Landscape and Urban Planning 214 (2021) 104171

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

Research Paper

Combining land cover, animal behavior, and master plan regulations to assess landscape permeability for birds

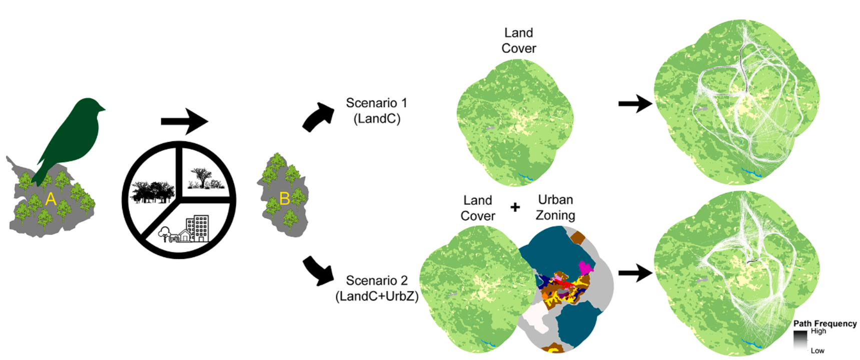
Tulaci Bhakti [a,b,*], João Carlos Pena [c,d], Bernardo Brandão Niebuhr [c,e,f,g], Juliana Sampaio [h], Fernando Figueiredo Goulart [i], Cristiano Schetini de Azevedo [a,j], Milton Cezar Ribeiro [c], Yasmine Antonini [a,j]

[a] Programa de Pós-Graduação em Ecologia de Biomas Tropicais, Laboratório de Biodiversidade, Instituto de Ciências Exatas e Biológicas, Universidade Federal de Ouro Preto, Rua Quatro, 786, 35400-000 Ouro Preto, Brazil
[b] Programa de Pós-Graduação em Ecologia Conservação e Manejo de Vida Silvestre, Laboratório de Ornitologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Avenida Presidente Antônio Carlos, 6627, 31270-901 Belo Horizonte, Brazil
[c] Spatial Ecology and Conservation Lab (LEEC), Department of Biodiversity, Instituto de Biociências, Universidade Estadual Paulista-UNESP, Rio Claro, Brazil
[d] Red de Ambiente y Sustentabilidad, Instituto de Ecología, A.C., Xalapa, Mexico
[e] Centro Nacional de Pesquisa e Conservação de Mamíferos Carnívoros, Instituto Chico Mendes de Conservação da Biodiversidade, Atibaia, Brazil
[f] Instituto Pró-Carnívoros, Atibaia, Brazil
[g] Swedish University of Agricultural Sciences, Uppsala, Sweden
[h] Instituto Federal de Educação, Ciência e Tecnologia de Minas Gerais, Campus Congonhas, Congonhas, Brazil
[i] Centro de Desenvolvimento Sustentável, Universidade de Brasília. Campus Darcy Ribeiro. Brasília, Brazil
[j] Universidade Federal de Ouro Preto, Departamento de Biodiversidade Evolução e Meio Ambiente, Instituto de Ciências Exatas e Biológicas, Ouro Preto, Brazil

HIGHLIGHTS

- We modeled least cost paths to assess landscape permeability of a South American city.
- We compared urban landscape permeability between two landscape resistance scenarios.
- The scenarios considered only biotic data and also included master plan regulations.
- Adding master plan regulations leads to more tortuous paths and higher paths' overlap.
- Master plan regulations are good predictors to assess urban landscape permeability.

GRAPHICAL ABSTRACT



ARTICLE INFO

Keywords:
Urban ecology
Urban planning
Understory birds

ABSTRACT

Cities are new and expanding ecosystems that harbor a variety of habitats with different degrees of permeability to the local fauna. However, the assessment of urban landscape permeability usually considers biotic and abiotic conditions, with sociopolitical dimensions (e.g., zoning regulations) – also important in shaping urban biodiversity – being underrepresented in the formulation of resistance surfaces. Our main goal was to compare urban landscape permeability for birds between two scenarios: one that considers only species' responses to land cover

* Corresponding author at: Present address: Programa de Pós-Graduação em Ecologia Conservação e Manejo de Vida Silvestre, Laboratório de Ornitologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Avenida Presidente Antônio Carlos, 6627, 31270-901 Belo Horizonte, Brazil.
E-mail address: tulaci.faria.duarte@gmail.com (T. Bhakti).

https://doi.org/10.1016/j.landurbplan.2021.104171
Received 11 February 2020; Received in revised form 20 May 2021; Accepted 13 June 2021
Available online 19 June 2021

Functional connectivity
South American city

for the formulation of resistance surfaces (LandC), and another that incorporates how birds would respond to different levels of occupation (i.e., amount of permeable area and maximum building height per individual lot) given the urban zoning regulations defined by the city's master plan (LandC + UrbZ). We used the software LSCorridors to simulate Multiple Least Cost Corridors (MLCC) for five forest bird species. We hypothesized that incorporating master plan regulations would better describe the variation on landscape resistance through the urban landscape. The simulations resulted in different MLCC among species and between scenarios, highlighted by differences in landscape permeability. As expected, simulations for scenario LandC resulted in more options for straighter paths than simulations for scenario LandC + UrbZ. Our results demonstrate the potential influences of sociopolitical aspects on landscape permeability modelling. Within cities, species movements are influenced not only by behavioral and environmental characteristics, but also by the urban landscape that was shaped by planning and management decisions throughout a city's history. Therefore, we emphasize that sociopolitical dimensions must be considered when assessing urban landscape permeability.

1. Introduction

Urban expansion profoundly modifies the composition and configuration of the landscapes, thus severely impacting biodiversity (Aronson et al., 2014). This process replaces natural areas such as forests and wetlands with human structures, leading to the loss and fragmentation of native habitats (Grimm et al., 2008) and to shifts in species composition and trophic interactions (Faeth, Warren, Shochat, & Marussich, 2005). Consequently, cities have become new and expanding ecosystems formed from a variety of natural and anthropogenic habitat types (Kowarik, 2011), where a new set of species interact, modulating ecological processes (e.g., pollination and seed dispersal; Faeth et al., 2005). In urban ecology, the study of the relationships between urbanization and ecological processes can improve our understanding of the functioning of cities in order to maintain biodiversity, as well as the benefits of human-nature interactions within the cities (e.g. increase in health and cognitive abilities, psychological well-being, increase in spiritual and social connections: Keniger, Gaston, Irvine, & Fuller, 2013). One of the processes altered in urban areas is the movement of organisms through urban landscapes, which is inherently linked to the landscape permeability, i.e., the opportunities in the landscape for organisms to move both within and between habitat patches. Landscape permeability can be promoted by the adequate management and planning of urban vegetation, for example, by enhancing quality, diversity and the density of street trees (Fernández-Juricic & Jokimäki, 2001; Pena, Martello, et al., 2017; Wood & Esaian, 2020). In an impermeable landscape, animals are prevented to find new foraging, shelter and reproduction sites, which ultimately increases competition and decreases survival (Suter, Bollmann, & Holderegger, 2007). Thus, the maintenance of landscape permeability in cities can enhance conservation opportunities, maintain important ecological services, such as pollination and seed dispersal, and increase human-nature interactions, ameliorating the overall well-being of both human and non-human populations.

Landscape permeability depends on an interplay between the spatial arrangement of the different land-cover types, such as houses, buildings, streets, and natural areas, and the ability of organisms to cross these different areas (Tremblay & St. Clair, 2009). Intraspecific factors such as mortality risk, energy costs or avoidance behavior determine the degree of permeability or resistance that each urban land cover type imposes on a given organism (Etherington & Penelope Holland, 2013). Therefore, understanding urban landscape permeability is of utmost importance for identifying the best paths or corridors for the movement of different species, thus contributing to the design of urban ecological corridors between natural areas and urban green spaces (Horta et al., 2018; Ignatieva, Stewart, & Meurk, 2011; Lynch, 2019). The identification of the best paths is the first measure to be taken to permit species' movement between natural and urban green spaces. However, other parameters, like the size of the vegetation patches, the width of the vegetation corridors, path connectivity, the strength of the edge effect, and the impacts of noise and other types of urban pollution are important for the use and persistence of species in these paths (Hennings & Soll, 2010). Larger, wider, more connected, and less polluted corridors are generally preferred by fauna (Hennings & Soll, 2010; Kettunen, Terry, Tucker, & Jones, 2007).

The approach that has been most often used to model species' paths through different land cover types is the Least-Cost Path (LCP) modeling (Simpkins, Dennis, Etherington, & Perry, 2017). However, one of the limitations of traditional LCP is that, given a pair of habitat patches, the method generates only one possible corridor, which is limited for many purposes. To bypass this limitation, a set of multiple path/corridor methods or tools has been developed, such as LORACS (Pinto & Keitt, 2009) and LSCorridors (Ribeiro et al., 2017). These methods allow the user to identify a set of most permeable routes, considering landscape resistance, the functional distance between pairs of sources and targets (e.g., habitat patches where species occur), and the assumption that animals have enough knowledge of the landscape to determine the multiple paths with the fewest risks and energetic costs (Ribeiro et al., 2017).

In this context, birds are frequently used as a model group for modeling connectivity and assessing the effects of urbanization on landscape permeability (LaPoint et al., 2015; Tremblay & St. Clair, 2011). One reason for this is that birds have a wide variety of responses to different types of urban land cover that can or cannot provide resources, be associated with different types of urban pollution, or represent physical barriers that hinder the movement of birds (Marzluff, 2017; Pena, Martello, et al., 2017). For example, landscape structure (e.g. types and the size of vegetation patches and the proximity to larger and continuous habitat fragments) can influence the ability of frugivorous birds to move through urban landscapes (Horta et al., 2018). Cities are shaped by sociopolitical decisions that can affect landscape permeability for birds by, for instance, influencing the diversity and density of street trees according to neighborhood income (Wood & Esaian, 2020). The streetscape can represent a barrier for the movement of bird species due to motorized traffic, the width of streets, and the level of noise exposure (Pena, Martello, et al., 2017; Tremblay & St. Clair, 2009). Furthermore, bird-window collisions are considered a threat for the survivability of birds in urban landscapes (Loss, Will, Loss, & Marra, 2014).

