ecological networks (Moreira et al. 2019). Across broader landscapes undergoing anthropogenic change, both temporal (Renner and Zohner 2018) and spatial decoupling (Schweiger et al. 2008) of interacting species have been shown. This decoupling is driven by climate change that induces species migration; and by land use, which creates migration barriers (but to different extents across species). In urban environments, phenological shifts to both earlier and later dates occur (Wohlfahrt et al. 2019) and might result in temporal decoupling of species interactions and associated ecosystem services (Sherry et al. 2007). Fragmentation and the abundance of novel ecosystems (Kowarik 2011) that are characterized by novel combinations of abiotic factors and species assemblages (Heger et al. 2019) might further modify existing networks, while the large share of generalist species present in urban environments might stabilize networks (Schleuning et al. 2016). Importantly, urbanization can affect various multi-trophic interactions in markedly different ways. For example, in one experiment urbanization reduced top-down control of aphids by the larvae of syrphid flies, partly driven by urban environmental conditions (Turrini et al. 2016). In contrast, while urbanization affected leaf chemical composition of English oak (*Quercus robur* L.), it was not related to decreases in leaf chewer damage (Moreira et al. 2019). These studies exemplify that an understanding of ecological networks is relevant for better determining both biodiversity-ecosystem function and biodiversity-ecosystem service relationships (Seibold et al. 2018). However, important questions remain, such as:

- How do multiple urban drivers interact to affect ecological networks, and to what extent, at different spatial scales?
- Do abrupt changes from diverse to simplified interaction networks occur in urban areas and under which conditions?
- What are the effects of abrupt disruptions to the network?
- How do urban-induced changes in ecological network complexity and diversity affect ecosystem functions and (dis-)services?
- What interventions and actions enhance ecological network structure and diversity in urban areas?

Overarching Considerations in Urban Biodiversity Research

Broaden the geographic focus of urban biodiversity research

The vast majority of urban biodiversity research to date has focused on urban areas in developed economies (McDonald et al. 2019). While we are not the first to say so, the bias remains. To truly understand how urbanization drives biodiversity and how we can design and manage for biodiverse urban areas, differences in historical legacies have to be addressed (Ramalho and Hobbs 2012), both within and between biogeographic realms. Special attention is required in regions where the most dramatic transformations associated with urbanization are expected to occur, particularly in Africa and Asia where most cities projected to become megacities by 2030 are located (e.g., Lahore, Pakistan, and Luanda, Angola; UN DESA 2016). Many of these megacities are situated in regions where biodiversity, poverty, and inequality intersect (Seto et al. 2012), and where detailed information about urbanization effects on social-ecological systems is scarce and underrepresented in the literature (Secretariat of the Convention on Biological Diversity 2012). Urban biodiversity patterns that hold for the Global North may not necessarily hold for the Global South (Silva et al. 2015). The interpolation of results from one part of the world to another or from large cities to small towns might not yield consistent or even appropriate outcomes (Duncan et al. 2011, Jung and Threlfall 2018). Also, the relevance of the topics that we present here will vary among regions – for example, the level and speed of technological change differs among countries and might take different trajectories in the future. Similarly, different ecosystem services will be prioritized in different urban areas.

Urban biodiversity research is progressing in less well-studied regions of the world (e.g., Wu et al. 2014, Chamberlain et al. 2018, Ofori et al. 2018, Guenat et al. 2019), paving the way towards a more holistic understanding that is not dominated by particular patterns of urban development or socioeconomic systems. However, this progression requires urban biodiversity researchers from the Global North to actively redress geographic inequities in representation by proactively seeking out research from, and research opportunities in, these under-represented regions.

Broaden the taxonomic focus of urban biodiversity research

Another common problem in all biodiversity research is taxonomic bias. Within disciplines such as wildlife ecology, there is strong bias for birds and mammals (Christoffel and Lepczyk 2012) and urban biodiversity research is similar (Marzluff 2016), with a focus on birds and vascular plants (Aronson et al. 2014). Other taxonomic groups are far less represented, particularly invertebrates and microorganisms, making our understanding of how organisms respond to urbanization incomplete. While work on less represented taxa exists (e.g., Niemelä & Kotze 2009, Paap et al. 2017, Merckx et al. 2018), results are often published in specialized regional or taxonomic journals of which the broader scientific community is not aware. Furthermore, research on multiple taxa in urban systems is rare (but see Sattler et al. 2010a,b, Concepción et al. 2016, Threlfall et al. 2017, Merckx et al. 2018). Finally, there is also a bias towards diurnal species and terrestrial or freshwater ecosystems, although a recent review highlights the potential for urban marine ecosystems to contribute to our understanding of urban biodiversity (Todd et al. 2019). Some unresolved questions on the geographic and taxonomic bias to be tackled by urban biodiversity researchers are:

- How and why do spatial and temporal patterns of biodiversity differ within and among urban habitats and regions?
- Do species of different taxa respond to urbanization in a similar way?
- Do urban areas and their green infrastructure need to be designed differently across regions, countries, continents, and cultures to maintain and enhance biodiversity?

