Urban Landscape Genetics: Are Biologists Keeping Up with the Pace of Urbanization?

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Abstract

Purpose of Review Urbanization has the potential to jeopardize the sustainability of populations of organisms living within and dispersing across urban areas. Landscape genetics approaches offer a great promise for quantifying how urban features affect ecological and evolutionary processes for species living within and around cities. In this review, we assess the current state (2015–2020) of urban landscape genetics research, examining what types of urban features are quantified, what genetic measures are used, what species are studied, and in which geographic regions they are conducted. We then make recommendations for future research.

Recent Findings We identified relatively few landscape genetic studies conducted within urban areas published in the last 5 years. We also found a publication bias towards certain taxa and geographic regions (mainly mammals studied in North America), based on results from relatively few molecular markers. These studies used varied measures of urbanization in their analysis, but the most common was urban land use/land cover measured at different resolutions, followed by buildings/development and transportation infrastructure (roads, railroads, and tramways). The results of these studies reflect previously conducted urban research findings that urban features may inhibit, facilitate, or have no correlation with gene flow, usually a product of which focal taxa is being studied, as well as what urban features are present/measured within variable cityscapes.

Summary We urge future research to directly measure urban features and stress the need for explicitly sampling within and around urban areas to gain full understanding of whether urbanization impedes, facilitates, or does not affect genetic differentiation between populations. To facilitate the development of robust theory, we urge the formation of a global network of urban landscape geneticists to collaborate and sample diverse taxa, in varied global landscapes and climates, and analyze genome-wide datasets for more robust conclusions about gene flow and genetic diversity. We advocate for analyzing urban features at multiple scales to allow broad conclusions about the effects of urbanization across studies, taxa, and regions. Finally, we recommend that study designs include social, cultural, and economic differences in human land use, which have the potential to affect how species disperse, survive, and reproduce in urban areas. Taking these factors into account, we can make novel advances in understanding how complex urban landscapes shape contemporary evolution.

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Introduction

Urbanization drastically affects how organisms survive in and move through the environment. Urban landscapes are comprised of complex heterogeneous features including roadways, buildings, and infrastructure with various intervening green spaces [1]. These "natural" areas within cities range in extent, quality, geological and topographic complexity, and in their potential to provide the resources necessary for native organisms to flourish. Additionally, the "grayspace" (i.e., the roads, buildings, and infrastructure) within cities may facilitate dispersal for human commensals and organisms that are

able to take advantage of these urban landscape features [2]. Many of these organisms can persist in urbanized habitats, either in remnant natural spaces or in and around human infrastructure. The socioeconomic and cultural influences of humans on landscapes also affect dispersal and gene flow [3]. For example, affluent areas with more green space will have a different species composition and create different spatial genetic patterns of wild populations, as opposed to city regions with densely packed, lower income public housing, and/or apartment complexes surrounded by greater amounts of impervious surface [3]. Recent work by Schell et al. [4] highlights economic and racial disparities that also influence abundance, diversity, and colonization of animal and plant species in cities. Empirical studies have shown reduced plant [5] and bird [6] diversity and lower species richness in urban regions of lower wealth. Specifically, historic "redlining" in the USA has drastically shaped urban landscapes. Redlining is a discriminatory practice in US cities that includes historical practices, as well as those still taking place today. Such practices include disinvestment by the Home Owners Loan Corporation (HOLC) in areas of cities with large African-American communities while providing resources for white residents. This practice often left African-American communities with limited patches of greenspace and large amounts of impervious surface coverage, even reducing tree canopy cover by half [7]. Thus, racial discrimination and the socioeconomic structure of urban areas could create direct limitations on available habitat for native species living within cities and consequently disrupt gene flow between populations of species remaining in these urban spaces [4].

Both anthropogenic and natural landscape features affect whether and, to what degree, an organism can disperse through their environment, ultimately influencing connectivity between populations. Identifying which features aid or deter movement through the landscape is important for understanding the ecology and evolution of wildlife populations within cities. The field of landscape genetics examines how landscape features affect genetic differences between individuals or populations. These studies use genetic material collected from organisms to assess functional connectivity, i.e., how dispersal affects gene flow, and assesses the physical components of landscape structure to determine how the landscape promotes or inhibits dispersal of individuals [8, 9]. The degree of gene flow between populations can influence population dynamics, species distributions, local adaptation, and an organism's ecological role in complex ecosystems [10]. This is especially true of heavily developed urban landscapes, which may promote or inhibit functional connectivity between populations depending on each organism's biological requirements.