Cities are highly complex and dynamic ecosystems, and their constant changes are determined by sociopolitical influences (Canedoli, Manenti, & Padoa-Schioppa, 2018; Ramalho & Hobbs, 2012). Economic and political interests shape urban expansion, which may lead to the development of areas without adequate planning, particularly in underdeveloped tropical countries (Bhakti, Pena, & Rodrigues, 2020; Pena, Assis, et al., 2017). Ideally, human occupation should consider the ecosystem's carrying capacity, hence reducing environmental degradation and maintaining ecosystem stability (Aguilar, 2008; Braga, 2001). Although the conservation of vegetation may be considered important in urban conservation, little importance is given to integral biodiversity maintenance, which may be related to inadequate or a lack of knowledge of stakeholders about ecosystem function and ecological processes (Sandström, Angelstam, & Khakee, 2006).

Biodiversity and ecological processes are essential for the maintenance of human well-being in cities, and therefore need to be considered as an essential element in planning and defining strategies for urban management (Sandström et al., 2006; Wu, 2014). One of the tools used to define guidelines and directives for appropriate occupation of the landscape is the formulation of urban master plans (Tian & Wang, 2016; City of Portland, 2012; Ouro Preto, 2006). Master plans define zones with multiple levels of urban restrictions, allowing specific land-use types, which have the objective of reducing socio-environmental impacts. Urban master plans have emerged as a strategy to meet the demands of Agenda 21, which defined directives for the sustainable development of the signatory countries (United Nations, 1992). Master plans are formulated according to the peculiarities of each city (geology, biodiversity, economic activities, etc.), and must be periodically revised (Brasil, 2001). Therefore, master plans can help cities to reconcile urban development with the maintenance of an ecologically functioning ecosystem (Pena, Assis, et al., 2017). Nevertheless, master plans rarely take into consideration the landscape permeability to animal movement and functional connectivity.

Few studies have focused on modeling connectivity and assessing the effects of urbanization on landscape connectivity and permeability, despite the growing interest in this topic (LaPoint et al., 2015). This is mostly true for tropical and developing countries, where urban landscapes are rapidly expanding (LaPoint et al., 2015; United Nations, 2018). Given this context, we emphasize that adequate planning and management decisions are only possible through an interdisciplinary process (Aronson et al., 2017; LaPoint et al., 2015). Ideally, one must consider not only biotic (e.g., species biology and natural history) and abiotic (*e.g.*, land use, landscape metrics) parameters when modeling landscape permeability, but also sociopolitical and economic aspects need to be combined to define functionally efficient urban ecological corridors. This is related to the fact that cities' sociopolitical and economic dimensions also modulate environmental conditions and, consequently, influence the distribution and diversity of organisms throughout urban landscapes (Leong, Dunn, & Trautwein, 2018; Wood & Esaian, 2020). In this investigation, we fill this gap by proposing a framework for urban permeability modeling, which integrates land cover, animal behavior, and the sociopolitical and economic dimensions of cities, translated into master plans and zoning regulations. This process allows us to assess the potential effects of urban expansion and to plan cities that are more sustainable and ecologically functional for biodiversity, which in turn may also benefit the urban human population. Our goal here is to exemplify this approach by comparing landscape permeability between two scenarios: (1) one that considers only species' responses to land cover, and (2) another that also incorporates how species would respond to different levels of occupation given the master plan regulations (proportion of impermeable area and the maximum building height within individual lots). We modeled landscape functional connectivity through the simulation of Multiple Least Cost Corridors (MLCCs) (Ribeiro et al., 2017; Schneiberg et al., 2020) for five forest-dependent bird species. These birds had different levels of sensitivity to urbanization, considering both the species' characteristics and the urban planning regulations. We expected a greater influence of landscape resistance values on the MLCCs simulated for the most sensitive species, than on the MLCCs simulated for the least sensitive species. Thus, for the most sensitive species, we expected that the simulated paths would avoid regions of low landscape permeability, presenting less straightness, higher accumulated cost, a reduced number of path options and higher overlap, in comparison with the least sensitive species. Since incorporating urban master plan regulations would define a larger range of resistance values for different areas of the landscape, particularly regarding the constructed areas, we also expected to find different MLCCs between the two scenarios. Consequently, the MLCCs generated by the scenario with the master plan regulations would present less straightness, higher accumulated corridor costs and greater overlap compared to the MLCCs simulated for the scenario based only on land cover.

2. Material and methods

2.1. Study area

Ouro Preto (Minas Gerais, Brazil) is a small-sized city (ca. 75,000 inhabitants), founded in 1711 during the Brazilian Gold Rush (Fig. 1). The city is considered a World Heritage Site by UNESCO because of its rich and well-preserved historic core (UNESCO, 1980); the city has since expanded somewhat around this center. Urban occupation within the oldest part of the city followed the Portuguese colonial architecture style, in which houses were built close to the curb, with no spaces between them (Castriota, 2009). Almost no importance was given to maintaining urban forests, and there is currently almost no space available for street trees in that part of the city. Within the historic center, the largest vegetation block is the Horto dos Contos Municipal Park (hereafter Horto dos Contos), a 6-ha botanical garden founded in 1799 (Pereira, 2015), which is composed of a mixture of managed and unmanaged native and exotic vegetation. As Ouro Preto expanded, additional green areas were preserved within its urban perimeter, especially native vegetation patches in areas with steep slopes and near watercourses and springs. In the urban and rural parts of the municipality, there are patches of native vegetation composed of mosaics of forest and grasslands, which is typical of the transition zone between the Atlantic Forest and Cerrado biomes, both considered biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Some of these areas are conservation units larger than 100 ha (Fig. 1).

To model MLCC through the Ouro Preto landscape, we selected five forest patches as sources and targets for animal movement simulations. Four patches were selected because they are well distributed throughout the peri-urban region, in different positions with respect to the urban perimeter: Itacolomi State Park (hereafter Itacolomi), Tripuí Ecological Station (Tripui), Brigida farm (Brigida), and Andorinhas Environmental Protected Area (Andorinhas) (Fig. 1). The Horto dos Contos is the only forest patch located within the urban perimeter and was selected to assess its importance in acting as a stepping stone, thus connecting habitat patches in the peri-urban region (Bhakti, Rossi, et al., 2021). All of these forest patches comprise an important network of conservation units for biodiversity conservation in the region (IEF/UFV, 2006; Silva et al., 2015).

2.2. Ouro Preto master plan and urban zoning

The Brazilian Statute of Cities is the Federal law that guides and regulates the formulation of master plans of Brazilian cities, in order to guarantee a democratic, transparent and participatory process (Brasil, 2001). Master plans divide the territory into zones – a process called macro zoning – allowing different levels of occupation, economic activities and land uses in accordance with socio-environmental and political attributes of the municipality. The macro zoning delimits, for example, environmentally sensitive areas, industrial and residential zones, and areas for urban expansion. Macro zoning also defines urban parameters and regulations according to the specific characteristics of each zone. Among the urban parameters generally used in Brazilian master plans are the Coefficient of Utilization (CoefU) and the Permeability Rate (PermR). The CoefU defines the potential for vertical construction or expansion of buildings, which can be more or less restrictive depending on the zone; the PermR defines the proportion of the soil permeability area that must be maintained in each individual lot, preferentially occupied by vegetation to enhance soil drainage and to contribute to the local climate (Belo Horizonte, 2019; Ouro Preto, 2006). Ouro Preto's macro zoning divides its urban perimeter into 11 zones, each of which allows different levels of CoefU and PermR (Table S-I in Supplementary Material I). Both CoefU and PermR indices are periodically reviewed and can therefore assume new values according to local proposals or needs. We used the latest values set by the municipality of Ouro Preto as a reference (Ouro Preto, 2006). The relationship between

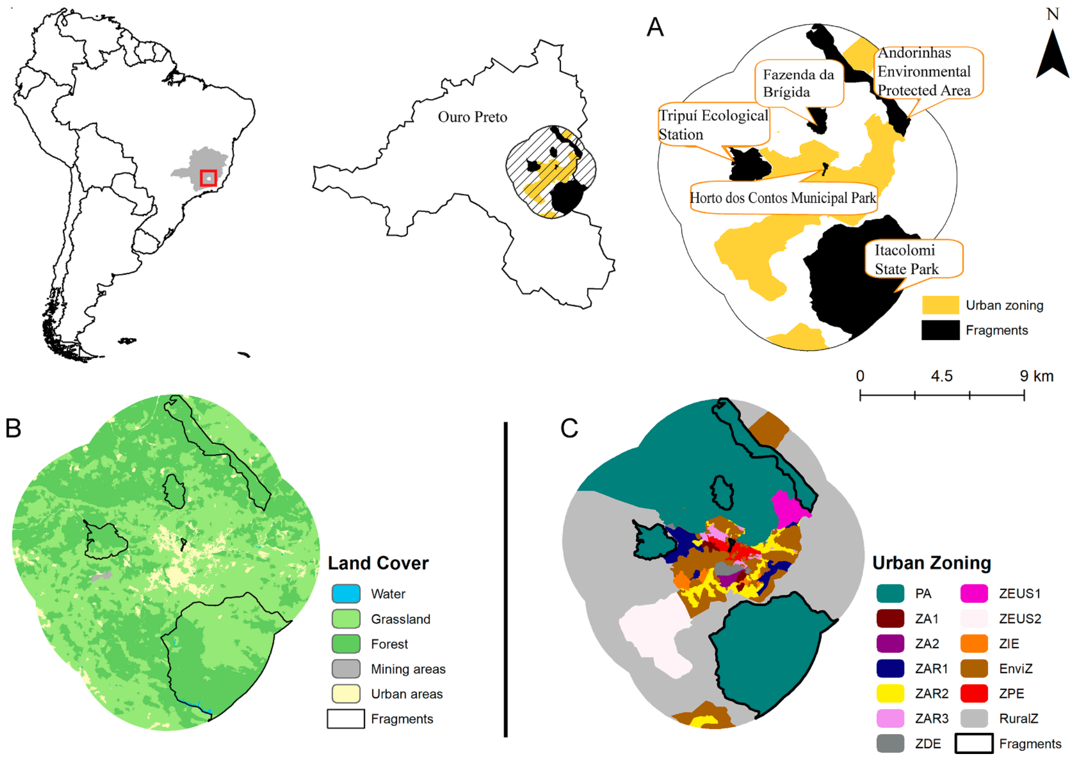


Fig. 1. Study area in the municipality of Ouro Preto, Minas Gerais, Brazil. A - Urban area delimited by the Master Plan (yellow) and forest fragments used for the simulations (Conservation Units, black). B – Land cover map of the study area. C - Map with the urban zones determined by the Ouro Preto Master Plan, with the different types of existing zones, represented by the zone code (for the complete information about the zone codes see Table S-I in Supplementary material I). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

these indices is a key point in simulations for connectivity, as they can indicate how much some zones can influence local biodiversity by hindering an organism's ability to move through the landscape (e.g. amount of available habitat, height of buildings). Since the city's macro zoning did not include the *peri*-urban and rural areas of the Ouro Preto territory, we added two classes to it: Conservation Units, which encompass protected areas (PA); and the Rural Zone (RuralZ), which encompasses the portion of our study area not occupied by urban zones or conservation units (Fig. 1, Table S-I in Supplementary Material I).