Gain a mechanistic understanding of urban biodiversity

There is a long-standing and repeated call for the need to move towards a more mechanistic understanding of how urban systems affect biodiversity (Shochat et al. 2006, McDonnell and Hahs 2013). While a range of drivers of urban biodiversity have been identified, in order to best manage and enhance biodiversity, we need to better understand the ecological processes that link drivers and responses. This call applies to all topics mentioned above, and although some progress has been made in this respect, urban biodiversity research is far from a comprehensive mechanistic understanding.

Great examples of mechanistic urban biodiversity research are investigations linking noise pollution to the abundance and traits of acoustically communicating species, where mechanisms can comprise shifts in behavioral traits such as temporal avoidance of traffic noise by birds (Nordt and Klenke 2013) or plastic or even genetically fixed adaptation (Lampe et al. 2014). Trait-based approaches are highly promising in the effort of gaining better mechanistic understanding (Lavorel and Garnier 2002), such as identifying functional groups of species that experience greater recruitment facilitation or limitation within urban environments (Piana et al. 2019). This will help explain how biodiversity responds to urbanization from individuals to populations to communities and ecological networks. Applying experiments in urban areas across the globe, as exemplified by GLUSEEN (Global Urban Soil Ecology and Education Network) for urban soil ecosystems (Pouyat et al. 2017) will help us identify mechanisms, find both generalities and particularities among taxa and regions, and yield synthetic understanding. The design of experiments needs to be extended beyond urban-rural gradients (McDonnell and Hahs 2008), as the complex mosaic of urban landscapes precludes “simple starting points and lines of argumentation to explain causal linkages between biological diversity and cities” (Werner and Zahner 2009, p. 56). Questions to be answered by mechanistic urban biodiversity research include:

- How does the response of functional traits to specific urban site factors influence observed patterns of species presence, abundance, and biodiversity?
- Are these responses observed across gradients of each site factor?
- How do site factors interact in affecting biodiversity?
- Is the functional response of species and communities to urbanization similar across regions, biomes, and taxa?

Beyond a research agenda for urban biodiversity

Communication and collaboration across fields and disciplines are necessary to solve the questions and research needs raised here and to put results into practice. To do so, a range of promising avenues exists. First, city administrations and scientists have started recognizing the importance of putting people of different disciplines together to solve complex problems. Such city-based initiatives must happen at both local (Table 1) and global scales. Second, community/ citizen science has become increasingly popular. For example, eBird (Sullivan et al. 2014) has triggered urban bird biodiversity research (e.g., La Sorte et al. 2014, Clark 2017), and BioBlitz (https://www.nationalgeographic.org/projects/bioblitz/) includes the City Nature Challenge specifically geared towards urban areas. Community/ citizen science efforts have the potential to increase public engagement with urban biodiversity and science more broadly (Bonney et al. 2016; Lepczyk et al. 2020). Similarly, urban biodiversity research and conservation can benefit from listening to community needs and aligning their goals with community values (Evans et al. 2005, Pandya 2012). Third, educational programs need to find a balance between providing a deep disciplinary understanding and integrating the teaching of ecology, landscape planning, public policy, and other relevant urban fields. Such programs can produce new generations of volunteers and professionals who will be knowledgeable about ecological issues and willing to build transdisciplinary partnerships, and thus be stronger in solving contemporary urban problems. Fourth, networks such as URBIO (Müller and Kamada 2011), the Society for Urban Ecology (www.society-urban-ecology.org), UrBioNet (Aronson et al. 2016; http://urbionet.weebly.com/), and CitiesWithNature (https://cwn.iclei.org/) connect different actors with an interest in urban biodiversity and provide a platform for data sharing and collaboration. They have the potential to fill the gaps highlighted here and ensure that their output is widely communicated. Finally, manipulative experimental approaches will pave the way towards a mechanistic understanding of how urban systems affect biodiversity. In the case of urban observational studies, much has been gained via comparative work across regions of the world such as the Globenet initiative (Niemelä and Kotze 2009). Recent promising experimental networks such as UWIN (Magle et al. 2019) or GLUE (www.globalurbanevolution.com/), that share a methodology in different urban areas across the globe, will identify generalities and yield synthetic understanding (Borer et al. 2014).

