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Urban biodiversity: State of the science and future directions

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Abstract

Since the 1990s, recognition of urban biodiversity research has increased steadily. Knowledge of how ecological communities respond to urban pressures can assist in addressing global questions related to biodiversity. To assess the state of this research field in meeting this aim, we conducted a systematic review of the urban biodiversity literature published since 1990. We obtained data from 1209 studies that sampled ecological communities representing 12 taxonomic groups. While advances have been made in the field over the last 30 years, we found that urban biodiversity research has primarily been conducted in single cities within the Palearctic and Nearctic realms, within forest remnants and residential locations, and predominantly surveys plants and birds, with significant gaps in research within the Global South and little integration of multi-species and multi-trophic interactions. Sample sizes remain limited in spatial and temporal scope, but citizen science and remote sensing resources have broadened these efforts. Analytical approaches still rely on taxonomic diversity to describe urban plant and animal communities, with increasing numbers of integrated phylogenetic and trait-based analyses. Despite the implementation of nature-based solutions across the world's cities, only 5% of studies link biodiversity to ecosystem function and services, pointing to substantial gaps in our understanding of such solutions. We advocate for future research that encompasses a greater diversity of taxonomic groups and urban systems, focusing on biodiversity hotspots. Implementing such research would enable researchers to move forward in an equitable and multidisciplinary way to tackle the complex issues facing global urban biodiversity.

Keywords

Biodiversity; Publication trends; Research bias; Sampling methodology; Systematic review; Urban gradient

Introduction

Anthropogenic changes to ecosystems globally, including unprecedented climate change (IPCC 2021), have pushed biodiversity to the brink of a sixth mass extinction. Despite calls from scientists and international policy organizations for actions to stem the rapidly accelerating loss of biodiversity around the world (e.g., Convention on Biological Diversity; United Nations 2015), little progress has been made in achieving established targets. In particular, biodiversity loss continues nearly unabated due to increases in human population size and accompanying land use change, particularly in the world's biodiversity hotspots (Mazor et al. 2018; Seto et al. 2012). Cities have the potential to play a critical role in conservation (Soanes and Lentini 2019; Spotswood et al. 2021) with initiatives that preserve species and habitats, improve landscape connectivity by creating and maintaining habitat corridors, mainstreaming urban environmental planning, and enhancing residents' knowledge and stewardship of biodiversity (Knapp et al. 2021; Nilon et al. 2017; Oke et al. 2021).

The conservation and management of biodiversity in cities requires knowledge of the ecological patterns and processes that drive species' responses and adaptation. Over thirty years ago, McDonnell and Pickett (1990) argued that ecological research should include urban areas as an additional context for addressing core ecological questions as well as understanding the impacts of urbanization on ecological function. Similar arguments had been made by German ecologists earlier, but had not received wide exposure in what was then a less globalized world

(Rebele 1994; Sukopp 2002; Sukopp and Weiler 1988). Urban ecologists have created a rapidly growing body of research on plant and animal communities in cities and towns. McKinney (2008) reviewed the effects of urbanization on plant and animal species richness, finding that species richness tended to decrease with high urbanization, while moderate levels of urbanization leads to diverging patterns in species diversity among taxonomic groups. Such patterns have been shown to occur on a global scale, where cities retain a subset of species from regional species pools (Aronson et al. 2014), but support non-native assemblages of varying diversity among different taxonomic groups. Interestingly, results of the few multi-taxonomic assessments in urban areas show that response to urbanization and to the management of green spaces vary among taxa (MacGregor-Fors et al. 2015; Sattler et al. 2014). Yet, the limited data available on taxa besides plants and birds have prevented the assessment of generalized patterns for other groups in urban areas.

Urban ecology has become an important focus across the ecological and environmental sciences (Cressey 2015), but there remain large gaps in our understanding of not only what species are found in cities, but also what enables them to persist or become established and adapt (Kowarik and von der Lippe 2018; Lepczyk et al. 2017; Rivkin et al. 2019). Therefore, urban biodiversity research is essential for understanding how intensive human activities affect the ecology and evolution of a region’s species, which in turn can inform conservation initiatives designed to mitigate biodiversity loss (McKinney 2002).

One recommendation to emerge from a workshop hosted by the Urban Biodiversity Network (UrBioNet) in March 2017 at Rutgers University, New Brunswick, New Jersey, was the need to assess the current state of urban biodiversity research in order to reflect on the work conducted since McDonnell and Pickett (1990) and McKinney (2002, 2008) by identifying areas of saturation and gaps in the literature. In response to this recommendation, we performed a systematic review of the literature with the goal of addressing three objectives: (i) document patterns of geographic and taxonomic foci, and methodology used in urban biodiversity research since 1990, (ii) examine how ecosystem function, management, and restoration are addressed in urban biodiversity research, and (iii) identify critical knowledge gaps for future research. Our emphasis in this review is on understanding the nature of research on biodiversity in cities conducted primarily through the ecological lens. While the past decade has seen more publications on how social-ecological dynamics influence urban biodiversity, research on the mechanisms underlying these complex dynamics remains relatively scarce (Kuras et al. 2020; Morelli et al. 2020; Schell et al. 2020), and is therefore not a focus of this paper. Our broader objective through these efforts is to provide information that will guide science and policy towards enhancing the biodiversity, sustainability, and resilience of urban regions.

Methods

Since 1990, many thousands of papers have been published that examine urban biodiversity from suborganismal to macroecological scales. Here we focus on biological communities (i.e., multiple interacting species in a shared space) as they capture the conservation needs of multiple species in a particular place and time. To address our objectives, we conducted a systematic literature search using PRISMA guidelines (PRISMA 2021) through the ISI Web of Science Core Collection for papers published between January 1990 - May 2018. The search included terms related to species richness and biodiversity composition, organized by taxa (Supplementary Information, Search Terms). Focal taxa included amphibians, ants, bats, bees, birds, butterflies, carabid beetles, mammals (excluding bats), plants, reptiles, snails, and spiders, because initial literature screening indicated that these taxa were the subject of the vast majority of urban biodiversity research and would be representative of the literature.

The search returned 7300 unique articles. We reviewed the titles and abstracts of each for relevance regarding emphasis on biological communities, inclusion of multiple sites, and urban focus. We focused our review on community-level patterns, thus studies that analyzed only a single species within the focal taxonomic groups or lacked a multi-species focus were excluded from further consideration. Likewise, we excluded studies that examined one site with multiple plots within that site, such as sampling multiple plots or transects within a single park. Only studies from areas described as urban, suburban, or peri-urban (often located at the periphery of cities, which tend to differ in their nature across the globe) were considered for analysis. For any abstracts where these conditions were unclear, the abstract was reviewed by a second individual and if still unclear, the corresponding paper was included in the full-text review so that the article's suitably for inclusion could be assessed with more detail. We included all papers in English, Spanish, and Portuguese. We excluded review papers to avoid replicating any studies in our analyses; however, we kept meta-analyses as they presented new analyses regarding urban biodiversity trends over larger spatial or temporal dimensions compared to single studies.