2.3. Bird species

For modeling MLCCs, we selected five forest-dependent birds among ten Atlantic forest endemic species recorded in 13 forest patches distributed throughout Ouro Preto landscape (Bhakti, Goulart, Azevedo, & Antonini, 2018b, Fig. S-I in Supplementary Material II). In each of these patches, bird sampling was performed using playback from January to April 2016 (Bhakti et al., 2018b). Four species are understory insectivorous birds (Sick, 1997): White-eyed Foliage-gleaner *Automolus leucophthalmus*, Rufous-breasted Leaftosser *Sclerurus scansor*, Lesser Woodcreeper *Xiphorhynchus fuscus*, and White-shouldered Fire-eye *Pyriglena leucoptera*. The fifth species is the Swallow-tailed Manakin *Chiroxiphia caudata*, a frugivorous species that forages in the intermediate strata of forest patches (Uezu, Metzger, & Vielliard, 2005). The bird species were classified as to their sensitivity to human disturbances, according to published reports (based on Stotz et al., 1996 and locally adapted by Bhakti et al., 2018b): highly sensitive (*A. leucophthalmus* and *S. scansor*), moderately sensitive (*X. fuscus*), and least sensitive (*C. caudata* and *P. leucoptera*). These levels of sensitivity are related to the bird species' dependence on arboreal vegetation structures and the little capacity to move through other vegetation types (Bradfer-Lawrence, Gardner, & Dent, 2018; Stratford & Stouffer, 2015). However, these species are able to move between forest fragments using small patches as stepping stones or even cross anthropogenic matrices for short distances (Boscolo, Candia-Gallardo, Awade, & Metzger, 2008; Ramos et al., 2020).

2.4. Resistance maps

To model MLCCs, it is first necessary to define a resistance surface, a raster map from a Geographic Information System – also known as a friction or permeability surface – which is used to represent the difficulty encountered by an organism in moving through the different land-cover types and landscape features within the landscape (Etherington & Penelope Holland, 2013; Zeller, McGarigal, & Whiteley, 2012). Cells with higher resistance values possess species-specific factors (such as mortality risk, energy costs or behavioral aversion) which reduce or impede the ability of a species to move (Etherington & Penelope Holland, 2013). To increase our ability to describe different aspects of landscape permeability for birds, we adopted a map algebra approach combining three different types of information. The first was the land-cover map of the study area produced by Bhakti, Goulart, Azevedo, and Antonini (2018a), which identified five main land cover classes: forest, grasslands, water, urban, and mining areas. Second, using the same RapidEye satellite image applied to produce the land-cover map (5-m resolution, WGS 1984, Transverse Mercator), we calculated the Red Edge Normalized Difference Vegetation Index (ReNDVI; values ranging from –1 to 1). This procedure allowed us to assign an estimate of vegetation quality, especially for the forest patches, through differences in photosynthetic activity which are related to the spectral signature (Sahana, Sajjad, & Ahmed, 2015) - an example which recently used vegetation indices to infer about habitat quality for terrestrial mammals is shown in Regolin et al. (2020). Finally, the third type of information was the macro zoning map of Ouro Preto, with the zones and their respective values of CoefU and PermR.

To simulate MLCCs, we produced two resistance maps for each bird species: a) scenario with *Land Cover* only – hereafter *LandC;* and b) scenario *Land Cover + Urban Zoning* – hereafter *LandC + UrbZ*. For each of the 13 forest patches in which bird surveys were conducted, we extracted the proportion of each land cover class from a 300 m radius buffer surrounding each site where the playback was made. The extent of this buffer followed Bhakti et al. (2018b), who showed that vegetation characteristics in this extent (e.g. proportion of forest cover) are related to the presence of bird species in these forest patches of Ouro Preto landscape. Thus, to assign a resistance value to each land cover class ($ResistLC_i$) for each species, we used the following equation:

$$\text{Resist } LC_i = \left(\frac{1-\text{LC}_\text{i}}{2}\right)*10 \tag{1}$$

where LC_i is the proportion occupied by the land cover class *i* within all buffers surrounding the playback sites where each species was observed (Table S-II in Supplementary Material I). By assuming that the dominant land cover class facilitates the presence of each bird species in these forest patches, and then their movement in the landscape, we assigned the lowest resistance value to the land-cover class that occupied the largest proportion within all buffers surrounding the sites in which each species occurred, and the highest resistance values to the land-cover class with less representation within the buffers. Since bird occurrence and frequency in the 13 forest patches varied between species, the resistance values attributed to each land cover class also varied between the bird species. Water and mining areas comprise a small proportion of the landscape and did not appear in the 300 m radius buffer. Thus, to produce the resistance surface, we decided to assign intermediate resistance level for water (5) and the maximum resistance value for mining areas (10) (Table S-II in Supplementary Material I). After this procedure, we produced map 1 for each species separately, in which the overall resistance values for land-cover classes ranged from 1.22 to 10 (Table S-II in Supplementary Material I).

Then, each map 1 was overlaid by the ReNDVI map and the values for the latter were subtracted from the values for the former; higher ReNDVI values are related to higher photosynthetic activity (ReNDVI values range from –1 to 1), resulting in five versions of map 2, which also represent the resistance maps for each bird species to be used to model MLCC in scenario LandC (Fig. S-II in Supplementary Material II). Using this last procedure, we were able to assign different resistance values (which are related to habitat quality) to the same land-cover class throughout the landscape. Although the ReNDVI map used in this procedure was the same for all bird species, the differences in resistance values between species in map 2 (or scenario LandC) were obtained by the different resistance values attributed to each land cover class for each species in map 1.

For the LandC + UrbZ scenario, first we defined a Construction Index (ConstI) from the zoning map of Ouro Preto, using the following equation:

$$\text{ConstI} = (\text{CoefU}/\text{PermR})*100 \tag{2}$$

the higher the values of PermR, the larger the area left to maintain soil water permeability within individual lots will be and therefore the lower the values of ConstI will be. Areas with lower ConstI values, i.e. with smaller buildings and larger permeable surface areas, would offer less resistance to the movement of bird species, since they would comprise areas with lower urbanization density, hence making it more suitable for a diverse bird community (Escobar-Ibáñez, Rueda-Hernández, & Macgregor-Fors, 2020). This process allowed us to represent, in the resistance maps, urban regions with small permeable areas, as well as different building sizes, both features which are not perceived in RapidEye imagery. Then, we multiplied the ConstI map by map 2 and obtained map 3 for each bird species, which is the resistance map for scenario LandC + UrbZ (Figure S-III in Supplementary Material II). Again, differences in resistance values between species were obtained from the different resistance values attributed to each land cover class in map 1. Although the height of the buildings may not have the same influence as a movement barrier for these bird species, all of them depend on vegetation strata to move through landscapes (Marini, 2010). Information on how urban landscape features, such as the height of buildings, influence these species are lacking. To deal with this limitation, the ability of these bird species to cross different matrix types was included in the model parameters, as described in the sections below. Finally, the resistance maps of each species and scenarios were rescaled to values between 1 and 100 to allow comparisons between scenarios.

2.5. Modeling multiple least-cost corridors

To assess landscape permeability, we used the software LSCorridors, which allows the simulation of multiple alternative paths between pairs of sources and targets, or multiple least-cost corridors (MLCCs) (Ribeiro et al., 2017; Schneiberg et al., 2020). With multiple possible solutions, it is possible to identify different areas of the landscape with higher permeability (or lower resistance) to the potential movements of each bird species, instead of only one solution that is generated by traditional LCP (Ribeiro et al., 2017). We performed 100 simulations for each pair of sources and targets for each bird species. Since Horto dos Contos is located in the middle of the remaining sources and targets, we did not perform simulations between pairs when the possible routes would cross this habitat patch. For example, we did not perform simulations between Brigida and Itacolomi, but only between Brigida and Horto dos Contos and between Horto dos Contos and Itacolomi (Fig. 1). This helped us to avoid overestimating the importance of possible routes between Horto dos Contos and the remaining habitat patches. Therefore, considering all species, all pairs of sources and targets, and both scenarios, we simulated 8000 MLCCs.