In summary, research has greatly increased the understanding of urban biodiversity. By highlighting some of the remaining knowledge gaps, we offer a research agenda that we hope will inspire and support future urban biodiversity research. Through new ways of partnering across disciplines and fields, urban biodiversity research can both improve the science and raise the number of biodiversity-friendly actions transferrable to urban areas around the world. Doing this can minimize the anthropogenic impacts causing biodiversity loss.

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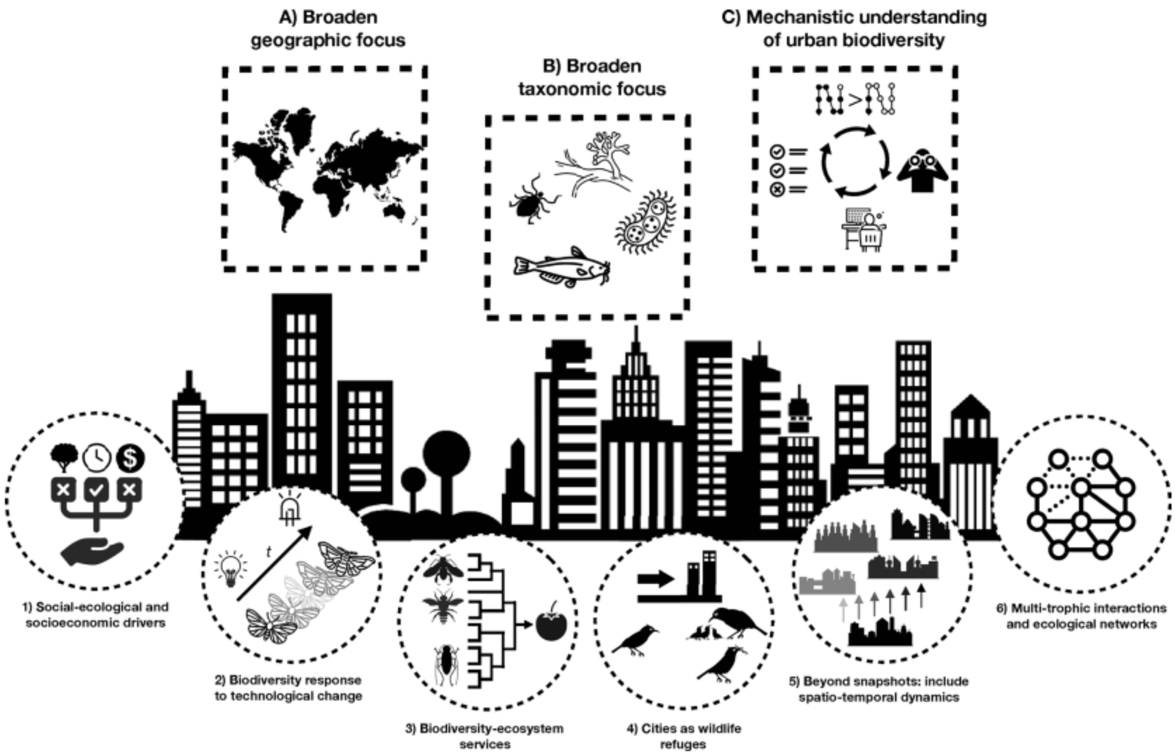

Fig. 1. A pictogram illustrating the six topics and three overarching considerations we have identified for future urban biodiversity research. Topics include the need 1) to understand how social-ecological and socioeconomic drivers interact to influence urban biodiversity, 2) to identify biodiversity response to technological change (in the circle representing this topic, *t*, refers to time), 3) to better link biodiversity to ecosystem services in urban planning and design, 4) to understand whether urban areas act as refugia for biodiversity, 5) to identify spatiotemporal dynamics in biodiversity (in the circle, time and space are presented by shading and different buildings, respectively), and 6) to investigate ecological networks. Overarching considerations include the need to A) broaden the geographic and B) taxonomic focus of urban biodiversity research and to C) gain a mechanistic understanding of urban biodiversity (with symbols in the box representing a circle of question, study, analysis, and adaptation).

Table 1. A toolbox with examples on how to approach the questions suggested in the article for future urban biodiversity research.

Topics	Questions to solve	Approaches
Socioeconomic and social–ecological drivers	Which factors modulate the strength of relationships between social–ecological, socioeconomic, and environmental drivers with biodiversity at different spatial scales?	Combine qualitative and quantitative social data collection via interviews or questionnaires with ecological data capture at various scales
Response to technological change	How does artificial lighting interact with climate change to create larger trophic mismatches than expected with just climate change?	Establish common garden experiment where light, temperature, etc. can be manipulated, measure phenological response of species
Relationships with ecosystem services	Which synergies and trade-offs among biodiversity and ecosystem services exist in urban environments?	Establish experimental species communities mimicking urban communities with varying levels of diversity, measure target ecosystem services
Urban areas as refugia	How do species that migrate into and through urban areas affect existing urban biodiversity and ecosystem functioning?	Identify migrators, apply experiments including/excluding them from selected plots/experimental species communities, measure target functions
Spatiotemporal	Can urban areas harbor self-sustaining populations of species of conservation concern and in which habitats or under which conditions is this possible?	Establish long-term monitoring across habitats/gradients of urban environmental conditions
Ecological networks	How do urbanization-induced changes in ecological network complexity and diversity affect ecosystem functions and services or disservices?	Exclusion experiments (excluding predator, herbivore, pollinator) combined with measurements of target ecosystem function or (dis-)service

Note: Exemplarily, one question per topic is shown with suggested approaches.

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Table 2. A nonexhaustive list of examples of local and international programs aimed at understanding and protecting urban biodiversity.

Category	Program	Description
City-based initiatives	Kommunen für biologische Vielfalt ("Municipalities for biological diversity"; www.kommbio.de)	More than 260 German municipalities formed a network where they identify fields of action for biodiversity conservation and exchange best-practice examples.
	Local Action for Biodiversity: Wetlands South Africa (cbc.iclei.org/project/lab-wetlands-sa)	Eleven municipalities in South Africa joined a program to protect wetlands by incorporating wetland ecosystem services into local planning and implementing projects.
	WildlifeNYC (www1.nyc.gov/site/wildlifenyc/index.page)	A campaign to increase public awareness about wildlife in the City of New York, which includes a website and billboards across the city to educate the public on common urban wildlife species.
	Grünbuch ("Green book") Zurich (www.stadt-zuerich.ch/ted/de/index/gsz/ueber-uns/gruenbuch.html)	A strategic paper informing politics that serves as a guideline for the city's service departments in the planning and implementation of projects concerning green and open spaces.
Community or citizen science	Attitudes toward foxes in an urban environment (Scott et al. 2014)	A TV media campaign invited the public to submit sightings of red foxes in urban areas during a 2-week period in 2012 to conduct a broad survey of fox distribution in England and Wales.
	NOISE MAPS (https://actionproject.eu/citizen-science-pilots/noise-maps)	Citizens record and analyze urban sound data by combining tested and novel technological approaches. Although not specifically focused on biodiversity such projects can help us understand noise-induced selection pressure on biodiversity.
Education	Crosstown Walk (https://sites.rutgers.edu/urbionet/resources/crosstown-walk-project/)	This teaching framework invites students to study urban ecological and environmental variables by walking along urban and socioeconomic gradients in their town or city.
Collaborative networks	Global Urban Biological Invasions Consortium (GUBIC, www.utsc.utoronto.ca/projects/gubic)	A multidisciplinary global consortium analysing how urbanization shapes and is shaped by the movement of species around the world. GUBIC provides a platform to share data and ideas, and to get researchers together for collaboration and discussion.
	International Network in Urban Biodiversity and Design (URBIO; Müller and Kamada 2011)	Facilitates the exchange of knowledge between researchers, practitioners and stakeholders.
	Society for Urban Ecology (SURE; www.society-urban-ecology.org)	Facilitates connections between researchers and practitioners engaged in urban ecology research and management.
	Urban Biodiversity Research Coordination Network (UrBioNet, https://sites.rutgers.edu/urbionet)	Connects researchers, practitioners, and students from around the world to expand global coverage of urban biodiversity data and develop recommendations for managing urban biodiversity.
Global experiments	Global Urban Evolution Project (GLUE; www.globalurbanevolution.com)	Large scale, replicated test of parallel evolution focusing on *Trifolium repens*.
	Global Urban Soil Ecology and Education Network (GLUSEEN; Pouyat et al. 2017; www.gluseen.org)	An experimental global network examining urban soil systems and their biota.
	Urban Wildlife Information Network (UWIN; Magle et al. 2019)	Partnership of researchers utilizing a shared methodology to study urban wildlife.