There are general trends in how urban ecologists and evolutionary biologists quantify the influence of urbanization, such as measuring the amount of impervious surface or human population density across study sites. However, comparisons across studies are difficult because researchers often use different metrics or landscape variables to examine urbanization. Features that have been used to define the urban landscape include the following: human population density [11], commercial and industrial development [12], transportation infrastructure [13], roadways [14–16], and impervious surface [9, 17]. Each of these landscape features influences dispersal in taxon-specific ways. For example, buildings and roads may reduce gene flow in urban salamanders [18] but facilitate gene flow in feral pigeons [19]. There is currently a lack of consensus on how to define an urban area, and relatively few studies have incorporated social, cultural, and political attributes of urban human populations.

While the influence of humans has been explored in the landscape genetics literature in recent years [20], urbanization has seldom been the main focus of landscape genetics studies. For example, Storfer et al. [21] identified only 7% of landscape genetic studies (12 of 655 articles) that included urban areas. Zeller et al. [22] reported that urban features of interest are typically roads or other linear features (explored in 37 of 96 studies), or development (buildings, coverts & weirs; explored in 11of the 96 studies). Reviews of landscape genetics research have consistently argued that future studies need to explicitly state hypotheses and objectives [10, 23], use the newest genetic datasets [21, 24], conduct comparative analyses across a diverse set of landscape variables [10] over a greater variety of taxa [21–23, 25–27], and need to investigate a broader range of geographic regions [10, 24], particularly outside of Europe and North America. Here, we assess whether researchers have incorporated these recommendations into recent studies.

In this review, we assess (i) geographic diversity, (ii) taxonomic diversity, (iii) types and numbers of molecular markers, (iv) types of urban landscape features measured, and (v) the overall results from recent urban landscape genetic studies to produce a snapshot of how urbanization affects genetic connectivity of species living in cities. We then make suggestions on how to move this field forward given the trends we observed in the literature.

Methods

A review by LaPoint et al. [10] focused on ecological connectivity in urban areas through 2015. Thus, we sought to assess how urban landscape genetics has progressed in the 5 years since that effort (2015–2020). To guide our search for relevant studies, we used the definition for landscape genetics from Storfer et al. [25]: "research that explicitly quantifies the effects of landscape composition, configuration and matrix quality on gene flow and spatial genetic variation."

To identify relevant studies, we searched Google Scholar using the terms "urban" OR "city" OR "development" OR "anthropogenic" AND "landscape genetics" (accessed June 2020) from January 1, 2015, to June 22, 2020. This search identified 470 scientific articles. We filtered out duplicate articles and only retained studies that were published in peer-reviewed scientific journals (i.e., theses, dissertations, and reports were excluded). After this initial filtering, articles had to meet three further criteria to be included: first, the study needed to include a direct measure of genetic distance or genetic diversity; second, the study had to include direct assessment of an urban landscape feature's influence on gene flow or genetic differentiation. We included research that deliberately measured some type of urban landscape feature and specifically quantified, assessed, or modeled how that feature affected gene flow and/or genetic diversity. We excluded studies that used population genetic metrics and/or spatial genetic analyses without landscape metrics, considering these studies generally made only hypothetical inferences about urban landscape effects on populations. We also excluded studies that focused on other aspects of anthropogenic activity such as deforestation or agriculture, since these phenomena are not limited to urban areas. The third criteria was that the study had to have been performed at least partially in an urban area (i.e., areas densely populated with humans, sampling locations near city centers, or sampling within an area mostly surrounded by buildings and/or impervious surface). This urbanized area was qualitatively assessed based on each studies' sample area map and cross referenced to an aerial view of the study area in Google Maps (when their sample area map did not give extensive detail on urban development). For example, if the sample locations were retrieved within a national park, and the analysis was examining the impacts of roads on gene flow, then we omitted this study as it was not focused within an urban area. We also avoided extensive analysis and discussion on landscape genetic methods because they have been recently reviewed by Munshi-South and Richardson [20].

After filtering using these criteria, we retained 32 relevant articles that represent the state of urban landscape genetics literature within the past 5 years. For each article, we made note of the class, order, family and/or genus and species studied, the continent and geographic region/city studied, the molecular markers used (mitochondrial regions, number of microsatellite loci, and/or number of SNPs), the urban features that were measured and tested, and the overall results regarding how urban features affected gene flow or genetic differentiation. From here, we assessed if and how these studies took into account suggestions made by past reviews; then we evaluated the overall knowledge gaps that still exist and need to be addressed in future urban landscape genetic studies.

Results

Upon filtering 470 studies in our search for "urban," "landscape genetics" research articles, we identified only 32 peer-reviewed studies focused directly within urban areas, which is approximately 6.8% of the recent landscape genetics literature (summarized in Supplemental Table S1). There were many theses and dissertations that explored urban taxa in urban environments, although they did not meet our requirements for this review. Therefore, the prospect of additional published urban landscape genetics studies may be on the horizon.