In LSCorridors, it is possible to define a scale of the influence of the surrounding landscape on the perception (and hence on the movement) of each species (Ribeiro et al., 2017). This is done by calculating summary statistics (minimum, maximum, or mean) of the landscape resistance at a scale of interest (in meters) around each pixel of the resistance surface. Therefore, the simulations not only account for the surrounding pixels but also consider the influence of the different land-cover types in the surrounding landscape perceived by the species. For example, for a forest specialist bird species, a pixel representing forest cover would indicate lower resistance to its movement. However, if this pixel is close to an urban area, which would be strongly avoided by the species, within a radius that represents its landscape perception, simulations may lead to other movement options to nearby pixels surrounded with less resistant land-cover types (Ribeiro et al., 2017). Ribeiro et al. (2017) proposed three approaches to test the influence of landscape on species movement. When the goal is to represent the movement of a highly sensitive species, they suggested the parameter MLmax (Measures by Landscape – maximum resistance value given a scale of influence), in which each pixel is replaced by the highest pixel value of a square of N × N pixels around it, with N being the window size that will be used to calculate the resistance of the central pixels (Ribeiro et al., 2017). This accounts for the species' avoidance of habitat areas close to highly stressful land-cover types. In line with this idea, and in order to represent the movement of a species with moderate sensitivity to human disturbances, the authors suggested the use of the method MLavg (average resistance value given a scale of influence), which would increase the number possibilities of movement. Finally, for the least sensitive species, the authors suggested the method MLmin (minimum resistance value given a scale of influence), which would facilitate species movement through the landscape since it replaces the central pixels by the lowest resistance values. Therefore, for *A. leucophthalmus* and *S. scansor*, we adopted the method MLmax; for *X. fuscus*, MLavg; and for *C. caudata* and *P. leucoptera*, MLmin. We defined the scale of influence using published reports for each bird species (Goulart, Takahashi, Rodrigues, Machado, & Soares-Filho, 2015; Marini, 2010). Since we are dealing with a highly heterogeneous landscape, we decided to use intermediate values of movement capacity as reported in the literature for different land-cover types (Table S-III in Supplementary Material I). For the sensitive species *A. leucophthalmus*, we also simulated corridors with different parameters to assess how the corridor modeling assumptions affect the results. We ran corridors with no landscape influence on species movement (method MP) and considering the average and maximum methods for including landscape influence (MLavg, MLmax), using different scales of influence (150 and 400 m). We selected this species for sensitivity analysis because we expected it to be one of the most affected by the inclusion of master plan regulations on corridors modeling.

After MLCC simulations in LSCorridors, an output for each species is provided in raster format, the Route Selection Frequency Index (RSFI), which represents the number of corridors that cross each pixel, considering all corridor simulations. Pixels with high RSFI indicate the most selected paths between the pairs of habitat patches, i.e. areas of the landscape that are more likely to be used as corridors according to species requirements given a resistance surface, and should therefore receive special attention (Ribeiro et al., 2017). We used the default value for the Variability parameter (2.0) in LSCorridors during the simulations, in order to include some stochasticity in the MLCC simulations (Ribeiro et al., 2017).

To identify the simulated paths through the Ouro Preto landscape with higher permeability for birds to move between the selected habitat patches, we calculated, for each scenario, the Paths Frequency – the sum of all RSFI maps, indicating the frequency with which pixels were selected by the MLCC simulations for all species combined. We also calculated the Paths' Species Rate, by transforming the RSFI maps into binary maps and then adding them. Thus, we obtained the number of species that crossed each pixel of the landscape.

2.6. Statistical analysis

Qualitative comparisons between the simulated corridors in both scenarios were performed using the RSFI maps for each species. We superimposed the output obtained for each species onto the land cover and onto the macro zoning maps, and constructed histograms to assess the frequency with which each land-cover type and urban zone was crossed by the simulated MLCC in each scenario.

To assess the differences between ecological corridors simulated in both scenarios (LandC and LandC + UrbZ), we calculated the corridor straightness. The corridor straightness index is the ratio between the Euclidean distance between the starting and ending locations of the corridor and the corridor length. Corridor straightness equals 1 if paths are straight lines and decrease as the path length increases. In addition, we calculated the relative corridor cost, which is the ratio between the total corridor cost (the sum of the resistance of all pixels crossed by the corridor) and the Euclidean distance between the starting and ending locations of the corridors. The relative corridor cost would increase as the paths become longer and pass through land cover types with higher resistance. We compared the magnitude of the straightness and relative cost values between species and scenarios (effect sizes), but did not perform statistical tests, as these are not appropriate for simulation studies (White, Rassweiler, Samhouri, Stier, & White, 2014).

Finally, to assess the spatial congruence of MLCCs, we quantified the overlap between the corridors modeled in the two scenarios, with land cover only (LandC) and including urban zoning (LandC + UrbZ), for each species. We also quantified the spatial congruence of corridors between pairs of species in the two scenarios. To do so, we first transformed the RSFI maps into maps of probability of movement by dividing them by the sum of all pixels, so that the probability of using any pixel in the landscape equals 1. Then, we calculated the overlap of corridors between scenarios or species using:

$$overlap(p_1, p_2) = \iint_{\Omega} min[p_1(x, y), p_2(x, y)]dxdy, \tag{3}$$

where p_1 and p_2 are the maps of probability of movement (in the two scenarios for a single species or for two species in a given scenario), and Ω is the study area. Then, the overlap accounts not only for the spatial congruence between corridors, but also for the number of routes that cross the same areas. More details on the calculation of the overlap are presented in Supplementary Material III.

3. Results

The simulations resulted in different MLCC between species – especially when considering levels of sensitivity – and between scenarios (Fig. 2, Fig. S-III in Supplementary Material II). Overall, the paths for highly sensitive species mostly crossed areas comprising forest cover; the paths were even more apparent in these forest areas and less present in the urbanized area when the urban zoning (scenario LandC + UrbZ) was included. In general, when comparing the two scenarios, multiple paths showed higher or lower overlap in different areas of the city, depending on the spatial configuration of the surrounding landscape (Fig. 2). Moreover, the paths for highly sensitive species showed low overlap when compared between scenarios LandC and LandC + UrbZ (overlap = 0.09 for *A. leucophthalmus* and 0.10 for *S. scansor*) indicating a low spatial congruence (Fig. 2). For least sensitive species, the simulated paths showed only small changes in the frequency of use of the different land-cover types (Figs. 2 and 4, Fig. S-III in Supplementary Material II) and showed higher overlap in the paths simulated under LandC and LandC + UrbZ (overlap = 0.24 for *C. caudata* and 0.15 for *P. leucoptera*) (Fig. 2). In the scenario LandC + UrbZ, the overlap was higher for all species due to fewer permeable options for paths between the source and target habitat patches (Fig. 3; Tables S-IV and S-V in Supplementary Material I). For example, for *X. fuscus* (moderately sensitive species), the scenario LandC + UrbZ reduced the permeability of the urbanized area and showed higher MLCC overlap than in the scenario LandC (Fig. 2).

Considering MLCC simulated for all species, the differences in landscape permeability between scenarios can be observed in the path frequency (Fig. 3) and number of species crossing each location (Paths' Species Rate) (Fig. S-III in Supplementary Material II). In scenario LandC, several relatively straight paths suitable for all species crossed the urbanized area (Fig. 3, Fig. S-III in Supplementary Material II). As expected, in scenario LandC + UrbZ, a smaller set of routes is crossed by several species (higher values of paths' frequency) within the urbanized area, indicating the reduction in the overall landscape permeability (Fig. 4), and therefore in the options for suitable routes between habitat patches (Fig. 3). This is followed by a reduction in the overlap between paths modeled for each species (Fig. 3, Tables S-IV and S-V in Supplementary Material I). This is evident for highly sensitive species, for which MLCC avoided the urbanized area, generating less straight paths, which preferentially crossed forest vegetation patches (Figs. 1 and 2) and herbaceous cover (Figs. 3 and 4) to move through the landscape.

An assessment of the frequency with which each land cover and urban zone was crossed during MLCC simulations revealed the differences in landscape permeability (Fig. 4). When considering urban zoning regulations (scenario LandC + UrbZ), the MLCC for highly and moderately sensitive species crossed fewer urban pixels and more frequently crossed herbaceous cover to move between habitat patches (Fig. 4). Surprisingly, we observed a reduction in the frequency of paths crossing forest cover (Fig. 4). Since the paths assumed avoidance of the urbanized area, they also rarely crossed urban forest vegetation patches, and passed through the herbaceous cover in the rural zone instead. For least sensitive species, we found no remarkable differences between the two scenarios in the frequency with which the paths crossed urban pixels (Fig. 4). Considering the urban zones in scenario LandC + UrbZ, all species preferentially crossed land-cover classes within conservation units (Fig. 4). Some urban zones that were crossed in scenario LandC were avoided in scenario LandC + UrbZ, especially by highly sensitive species (Figs. 2 and 4). These species crossed fewer Environmental