The abstract review resulted in 1624 possible articles, some of which were duplicates if they covered more than one of the focal taxa (Table 1). We distributed the abstracts among our research group members for thematic analysis of the full-text. Additional articles were identified through relevant references within these articles. From these articles, we collected a set of basic data in a shared Google Form (Supplementary Information, Table S1). All research group members followed guidelines provided by MFJA to ensure consistency for data entry. Once all articles were processed, quality control and assurance were performed by CCR-B and MFJA for errors or duplication, resulting in 1209 unique papers containing 1498 studies, as a single paper may have presented results from multiple taxa (Table 1). For papers that examined multiple taxa, we performed the thematic analysis individually by taxon. Studies were classified by publication year, journal, location(s) (city, country, biogeographic realm, or multiples of each), city of the lead author's institution, urban comparison type (urban only, gradient, urban vs. rural), how the urban area was defined (e.g., municipal boundary, land use, road density, population density), sampling effort (number of locations and duration) and methodology, land use and habitat types sampled, biodiversity metrics analyzed (e.g., species richness, taxonomic, functional, and/or phylogenetic diversity), data availability (e.g., species, traits, and/or coordinates identified), linkages to restoration and management techniques and/or ecosystem service provision. Additional details for each study and the thematic analysis are included in the Supplementary Information.

Results & Discussion

Urban biodiversity studies have increased steadily each year since 1990 and approximately doubled in the last five investigated years from 91 studies in 2012 to 176 in 2017 (Fig. 1). While the first journals to publish urban biodiversity studies included general ecology journals (e.g., *Economic Botany, Environmental Conservation, Oikos, Journal of Applied Ecology, Studies on Neotropical Fauna and Environment, Ecography*), urban biodiversity studies started to be published in urban-focused journals established in the late 1990s and early 2000s (Fig. 1), when, for example, *Urban Ecosystems* and *Urban Forestry & Urban Greening* published their first issues. The journals most frequently publishing urban biodiversity studies included *Urban Ecosystems* (13%), *Landscape and Urban Planning* (11%), *Urban Forestry & Urban Greening* (5%), and *Biological Conservation* (4%). Overall, 30% of urban biodiversity studies were published within urban-focused journals. Increases in publications after 2010 in both the urban and general ecological literature reflect increasing interest in and realization of the importance of urban ecological science as well as the recognition of cities as places for biodiversity conservation (Collins et al. 2021; Cressey 2015; Wu 2014). It is important to note that our search was primarily performed in the Web of Science Core Collection, which comprises a subset of papers published in journals indexed in that collection. Given that in the Global South there is an important wealth of information published in local and regional journals and theses/dissertations, often not in English, our results ought to be considered and interpreted from this lens, as information published in the "gray literature" - including high-quality science journals in a language other than English - is neglected (Haddaway et al. 2015). By including papers written in either English, Spanish, or Portuguese, we aimed to alleviate at least some of the linguistic, if not geographic, bias.

Geographic focus

Overall, 1745 unique urban areas were studied around the world, but only 21% of studies compared biodiversity across multiple cities/urban regions and only 5% surveyed locations across multiple countries. Chicago (USA), Melbourne (Australia), Phoenix (USA), Sydney (Australia), Helsinki (Finland), New York City (USA), and Prague (Czech Republic) were the most studied cities (Fig. 2), illustrating the bias towards sampling larger cities (Kendal et al. 2020). Research in urban biodiversity was dominated by studies performed in the Palearctic (38%) and Nearctic (27%) realms, followed by the Neotropics (13%) and Australasia (10%), confirming published trends on the distribution of urban ecology studies (Collins et al. 2021; Magle et al. 2012). Most of these studies were performed in the USA (20%), Australia (7%), and China (5%). These trends confirm the challenges facing the study of biodiversity in the Global

South, where the majority of people on earth reside (with elevated levels of poverty), and where most of the world’s natural resources, including biodiversity, are located (Nagendra et al. 2018). These challenges include (but are not limited to): lack of recognition of urban biodiversity as worthy of examination by researchers, limited national and international funding (Nagendra et al. 2018), reduced access to scholarly literature and data (Trisos et al. 2021), and overall less developed research infrastructure than in the Global North. While we do acknowledge that biodiversity assessments occur within these regions, our search criteria may have restricted some studies from inclusion in this review. Even so, a lack of information within the literature on urban biodiversity in these biodiverse regions potentially skew our understanding of patterns and processes in the urban milieu. For instance, there were few studies from Oceania (0.2%), Afrotropic (5%), or Indo-Malay realms (7%), with only 2.2% of papers surveying urban biodiversity across multiple realms. Recently, a number of important urban ecological studies have acknowledged this geographic bias as the field works towards closing this gap in the literature (see Nagendra et al. 2018, Shackelton et al. 2021).

Similar geographic patterns were found for each focal taxon (Supplementary Information, Fig. S1). Of the few urban reptile studies, research in the Nearctic region (44%) and Australasia (25%) dominated, which was unique among the focal taxonomic groups. Considering most of the world’s biodiversity is found in the equatorial bands of the Neotropics, Indo-Malay, and Afrotropics, limited coverage of possibly the most diverse cities remains a significant gap (Aronson et al. 2016; Beninde et al. 2015). Only through additional studies and monitoring schemes that include those regions that are under-represented, will it be possible to maximize the potential of urban biodiversity while achieving conservation goals, and improving local and global urban governance (Secretariat of the Convention on Biological Diversity 2012).

Unlike biodiversity studies in natural areas, such as those in the tropics in which biodiversity is often assessed by scientists from foreign institutions (e.g., Reboredo Segovia et al. 2020), the science of urban biodiversity was primarily conducted in the city where the lead author's institution was located (58%). Very few lead authors were located outside of the country (7%) or region (4%) in which the study took place, potentially due to convenience or funding limitations. As a local or "backyard" science, the study of urban biodiversity allows for opportunities for education and engagement with communities surrounding universities and other research institutions, which likely enhance conservation interest by urban residents, even for biodiversity beyond the city and in natural areas (e.g., Narango 2020). Urban biodiversity studies conducted locally further enable direct contribution to city government conservation and monitoring programs. However, the trend towards sampling in the city in which an author lives or works has led to biases in the evidence base and limits our understanding of biodiversity responses in smaller cities and towns (Kendal et al. 2020).

Taxonomic focus

Plants (38%) and birds (19%) remain the most studied taxa (Fig. 3), with a notable increase in publications around 1998. However, other taxonomic groups have increasingly been represented in the literature beginning around 2006-2007 (Supplementary Information, Fig. S2). While publications on the remaining focal taxa either steadily rose slowly over time (e.g., ants, bats, bees, butterflies) or occurred periodically during our sampled period (e.g., amphibians, carabid beetles, other mammals, reptiles, snakes, spiders), yearly publication rates did not surpass 20 publications in any year. Studies on urban snail communities were limited (n = 7). The underrepresentation of snails is a particular gap in the literature, as they are good indicators of local environmental and habitat determinants for urban green spaces (Barbato et al. 2017;

Lososová et al. 2011), and of adaptation to a changing climate (Silvertown et al. 2011). Even so, the bulk of our surveyed species are becoming better studied over time, albeit slowly, due to standardizations in global sampling protocols (e.g., carabids with GLOBENET; Niemelä et al. 2000), growing interest in the ecosystem services they provide (e.g., insect pollinators; Hall and Martins 2020; IPBES 2019), recognition of the critical gap in knowledge of these species within urban ecosystems (e.g., amphibians and reptiles; French et al. 2018; Hamer and McDonnell 2008), citizen science programs (Yang 2020), and access and availability of advanced technology to survey in complex environments. Publications that focus on echolocating bats, for example, increased from the mid-2000's due to technological advances in the acoustic equipment used to survey them; however, these studies are geographically biased towards countries and cities where researchers had access to such equipment. Other taxa beyond our focal subset had a minor presence within our database, such as mosquitoes, wasps, true bugs, lichens, molluscs, diatoms, earthworms, and odonates. However, these taxa should continue to be explored due to their diversity and important roles for urban ecosystem function, services, and disservices (e.g., Koch et al. 2019; Monteiro Júnior et al. 2015; Mutinova et al. 2020).