(i) Geographic Distribution of Studies Recent urban landscape genetics literature is heavily biased towards studies conducted in North America and Europe. Fourteen of the studies were conducted in North America, 11 in Europe, and only five in Asia, one in Australia, one in South America, and zero in Africa. One study was conducted in Egypt and Jordan [28]; however, because samples were collected east of the Suez Canal, we concluded that this study was conducted in Asia and not Africa. North American studies were conducted almost exclusively in the USA with a single study [29] examining cities in both the USA and Canada. Within Europe, four studies were conducted in France, while the remaining studies included two conducted in Germany, one in Belgium, one in Denmark, one in Scotland, one in Spain, and one in Switzerland.

(ii) Taxa Sampled We examined the class and order of organisms studied in recent urban landscape genetics publications. Half of the articles (16 of the reviewed studies) examined mammals, with three papers investigating Artiodactyla (even-toed ungulates), five papers investigating Carnivora, three investigating Rodentia, two investigating Eulipotyphla (hedgehogs, shrews, moles, and solenodons), one investigating Lagomorpha (rabbits, hares, and pikas), and one investigating Chiroptera (bats). An additional paper investigated both Carnivora and Ortervirales (single-stranded RNA viruses; 31). Four papers examined Amphibia, with two looking specifically at Anura (frogs and toads) and two comparing Anura and Urodela (salamanders). Two papers researched Aves (birds), two researched Insecta, and two researched Reptilia. Three of the final five papers covered Actinopterygii (ray-finned fishes), Clitellata (ragworms, earthworms, and leeches), and Gastropoda (snails and slugs), while three included plants as their subject of study, specifically two examining Liliopsida (monocots) and one examining Magnoliopsida (dicots).

All of the taxa covered by these studies were sampled in their native range except for studies by Baudouin et al. [30], Alvarado-Serrano et al. [31] and Arredondo et al. [32]. Baudouin et al. [30] examined invasive Eastern subterranean termites (*Reticulitermes flavipes*) in France that are native to

the southeastern USA. Alvarado-Serrano et al. [31] investigated the common morning glory (*Ipomoea purpurea*), which is native to Mexico but is a widespread invasive species in the USA. Similarly, Arredondo et al. [32] conducted their study on the slender false brome (*Brachypodium sylvaticum*) which is a bunchgrass that is native to parts of North America, but was studied in its invasive range in Oregon.

(iii) Molecular Marker Type All but three of the studies we reviewed [11, 31, 32], made use of microsatellite markers to measure genetic differentiation or genetic diversity. The number of microsatellite loci ranged from 5 to 19. Six studies examined SNPs instead of, or in addition to, microsatellite markers [9, 32–36]. Some studies looked at mitochondrial DNA, such as Sacks et al. [35], who used 696 base pairs of mitochondrial DNA (*cytb* and *D-loop*) to estimate gene diversity and haplotype frequencies and to compare F_{ST} estimates to microsatellite data, as did van Rees et al. [34], who used 520 base pairs of *ND2* to confirm that their model support was consistent across both microsatellites and mitochondrial DNA. Beninde et al. [9] used 450 base pairs of *cytb* to confirm that all the individuals sampled were native, and Evans et al. [36] used the *cytb* mitochondrial gene region to confirm that their hair samples were from the correct species under investigation for their particular study. Fountain-Jones et al. [33] also used two specified gene regions (in the retroviral genome) to build a phylogeny for feline immunodeficiency virus (FIV).

Only three studies used next generation sequencing to retrieve genetic diversity or genetic differentiation measures to incorporate into their landscape analyses. Alvarado-Serrano et al. [31] constructed a genome-wide, Genotype By Sequencing (GBS) library and recovered 263,658 SNPs in addition to the 15 microsatellite markers they amplified. Arredondo et al. [32] also used GBS to genotype 2187 SNPs for population and landscape genetic analyses. Finally, Rasmussen et al. [11] conducted reduced representation genome sequencing using a Restriction site Associated DNA sequencing (RADseq) protocol and recovered 2902 SNPs (after filtering) to assess genetic variability.