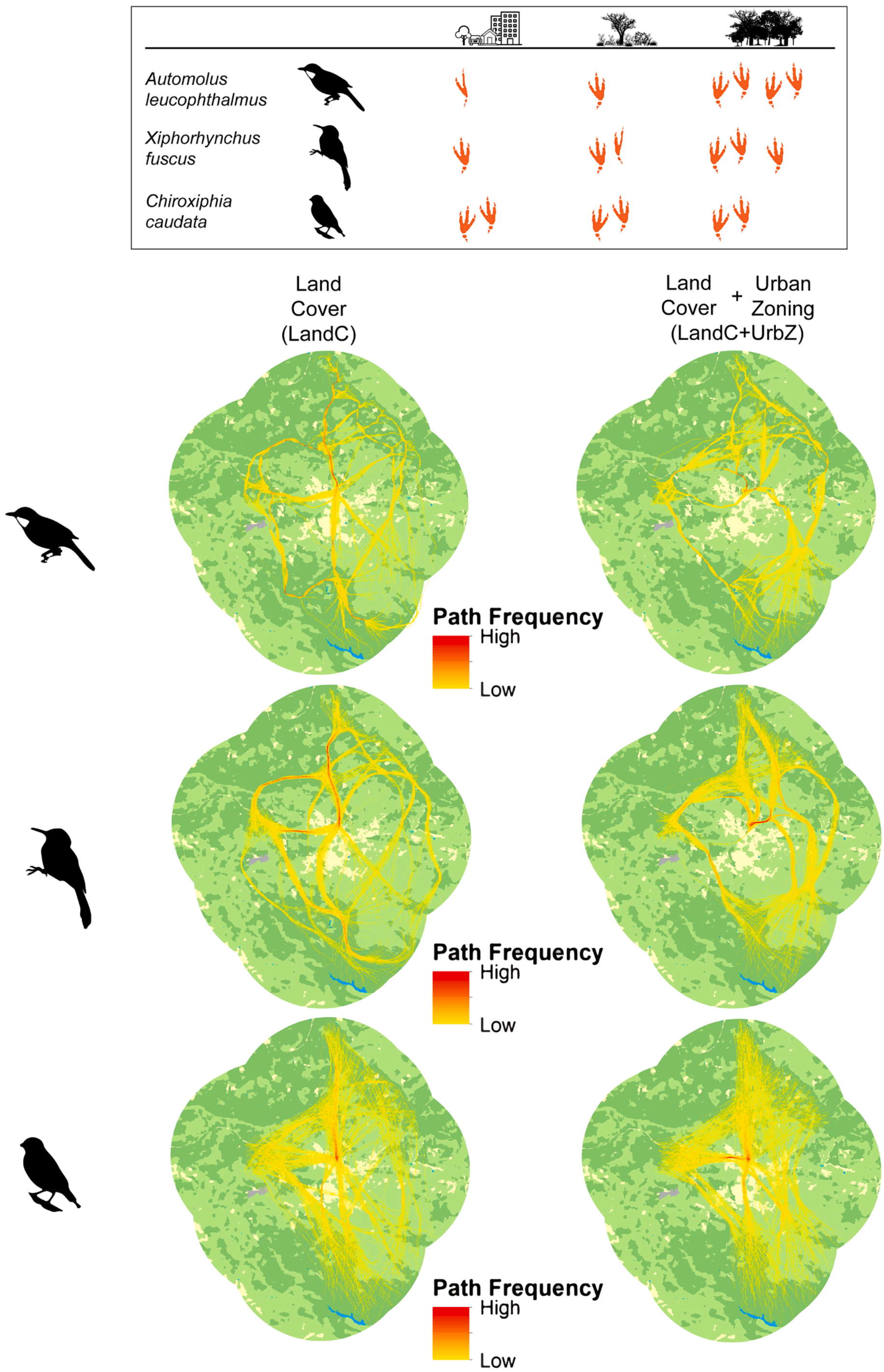


Fig. 2. Multiple least-cost corridors (MLCC) simulated for the two scenarios, Land Cover (LandC) and Land Cover + Urban Zoning (LandC + UrbZ), using as an example three bird species with different levels of sensitivity and estimated movement in the landscape. These species are, from higher to lower sensitivity to habitat disturbance (and from top to bottom): *Automolus leucophthalmus*, *Xiphorhynchus fuscus* and *Chiroxiphia caudata*. The table on the top presents three major possible land covers for the movement of birds in the study area: urban areas, grassland vegetation, and forests. The landscape permeability of each land cover type is represented by the number of *bird feet*.

Protected Zones within the urban area (EnviZ), avoiding urban zones and preferentially crossing the rural area (RuralZ) (Fig. 4).

As expected, MLCCs simulated in scenario LandC were generally straighter than those simulated in scenario LandC + UrbZ, with remarkable differences for *X. fuscus* and *P. leucoptera* (Fig. 5). In scenario LandC, highly sensitive species presented the least straight paths, compared to moderately and least sensitive species (Fig. 5). The two highly sensitive species and the least sensitive species *C. caudata* showed very small differences in average straightness between scenarios (the straightness index varied less than 1%). On the other hand, for the moderately sensitive species and the least sensitive *P. leucoptera*, the corridor average straightness decreased by 8% in the scenario LandC + UrbZ, and were even lower than the straightness of the sensitive species corridors (Fig. 5). Considering the relative corridor cost, the result was different from what we had expected: the cost was lower in scenario LandC + UrbZ than in scenario LandC (Fig. S-IV in Supplementary Material II). In the LandC + UrbZ scenario, relative corridor cost was about 80% lower for the sensitive species, 64–68% for the moderately and one of the least sensitive species (*P. leucoptera*), and 50% the other least sensitive species, *C. caudata*.

As for the assessment of model assumptions for the sensitive species *A. leucophthalmus*, the simulation methods highly affected the corridor trajectories and their straightness (Figs. S-V and S-VI in Supplementary Material II). When no landscape influence was considered (method MP),

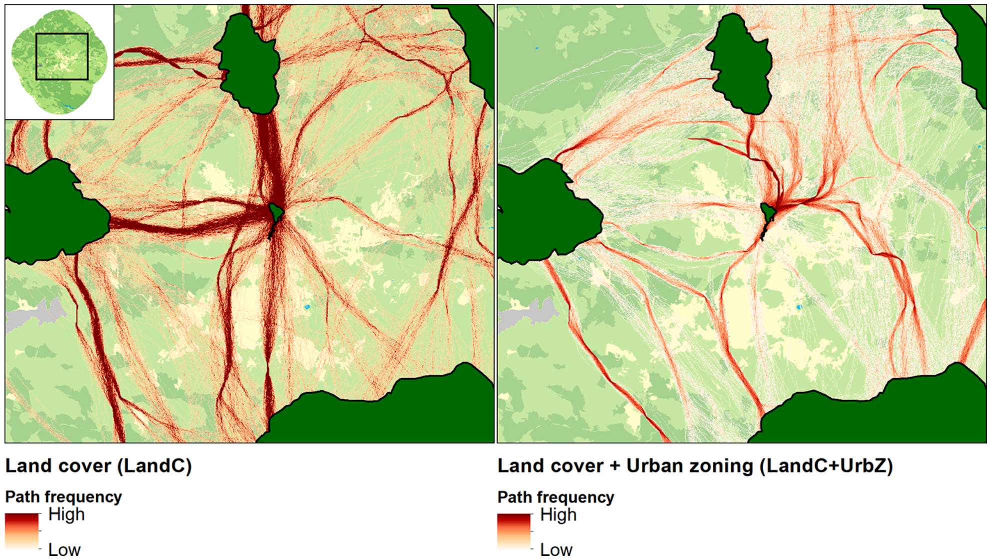


Fig. 3. Paths' frequency analysis considering the MLCC simulations of the five bird species for the two scenarios: Land Cover (LandC) and Land Cover + Urban Zoning (LandC + UrbZ).

the corridors continued passing through the urban area, even in the LandC + UrbZ scenario, contrary to our main findings (Fig. S-V in Supplementary Material II). On the other hand, as the size of the entire physical area used for analysis increased (when we applied MLavg and MLmax methods using the scales of landscape influence of 150 and 400 m), the corridors rarely crossed the urban area and their straightness decreased in LandC + UrbZ, compared to LandC (Fig. S-V in Supplementary Material II). While the straightness showed no change between scenarios at the scale of 150 m of landscape influence, it decreased by 2 and 9% in the LandC + UrbZ scenario for the MLavg and MLmax methods, at the scale of 400 m (Fig. S-VI in Supplementary Material II). The results for the relative corridor cost did not change qualitatively with the simulation parameters (Fig. S-VII in Supplementary Material II).

4. Discussion

We demonstrated that combining species biological data for individual species, land cover, and master plan regulations can influence landscape permeability modeling and, therefore, estimates of functional connectivity. When considering the construction index (ConstI) in scenario LandC + UrbZ, most of the simulated MLCCs avoided urbanized areas and were spread through the rural and peri-urban regions. By including the height of buildings [which can be considered a mortality risk factor for birds due to window collisions (Loss et al., 2014)] and the proportion of permeable surface [which are related to the degree of urbanization intensity, which affect urban bird communities (Escobar-Ibáñez et al., 2020)] we described a greater number of resistance classes. Thus, scenario LandC + UrbZ allowed us to identify areas in the Ouro Preto landscape that would be more permeable routes for the movement of bird species. In this scenario, the few MLCCs that crossed the urban area preferentially indicated routes through forest vegetation patches, leading to lower straightness and overlapping paths. This result highlights the importance of Horto dos Contos as a stepping-stone or connecting hub between peri-urban and rural habitat patches, reinforcing previous findings that this conservation unit is fundamental for conserving biodiversity within Ouro Preto's urban area (Bhakti et al., 2021). Furthermore, patches of herbaceous vegetation, located in the rural area and in conservation units, proved to be important for landscape permeability when considering the different resistances of the urbanized area. Therefore, master plan regulations can be considered an appropriate tool when assessing landscape permeability at the municipality level, assisting in the formulation of urban ecological corridors.

Cities are highly heterogeneous ecosystems, and the influences of urbanization on species movement may differ through the urban landscape. When considering the urban parameters in MLCCs simulations, we defined a hierarchy for different urban zones with respect to landscape permeability. On the city level, studies that modeled the Least Cost Paths have attempted to represent the variety of influences of urbanization on the simulated movement of species, by incorporating information on different human-made structures (buildings, streets, avenues) and/or habitat quality and vegetation structure (Balbi et al., 2019; Teng, Wu, Zhou, Lord, & Zheng, 2011). However, it is also important to consider this heterogeneity at the municipality level, representing that different species perceive the environment as a continuous habitat quality that reveals complex and multiple possibilities to analyze within urban landscapes. In Ouro Preto, areas with a lower construction index (ConstI) would have more vegetation in gardens and green spaces that were not identified by the resolution of our mapping process. Thus, we produced a better representation of the landscape for estimation of the most appropriate simulated routes for the movement of bird species after incorporating master plan regulations.

Simulated MLCCs presented higher overlap when considering master plan regulations, which means that urbanization generally decreases possible routes for birds across urban and peri-urban areas. Also, the MLCCs simulated in scenario LandC were straighter than in scenario LandC + UrbZ. This is related to the wider variety of resistances of the land cover classes, thus leading to lower relative resistance values of the most permeable classes – forest and herbaceous vegetation – especially within rural areas and conservation units. Consequently, the simulated paths (especially for highly sensitive species) rarely crossed pixels related to urban cover. Most of the paths circled around the urbanized area, and those paths that crossed the city passed through the Horto dos Contos and other urban vegetation patches, indicating their importance for maintaining landscape permeability. Thus, these forest patches can be considered priority conservation areas that can be used, for example, to design urban ecological corridors.