Most publications that assessed carabid beetles (94%), ants (89%), and snails (86%) surveyed the entire taxonomic group for inclusion within their analyses, compared to few mammal (29%) and plant (47%) studies that only sampled a subset of those respective taxa (e.g., sampling trees rather than the entire plant community). While we recognize the barriers preventing sampling of entire communities (i.e. taxonomic breadth and the requirement for multiple sampling techniques and time periods), trends obtained from such studies would be much more informative for an ecosystem-scale understanding of urbanization, in terms of both species assembly and ecosystem functioning (Aronson et al. 2016). Additionally, 19.8% of studies sampled more than one taxon (of the 12 focal taxa), with the most common pairings between plants and birds (29% of multi-taxonomic studies), plants and bees (15%), plants and butterflies (13%), and birds and mammals (9.2%). The lack of multi-species and multi-trophic surveys has been highlighted in the urban biodiversity literature (Beninde et al. 2015; Knapp et al. 2021; MacGregor-Fors et al. 2015; Melliger et al. 2017; Pinho et al. 2021). Addressing this knowledge gap would provide a more comprehensive view of the impacts of urbanization on biodiversity, especially by taking broad ecological networks into account (e.g., mutualistic and antagonistic interaction networks as well as entire food webs endangered by global change; Heleno et al. 2020).

Urban Biodiversity-Ecosystem Function and Service Relationships

Over the past two decades there have been repeated calls for deeper mechanistic understandings of the social-ecological drivers of biodiversity (Knapp et al. 2021; McDonnell and Hahs 2013; Schell et al. 2020; Shochat et al. 2006), including elucidation of relationships and processes that link biodiversity with ecosystem function and ecosystem services (Pinho et al. 2021; Schwarz et al. 2017). While the study of biodiversity–ecosystem function relationships are common in the general ecological literature and ecosystem services (ESS) and nature-based solutions have taken center-stage in urban ecological practice, we found that only 9% of urban community studies implicitly linked biodiversity and ecosystem functions/services (EF/ESS) in the research question. Only 5% of studies compared biodiversity outcomes with explicitly measured EF/ESS (e.g., pollination, carbon storage, pollutant removal, food production/social services). Plant biodiversity was most commonly linked to measured EF/ESS (63%), with the remaining taxa represented with few papers in these efforts (i.e., birds, 8%; bees and ants, 7%; butterflies, 5%; spiders, mammals, and carabid beetles, 3%). In a next step forward for urban biodiversity research, studies that examine community patterns in multi-trophic interactions (e.g., pollination, predation, decomposition; Frey et al. 2018; Seibold et al. 2018; Tresch et al. 2019) and those that examine biodiversity of taxa closely associated with ecosystem function (e.g., soil microbial diversity), should be prioritized with biomonitoring surveys in taxa that are well studied (e.g., bees, birds). With the current emphasis on nature-based solutions to address environmental hazards and the effects of extreme weather events, understanding how biodiversity may drive the mechanisms behind ecosystem function in natural and artificial urban ecological systems should be emphasized in urban ecological research.

Methodology of Urban Biodiversity Studies

Early urban biodiversity research demonstrated that communities change between urban and non-urban areas or across urban-rural gradients in ways that result in novel species assemblages (Gaertner et al. 2017; Kowarik 2011; McKinney 2008). The urban gradient approach has been a prominent paradigm for studying urban ecology since 1990 (McDonnell and Pickett 1990) and has continued to spur on exciting ecological questions, experimentation, and collaboration with other disciplines. However, in the last five years, within-city studies have increased (e.g., those that do not have a non-urban component included in the study design), becoming the dominant type of study across taxa. Of the studies published between 1990-2018, 53% sampled exclusively within cities, while only 26% sampled an urban-rural gradient, and 21% contrasted biodiversity in sites within urban/suburban land uses to rural land uses. Over this 30-year period, the number of gradient and contrast studies leveled off, while studies within cities increased, especially since the early 2010s (Fig. 4). This new direction in urban biodiversity research, where studies are conducted entirely inside city boundaries, highlights the diversity and complexity of urban habitats and land uses within the city itself, and the necessity to look at urban areas from a regional perspective. Such a perspective is also crucial when thinking about the tight urban-rural linkages that connect humans, goods, services (Kroll et al. 2012), resources, species (Seebens et al. 2015), and more (Haase 2019) beyond municipal boundaries (McDonald et al. 2020).

Defining what constitutes "urban" has been a challenge in many disciplines (e.g., demography, sociology, geography) including ecology and the environmental sciences (Lepczyk et al. 2017; MacGregor-Fors 2011; McIntyre et al. 2000). The United Nations' (1955) view that ''*There is no point in the continuum from large agglomerations to small clusters of scattered dwellings where urbanity disappears and rurality begins; the division between urban and rural populations is necessarily arbitrary*'' remains as true today as it did 70 years ago. Thus, we see a variety of ways that researchers have defined urban in their work with the most common delineations of the urban landscape being the use of municipal boundaries (41%), land use (35%) or land cover (25%), and population density (13%), while 4% of studies did not define urban with any metric or description. Other quantitative variables, such as distance from the city center (9%), impervious cover (8%), building density (2%), road density (1%), and distance to roads (0.5%), were less frequently utilized as urbanization metrics. Non-urban was mostly characterized as "rural" (39%), by vegetation type (24%; e.g., forest, grassland, desert), or agricultural land use (17%; e.g., cropland, pasture, farm). Other terms used to characterize non-urban landscapes included peri-urban, natural/native/pristine, suburban, protected, and exurban (Supplementary Information, Table S2). Urban gradients were most often defined by land cover (41%), land use (30%), distance from the city center (20%), impervious cover (14%), building density (9%), and population density (9%) (Supplementary Information, Table S3). Such variation in the factors used to delineate 'urban' is unsurprising given the lack of a strict definition of what encompasses an urban area. Notably, there is no simple or elegant way to strictly denote what constitutes an urban setting, thus a good fraction of studies (20%) utilized multiple characteristics to quantify their urban sampling locations instead of using land use categories such as “urban” or “rural” (MacGregor-Fors 2011; MacGregor-Fors and Vázquez 2020). Nevertheless, the lack of simple, consistent, or agreed upon methods to define urban poses a challenge for comparative urban ecology.

Studying biodiversity within multiple land uses and vegetation habitat types within and across cities and towns allows for a more complete understanding of the effects that cities have on biodiversity, the value of cities for conservation, and applications in design and planning of cities for biodiversity (Filazzola et al. 2019). Increasing land use and habitat types sampled within one city can also broaden our understanding of the response of biodiversity in different socio-ecological contexts. Within cities, the most common land use types surveyed were remnant natural areas (56%), residential areas (44%), and parks (33%). Rare land use types/categories included brownfields (3%), roads (3%), and vacant lots (6%). Multiple land use types (≥3) were sampled in only 27% of studies, while 23% of the papers sampled multiple habitat types. Seven percent of studies did not specify the land use types sampled (e.g., city-wide surveys), and of those, a handful (0.4%) only specified the rural land uses and failed to specify the contrasting urban land use(s) (Supplementary Information, Table S4). Defining the specific land use surveyed in urban biodiversity studies is imperative to provide the socioeconomic and cultural contexts of a city (Kuras et al. 2020), and to compare trends across cities.

Close to half of all studies that specified the type of vegetation surveyed sampled forests (46%), followed by highly managed public landscapes (e.g., mowed/landscapes within parks, golf courses; 29%), or private yards and gardens (23%). The dominance of forest habitats may be a consequence of the geographic bias towards sampling temperate cities in North America and

Europe (Fig. 2). Approximately 5% of studies sampled anthropogenic habitats unique from other categories, such as green roofs, bioswales, and stormwater ponds. The least common habitats studied included ruderal vegetation (1%), coastal dunes (1%), saline wetlands (2%), field margins (2%), and deserts (2%). Furthermore, we found that many studies confound land use and habitat type or define only one. For example, studies may have evaluated forest patches in commercial areas, but only "commercial" was used to describe the sample locations. Cities are mosaics of different land uses and habitat types (Niemelä 1999), which calls for additional studies that highlight land use and habitat diversity within urban areas and a typology of land use and habitat types that can be used across all cities for better comparative studies (i.e., similar to urban climate typology described in Stewart and Oke 2012). While focusing on one land use or habitat type is informative, especially for undersampled green space types, the lack of diversity in land use and habitat types reflects gaps in our understanding of how cities can act as refugia for biodiversity (Knapp et al. 2021), how multiple habitat types contribute to overall taxonomic and functional diversity (Casanelles-Abella et al. 2021; Fournier et al. 2020), which land use and habitat types act as ecological traps or population sinks, and how urban green spaces may be designed and managed to support biodiversity and in the long term (Kowarik and von der Lippe 2018; Lepczyk et al. 2017).

We also examined the methods utilized in urban biodiversity studies. Across all taxa, the median number of sites surveyed was 24 (mean = 790, mode = 3). The number of sites ranged from 2 to 880,310 (eBird; e.g., La Sorte et al. 2017). The largest sample sizes are from citizen science studies (e.g., Border et al. 2017; Fontaine et al. 2016; La Sorte et al. 2017). Excluding studies that utilized data from citizen science programs or museum specimens, the median number of sites surveyed across all taxa drops only slightly to 23 (mean = 104, mode = 3). Birds were sampled from the greatest number of sites, skewed again by eBird and other citizen science projects. Reptiles, spiders, carabid beetles, and ants were surveyed in the fewest number of locations (constrained in number and geography; Supplementary Information, Fig. S1), possibly due to the more time-intensive or handling-intensive survey methods needed for them and more limited taxonomic expertise in these groups.

Common sampling methods utilized in urban biodiversity research included point counts (birds, 54% of studies), transects (butterflies, 48%), physical traps or nets (amphibians, 43%; ants, 77%; bees, 72%; carabid beetles, 90%; mammals, 41%; reptiles, 46%; spiders, 86%), acoustic (amphibians, 43%; bats, 75%), and quadrats/relevés (plants, 65%). Other methods not commonly utilized across any taxon included physical evidence (e.g., tracks, scat), museum collections, atlas data, and citizen science (albeit increasing for birds and butterflies). For all taxa, most surveys occurred within one year, and except for butterflies (13%) and mammals (12%), < 5% of studies surveyed taxa over a period of five years or more. The longest duration studies utilized historical databases or museum specimens. For example, Knapp et al. (2017) utilized herbarium specimens, published historical and recent floras, and unpublished species lists and manuscripts, to examine 320 years (1687-2008) of vegetation change in the city of Halle, Germany. The limited number of long-term studies and low median survey sample size highlights the need to increase our understanding of spatiotemporal dynamics of urban biodiversity (Knapp et al. 2021). However, increasing rates of citizen science, broad-scale databases, and coordinated global research networks in the past decade could help to address this need (Amano et al. 2016; Poisson et al. 2020). Furthermore, we still lack any long-term, consistent urban biodiversity monitoring programs that can provide the information needed to evaluate many ecological relationships and assess temporal trends of populations.

Abundance was assessed for the sampled taxa in 72% of the studies, with 40% also utilizing traits to describe species' role in their community. The use of taxonomic diversity metrics, including species diversity and richness (85%) was overwhelmingly more common than functional (3%) or phylogenetic (1%) diversity metrics. Urban functional diversity studies became an important component of urban biodiversity science in the mid-2010s with over half of the studies focusing on the functional diversity of either plants or birds (62%) (Fig. 5). Phylogenetic diversity studies were rare until 2018 (1% of all studies), with plants serving as the dominant taxon analyzed (52%). Functional and phylogenetic diversity reflects evolved strategies for survival and use of available resources, differences among cities in how they support or filter out species from regional species pools, and allow for better comparisons across cities and taxa (Dolan et al. 2017; Hensley et al. 2019; La Sorte et al. 2018; Morelli et al. 2016; Vandewalle et al. 2010). These characteristics could be important for planning and design of biodiverse green spaces that support ecosystem functions and services (MacIvor et al. 2016).

Data Transparency

Public data availability has become an increasingly important factor in scientific publication (Trisos et al. 2021) and collaborative urban biodiversity research. Species lists were reported in 65% of studies. However, we found that only 9.4% of studies published site coordinates and 6% reported species lists by site coordinates in either the paper, supplementary materials, or other online data repositories. Many urban ecological studies are conducted on residential property and sharing coordinates might infringe on privacy. As well, publishing localities of rare species may drive collectors or other activities that cause harm. However, such data transparency would allow tackling research questions related to environmental change over time and space or relate biodiversity data to socio-ecological and socioeconomic context of different areas of cities and so innovative approaches (e.g., beyond jittering coordinates) are needed. Additionally, of papers that examined species traits, only 31% of those reported the traits of those species. Despite broad calls for data sharing across scientific communities (Costello et al. 2013; Reichman et al. 2011; Trisos et al. 2021), very few scientists share trait data, even for common, broadly distributed species. While some of these trait data are published in online repositories (e.g., PanTHERIA, Jones et al. 2009; TRY, Kattge et al. 2011), many taxa are not represented, and existing databases are not complete. Further, for some taxa, traits are tied closely to local conditions, and urban conditions are not well represented. Biodiversity science, particularly in urban areas, can only be enhanced with open data sharing and collaboration. This underlines the importance of research networks such as UrBioNet (Aronson et al. 2016; https://sites.rutgers.edu/urbionet) that are valuable, particularly to share data and findings with and link scientific and practitioner communities. This is particularly crucial if urban ecology is to become more inclusive and representative of cities in the Global South. However, funding is currently limited for long-term conglomerate research and networking that would properly support scholars and practitioners from the Global South as equal collaborators.

Linking Biodiversity to Management and Restoration

Although we did not specifically search for management and restoration case studies, we did evaluate how urban biodiversity studies addressed these. The effects of restoration or management strategies were tested in 8.5% (103) of urban biodiversity studies. An additional 4.6% of studies surveyed biodiversity of restored sites (but did not test any restoration or management strategies). The effects of restoration/management strategies were most often studied on plant (57%) and bird (12%) communities, and in forest (41%) and lawn/garden (29%) habitats within residential land uses (47%), remnant natural areas (41%), and parks (28%).

Forests (48%) and freshwater wetlands (18%) were the most surveyed restored site habitats. The UN Decade on Ecosystem Restoration 2021-2030 highlights the need to prevent, halt and reverse the degradation of ecosystems across the globe, including in urban areas (United Nations Environment Programme 2021), but the paucity of studies that test restoration and management outcomes on ecological communities in urban areas needs to be addressed. Some countries (e.g. Germany) and cities (e.g. Toronto) even launched programs to enhance biodiversity friendly management within urban areas. Thus, individual municipalities are implementing biodiversity friendly management of green spaces, by mowing of parklands less frequently to benefit insect diversity or support the installation of artificial roosting sites for birds and bats by private owners. Yet, the effect of such management strategies within cities and towns is not systematically monitored. Furthermore, the urban bird ecology literature focusing on or providing management, planning or conservation suggestions based on their results indicates that their recommendations are often not implemented in meaningful ways (MacGregor-Fors et al. 2020). Early collaboration during the research process with practitioners, decision-makers, and community members and stakeholders can help co-produce and implement management and restoration strategies that are effective in urban areas (Apfelbeck et al. 2020). Transparently collaborative approaches that include more representative and diverse human communities living in cities in the co-production of urban biodiversity research are more likely to result in effective long-term management action (Trisos et al. 2021) to sustain biodiversity in cities.

The Way Forward

Since McDonnell and Pickett’s (1990) landmark publication outlining the possibilities of urban areas as locations for biodiversity and its conservation, urban ecology has become a significant component of the ecological literature. Even so, more work is required to advance the field, which is taking on greater urgency during an era of rapid urbanization, global biodiversity loss (Knapp et al. 2021), and climate change (IPCC 2021). We applaud the progression of urban biodiversity research in its geographic, taxonomic, and methodological scope. However, pushing these boundaries will continue to allow us to obtain a more comprehensive understanding of urban biodiversity, especially as cities, in some cases, are being identified as biodiversity refugia (Hall et al. 2017; Knapp et al. 2021; Soanes and Lentini 2019; Spotswood et al. 2021). Nonetheless, we echo calls of many authors to expand the geographic representation of research (e.g., Collins et al. 2021; La Sorte et al. 2014). The current geographic and study systems investigated (e.g., taxa, vegetation habitat, land use) bias our understanding of urban biodiversity towards birds and plants, forested ecosystems, the Global North, and areas of intense habitat management. We also recommend researchers and practitioners continue to broaden taxonomic representation in urban biodiversity research for understudied urban taxa (e.g., snails, spiders, reptiles, soil invertebrates, microbes) as these groups play important functional roles within urban ecosystems, as well as research that examines interactions of multiple taxa across trophic levels. We call for an expansion of sampling efforts beyond single year studies, examining differences among and within different urban habitat and land use types, and exploring new means of analyzing biodiversity. Finally, experimental studies, particularly those that test restoration and management outcomes in urban habitats, as well as those investigating biodiversity and ecosystem functions / services relationships, are needed to elucidate the mechanisms that lead to resilient communities, but these are rare and even fewer multi-city experimental studies have been performed.

While we did not explicitly examine social drivers of urban biodiversity in this study, we acknowledge that biodiversity is also shaped by peoples’ social, cultural, political, and stewardship practices (Aronson et al. 2016; Kuras et al. 2020). Such drivers warrant further examination to better our understanding of the distribution of urban biodiversity, especially in the Global South. Additionally, Schell et al. (2020) highlighted the importance of going deeper into the social drivers of biodiversity, beyond socioeconomic gradient approaches (Leong et al. 2018), to considering the impacts of the racial and ethnic geography of cities on ecology and evolution of diverse taxa inhabiting cities. Funding agencies ought to support both fundamental and applied urban biodiversity projects, and with emphasis on the Global South, if we aim for the discipline to further develop and its applicability to materialize at faster rates.

Several of the journals included in our analysis have added new formats where paper submissions are encouraged from collaborative teams including researchers and practitioners involved in hands-on management (e.g., Practitioner's Perspective, *Journal of Applied Ecology*). Another recently developed tool by the British Ecological Society, *Applied Ecology Resources*, is a searchable database of grey literature where practitioners can host their materials now accessible to ecological researchers. We believe these represent an important opportunity to fill in some of the gaps identified in our review and by other recent calls for greater inclusivity and representation (Nagendra et al. 2018; Trisos et al. 2021). Action-oriented research projects designed with practitioners to ensure the results have impact may be a way forward in this area. In particular, the inclusion of local communities in decision making (e.g., Apfelbeck et al. 2020) will raise the acceptance for biodiversity-friendly urban planning that is equitable and considerate of different cultural and socioeconomic backgrounds. Recent research demonstrates that urban biodiversity conservation initiatives are most successful when practitioners actively engage communities to understand people’s needs and embrace the diversity of values the public hold towards biodiversity (Taylor et al. 2021). Such information would be enormously valuable to advance the application of future urban biodiversity research towards more sustainable solutions tackling the global challenge to reconcile urbanization trends with conservation goals. We also encourage public data access, both the raw data and in secure open-access data repositories (e.g., Dryad; datadryad.org) or in supplementary materials and through the development and expansion of data sharing networks. Where possible, data and study results should be accessible to non-scientists, through web-based applications (e.g., R Shiny; Chang et al. 2021) to further enable transparency and engagement with all stakeholders. In doing so, we can commit to understanding biodiversity in cities and continuing to expand the scope, multidisciplinarity, equity, inclusivity, and rigor of urban ecological research within a rapidly urbanizing world, which could help pave the way to obtaining healthier, livable cities.

Declarations

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Conflicts of interest

We certify that we have no conflicts of interest regarding this work.

Ethics approval

Not applicable

Consent to participate

Not applicable

Availability of data and material

The dataset will be available via the UrBioNet Database on the University of Missouri's MOspace at https://mospace.umsystem.edu/xmlui/handle/10355/46235

Code availability

Web of Science search terms are provided within the Supplementary Information.

Authors' contributions

This study was developed during the UrBioNet workshop held at Rutgers, the State University of New Jersey, New Brunswick, New Jersey, 27-31 March 2017. All authors either designed the study, conducted the literature search, and/or reviewed studies resulting from the literature search. CCR-B, MFJA, MRP, AKH, and NSGW analyzed the data. CCR-B and MFJA wrote the first draft of the manuscript. All authors reviewed and edited the manuscript, and approved its final form.

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Table 1. Literature search process by taxa for inclusion in systematic literature review of urban biodiversity studies. Numbers for articles included can exceed numbers of articles shortlisted because additional papers were identified through relevant references within shortlisted articles.

Taxa	**Articles identified by Web of Science search**	→	**Articles shortlisted based on abstract and review criteria**	→	**Articles included**
Amphibians/Reptiles	288		83		92
Ants	392		77		79
Bats	138		57		81
Bees	398		167		102
Birds	1338		284		279
Butterflies	213		116		104
Carabids	164		96		70
Mammals	388		101		63
Plants	3794		567		564
Snails	52		20		7
Spiders	135		56		56

Graphical Abstract: Word cloud from titles of 1209 publications on urban biodiversity from 1990-2018.

Fig 1. All publications (n=1209) and number of unique journals publishing urban biodiversity studies by year and journal focus (urban topical journals and general ecological journals) from 1990-2017 and papers up to May 2018.

Fig 2. Urban biodiversity studies by country and city (cities with ≥10 studies displayed). This figure highlights the geographical bias of the current urban biodiversity literature towards the Palearctic and Nearctic regions, and the predominant focus on large cities.

Fig. 3. Proportion of studies by taxa group.

Fig 4. Annual changes in the number of publications that surveyed urban biodiversity as a contrast against non-urban regions, along a gradient, or within a city.

Fig. 5. Numbers of publications evaluating taxonomic, functional, and phylogenetic diversity change over time. A single paper may have multiple diversity measures. Patterns hold across all studied taxa.


URBAN
COMMUNITY
DIVERSE
BIRD
SPECIES
FOREST
LANDSCAPE
HABITAT
PLANT
AREA
RICH
CITY
USE
BAT
GREEN
BIODIVERSE
ABUNDANCE
LAND
PARK
BEE
AVIAN
STRUCTURE
FRAGMENT
ASSEMBLAGE
GRADIENT
GARDEN
LOCAL
RURAL
TRAIT
TREE
ANT
HUMAN
LARGE
CONSERVING
ARTHROPOD
PATTERN
WETLAND
FUNCTION
MANAGE
SPACE
SMALL
SPATIAL
EXOTIC
LEVEL
RESTORE
THREE
CALIFORNIA
PREDATOR
CONTRASTS
GRASSLAND
ECOSYSTEM
ECOLOGY
NATIVE
MAMMAL
DRIVER
FLORA
CHINA
FORAGING
ROAD
ROOF
EDGE
FLOWER
SOUTH
REGION
BRAZIL
AFRICA
NEST
FAUNA
STREAM
YEAR
ALIEN
DISTRIBUTION
PATCH
SHAPE
UK
AMPHIBIAN
POLLINATOR
SOIL
VALUE
WESTERN
DEVELOPED
ACTIVE
SCALE
RIVER
CASE
SPIDER
BEETLE
COMPOSITION
BUTTERFLY
GROUND
GLOBAL
CENTRAL
CARABID
SIZE
RESERVE
RIPARIAN
USA
LINK
SITE
VEGETAL
TROPICS
DENSITY
SOUTHERN

Fig1

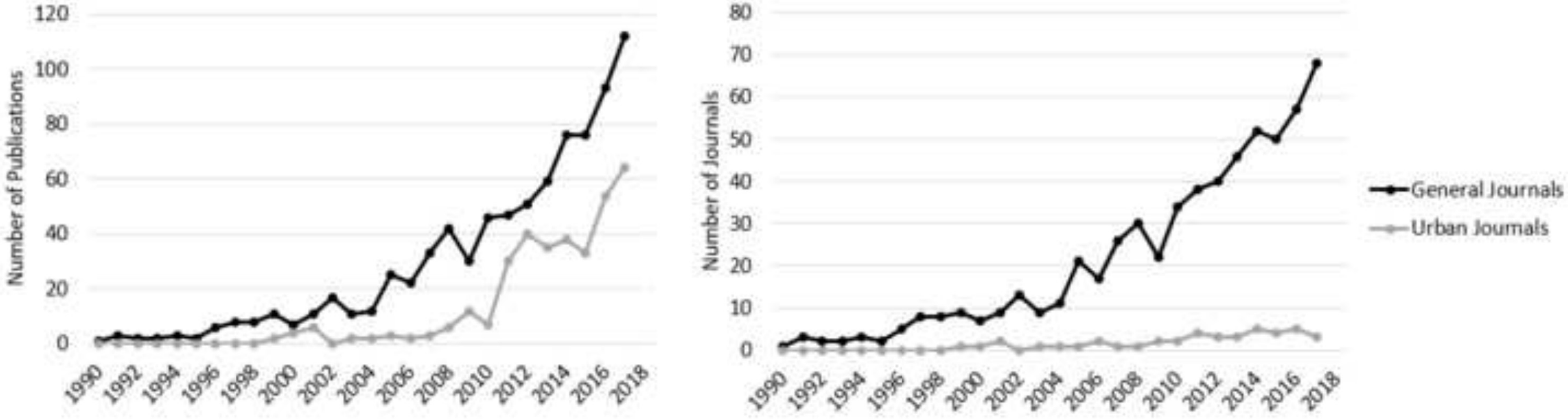

Number of Publications
120
100
80
60
40
20
0
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Number of Journals
80
70
60
50
40
30
20
10
0
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
General Journals
Urban Journals

Fig2

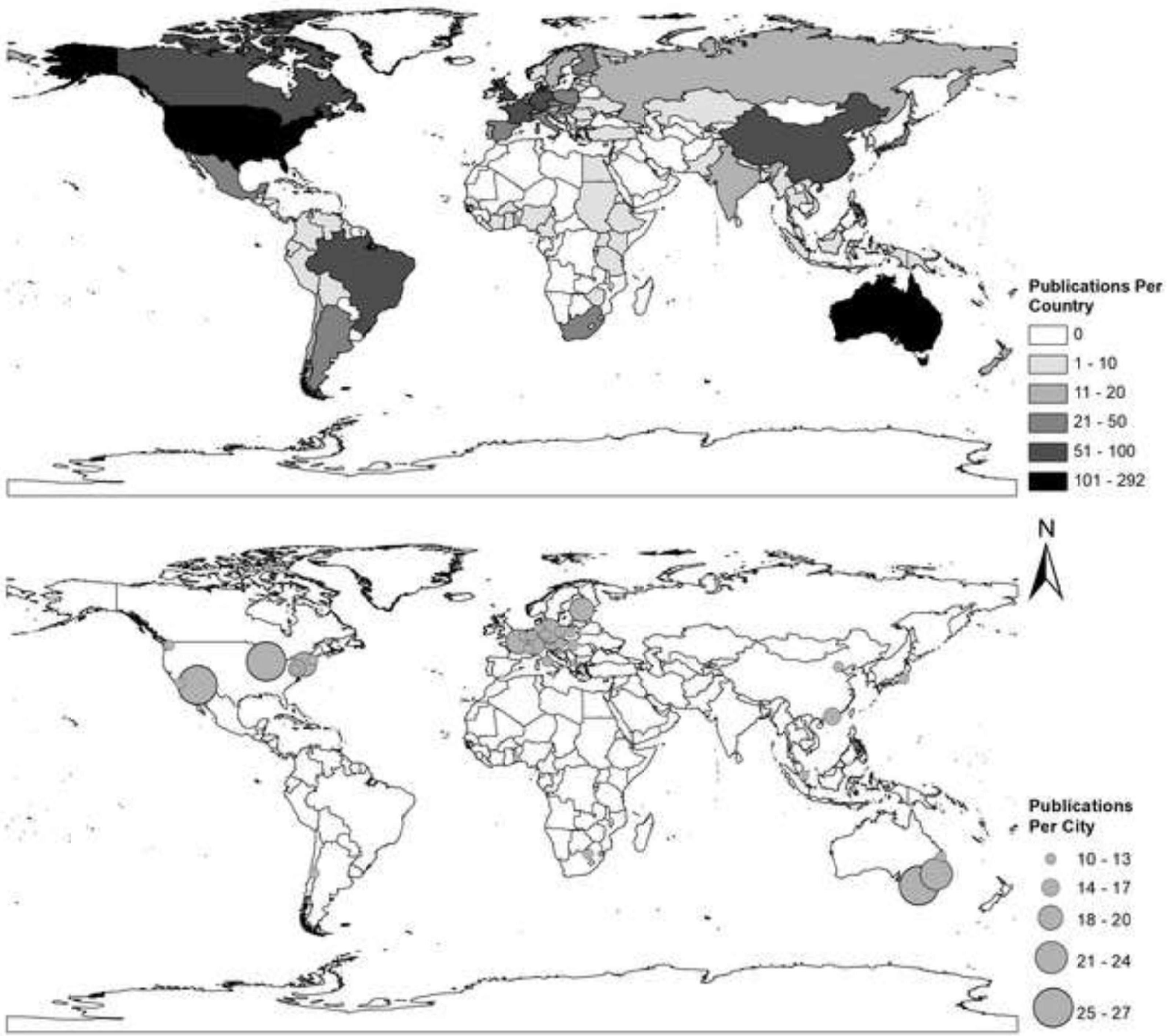

Publications Per Country
0
1 - 10
11 - 20
21 - 50
51 - 100
101 - 292
N
Publications Per City
10 - 13
14 - 17
18 - 20
21 - 24
25 - 27

Fig3

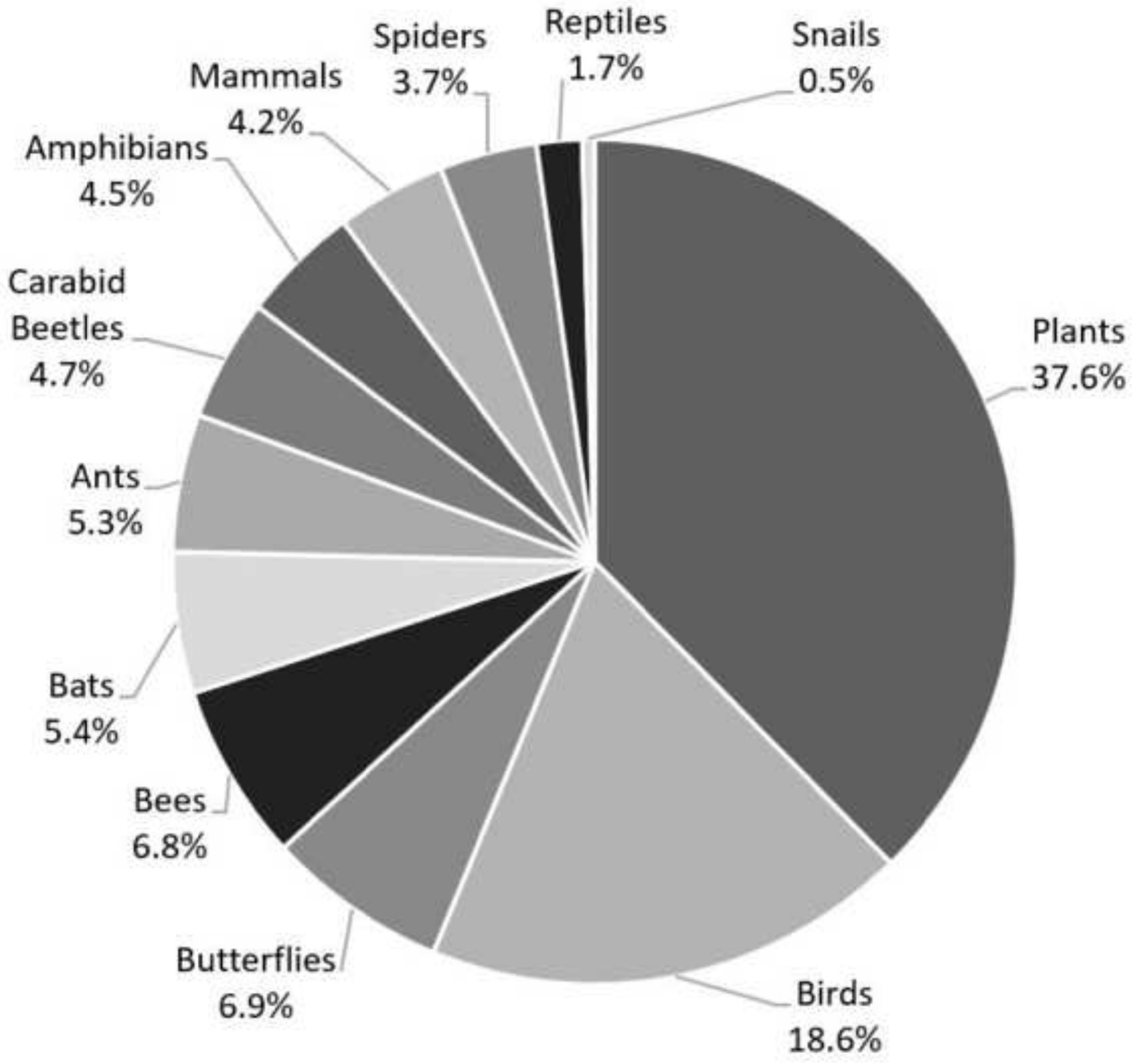

Spiders
3.7%
Reptiles
1.7%
Snails
0.5%
Mammals
4.2%
Amphibians
4.5%
Carabid
Beetles
4.7%
Plants
37.6%
Ants
5.3%
Bats
5.4%
Bees
6.8%
Butterflies
6.9%
Birds
18.6%

Fig4

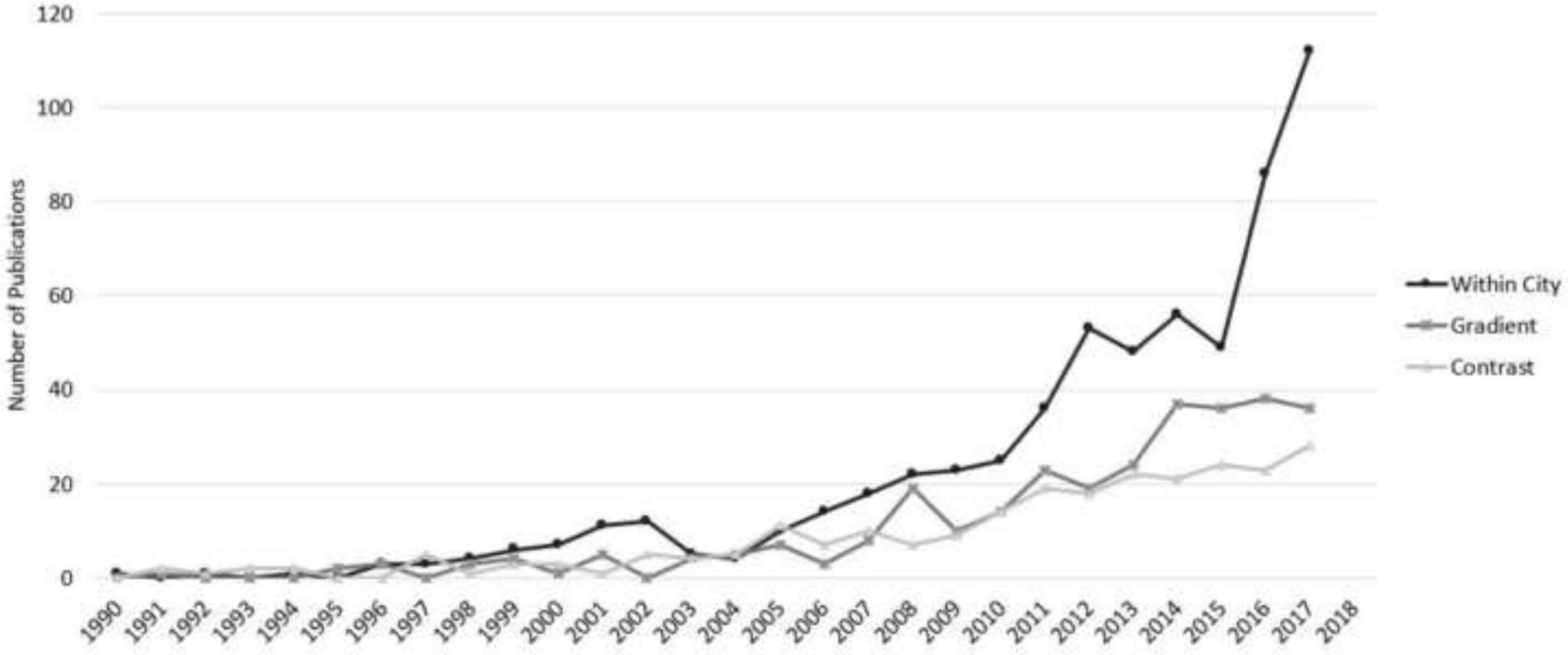
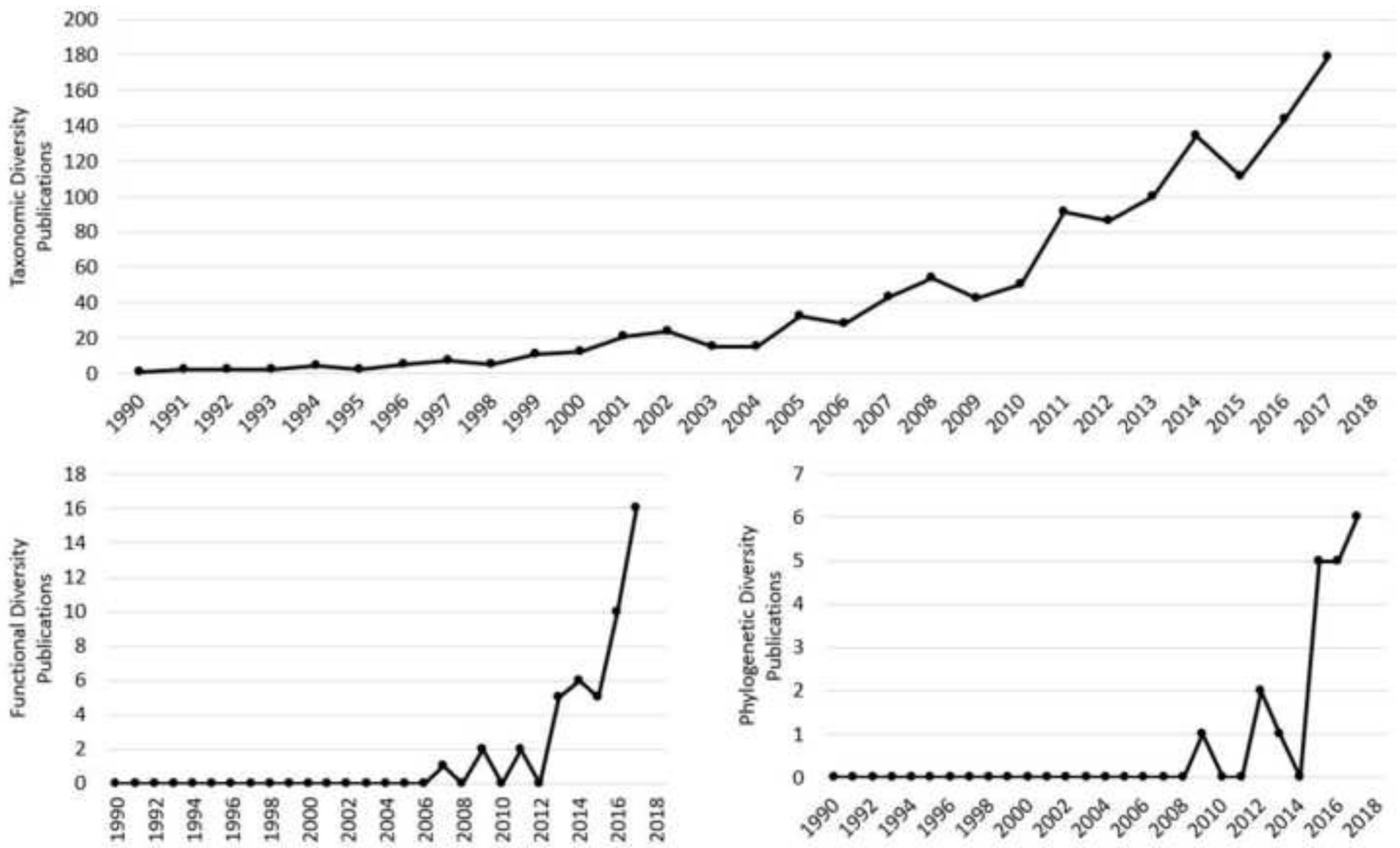

120
100
80
60
40
20
0
Number of Publications
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Within City
Gradient
Contrast

Fig5


Taxonomic Diversity
Publications
200
180
160
140
120
100
80
60
40
20
0
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
Functional Diversity
Publications
18
16
14
12
10
8
6
4
2
0
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Phylogenetic Diversity
Publications
7
6
5
4
3
2
1
0
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018