(iv) Urban Landscape Features Measured The studies reviewed here included a diverse set of urban landscape features used for landscape genetic analyses. All of the studies included variables collected from either remote-sensed datasets and/or field-collected spatial data to describe urban areas. Sixteen of the studies (half of the total studies examined here) used what they termed "urban land use/land cover" layers often derived from pre-existing publicly available remotely sensed datasets that included a pre-defined "urban" land use category. Of the 13 US studies, six retrieved urban-related variables from USGS (the United States Geological Survey) or NLCD (National Land Cover Database; Homer

et al. [37, 38]), four used the NOAA C-CAP data (National Oceanic and Atmospheric Administration's Coastal Change Analysis Program), and the remaining three used state-specific datasets. Of the 11 European studies, two used country-wide data to explore urban features from CORINE (the Copernicus Land Monitoring Service's Land Cover), the remotely sensed data inventory, [39] whereas others used country-specific shapefiles collected from national geographic information institutes. Of the five studies in Asia, two used country-specific remotely sensed datasets, and the others used global datasets like NASA's MODIS (Moderate Resolution Imaging Spectroradiometer) and WorldClim data to identify and describe urbanization. The single South American study used NASA's LANDSAT Imagery to represent anthropogenic effects to the landscape, and the single Australian study used country-specific data from the Australian National Catchment and Stream Environment Database to describe human influence in and around a waterway.

These remotely sensed pre-defined maps and shapefiles represent urbanization using either a single variable or a conglomeration of measurements, such as percent impervious surface, human population density, and/or amount of buildings/infrastructure or built-up areas. For example, Kimmig et al. [40] used Copernicus Urban Atlas categories to define "artificial surface" land cover. This measure included a combination of categories, such as continuous and non-continuous urban fabric (describing impervious surface coverage); industrial, commercial, public, military, and private units; the presence of mine, dump, and construction sites; and non-agricultural vegetated areas such as urban green space and sports and leisure facilities. Adavodi et al. [41] and Roy and Gregory [42] used measures of anthropogenic influence via the "human footprint" metric derived from the Wildlife Conservation Society [43], which involves multiple measures of urbanization and human land use practices to describe and measure human influence on the landscape [41, 42].

Other metrics commonly used to describe urbanization were stand-alone categories defining built-up areas often termed "development" on the landscape (which was sometimes incorporated into their urban land use/land cover layer) and/or the specific presence or density of transportation infrastructure. Measurements of development were often defined by the presence of buildings, other built structures, or measures of residential housing density. Measures of transportation infrastructure included presence or density of road, rail, or tramways. To analyze transportation infrastructure, studies conducted in the USA used data from the U.S. Census Bureau TIGERLINE shapefiles to map roadways, while studies conducted in Europe, Asia, and South America used resources such as Google Maps [44] or country-specific transport maps [45–47]. Many of these studies hypothesized roads as potential barriers to gene flow, and some predicted

transportation as potential corridors (depending on species-specific dispersal strategies). Some also assessed the effect of road density and/or traffic volume on genetic differentiation. For example, Amaral et al. [48] hypothesized roads as barriers for New England cottontail (*Sylvilagus transitionalis*) dispersal and gene flow, yet hypothesized linear features such as roadsides, railways, and powerline passages as conducive to gene flow (assigning it a lower resistance value) based on what is known about cottontail dispersal and movement ecology along edge habitat.

Lastly, a few studies incorporated very distinctive urban landscape features into their analysis. Mapelli et al. [49], who studied gene flow in tuco-tucos (*Ctenomys* spp.), examined anthropogenic landscape change to understand how a temporal element of human development affects genetic differentiation for a subterranean rodent existing in a continually developing region of Argentina. In a similar vein, Baudouin et al. [30] used building age, as well as urban greenspace as landscape features that potentially affect genetic diversity and infestation by termites in Paris, France. Specific to the ecology of a marsh bird, van Rees et al. [34] included linear man-made drainage ditches in their analysis to explore how this feature affected genetic connectivity for the Hawaiian gallinule (*Gallinula galeata sandvicensis*). Lastly, Braaker et al. [50] specifically investigated how urban greenspace affected European hedgehog (*Erinaceus europaeus*) dispersal.

(v) Summary of the Effects of Urban Landscape Features

Across the articles reviewed here, features related to urbanization were either restricted, facilitated, or had no correlation with gene flow or genetic divergence. Twenty-five of the studies found at least one urban feature that restricted gene flow or had a correlation with increased genetic divergence. For example, Thatte et al. [46] found both the presence of human settlements and heavy roadway traffic resulted in increased genetic distance between tiger (*Panthera tigris*) populations in protected areas across India. Conversely, eight studies found at least one urban variable that facilitated gene flow for their species of interest. Sacks et al. [35] found that urban areas facilitate high levels of gene flow between fox populations across Southern California.

Only two studies found urban features that were measured, to have no correlation with genetic differentiation or gene flow [11, 32]. Most other studies, when testing multiple urban-related variables, found mixed results—some features aiding, others impeding, and/or finding features that have no effect on genetic differentiation between sampled populations or individuals. For example, mean human population density was a significant factor affecting genetic distance for populations of striped field mice (*Apodemus agrarius*) in South Korea [51]. Yet other urban features measured in this study (railroad system, highways, all paved roads, traffic volume, and distance to big cities with 100,000 residents) showed no significant

correlation with genetic distance. On the other hand, European hedgehog (*Erinaceus europaeus*) gene flow was found to be facilitated by urban greenspace throughout Zurich, Switzerland, yet main transportation axes showed no hindrance of hedgehog dispersal [50]. There is even a single case where roads were significant barriers to gene flow in one species of earthworm (*Allolobophora chlorotica*), but had no effect in another (*Aporrectodea icteric*) within the same city in France [44]. Another interesting finding was that urban features were found to either significantly or not significantly affect genetic distance for black needlerush (*Juncus roemerianus*) based on which genetic metric was employed (*Dch*, Cavelli-Sforza chord distance or Wright's F_{ST} distance; 53) [53].

The specific urban features identified to restrict gene flow were mostly related to "urban areas" and/or development (pre-defined urban land cover/land use, human settlements, housing density, developed lands, or towns; reported in 14 of the 32 studies reviewed), followed by roads/transportation (10 of the 32 studies reviewed). For example, one study found buildings act as a barrier and restricted gene flow [9], and another reported mean human population density (which is often used as a proxy for urban areas) correlated with increased genetic distance between populations [51]. Urban features that facilitated gene flow included urban/anthropogenically altered land (4 of the 32 studies reviewed), transportation infrastructure (3 of the 32 studies reviewed), buildings (2 of the 32 studies reviewed), and urban green space (1 out of the 32 reviewed). Lastly, features that were found to have no significant correlation with genetic divergence or gene flow included roads, development/land use, and human population density (see Supplemental Table S1). Of note, throughout all of these studies, there were other natural landscape features or variables that were also found to significantly affect gene flow in varied ways (not just urban features alone). Overall, the summary of these results mirrors the gradient of results reported in previous urban landscape genetic research (prior to 2015) and also echoes the diverse mixture of natural and anthropogenically modified landscape features that have the potential to affect evolution of wild populations in urban environments.

Discussion

Both natural and human-created features within the landscape have the potential to affect gene flow between populations of a variety of organisms living in cities around the world. We reviewed 32 peer-reviewed articles published over a 5-year period that analyzed how urban features affect gene flow or genetic differentiation within and between urban populations. We found a bias towards studying native mammalian taxa in North America and Europe; the use of microsatellite loci for genetic analysis; and the use of either pre-defined "urban"

land cover/land use categories, development, or roadways to describe urban landscapes. The studies reviewed here demonstrate a continued bias in the choice of taxa, geographic region, type of molecular marker, and urban landscape features explored in current literature (Fig. 1). Studying landscape genetics on a wider variety of urban species, in different global regions, and the use of more genetic markers will strengthen our understanding of how urban landscapes shape the spatial genetic patterns of native and non-native organisms (Fig. 1). With the exponential growth of the human population and continued expansion of urbanization around the world, landscape genetics research should focus more effort on expanding the only 7% of current landscape genetic studies focused within urban areas. Insights gained from a larger effort to understand urban landscape genetics will allow conservation biologists, city planners, and urban ecologists to better understand and predict the needs of urban wildlife. Equitable restoration of urban habitat, supported and implemented by city planners across the expanse of cities, could benefit wildlife population connectivity, support diverse urban ecosystems, and promote access to natural spaces for humans in marginalized communities [4].

Geographic Bias Urban areas are expected to grow by 2.5 billion human inhabitants in the next 30 years, with most of this growth occurring in Asia, Africa, and South America

[52]. Very few urban landscape genetics studies are being conducted on these continents [54]. With the urban expansion that is expected to take place in these regions, now and in the near future, studies in Asia, Africa, and South America have the potential to provide pre- and post-development models of the effects of urbanization on gene flow. Cities in these regions vary in climate, time since urbanization, rates of urban expansion, and local politics, leading to powerful cross-city comparisons for landscape genetics. Comparing species in and between cities around the world will allow us to better grasp which aspects of urban landscapes, socioeconomic differences, and human culture affect gene flow.

Taxon Bias We found a clear bias in the urban taxa that were studied, with almost all of the focus on terrestrial vertebrates (mainly mammals). Given that fish make up almost half of all vertebrates, and arthropods make up the vast majority of animal species [55], we found it surprising that these taxa, along with plants, were underrepresented in current urban landscape genetics studies. While marine and freshwater fishes may often be overlooked as part of the urban community, recent research has shown that these organisms are heavily impacted by urbanization [56, 57]. Additionally, invertebrates play an extremely important foundational and functional role in maintaining urban ecosystem quality, and they respond rapidly to environmental change due to short generation times, making

Fig. 1 Conceptual diagram illustrating the current state of urban landscape genetics research and the recommendations for future research programs. The inner dashed circle visualizes the current state of urban landscape genetics research, which is heavily biased towards studies of mammals (green), single cities (pink), urban metrics that are often limited to roads and development (yellow), microsatellites (blue), and North America (orange). The outer circle represents our recommendations for future research, including a greater diversity of taxa (green); comparison of multiple cities with different socioeconomic demographics (pink); the inclusion of multiple measures of urbanization including socioeconomic metrics (yellow); the use of genome-wide SNP datasets (blue); and a focus on Asia, Africa, and South America where urbanization is accelerating at the most rapid rates
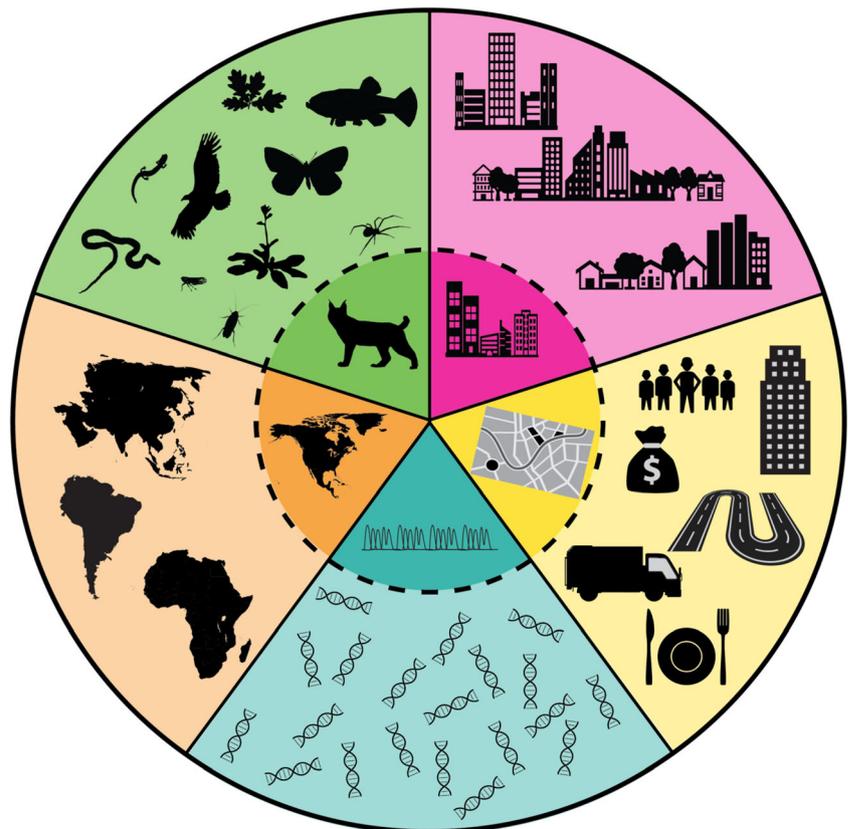
them prime study taxa in rapidly changing urban environments [58]. We also found minimal research investigating plant communities in urban areas. Promoting connectivity and gene flow among plant populations bolsters diverse plant communities and thus provides a multitude of ecosystem services that strengthen the urban ecosystem [59].

Understanding connectivity of native taxa across urban areas is important for conservation efforts, yet there is also interest in the use of landscape genetics for studying patterns of gene flow and range expansion in invasive species since their dispersal is often human-mediated [32]. We found only three recent landscape genetics articles focusing on invasive species [30, 31, 41] in urban areas. Rapid invasion of non-native species is one of the many reasons for biodiversity loss [26], making this a particularly important direction for urban landscape genetics research. Landscape genetic studies can aid in understanding the evolution of invasive species dispersal in an urban setting [60] and current invasive species distribution in cities and help target areas of potential dispersal/invasion fronts through cityscapes for management purposes [25]. Overall, we encourage future studies to explore the wide range of taxa that are present in urban areas (both native and non-native) so that we can draw clearer conclusions about the ways urbanization plays a role in shaping community ecology and the spatial genetic patterns of wild organisms.

Through this review, we did uncover a few studies that focused their efforts on understudied taxa in understudied geographic regions, such as bats and reptiles in Asia and insects in Europe. These studies revealed that anthropogenically altered habitats did not affect gene flow for urban fruit bats in Jordan and Egypt [28] or for pit vipers across areas of Iran, where "human footprint" had minimal effect on gene flow [41]. These studies found urban fruit bats frequently make use of anthropogenically altered habitat [28], and forest cover had a greater effect on gene flow for pit vipers than did human activity. These findings reveal both important information about the way these species are utilizing habitat space within cities, as well as evidence that different measures of urbanization can have different effects on evolutionary dynamics. Branching out from the more commonly studied terrestrial species will help researchers prioritize which species is negatively or positively affected by urbanization and help make future predictions about similar closely related taxa. Combining this knowledge with an expansion of research into different geographic locations/climates will provide a more comprehensive understanding of how a variety of wild organisms cope with urban development in cities with different spatial structure and different anthropogenic pressures.

Marker Choice Advances in high-throughput genomic sequencing offer low-cost discovery and genotyping of thousands of loci, or even whole genomes [61] which have been incorporated into high resolution population genetic analyses.

Yet we identified a lack of genome-wide datasets incorporated into recent urban landscape genetic studies. The majority of landscape genetic studies reviewed here rely on microsatellite markers for measures of genetic differentiation and genetic diversity in assessing how the landscape affects genetic patterns. The advancement in our ability to explore thousands, not just a handful, of molecular markers has increased the power to more precisely identify individual-based movement and gene flow through the landscape, and understand the potential for local adaptation in urban areas [62–64].

Analyses of genome-wide SNP datasets may also detect genetic differentiation and structure that are missed by microsatellites [65]. For example, McCartney-Melstad et al. [66] identified roads as strong predictors of genetic divergence in Eastern tiger salamander (*Ambystoma tigrinum*) populations using a SNP dataset, but not when using microsatellites. Analysis of genome-wide datasets enables the detection of subtle effects of urban landscape features that may ultimately play a large role in the evolutionary trajectory of urban populations. Genomic data provide greater accuracy in genome-wide estimates of diversity [24] for studies in urban areas and are necessary to estimate genetic differences under complex demographic scenarios [54] that may be present in urban populations.

Usual Suspects and Unexplored Urban Landscape Features
Urban areas can be defined by human population density, remotely sensed features such as impervious surface versus vegetation, socioeconomics, or physical attributes and composition [1]. Because of the inherent complexity of urban landscapes, there have been few attempts to standardize quantification of urbanization in the literature, further complicating the development of theory, comparisons across studies, and how management strategies are implemented for conservation [67].

Many of the studies identified in this review have used different metrics for measuring urbanization; the most common metric was a pre-defined urban land cover/land use category retrieved from remote-sensing datasets. However, the scope of these datasets varies from state to national to global and varies in terms of date when the remote sensing was conducted. The other studies reviewed here included other more specified measures of anthropogenic influence such as human population density [41, 42, 46, 51], housing density [33, 36], the presence of development or buildings [9, 13, 28, 30, 40, 45, 46, 68], percent impervious surface [13, 32, 69, 70], or artificial light at night (ALAN; 41,45) to measure urban influence on the landscape. With such a wide array of measures, choosing standardized metrics to use across the field will be challenging since all urban landscape features (and all scales they are measured at) may not be relevant for the species in question. For example, human population density may not be directly applicable to stream salamander

population dynamics and dispersal, yet it may be a crucial element influencing survival and gene flow for rats or cockroaches. The complex and variable nature of "urban" metrics employed in wildlife research has been extensively explored by Moll et al. [67]. As they express in their review, we also suggest the use of multiple measures of urbanization, measured at multiple scales to retrieve sound results about how the urban landscape affects organisms. For urban landscape genetic analyses, this will help capture both the complexity and variation of the cityscape and how it affects species with variable life histories and dispersal biology. Multidimensional study designs will help to make robust inferences about how urbanization affects ecological and evolutionary processes and aid in developing theory about the general effects of urbanization on gene flow.

We found some studies using measures such as "human footprint" which involves a conglomeration of structural, social, and physical modifications to the landscape that cannot be easily teased apart to determine which specific urban feature affects gene flow. Other urban features, such as percent impervious surface [70], provide a more direct measurement that is relatively easy to measure and has known impacts on species since it involves replacement of native vegetation and often cannot be used directly as habitat. We discourage the use of umbrella measures such as "human footprint" for landscape genetics because they may underestimate, overestimate, or even miss the effect of specific aspects of urbanization on gene flow. We encourage the utilization of more targeted measures of urbanization while also expanding the scope and types of urban features that could potentially affect species' dispersal across the cityscape (Fig. 1).

Transportation networks such as roads and railways may result in substantial mortality for many different species and thus are one of the most common variables hypothesized to negatively influence gene flow. As urban human populations become denser, transportation networks will, by necessity, also comprise a greater portion of the landscape. While we recognize the importance of including transportation variables in analyses, as well as readily available data from public sources, we caution researchers in using only this metric to assess urban landscapes. Roads may be impenetrable barriers to dispersal impeding gene flow for some species, where others easily traverse across roadways (despite the risk of mortality). Roadways as an urban landscape feature depends on habitat preference or dispersal strategy of the focal species who may never contact a roadway during movement across their environment (i.e., pigeon or fish). Also, transportation routes alone do not make a landscape "urban," especially considering transportation networks that often span suburban and rural areas as well as urban hubs.

The choice of scale for measuring the effect of urban features on gene flow can greatly affect the generalizability of landscape genetic results. The study scale should be relevant to the biology of the species, but out of necessity may also be constrained by the scale at which landscape data are available. For example, New York City now has percent impervious surface data at one m^2 resolution (https://edg.epa.gov/EPADataCommons/public/ORD/EnviroAtlas/) allowing for fine-scale investigation into how organisms disperse within the city. However, these data are not available outside the political boundaries of NYC, and other US cities may only have data on percent impervious surface down to 30 m^2 resolution, such as that provided in the USA via the National Landcover Dataset [37]. Due to differences in dispersal ability and the scale at which organisms are influenced by the landscape, a 30 m^2 resolution may lead to underestimating the effect of urban features on gene flow. Going forward, we suggest that urban landscape genetic studies should measure gene flow at multiple scales. Researchers should be explicit in reporting how and why the scale was chosen for analysis. This reporting will allow for cross-city comparisons in similar taxa and cross-species comparisons for those who disperse at the same scale, to ultimately draw conclusions on how urban landscapes affect spatial genetic patterns.

In this review, we noted that recent papers have rarely attempted to incorporate social, political, or cultural aspects of urban human populations into landscape genetic analyses. Munshi-South and Richardson [20] recently summarized the potential effects of socioeconomic status that could shape spatial genetic patterns within and across cities. We suggest that urban landscape genetics studies integrate more specific information on human activity (not just residential density) within urban spaces where humans are constantly present, such as heavily trafficked pedestrian corridors (sidewalks/bike paths) and urban parks. Areas in cities used for dining and disposing of anthropogenic food waste (in trash bins, curbsides trash piles, and dumpsters) as well as frequency of garbage pickup are other features that could affect dispersal. We suggest that researchers incorporate socioeconomic, political, and cultural variables that are relevant to their focal species. For example, Combs et al. (personal communication) are currently incorporating human variables (e.g., fine-scale human population density, income/slum proxy, and restaurant density) into landscape genetic studies of brown rats (*Rattus norvegicus*) in multiple cities. The incorporation of social variables into landscape genetic analyses could greatly improve our understanding of how the choices and attributes of humans in cities influence other species.

Barriers to Development of the Field As we urge the field forward, we understand that there are multiple impediments to the progression of urban landscape genetics research. For example, the lack of studies conducted to date in certain geographic areas is likely due to lack of funding rather than a lack of interest. To combat this, we encourage international cooperation and funds to study developing regions that have been

previously neglected. Along these lines, the formation of a global network of urban landscape geneticists would encourage communication [71], collaboration, and yield useful datasets for comparative studies between taxa and across cities. Additionally, steering away from only answering the "safe" questions about evolution, often using common, charismatic, or model organisms, will expand our knowledge about the evolution of diverse wild populations within intricate and complex urban ecosystems.

Conclusion

A rapid increase in urban landscape genetic studies is needed to keep pace with the rate of urban growth around the globe. Moreover, the relatively few studies conducted to date means that there are a plethora of taxa and cities where new discoveries can be made. The studies reviewed here continue to be characterized by limited taxonomic and geographic scope, small molecular datasets, and the use of idiosyncratic urbanization metrics. In addition to using next generation sequencing, and focusing on a wider array of taxa and geographic locations, future research should better integrate the human social and economic patterns that contribute to the spatial genetics patterns of urban organisms [3].

We echo the concerns put forth by Munshi-South and Richardson [20] that advancements in understanding gene flow in urban environments should include comparisons of multiple cities and species. We also agree with Donihue and Lambert [72] who argued that the incorporation of genomic datasets into studies of urban evolution will answer questions about adaptation and that of Lambert and Donihue [73] that express the importance of exploring evolutionary patterns for species in urban landscapes to conserve and maintain urban biodiversity. We also acknowledge the importance of exploring different spatial scales in urban landscape genetic research to appropriately assess the effects of specific urban features on gene flow [74], especially in regard to how subtle features (that may need to be measured in the field at finer scales) can affect species with smaller home ranges [75]. Lastly, we stress the importance of the findings in Schell et al. [4] that historic legacies of racism leading to economic and wealth disparity is an underlying mechanism that ultimately affects the ecology and evolution of urban wildlife. We see the field of urban landscape genetics moving forward through the integration of human social patterns to reveal how these social drivers affect evolutionary processes in urban wildlife. Altogether, continual urban growth and modification of the landscape provide a flourishing area of unexplored research for different species and unique urban elements that could be affecting the evolution of wildlife populations residing in urban areas.

Declarations

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