Beyond that, we can also infer the influence of changes on landscape permeability by assessing the variation of MLCC in areas currently covered by arboreal and herbaceous vegetation and in which human occupation is allowed. It is also possible to model the potential influences of proposed changes in urban parameters on landscape permeability. Therefore, the use of ConstI has great potential for

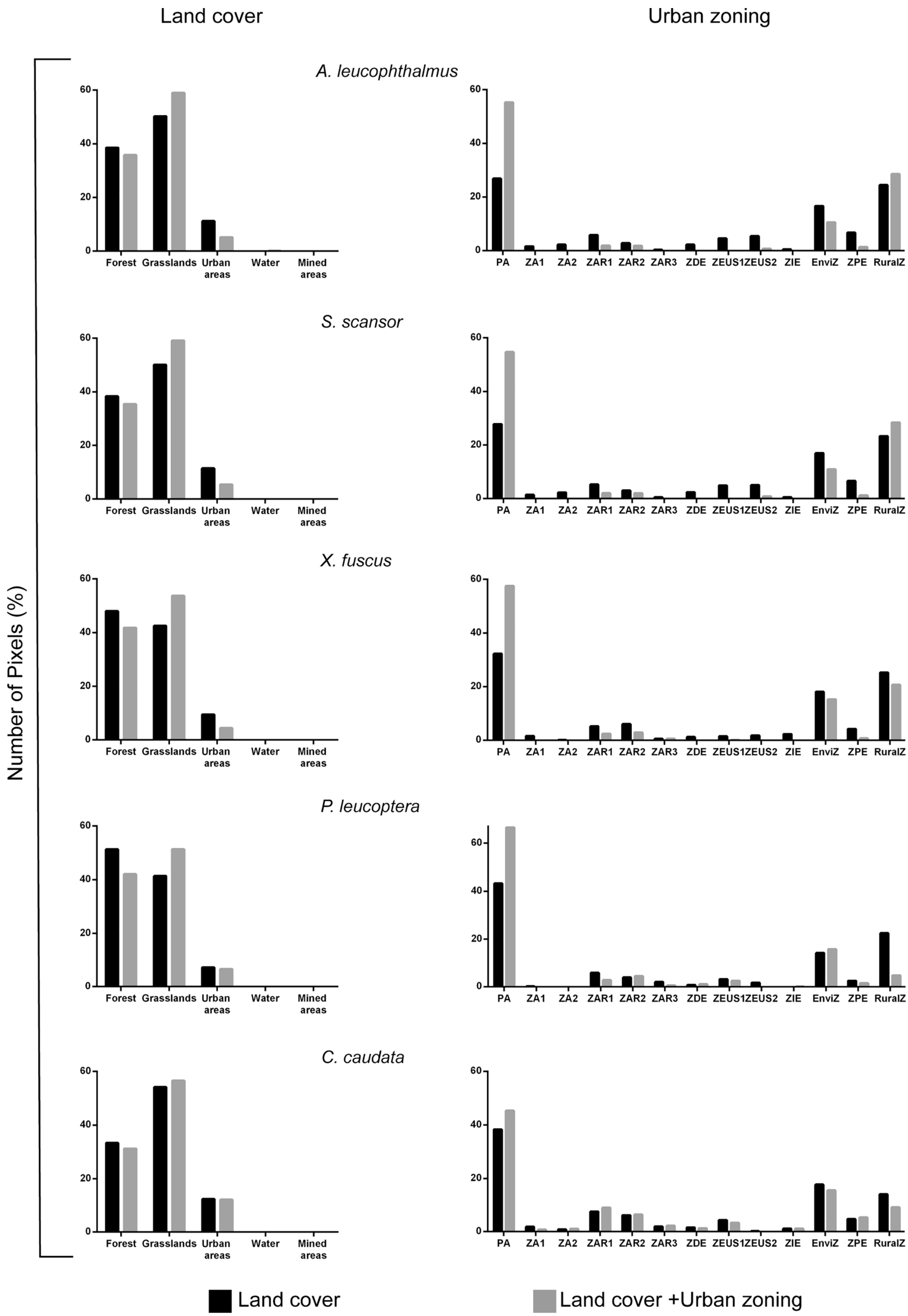


Fig. 4. Frequency of pixels crossed by the MLCC simulations for each bird species. The first column presents the frequency of pixels of each land cover type crossed by the simulated MLCC in both the Land Cover (LandC, black) and the Land Cover + Urban Zoning (LandC + UrbZ, gray) scenarios. The second column presents the frequency of pixels of each urban zoning category crossed by the simulated MLCC in both scenarios (for the complete information about the zone codes see Table S-I in Supplementary material I).

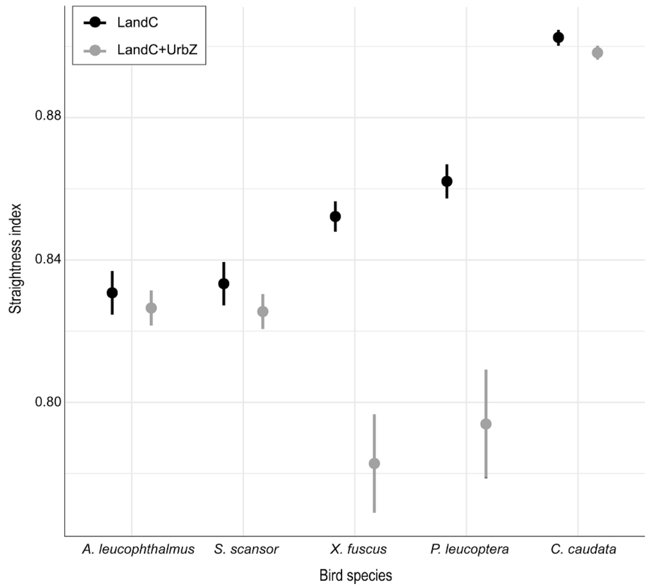


Fig. 5. Straightness index (average and 95% confidence interval) of the simulated MLCC for each bird species in both scenarios, Land Cover (LandC) and Land Cover + Urban Zoning (LandC + UrbZ).

measuring current landscape permeability, and as a tool to assess the consequences of urban expansion for landscape permeability. Future studies should focus on understanding *in situ* the movement of bird species through Ouro Preto's landscape and whether and how regions under different master plan regulations would influence the movement of bird species.

Although the studied bird species preferentially occupy forest vegetation types (Pinto & Keitt, 2009), some forest bird species may be adapted to move through grasslands and herbaceous vegetation between forest fragments in naturally patchy landscapes (Marini, 2010). This characteristic is especially important in landscapes composed of a mosaic of different vegetation types (Neuschulz, Brown, & Farwig, 2013), as in the transition zone between the Cerrado and Atlantic Forest biomes where Ouro Preto is located. In our study, the simulations indicated not only the potential of birds to use the herbaceous vegetation as routes between forest patches, but that these areas may be alternatives to cross urbanized regions. These results have the potential to guide the adequate delimitation of regions for urban expansion, reducing the negative influences of urban expansion on landscape permeability.

Selecting the appropriate set of species, i.e. with different levels of sensitivity to anthropogenic disturbances, it is important to produce more accurate models for MLCC simulations (Groves et al., 2002; Ribeiro et al., 2017). This process led to different MLCC results between species and scenarios in our study. The incorporation of master plan regulations increased the resistance of the urbanized area, especially for highly sensitive species, for which only a few simulated paths crossed this area. On the other hand, simulations for the least sensitive species produced straighter corridors. Even with differences between simulated MLCCs, our analysis identified the best possible routes that included all bird species, with different requirements for habitat quality. The results from the path-frequency and path species rate analyses can be used to indicate forest patches for the maintenance of urban landscape permeability and potential ecological corridors between peri-urban and rural habitat patches. This process highlighted the importance of small habitat patches and green spaces for biodiversity conservation within cities (Amaya-Espinel, Hostetler, Henríquez, & Bonacic, 2019), especially close to the urban fringe (Bhakti, Pena, et al., 2020). In our study, these habitat patches may represent convergence areas and stepping-stones through which species access the urban perimeter. Some of these areas are classified as Environmental Protected Zones within the urban area (EnviZ) in the Ouro Preto Master Plan and are conserved due to their importance for soil stability (Ouro Preto, 2006). Here, we highlight their additional importance for increasing landscape permeability. In scenario LandC + UrbZ, we observed that the paths crossed EnviZ areas less frequently than in scenario LandC. This is related to their isolation from other green areas, due to the high resistance of the surrounding urban land uses. Thus, increasing forest cover in urban zones located in the urban fringe may facilitate the access of bird species in the Ouro Preto urban perimeter.

The relative corridor cost was lower in scenario LandC + UrbZ than in scenario LandC, contradicting our expectations. We consider that this result was related to an artefact after we rescaled the resistance maps. To guarantee that we could compare the relative corridor costs between LandC and LandC + UrbZ, we normalized the resistance values to be in the same range [1–100] in both scenarios. Consequently, the relative resistance value decreased in scenario LandC + UrbZ instead of increasing, for many areas under different land-use classes, depending on which urban zone overlapped them. Since we are assessing differences in landscape permeability between scenarios, this is not a drawback. The routes adopted by the corridors and the differences in straightness are able to demonstrate differences between scenarios. However, we suggest that future studies using this approach should consider the relative values of each land cover class when building the resistance maps.

We demonstrated that differences in the model assumptions led to changes in the MLCC simulations (Appendix A in Ribeiro et al., 2017). The main difference arose when ignoring the influence of the landscape on animal perception (method MP), in which case the corridors continued to pass through the urban area, even after including master plan regulations in the modeling process. Since most LCP methods are based on local resistance values, ignoring potential landscape influences (Ribeiro et al., 2017), we argue that the scale of animal perception and movement should be included when defining resistance maps or in the modeling process. The scale of landscape influence also changed the routes and straightness of the corridors. Therefore, it is important to set the most biologically meaningful scales for modeling corridors for each species, taking information from the literature or from direct behavioral studies (Apfelbeck et al., 2020).

To produce resistance maps, we adopted a simple map algebra process that can be easily reproduced by urban planners with the assistance of biologists for different animal species. This method combines ecological knowledge, species characteristics, urban conditions and master plan regulations, in a procedure that is essential for a more sustainable urban development (Ahern, 2013). Furthermore, through our simulations, we highlight the importance of urban conservation units, such as the Horto dos Contos, for the maintenance of landscape permeability. Peri-urban and rural habitat patches are also essential for biodiversity conservation, providing habitats and allowing the movement of more-sensitive species (Xun, Yu, & Wang, 2017). Thus, by combining biological data and urban parameters through master plan regulations, better MLCC simulations can be produced for urban landscapes, leading to better urban planning and management decisions.

By applying our framework, we believe it is possible to:

- Define better urbanistic parameters to increase or maintain landscape permeability, such as the height of buildings (CoefU) and the proportion of the permeable surface area (PermR) in individual lots;
- Support, stimulate and guide tree planting to increase the area occupied by the urban forest when formulating cities' Master Plans. By reducing the CoefU, increasing the PermR and stimulating the use of native tree species in private gardens, several benefits can be achieved, such as the enhancement of landscape aesthetics and abiotic quality, and the reduction of surface temperature. Such practices have already been adopted in cities worldwide, including in the Minas Gerais State capital, Belo Horizonte (Belo Horizonte, 2019), Toronto - Canada (City of Toronto, 2013), Phoenix - USA

(Middel, Chhetri, & Quay, 2015), and Barcelona - Spain (City of Barcelona, 2017);

- Define forest and other vegetation patches as protected areas both within the city and at the urban fringe, allowing species to access the urban perimeter and thus, their mobility through the urban landscape;
- Define ecological corridors either for new urban developments or in the consolidated urban area. Ecological corridors can be multifunctional, i.e., they can integrate different urban land uses (e.g., gardens, squares, and streets) and bring other benefits (e.g., food security, urban mobility), while increasing urban landscape permeability for biodiversity.

5. Conclusions

We developed a framework to model MLCCs and assess urban landscape permeability at the municipality level which also considers sociopolitical characteristics through zoning and master-plan regulations. Thus, planning and management decisions can be made based not only on biotic and abiotic parameters, but also on how planning and management decisions may potentially influence species movement. In Ouro Preto, our results can guide urban expansion by defining an adequate set of urban parameters and maintaining access points and stepping-stones that allow different forest bird species to access and exploit the urban landscape. Our framework can also be applied worldwide, by every city possessing a master plan, land use maps and biodiversity data at a municipality level. A more permeable city allows an increase in human-bird encounters, which increases the sense of human well-being (Kareiva, Watts, McDonald, & Boucher, 2007; Russell et al., 2013). In other words, a more permeable urban landscape would be good for both humans and birds and should be considered by governments. Currently, more than half of the world's population lives in cities; this proportion is expected to reach 66% by 2050 (Cohen, 2003; United Nations, 2018), while this rate is already over 80% in some Latin American countries (Jaitman, 2015). Therefore, it is essential to plan the expansion of our cities using more sustainable practices (Aronson et al., 2017; Lepczyk et al., 2017). To reach this goal we need to reduce the gap between scientific knowledge and the formulation of public policies (Pena, Assis, et al., 2017). Thus, the formulation of cities' master plans, also taking into account ecological processes (such as functional connectivity), can be considered opportunities to apply the outcomes of interdisciplinary research for a more sustainable and ecologically responsible urban development.

CRediT authorship contribution statement

Tulaci Bhakti: Conceptualization, Writing - original draft. **João Carlos Pena:** Conceptualization, Writing - review & editing, Supervision. **Bernardo Brandão Niebuhr:** Writing - review & editing. **Juliana Sampaio:** Writing - review & editing. **Fernando Figueiredo Goulart:** Writing - review & editing. **Cristiano Schetini de Azevedo:** Writing - review & editing. **Milton Cezar Ribeiro:** Writing - review & editing, Supervision. **Yasmine Antonini:** Writing - review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thanks to IEF for the license for access to the protected areas (state parks) (license number 064/2015). Tulaci Bhakti received scholarships from CAPES (Brazilian Federal Agency for Support and Evaluation of Graduate Education – process # 88887.364396/2019-00) and the Student Grant Program of the Neotropical Grassland Conservancy. João Carlos Castro Pena is founded by FAPESP (grant numbers 201822215-2, 2018/00107-3). FFG received a post-doctoral scholarship from Capes – Finance code 001). MCR thanks FAPESP (processes #2013/50421-2; #2020/01779-5), CNPq (processes # 312045/2013-1; #312292/2016-3; 442147/2020-1) and PROCAD/CAPES (project # 88881.068425/2014-01) for their financial support. Yasmine Antonini is granted by CNPq (research scholarship). We would like to thank the associate editor Christopher Lepczyk and two anonymous reviewers for helpful comments on an earlier version of the paper.

Data accessibility

All the data and code used in this study is available in the Github repository https://github.com/LEEClab/ms_landscape_permeability_urban_landscapes (http://doi.org/10.5281/zenodo.4271378, Bhakti et al., 2020).

Bhakti, T.; Pena, J.C.; Niebuhr, B.B.; Sampaio, J.; Goulart, F.F.; Azevedo, C.S.; Ribeiro, M.C., and Antonini, Y. (2020). Code and Data from Bhakti et al. on landscape permeability of urban landscape (Version 1.0) [Code and data set]. Zenodo. http://doi.org/10.5281/zenodo.4271378.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2021.104171.

References

Aguilar, A. G. (2008). Peri-urbanization, illegal settlements and environmental impact in Mexico City. *Cities, 25*(3), 133–145. https://doi.org/10.1016/j.cities.2008.02.003.

Ahern, J. (2013). Urban landscape sustainability and resilience: The promise and challenges of integrating ecology with urban planning and design. *Landscape Ecology, 28*(6), 1203–1212. https://doi.org/10.1007/s10980-012-9799-z.

Amaya-Espinel, J. D., Hostetler, M., Henríquez, C., & Bonacic, C. (2019). The influence of building density on Neotropical bird communities found in small urban parks. *Landscape and Urban Planning, 190*, 103578. https://doi.org/10.1016/j.landurbplan.2019.05.009.

Apfelbeck, B., Snep, R. P. H., Hauck, T. E., Ferguson, J., Holy, M., Jakoby, C., … Weisser, W. W. (2020). Designing wildlife-inclusive cities that support human-animal co-existence. *Landscape and Urban Planning, 200*, 103817. https://doi.org/10.1016/j.landurbplan.2020.103817.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences, 281*(1780), 20133330. https://doi.org/10.1098/rspb.2013.3330.

Aronson, M. FJ., Lepczyk, C. A., Evans, K. L., Goddard, M. A., Lerman, S. B., MacIvor, J. S., … Vargo, T. (2017). Biodiversity in the city: Key challenges for urban green space management. *Frontiers in Ecology and the Environment, 15*(4), 189–196. https://doi.org/10.1002/fee.2017.15.issue-410.1002/fee.1480.

Balbi, M., Petit, E. J., Croci, S., Nabucet, J., Georges, R., Madec, L., & Ernoult, A. (2019). Ecological relevance of least cost path analysis: An easy implementation method for landscape urban planning. *Journal of Environmental Management, 244*, 61–68. https://doi.org/10.1016/j.jenvman.2019.04.124.

Belo Horizonte. (2019). Plano Diretor do Município de Belo Horizonte - Lei no 11.181/2019. Retrieved from http://portal6.pbh.gov.br/dom/iniciaEdicao.do?method=DetalheArtigo&pk=1215565.

Bhakti, T., Goulart, F., Azevedo, C. S., & Antonini, Y. (2018a). Land use classification of Ouro Preto MG/Brazil. *Mendeley data, 1*. https://doi.org/10.17632/4nc59x3v8c.1#folder-bfc6622a-1b47-442c-8942-14ff3139b68b.

Bhakti, T., Goulart, F., Azevedo, C. S., & Antonini, Y. (2018b). Does scale matter? The influence of three- level spatial scales on forest bird occurrence in a tropical landscape. *PLoS ONE, 13*(6), e0198732. https://doi.org/10.1371/journal.pone.0198732.

Bhakti, T., Pena, J. C., & Rodrigues, M. (2020). Unplanned urban growth and its potential impacts on bird species in a South American city. FLORAM, 27(2), e20190111. https://doi.org/doi.org/10.1590/2179-8087.011119.

Bhakti, T., Rossi, F., de Oliveira Mafia, P., de Almeida, E. F., Fujaco, M. A. G., & Azevedo, C. S. de (2021). Preservation of historical heritage increases bird biodiversity in urban centers. *Environment, Development and Sustainability, 23*(6), 8758–8773. https://doi.org/10.1007/s10668-020-00993-7.

Boscolo, D., Candia-Gallardo, C., Awade, M., & Metzger, J. P. (2008). Importance of interhabitat gaps and stepping-stones for lesser woodcreepers (*Xiphorhynchus fuscus*) in the Atlantic forest, Brazil. *Biotropica, 40*(3), 273–276. https://doi.org/10.1111/j.1744-7429.2008.00409.x.

Bradfer-Lawrence, T., Gardner, N., & Dent, D. H. (2018). Canopy bird assemblages are less influenced by habitat age and isolation than understory bird assemblages in Neotropical secondary forest. *Ecology and Evolution, 8*(11), 5586–5597. https://doi.org/10.1002/ece3.4086.

Braga, R. (2001). Política urbana e gestão ambiental: Considerações sobre o plano diretor e o zoneamento urbano. In P. F. de Carvalho, & R. Braga (Eds.), *Perspectivas de Gestão Ambiental em Cidades Médias* (pp. 95–109). Rio Claro: LPM-UNESP. Retrieved from http://www.redbcm.com.br/arquivos/bibliografia/política urbana e gestão ambiental.pdf.

Brasil. (2001). Estatuto da Cidade - Lei n. 10.257, de 10 de julho de 2001, que estabelece diretrizes gerais da política urbana, Câmara dos Deputados. *Coordenação de Publicações*.

Canedoli, C., Manenti, R., & Padoa-Schioppa, E. (2018). Birds biodiversity in urban and periurban forests: Environmental determinants at local and landscape scales. *Urban Ecosystems, 21*(4), 779–793. https://doi.org/10.1007/s11252-018-0757-7.

Castriota, L. B. (2009). Nas encruzilhadas do desenvolvimento: A trajetoria da preservação do patrimônio em Ouro Preto (MG). In L. B. Castriota (Ed.), Patrimônio Cultural: Conceitos, políticas, instrumentos (pp. 131–152). Belo Horizonte: IEDS: UFMG.

City of Barcelona. (2017). Master Plan for Barcelona's Trees 2017 - 2037, Àrea d'Ecologia Urbana. Ajuntament de Barcelona. Retrieved from https://ajuntament.barcelona.cat/.

City of Portland. (2012). The Portland Plan. Adopted by the Portland City Council by Resolution 36918. Retrieved from http://www.portlandonline.com/portlandplan/.

City of Toronto. Sustaining and Expanding the Urban Forest: 2013-2032 (2013). Retrieved from https://www.toronto.ca/.

Cohen, J. E. (2003). Human population: the next half century. *Science, 302*(5648), 1172–1175. https://doi.org/10.1126/science.1088665.

Escobar-Ibáñez, J. F., Rueda-Hernández, R., & Macgregor-Fors, I. (2020). The greener the better! Avian communities across a Neotropical gradient of urbanization density. *Frontiers in Ecology and Evolution, 8*, Article 500791. https://doi.org/10.3389/fevo.2020.500791.

Etherington, T. R., & Penelope Holland, E. (2013). Least-cost path length versus accumulated-cost as connectivity measures. *Landscape Ecology, 28*(7), 1223–1229. https://doi.org/10.1007/s10980-013-9880-2.

Faeth, S. H., Warren, P. S., Shochat, E., & Marussich, W. A. (2005). Trophic dynamics in urban communities. *BioScience, 55*(5), 399. https://doi.org/10.1641/0006-3568(2005)055[0399:tdiuc]2.0.co;2.

Fernández-Juricic, E., & Jokimäki, J. (2001). A habitat island approach to conserving birds in urban landscapes: Case studies from Southern and Northern Europe. *Biodiversity and Conservation, 10*(12), 2023–2043. https://doi.org/10.1023/A:1013133308987.

Goulart, F. F., Takahashi, F. S. C., Rodrigues, M., Machado, R. B., & Soares-Filho, B. (2015). Where matrix quality most matters? Using connectivity models to assess effectiveness of matrix conversion in the Atlantic Forest. *Natureza & Conservação, 13*(1), 47–53. https://doi.org/10.1016/j.ncon.2015.03.003.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. *Science, 319*(5864), 756–760. https://doi.org/10.1126/science.1150195.

Groves, C. R., Jensen, D. B., Valutis, L. L., Redford, K. H., Shaffer, M. L., Scott, J. M., … Anderson, M. G. (2002). Planning for biodiversity conservation: Putting conservation science into practice. *BioScience, 52*(6), 499–512. https://doi.org/10.1641/0006-3568(2002)052[0499:Pfbcpc]2.0.co;2.

Hennings, L., & Soll, J. (2010). *Wildlife corridors and permeability – A literature review*. Portland, OR: Metro.

Horta, M. B., Bhakti, T., Cordeiro, P. F., Carvalho-Ribeiro, S. M., Fernandes, G. W., & Goulart, F. F. (2018). Functional connectivity in urban landscapes promoted by *Ramphastos toco* (Toco Toucan) and its implications for policy making. *Urban Ecosystems, 21*(6), 1097–1111. https://doi.org/10.1007/s11252-018-0789-z.

IEF/UFV. (2006). *Zoneamento Ecológico-Econômico da Área de Proteção Ambiental Cachoeira das Andorinhas*. Viçosa, MG: Instituto Estadual de Florestas / Universidade Federal de Viçosa.

Ignatieva, M., Stewart, G. H., & Meurk, C. (2011). Planning and design of ecological networks in urban areas. *Landscape and Ecological Engineering, 7*(1), 17–25. https://doi.org/10.1007/s11355-010-0143-y.

Jaitman, L. (2015). Urban infrastructure in Latin America and the Caribbean: Public policy priorities. *Latin American Economic Review, 24*(1), 1–57. https://doi.org/10.1007/s40503-015-0027-5.

Kareiva, P., Watts, S., McDonald, R., & Boucher, T. (2007). Domesticated nature: Shaping landscapes and ecosystems for human welfare. *Science, 316*(5833), 1866–1869. https://doi.org/10.1126/science.1140170.

Keniger, L. E., Gaston, K. J., Irvine, K. N., & Fuller, R. A. (2013). What are the benefits of interacting with nature? *International Journal of Environmental Research and Public Health, 10*(3), 913–935. https://doi.org/10.3390/ijerph10030913.

Kettunen, M., Terry, A., Tucker, G., & Jones, A. (2007). Guidance on the maintenance of landscape connectivity features of major importance for wild flora and fauna. *Institute for European Environmental Policy*, 1–155.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. Environmental Pollution, 159, 1974–1983. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/21435761.

LaPoint, S., Balkenhol, N., Hale, J., Sadler, J., Ree, R., & Evans, K. (2015). Ecological connectivity research in urban areas. *Functional Ecology, 29*(7), 868–878. https://doi.org/10.1111/fec.2015.29.issue-710.1111/1365-2435.12489.

Leong, M., Dunn, R. R., & Trautwein, M. D. (2018). Biodiversity and socioeconomics in the city: A review of the luxury effect. *Biology Letters, 14*(5), 20180082. https://doi.org/10.1098/rsbl.2018.0082.

Lepczyk, C. A., SorteLa, F. A., Aronson, M. F. J., Goddard, M. A., MacGregor-Fors, I., Nilon, C. H., & Warren, P. S. (2017). Global patterns and drivers of urban bird diversity. In E. Murgui, & M. Hedblom (Eds.), *Ecology and Conservation of Birds in Urban Environments* (pp. 13–33). Springer. https://doi.org/10.1007/978-3-319-43314-1.

Loss, S. R., Will, T., Loss, S. S., & Marra, P. P. (2014). Bird–building collisions in the United States: Estimates of annual mortality and species vulnerability. *The Condor, 116*(1), 8–23. https://doi.org/10.1650/CONDOR-13-090.1.

Lynch, A. J. (2019). Creating effective urban greenways and stepping-stones. *Journal of Planning Literature, 34*(2), 131–155. https://doi.org/10.1177/0885412218798334.

Marini, M.Â. (2010). Bird movement in a fragmented Atlantic Forest landscape. *Studies on Neotropical Fauna and Environment, 45*(1), 1–10. https://doi.org/10.1080/01650521003656606.

Marzluff, J. M. (2017). A decadal review of urban ornithology and a prospectus for the future. *Ibis, 159*(1), 1–13. https://doi.org/10.1111/ibi.2017.159.issue-110.1111/ibi.12430.

Middel, A., Chhetri, N., & Quay, R. (2015). Urban forestry and cool roofs: Assessment of heat mitigation strategies in Phoenix residential neighborhoods. *Urban Forestry and Urban Greening, 14*(1), 178–186. https://doi.org/10.1016/j.ufug.2014.09.010.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853–858. https://doi.org/10.1590/2179-8087.011119.

Neuschulz, E. L., Brown, M., & Farwig, N. (2013). Frequent bird movements across a highly fragmented landscape: The role of species traits and forest matrix. *Animal Conservation, 16*(2), 170–179. https://doi.org/10.1111/acv.2013.16.issue-210.1111/j.1469-1795.2012.00582.x.

Ouro Preto. (2006). Plano Diretor do Município de Ouro Preto. Lei Complementar no 29. Prefeitura Municipal de Ouro Preto. Altered by Lei Complementar no 93 (2011).

Pena, J. C.de. C., Assis, J. C.de., Silva, R. A.da., Honda, L. K., Pagani, M. I., & Ribeiro, M. C. (2017). Beyond the mining pit: The academic role in social deliberation for participatory environmental planning. *Perspectives in Ecology and Conservation, 15*(3), 194–198. https://doi.org/10.1016/j.pecon.2017.06.006.

Pena, J. C.de. C., Martello, F., Ribeiro, M. C., Armitage, R. A., Young, R. J., Rodrigues, M., & Chapman, M. G. (2017). Street trees reduce the negative effects of urbanization on birds. *PLoS ONE, 12*(3), e0174484. https://doi.org/10.1371/journal.pone.0174484.

Pereira, M. M. (2015). Horto Botânico de Villa Rica: Algumas considerações sobre um espaço das ciências nos sertões do ouro. IV EJIHM 2015 Porto, 1–15.

Pinto, N., & Keitt, T. H. (2009). Beyond the least-cost path: Evaluating corridor redundancy using a graph-theoretic approach. *Landscape Ecology, 24*(2), 253–266. https://doi.org/10.1007/s10980-008-9303-y.

Ramalho, C. E., & Hobbs, R. J. (2012). Time for a change: Dynamic urban ecology. *Trends in Ecology and Evolution, 27*(3), 179–188. https://doi.org/10.1016/j.tree.2011.10.008.

Ramos, D. L., Pizo, M. A., Ribeiro, M. C., Cruz, R. S., Morales, J. M., & Ovaskainen, O. (2020). Forest and connectivity loss drive changes in movement behavior of bird species. *Ecography, 43*(8), 1203–1214. https://doi.org/10.1111/ecog.2020.v43.i810.1111/ecog.04888.

Regolin, A. L., Ribeiro, M. C., Martello, F., Melo, G. L., Sponchiado, J., Campanha, L. F. de. C., … Cáceres, N. C. (2020). Spatial heterogeneity and habitat configuration overcome habitat composition influences on alpha and beta mammal diversity. *Biotropica, 52*(5), 969–980. https://doi.org/10.1111/btp.v52.510.1111/btp.12800.

Ribeiro, J. W., Silveira dos Santos, J., Dodonov, P., Martello, F., Brandão Niebuhr, B., & Ribeiro, M. C. (2017). LandScape Corridors (lscorridors): A new software package for modelling ecological corridors based on landscape patterns and species requirements. *Methods in Ecology and Evolution*. https://doi.org/10.1111/2041-210X.12750.

Russell, R., Guerry, A. D., Balvanera, P., Gould, R. K., Basurto, X., Chan, K. M. A., … Tam, J. (2013). Humans and nature: How knowing and experiencing nature affect well-being. *Annual Review of Environment and Resources, 38*(1), 473–502. https://doi.org/10.1146/annurev-environ-012312-110838.

Sahana, M., Sajjad, H., & Ahmed, R. (2015). Assessing spatio-temporal health of forest cover using forest canopy density model and forest fragmentation approach in Sundarban reserve forest. *India. Modeling Earth Systems and Environment, 1*(4), 49. https://doi.org/10.1007/s40808-015-0043-0.

Sandström, U. G., Angelstam, P., & