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METHODOLOGICAL DEVELOPMENTS IN LANDSCAPE ECOLOGY AND RELATED FIELDS (Y WIERSMA AND J HOLLISTER, SECTION EDITORS)

Connectivity in the Urban Landscape (2015–2020): Who? Where? What? When? Why? and How?

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Abstract

Purpose of Review This review uses a combination of narrative and systematic review techniques, including automated content analysis (ACA), to summarize the last 5 years of research on urban connectivity. It addresses the evolution of the field relative to prior reviews, identifies common themes and research gaps in the studies, and assesses the use of novel methods and data.

Recent Findings We found a broadening of geographic and taxonomic scope in recent studies, including more research from Chinese cities and on multiple species. We also found more studies that covered multiple time periods than have been documented in prior reviews. However, we observed a continuing reliance on best professional judgment rather than empirical field data to parameterize models and on analytic methods that are 10–20 years old. Our review framework identified several distinct conceptual themes in the literature including foci on land cover, including roads, water, and vegetation; green spaces and infrastructure; ecological conservation, planning, and management; habitat structure and function; and species movement.

Summary Urban areas offer the opportunity to leverage unique data sets and novel analytical methods that incorporate both human and other biological needs for connectivity, acknowledging that these two needs may not always align. In terms of data, few of the connectivity results were supported by or tested with empirical data. While nearly two-thirds of the papers reviewed included some measure of functional connectivity, which is an increase from previous reviews, future research would benefit from new modeling approaches that explicitly incorporate the challenges of measuring landscape connectivity within the urban context and from a clear set of shared objectives and goals.

Keywords City · Conservation · Corridors · Green space · Network

Introduction

Landscape connectivity, or the degree to which the landscape facilitates movement of organisms, has been of interest to ecologists for several decades [1, 2]. It has been recognized for its importance to dispersal, foraging, species interactions, population persistence, gene flow, and evolution [3]. Because these processes are notoriously difficult to observe empirically, measures of landscape connectivity often serve as coarse proxies [4]. Measuring and maintaining these ecological processes may be more important than ever in the face of intense anthropogenic impacts, such as climate and land cover changes [5].

Urban ecosystems have unique properties and have the potential to uniquely contribute to local, regional, and global biodiversity. For example, cities can release species from the pressures they face in the surrounding landscape, increase regional habitat heterogeneity, provide stopover habitat for migratory species, and contribute to species genetic diversity and adaptation to climate change [as reviewed in [6]. Urban areas also pose unique challenges for measuring landscape connectivity, due to their fine-scale heterogeneity, novel land cover types and stressors, and potentially inhospitable matrix (Fig. 1). The effects of urbanization on connectivity

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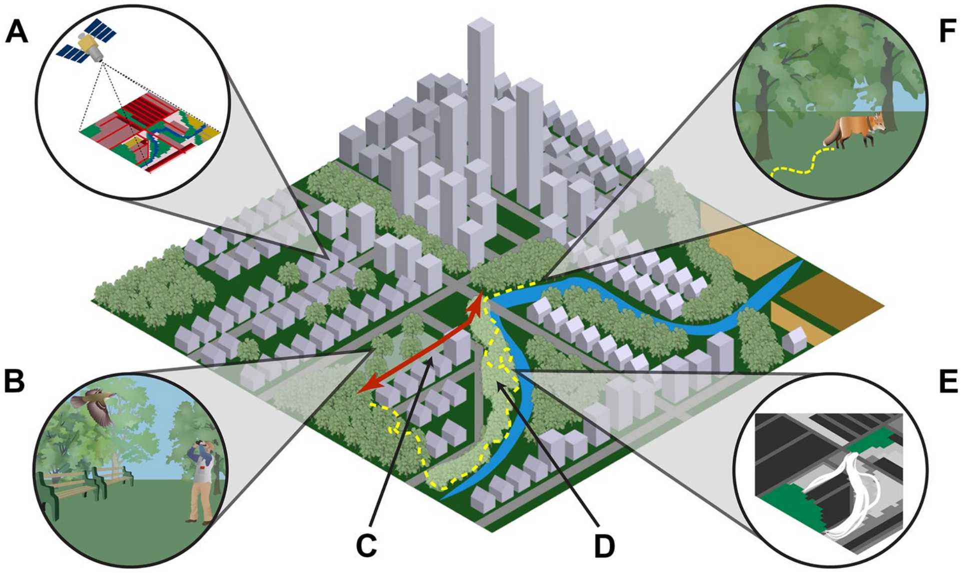

Fig. 1 Urban areas pose unique challenges for measuring landscape connectivity, due to their fine-scale heterogeneity (**A**) and novel land cover types (**B**). The degree to which the urban landscape facilitates or inhibits movement of organisms between two patches can be modeled through structural connectivity measures (e.g., **C**, Euclidean distance), functional connectivity measures (e.g., **D**, least-cost path corridor; **E**, circuit theory), or observed empirically (**F**) through radio-tracking or other methods. Symbols and images courtesy of the integration and application network, University of Maryland Center for Environmental Science (ian.umces.edu/media-library/symbols/) used under CC BY-SA 4.0

are still unclear. For example, landscape genetics studies have shown that urban features can inhibit, facilitate, or have no correlation with gene flow, depending on the organism and specific urban feature studied [7]. Furthermore, lessons learned from other systems may or may not apply to highly disturbed urban systems with distinctive socio-economic and biophysical forces and interactions [8]. However, urban areas are pervasive and growing, and landscape connectivity is one of the key drivers that shape urban evolutionary dynamics [9]. Understanding the impact of urbanization on movement of organisms and eco-evolutionary processes will be important for long-term sustainability of urban areas and global biodiversity.

Connectivity is often a desired outcome of urban planning efforts, as seen in planning strategies such as greenbelts, greenways, and green-blue networks [10]. In social-ecological systems such as cities, landscape connectivity may be an indicator of resilient systems that are able to persist, adapt, and transform in response to disturbances and change [11, 12]. Landscape connectivity can be directly beneficial to humans, through the creation of connected trails and greenways, and is thought to increase the provisioning of a variety of ecosystem services [13]. Conversely, connectivity could lead to the spread of undesirable species or disease, although positive effects of connectivity are generally thought to outweigh negative effects [14].

In 2015, LaPoint et al. [15••] reviewed 36 years of ecological connectivity research in urban areas. They identified 174 papers that investigated urban ecological connectivity, with the number of papers published annually generally increasing after 1996. Despite the growing literature, they noted that the understanding of ecological connectivity in urban landscapes appeared limited. They reported a strong geographic and taxonomic bias in research, with most studies taking place in North America and Europe and focusing on mammals, especially large-bodied ones. Papers that directly investigated plant or insect dispersal or migratory movements were rare, as were papers that made use of state-of-the-art genetic and biotelemetry techniques. Most papers focused on land-cover/use types and ignored other factors that could influence ecological connectivity in urban areas, such as land-use intensity, traffic volumes, noise, and lighting. While many studies highlighted the importance of structural connectivity to land-use planning and the importance of functional connectivity to ecological processes, far fewer directly addressed both aspects, thereby limiting the application of the research to urban planners.

In this paper, we follow up on LaPoint et al. [15••] with an examination of urban connectivity literature over the last 5 years. We ask:

- What is the geographic and taxonomic scope of recent studies within the urban connectivity literature? Are there regions or organisms not being adequately studied?
- What are the objectives of the studies? Are they clearly defined and articulated?

- How are the studies making use of state-of-the-art techniques to assess connectivity? Are genetic, biotelemetry, and novel urban data sets being incorporated to assess not just connectivity but also the consequences of connectivity?

In general, we ask how the field has evolved since 2015. We use a combination of narrative and systematic review techniques and employ a concept mapping approach to identify common themes and analytical approaches in the literature. In describing future research needs, we assess the relative merits and drawbacks of various new tools and approaches that are just now finding their way into the literature.

Methods Used for This Review

Using the Web of Science database, we searched for articles using the phrase "'Landscape Connectivity' AND 'Urban'" between January 1, 2016, and December 31, 2020, limiting the search to papers classified as belonging to one or more of the following Web of Science categories: biodiversity conservation, environmental sciences, environmental studies, ecology, geography, and physical geography. To be included in our list, the articles needed to meet these criteria:

(1) The authors explicitly stated that they conducted a connectivity analysis;
(2) The research was based in a specific city or metropolitan region rather than a larger region that was primarily comprised of rural areas; and
(3) The article presented a case study that directly measured or modeled connectivity of a focal landscape.

For each paper included in the review, we recorded variables addressing the paper's spatial and temporal scope, author and reference information, object studied, objectives, use of data, and methods (Table 1). Most information was extracted directly from the text, based on the authors' descriptions of their methods. Some variables were restricted to a limited set of possible values to analyze general trends in the literature, while others allowed a wider range of possible values to demonstrate the uniqueness of individual papers. Each paper was reviewed independently by at least two people, and any disagreements were discussed with a third co-author present.

Table 1 Description of variables assessed in the review. Where relevant, a list of possible values for each review category is provided

Review category	Description	Possible values
Location	Where did the study take place?	Country and city
Lead author affiliation	What were the department and institutional affiliation of the lead author?	Department and institutional affiliation
Reference information	What sources were referenced by the study?	Complete reference list
Object studied	What object was the focus of the paper?	Species, green space, ecosystem services, abiotic elements
Object studied—detail	What types of species, green space, ecosystem services, or abiotic elements were studied?	E.g., taxonomic group of species
Time period	Over what time period does the study observe or predict?	Dates
Objectives	What was the main objective of the paper?	Land use/land cover change, conservation, restoration, ecosystem services, basic science
Connected features	What was the element of the landscape that was connected or not connected?	Patch, pixel, point
Connected features defined	How were patches, pixels, or points defined?	land use/land cover data, species distribution model, empirical field data
Type of connectivity	What kind of connectivity did the paper focus on?	Structural or functional (potential, empirical, hydrologic)
Empirical data	What type of empirical field data were used for defining or validation connectivity, if any?	Direct observation, mark-recapture, playback experiments, radio tracking, GPS, genetic testing, other
Analytic approaches	What was the general approach to measuring connectivity?	Empirical, landscape metrics, least-cost path, circuit theory, graph theory, MSPA, gravity model, others
Cost surface defined	If a cost surface was used, how were costs assigned?	Literature, field observations, expert opinion survey, best professional judgment, undefined
Metrics	What metrics were used, if any?	Cohesion index, graph diameter, number of components, number of links, Harary index, integral index of integrity, other
Tools and software	What tools and software were used to assess connectivity?	Guidos, Conefor, FRAGSTATS, PANDORA, other

To further our understanding of the thematic composition of the literature, we performed an automated content analysis (ACA) on the selected articles using the ACA software system LexiPortal 5.0 (Leximancer Pty Ltd., Brisbane, Australia). ACA is a literature synthesis technique that uses text-parsing and machine learning algorithms to identify topics frequently discussed in a body of literature and how these topics are related to each other in the literature [16, 17]. An ACA is executed in three stages. In the first stage, frequently utilized words are identified in the text and used to create a list of "concept seeds." For our analysis, we excluded "urban," "connectivity," and "landscape" as concept seeds, as these terms were used to select the articles included in the corpus. In the second stage, a topic-modeling algorithm uses a co-occurrence matrix of concept seeds to designate "concepts," or groups of words that are strongly associated in the literature and that represent important topics discussed. In the third stage of the process, segments of text (i.e., 2–3 sentences) are classified by concept based on the concept seed words present in the segment. The use of concepts, as opposed to single word counts, is advantageous for our purposes, as it accounts for semantic and linguistic complexities, including synonyms, homonyms, and sentence construction [18].

Here, we performed an ACA following the protocols detailed in Nunez-Mir et al. [17] to identify the top concepts discussed in the literature reviewed. We used this information to produce a concept map of the top 50 concepts. This concept map is a two-dimensional projection of a co-occurrence matrix among concepts, akin to multidimensional scaling techniques that operate on distance matrices. In a concept map, the distance among concepts in map space is directly related to the strength of association among concepts. Dominant themes and concepts identified in the ACA were explored in greater detail during the systematic review of individual papers.

Overview of Results

Our search yielded 121 articles, of which 36 were discarded based on abstracts for clear irrelevance to our criteria. An additional 22 papers were discarded for irrelevance after reading them during the review process, leaving us with 63 case studies of urban landscape connectivity that met our three criteria (Appendix 1). Our findings were consistent with the trend of increasing publications in this field reported in prior reviews [15••, 19, 20]. The number of relevant publications per year increased from five in 2016 to 21 in 2020.

The automated concept analysis (ACA) provided an integrated overview of the literature. The terms "habitat," "green," "land," and "ecological" were the concepts most frequently discussed in the papers, identified in more than 1600 text segments each (Appendix 2). These concepts formed the centers of four distinct thematic clusters (colored bubbles in Fig. 2). A fifth distinct cluster was comprised of species movement concepts such as dispersal, distance, and least-cost, although the frequency of occurrences was generally lower for this portion of the concept map with dispersal (identified in 485 text segments) and movement (identified in 464 text segments) being only the 40th and 41st most common concepts in the selected literature (Appendix 2).

We used the ACA results as hypotheses for the types of studies we expected to find as we dug deeper into the literature. For example, one group of studies we anticipated were analyses focused on the spatial distribution of land cover, including roads, water, and vegetation. Other thematic clusters focused on green spaces and infrastructure; ecological conservation, planning, and management; and species habitat structure and function, including concepts of patches, corridors, and fragmentation.

We additionally included "China," "Europe," and "USA" in the concept map, even though only China (referenced 392 times) fell within the top 50 most-mentioned concepts (Appendix 2). Notably, these geographic areas were located in very different regions of the concept map and were aligned with different thematic clusters. The European papers were most closely aligned with the habitat thematic cluster, China was aligned with the green space cluster, and USA was most closely associated with the land cover thematic cluster (Fig. 2).

Below, we provide a systematic review of the studies with respect to their author and reference information (who), locations (where), object studied and taxonomic focus (what), temporal scope (when), and objectives and motivations (why). We then provide a detailed accounting of the common tools and methods (how), including how patches were defined, how connections were defined, and what data, analytical models, and software were used. We follow this section with additional discussion of exciting methodological developments in the past 5 years and provide recommendations for future research directions.

Who and Where?

The first authors of each paper were affiliated with a diverse array of academic departments and institutions, illustrating the breadth of interest in the topic. Approximately a quarter of the authors were from academic departments with biology/ecology in their name, half were from an academic department focused on some kind of applied environmental science (e.g., forestry, natural resources), and the remainder were from a mix of departments and institutions including geography, urban planning, and engineering departments; a botanical garden; and a zoo.

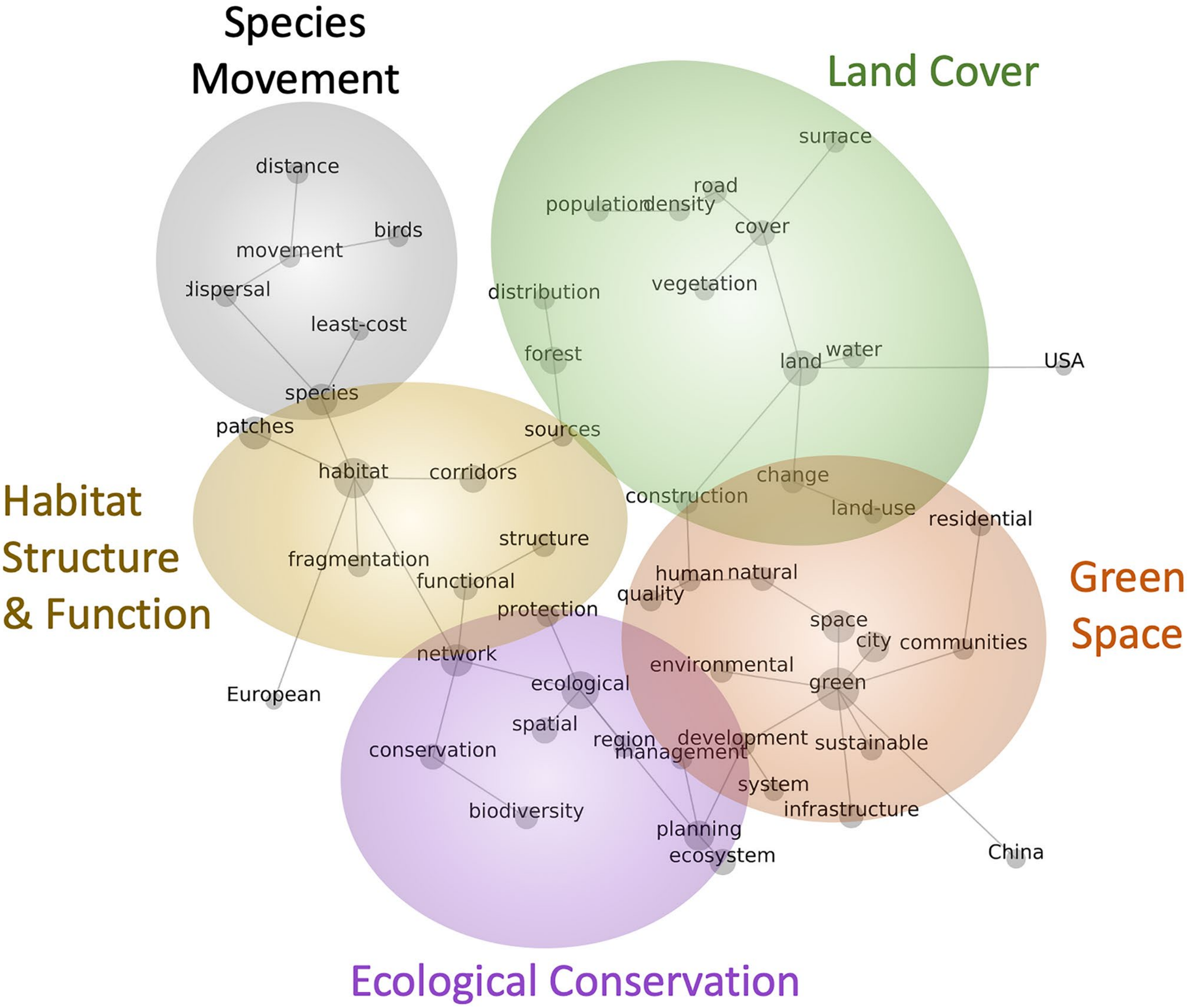

Fig. 2 Concept map of the 63 papers on urban landscape connectivity displaying the 50 most frequently discussed concepts in the text. The position of each concept in the figure is indicative of the strength of its association to other concepts. Circle size indicates the frequency of concept occurrence throughout the literature. Solid lines represent the strongest direct associations among concepts. Colored bubbles show clusters of concepts that appeared to represent a common theme. 'China' (referenced 392 times), 'Europe,' (116 times), and 'USA' (74 times) were included in the concept map as the most common geographic references

Looking at who was being referenced by these studies, the ten most commonly cited papers were almost all methods-based papers that introduced metrics or modeling approaches for assessing connectivity (Table 2). Furthermore, all of these highly cited papers were at least 10 years old, and three of them were at least 20 years old. While older citations in a paper do not necessarily indicate older methods, we found in our reading of the papers that older methods still dominate the literature. These methods are described in more detail in the "how?" section below. Given that landscape connectivity studies are dependent on metrics and models, we believe that the field is ripe for new innovation and approaches. We describe some of these new approaches in the "how?" section but also argue for future studies that make greater use of the unique attributes of urban landscapes in conducting connectivity analyses.

The papers focused on 18 different countries on all inhabited continents, but only three continents had more than two papers: North America, Europe, and Asia (Fig. 3). These regions were consistent with the most common geographic terms identified in the ACA. Over one-third of the papers ($n = 25$) focused on China. The geographic distribution of studies has changed substantially since the previous review of urban connectivity literature by LaPoint et al. [15••]. In particular, the percent of studies conducted in North America decreased from almost 50% in the previous review to 16% in this review, while the percent of studies conducted in Asia and Australia increased from 19 to

Table 2 The ten most cited papers in the 63 papers included in the literature review

Number of citations	Paper
19	Adriaensen et al. 2003. The application of "least-cost" modeling as a functional landscape model
15	Kong et al. 2010. Urban green space network development for biodiversity conservation: identification based on graph theory and gravity modeling
14	Saura & Pascual-Hortal. 2007. A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study
13	Saura & Torne. 2009. Conefor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity
12	Taylor et al. 1993. Connectivity is a vital element of landscape structure
11	Minor & Urban. 2008. A graph-theory framework for evaluating landscape connectivity and conservation planning
10	Tischendorf & Fahrig. 2000. On the usage and measurement of landscape connectivity
10	Urban & Keitt. 2001. Landscape connectivity: a graph-theoretic perspective
10	Pascual-Hortal & Saura. 2006. Comparison and development of new graph-based landscape connectivity indices: towards the prioritization of habitat patches and corridors for conservation
10	Saura et al. 2011. Network analysis to assess landscape connectivity trends: application to European forests (1990–2000)

48%. The percent of studies conducted in Europe remained nearly constant at approximately 30%. This trend is encouraging, as it better reflects the location of urban centers around the world (Fig. 3). However, our search did not uncover any studies in other areas of dense human population such as South Asia, and we found few papers focused on Africa and Southeast Asia (Fig. 3). We found only four studies in the entire southern hemisphere, a trend that has been previously noted in urban ecology [21, 22].

What, When, and Why?

Approximately half ($n = 33$) of the papers focused on connectivity for one or more species. We found that mammals and birds were the two most studied taxonomic groups. Large and small mammals were evenly studied. Few papers focused on invertebrate animals ($n = 2$; 3%) or plants ($n = 5$; 8%); perhaps, because there is less knowledge about how these taxa move across the urban

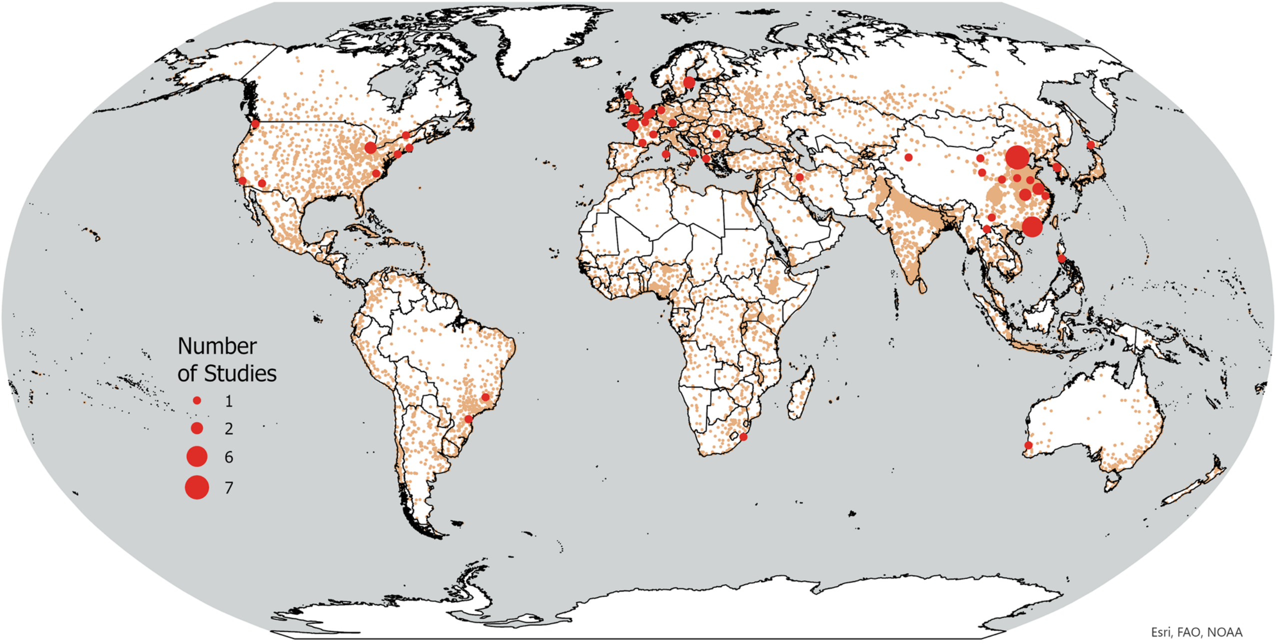

Fig. 3 Locations of urban connectivity studies. Marker sizes correspond to the number of studies at that location; larger markers indicate more studies. Background shading shows urban areas as defined by Kelso and Patterson [86]

landscape. Previous reviews have noted similar taxonomic biases. LaPoint et al. [15••] noted that most papers in their review were focused on large mammals, especially large predators. Similarly, in their more general review of habitat connectivity, Correa Ayram et al. [19] observed a taxonomic bias towards vertebrates, especially mammals.

Although a focus on a single species is sometimes well-justified, Diniz et al. [23] noted that a single surrogate species cannot represent the connectivity demands of all co-occurring species. We found 22 papers (35%) that analyzed connectivity for multiple species, indicating that recent urban landscape connectivity studies are often using a diverse and multi-species perspective. These studies included disparate taxa of birds and mammals [24], plants and animals [25], and vertebrates and invertebrates [26]. They included comparative ecological network analysis among species [27] and the construction of multi-species habitat networks [28].

In cities, humans and their demands for abiotic resources may be the most relevant focus for many connectivity studies, though it is important to recognize that human and wildlife use are often in conflict [29, 30]. We found relatively few papers focused on connectivity with respect to an abiotic factor or process (e.g., water; $n = 7$; 11%) or connectivity with respect to ecosystem services ($n = 4$; 6%). The remaining papers ($n = 19$; 30%) focused on connectivity of green space in general, without analyzing any particular species or process.

We identified regional differences in the objects studied in the papers that were consistent with our ACA (Fig. 4). In particular, the majority of European papers (15 of 19) focused on connectivity of species habitat, while most of the studies that focused on green space (13 of 19) were in Asia. North America was situated between Europe and China in the concept map (Fig. 2) and studies from this region had an equal focus on species habitat and green space (Fig. 4).

Zeller et al. [31] identified dynamic connectivity modelling as an underused but emerging area of research. Although most of the papers that we reviewed assessed connectivity for a single point in time, we were encouraged by

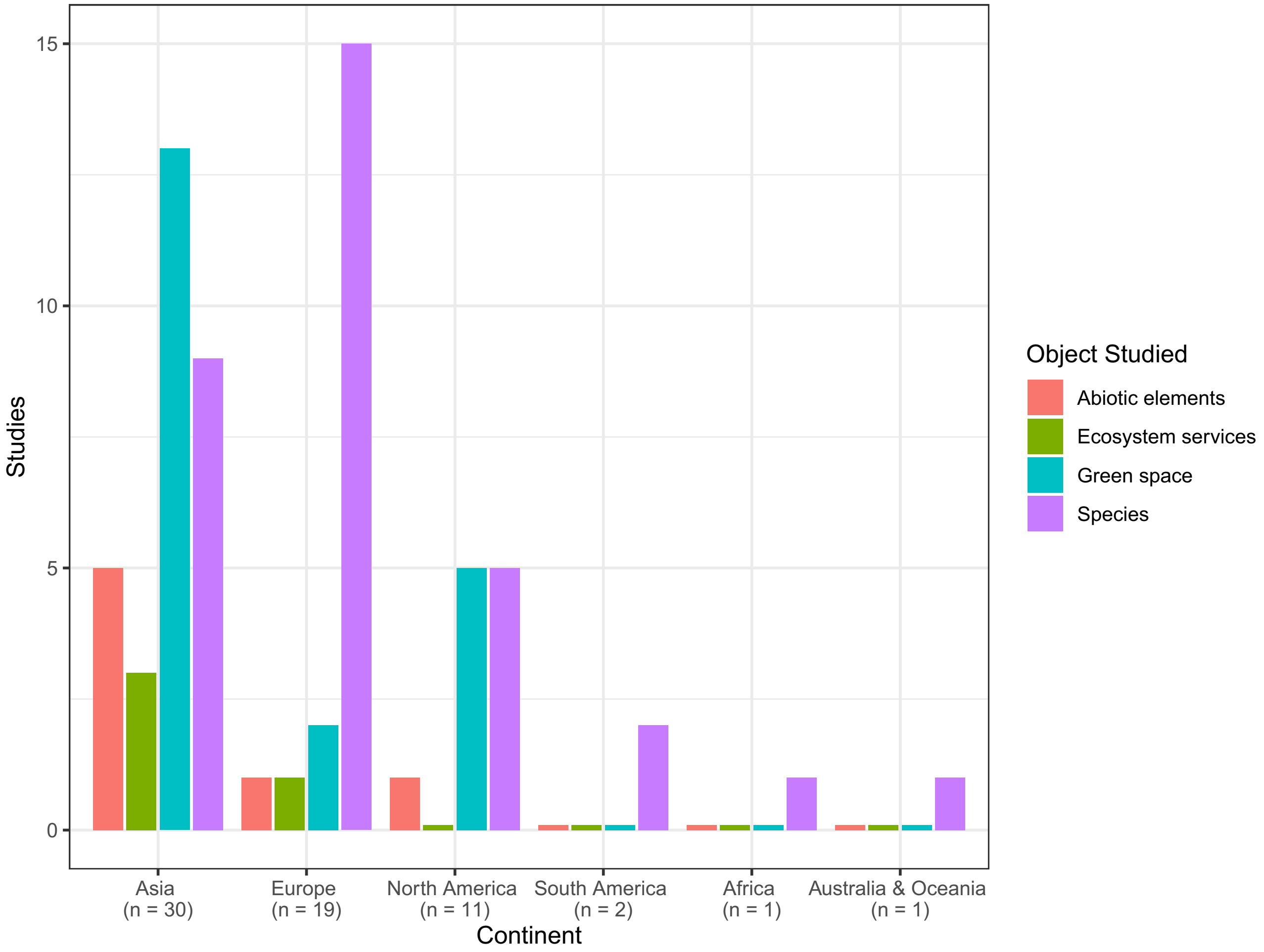

Fig. 4 The number of studies on each continent focused on the four urban connectivity objects or emphases we identified in the literature: species, green space, ecosystem services, and abiotic elements. Meerow [71], who investigated green space in both the USA and the Philippines, was counted as both a North American and Asian study, resulting in 64 studies from 63 papers identified in the literature

new methods that took a more dynamic approach to their connectivity assessments. We found eight papers that looked at empirical changes in connectivity over multiple years, with time periods extending as far back as 1904 in one case [32]. These papers emphasized the importance of dynamic connectivity models that incorporate change over time and provide more realistic recommendations for conservation and management.

As important as it is to look back in time, connectivity analyses can also be a valuable tool for assessing future landscape scenarios. An additional ten papers used novel simulations to explore the effect of alternative scenarios on landscape connectivity extending forward in time as far as 2058. The purpose of these simulations varied from paper to paper, with several papers contrasting different urban growth scenarios and others examining innovative aspects of urban connectivity. For example, a study of Lille, France, evaluated the effect of different light-reduction scenarios on landscape connectivity for bats [33]. Another paper used simulations to examine how restoring vacant urban land could impact landscape connectivity [34•].

Overall, we found a general lack of clarity and consistency in study objectives. Few papers provided clearly and precisely formulated hypotheses and predictions with regards to connectivity, probably because few studies used a hypothesis-testing framework. This ambiguity makes it difficult to compare and generalize among studies. In attempting to assess the authors' motivations, we assigned the study objective to one of five categories (basic science, land-use change, ecosystem services, conservation, and restoration). Papers assigned as having basic science objectives (n = 11; 17%) did not clearly address an obvious environmental issue but instead offered broad conclusions from their research that were focused primarily on understanding connectivity in urban areas rather than on specific environmental concerns. The papers included a mix of empirically based [33] and modeling studies [35]. Land-use change was the next broadest (and the most frequent) objective (n = 23; 37%), offering general suggestions about the effect of cover change on connectivity, oftentimes for planning purposes [36]. Other papers proposed planning strategies for more specific objectives. Ecosystem service papers (n = 11; 17%) aimed to increase the benefit of urban areas for humans [12, 37], while conservation papers (n = 12; 19%) aimed to improve the landscape for specific species or habitat patches [38]. Restoration papers (n = 6; 10%) examined the effects of landscape alterations or proposed restoration projects on connectivity [39].

How?

The majority of papers we reviewed relied on the delineation of discrete patches in a mostly inhospitable, if not always explicitly defined, urban matrix. Almost two-thirds of these papers delineated patches based solely on GIS-based land-use/land cover (LULC) variables, without including any species-specific information. This approach is consistent with the large land cover concept cluster in Fig. 2. The remainder of the papers delineated patches based on empirical field data (n = 9; 14%) and/or habitat suitability models (n = 11; 17%), many of which also incorporated LULC data into their patch delineation. It was relatively common for patches to be defined as survey locations (for example, ponds) in which species were present [40]. In other instances, patches were weighted by habitat quality scores derived from field surveys [25]. In yet other cases, field data were simply used to validate the underlying land cover map from which patches were derived [41]. One novel use of data to define patches was a field survey requesting pedestrians' favorite green spaces [42]. But overall, there were few creative uses of socio-environmental data to identify and delineate patches.

Approximately one-third (n = 22) of the papers used only structural measures of connectivity that were independent of species- or process-specific attributes. Most of these papers measured connectivity based on Euclidean distance between patches or other landscape metrics, although some identified least-cost paths based on human-defined resistance values, such as the suitability of a site for creating a corridor [e.g., 43]. Other papers incorporated more biological information into their connectivity measures by using functional measures of connectivity. Of the papers that measured potential connectivity—based on a combination of the spatial configuration of landscape elements and assumptions about movement behavior of species or processes of interest—most modeled resistance to different LULC types with least-cost paths or circuit theory. The majority of these papers modeled resistance values based on the authors' own professional judgment, the opinion of external experts, and/or published literature.

Only four papers used novel empirical data to identify (or define) connections across the landscape. These included direct observations of species movement between two patches using playback experiments of mobbing calls [44] and echo-location calls [38] and field-based observations of organisms used to define least-cost surfaces [33]. One of these papers [45] defined the edges in their population graphs using conditional genetic covariance.

Relative to the few papers that used empirical data to define connections, we found more papers that used empirical data to evaluate (or validate) connectivity impacts. Interestingly, several of these papers were studies of structural connectivity, oftentimes using straightforward landscape metrics, such as the number of other habitat patches within a predefined distance of the focal patch to first identify connected areas of the landscape [40, 46]. Empirical data, such as counts of species abundance, were then used to determine if there was a correlation between these landscape metrics and desired biological attributes. Field data were also used to validate estimates of potential connectivity, especially to evaluate whether species were moving within potential corridors by using radio-tracking [47••], road mortality [48], and mark-release-recapture methods [49]. Only two studies used genetic data and methods, including Wilk et al. [50•] who used genetic analysis to assess the potential implications of their connectivity analysis but found no significant relationship between Euclidean or resistance distance and genetic differentiation between populations. However, we note the growing number of papers about urban landscape genetics and urban evolutionary ecology, which were not detected by our search terms but are described further below.

The most common analytic approach used to measure connectivity was graph theory ($n = 26$; 41%), followed by landscape metrics ($n = 24$; 38%), and least-cost paths ($n = 19$; 30%). Eight papers (13%) used circuit theory and eight papers used other analytic methods including morphological spatial pattern analysis (MSPA) and gravity models. A total of 20 papers (32%) used more than one analytic method, e.g., least-cost path modelling and graph theory. The results of the analyses focused nearly equally on identifying patch attributes ($n = 26$; 41%), corridors ($n = 33$; 52%), and landscape-level characteristics ($n = 35$; 56%).

Many of these papers used ArcGIS to map what were perceived as important corridors as their final results. Others calculated the amount of land cover of a specified type surrounding focal patches. In addition to ArcGIS, Conefor ($n = 15$; 24%) and FRAGSTATS ($n = 13$; 21%) were the most common software tools. For the Conefor papers, probability of connectivity (PC) was the most common metric ($n = 11$; 17%). Nearest neighbor distance and contagion and cohesion indices were common metrics calculated in FRAGSTATS. Circuitscape ($n = 6$; 10%), Graphab ($n = 5$; 8%), and Guidos ($n = 4$; 6%) also were used in multiple articles. Four papers that focused on ecosystem services used PANDORA as a modeling framework. PANDORA is based on a system of ordinary differential equations that divides the landscape into bio-energy landscape units separated by barriers to ecological flow, such as roads and railways [51]. It then calculates the bio-energy fluxes among landscape units and estimates the ecosystem service value of each landscape unit.

Related Areas of Study

Urban landscape genetics and urban evolutionary ecology are two rapidly growing fields with close ties to landscape connectivity. These fields examine how urbanization affects gene flow, genetic drift, and evolution of populations [7, 9, 52, 53]. Gene flow and genetic drift may be influenced by urbanization either through "urban fragmentation" or "urban facilitation" [reviewed in [54]]. Urban fragmentation can reduce movement and gene flow for some species, potentially leading to reduced genetic diversity within populations and greater genetic differentiation between populations. This has been shown in species ranging from bumble bees [55] to pumas [56]. Conversely, urbanization may facilitate the movement of highly mobile or human commensal species, potentially increasing genetic diversity within populations and reducing genetic differentiation between populations. For example, feral pigeons (*Columba livia*) formed only two genetic clusters across six large cities in a northeastern "megacity" in the USA [57]. The geographic divide between the two genetic clusters corresponded to a break in the urban landscape, suggesting that urbanization facilitated gene flow in this species [57]. This body of literature provides insight into the extent to which various urban features act as barriers or conduits to gene flow and thus informs our knowledge of landscape connectivity. Although these topics were beyond the specific scope of our review, they provided meaningful context for interpreting the results, and urban landscape genetics and evolutionary ecology provide fruitful related areas of future exploration.

Lessons Learned

There has been considerable progress in the urban connectivity literature, which has continued to flourish in the past 5 years. Accompanying the increase in publications has been an apparent broadening of the geographic scope of studies. Although there has been a greater focus on Asian cities since LaPoint et al. [15••] published their review, especially from China, large portions of the planet remain understudied, notably most of the Global South [58]. However, we caution that the extent to which urban connectivity papers are being published in other languages was not considered in our review. It is likely that our review methods, including the database we used and the fact that we only searched for papers that were published in English, led to a geographic bias in publications.

As illustrated in Figs. 2 and 4, the studies from China are distinctive in their approach to studying connectivity and their focus on concepts such as green infrastructure and ecosystem services. For example, the vector-based analytical tools and models such as PANDORA being used in these articles to quantify patterns and processes represent a noteworthy advancement in the literature [43, 59]. Other advancements include ecological security pattern analyses that use a combination of graph theory to identify key nodes and least-cost path modeling (e.g., using ant colony algorithms) to identify strategic infrastructure between nodes [60–63]. A further diversification of geographic perspectives is likely to lead to additional novel methods and insights into the unique nature of connectivity in urban systems.

We also observed a greater taxonomic breadth in the object of study than observed previously. In their review of landscape connectivity studies focusing on biodiversity conservation, Correa Ayram et al. [19] reported that only 29% of studies that included focal species included more than one species. They further advised that studies should analyze a wider mix of a species, not just charismatic megafauna and large carnivores. Encouragingly, we found that two-thirds of the papers in our study that examined connectivity from a species perspective included multiple species in their analyses [e.g., 28, 64, 65]. We also found a more even mix of birds, small mammals, and large mammals than in previous review studies, while studies on plants and invertebrate species are still scarce [but see [26, 27]]. This taxonomic bias is somewhat surprising since plants and invertebrates were the most studied groups in a review of biodiversity in human-modified landscapes [66]. However, a different review of movement ecology found that plants and invertebrates were less often the focus of movement studies compared to vertebrates and tended to be studied at the population level rather than the individual level, presumably due to the difficulty of marking seeds and small larval invertebrates using current techniques [67].

Urban concerns extend well beyond that of just biological diversity, and we noted a distinct split in the literature between species-based papers and those that assessed connectivity of the abiotic landscape. Increasingly, urban heat islands and water resources are the focus of connectivity analyses. Three studies focused specifically on the relationship between connectivity and temperature [68–70], while an additional three studies included urban heat island mitigation as one of multiple factors (including landscape connectivity) to consider in green infrastructure planning [71–73]. Other studies examined the effect of connectivity on flow and health of urban rivers, streams, or lakes [35, 74, 75]. We expect this trend in publications to continue. Bridging the biotic and abiotic realms were papers focusing more generally on the structural connectivity of forest or other broad land cover types. We also welcome the increasing attention to the shared biotic, abiotic, and human needs for connectivity in cities. However, many of these studies of urban green space would have benefited from greater specificity and more ecological and/or human-centered data.

Urban areas offer the opportunity to leverage unique data sets. LaPoint et al. [15••] described how novel processes and pressures in cities warrant the incorporation of novel data sets into connectivity models. We found several studies that used data on urban stressors such as artificial light, building density, and chemical pollution [33, 74, 76, 77•] or potential urban amenities like desired green spaces [29, 78]. Other studies successfully highlighted how habitat can include private yards, vacant lots, and gardens in urban environments [34•, 38, 79]. More of these types of analyses are needed to better understand how cities are similar and different from other types of ecosystems.

The importance of studying connectivity over multiple time periods has been discussed in detail elsewhere [e.g., [31]]. For example, connectivity may be limited by dispersal constraints over short time periods but may be much greater when examined over longer time periods and when considering temporal variability in landscape conditions [14]. Some species also exhibit time lags in their responses to environmental conditions, and therefore, a longer view of the landscape is needed to adequately predict connectivity [80]. Capturing more than one snapshot is especially important to understand connectivity in urban landscapes, which by their nature are highly dynamic [81]. As over one-quarter of the papers that we reviewed considered multiple time periods or scenarios, we believe that the urban connectivity literature is moving in the right direction to address these knowledge gaps.

Future Research Needs

While the field of urban landscape connectivity has evolved in promising ways, we believe that there is room for growth. In particular, there are opportunities to collect and use more novel empirical movement data and to develop more sophisticated methods for modeling this movement. In describing these future needs, we underscore that the species movement cluster was the least frequently studied of the five concept clusters identified in our ACA (Fig. 2). We also describe how the ACA identifies other important research gaps for future study.

We were heartened that nearly two-thirds of the papers included some measure of functional connectivity, which is an increase from previous reviews. However, few measures of functional connectivity were supported or tested by empirical data, and many papers in our review took the "operational" approach described by Foltête et al. [82] by prioritizing making time- and cost-efficient recommendations over deriving novel ecological insight. Similar to our findings, Foltête et al. [82] documented how a relatively small proportion of landscape connectivity studies are using primary biological data and argued that connectivity studies are too often focused on the identification of corridors without paying sufficient attention to the value of those corridors. Correa Ayram et al. [19] found that, while 78% of studies proposed or identified potential corridors, no studies included an explicit evaluation of those corridors.

We suggest that the limited number of empirical studies may be partially due to the general assumption that connectivity is a positive attribute. Fletcher et al. [14] and Diniz et al. [23] also noted that most ecological connectivity studies assume that connectivity is a positive attribute without validating this assumption. However, in a review of studies that examined the empirical effect of connectivity, 20%

found a negative effect [14]. This percentage may be even higher in urban environments where, for example, nonnative invasive species are rampant [83, 84]. For this reason, validating the results of urban connectivity analyses remains very important and can be accomplished with genetic and telemetry data, among other approaches [85]. We found several good examples of studies that used empirical data to validate the results of connectivity analyses [47••, 49, 50•], but more studies are needed to better understand the value and implications of connectivity in urban systems.

In addition to these data needs, the field of urban landscape connectivity would also benefit from a broader incorporation of new modeling approaches. For example, we found that least-cost path modeling was among the most common approaches for assessing connectivity, as did Correa Ayram et al. [19] in their earlier review. However, the classic least-cost approach poorly matches animal dispersal for at least three reasons [23]: (1) sources and destinations among which individuals will disperse are rarely known; (2) the approach assumes that individuals have a clear destination as a goal, complete knowledge of the routes to that destination, and always travel by the "cheapest" one; and (3) the narrow paths designated by least-cost models may not be suitable corridors for many species. In other cases, depending on the pixel grain size, traditional least-cost path estimates may underestimate connectivity, especially for understudied taxa such as arthropods that can make use of many built and mixed-used components of the urban landscape. Some workarounds for these problems have been proposed, such as considering additional suboptimal routes, smoothing the least paths using a probability density function, or use of resistant kernels [23]. Based on our analysis, these workarounds are not being widely used in the urban connectivity literature. Instead, many of the cost surfaces used in the papers that we reviewed were created using best professional judgment and output from habitat suitability models. While habitat suitability models may be useful for delineating patches, they have been shown to be a poor predictor of dispersal and gene flow [82].

Many other urban connectivity studies still rely on GIS-based identification of structural corridors or FRAGSTATS-based studies of structural connectivity metrics. The need for a modernization in methods and models is partially illustrated by the publication dates of the most commonly cited papers in this body of literature (Table 2). These papers are nearly all methods-based papers, and these methods were introduced 10–20 years ago. We do not mean to imply that these approaches are no longer valid, as they provide a firm foundation for the field. However, landscape connectivity is a technology-based field, and the technological advances in the urban studies we analyzed were rather modest. We especially welcome new and novel analytic approaches such as PANDORA [51] that address connectivity of ecosystem services in urban environments.

Finally, we found it challenging to manually assess and characterize the overall objectives of many of the studies. As reviewers, it was not uncommon for two of us to assign different motivating objectives to the same paper. The unclear objectives are probably linked to the fact that many of the papers were largely descriptive and not hypothesis-driven. However, without clear and shared objectives, it is difficult to draw general conclusions that are robust across multiple cities and studies. Automated quantitative literature synthesis approaches, such as ACAs, provide bird's eye views of the current, shared conceptual and thematic foci of the literature reviewed. This information can be used to identify potential avenues for future research.

Connected terms and thematic concept bubbles in our ACA highlighted topical areas with robust example applications and areas in which more research is needed (Fig. 2). Foci of urban connectivity studies over the past 5 years include biodiversity conservation, identification of habitat corridors, green space and infrastructure planning, and land cover change analysis. Equally noteworthy were the infrequency and omissions of certain themes and concepts. For instance, the movement cluster was smaller and spatially separated from the other clusters in the concept map space, indicating a disconnect between the literature focused on modeling species movement and the rest of the urban connectivity research. The concepts within this cluster were also found to be less frequent in the literature as compared to others. Another interesting gap pertains to the omission of "climate change" in the top 50 concepts (Appendix 2). We only encountered one paper that explicitly considered how

Table 3 Summary of past, present, and future research in urban landscape connectivity

	Before 2016	2016 - 2020	Future research needs
Where?	North America and Europe	China, Europe, North America	The Global South
What?	Large-bodied mammals	Birds, small-bodied mammals, large-bodied mammals, multiple species, greenspace, ecosystem services	Plants, invertebrates
How?	Land-cover, land-use types, structural connectivity	Functional connectivity without empirical support, least cost path models, expert opinion, and habitat suitability models	Functional connectivity with support from telemetry and/or genetic data, new connectivity models, incorporation of abiotic processes and climate change scenarios

climate change might impact landscape connectivity [28]; this paper combined land-use simulations, graph theory, and regional climate projections to evaluate the robustness of habitat networks to future threats. As numerous studies outside of urban areas have incorporated future climate change into connectivity design [5], we can only speculate that urban researchers find climate change to be less of a concern than other stressors.

Conclusions

In this review, we evaluated the urban connectivity literature from the last 5 years. Our goal was to determine the state-of-the-art of the field and evaluate progress since the 2015 review by LaPoint et al. [15••]. In particular, we reviewed the literature with an eye to the research gaps, recommendations, and emerging areas noted by LaPoint et al. [15••] and other relevant reviews of the landscape connectivity literature [14, 19, 80]. In Table 3, we summarize our findings, the progress made, and lessons learned, as well as identify methodological developments and future research needs. We found a welcome expansion of the geographic regions and taxonomic groups being studied but a continuing need for research in the Global South and research on plants and invertebrates. We also observed an increase in studies of functional connectivity but a lack of empirical support for most of those studies. We found a few examples of new models being used to assess connectivity of ecosystem services, but a need for more explicit consideration of the connectivity of abiotic factors such as temperature and water, especially in response to changing climatic conditions. Future research on urban connectivity will hopefully collect and use more novel empirical movement data and develop more sophisticated methods for modeling species movement across these dynamic landscapes.

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- •• Of major importance

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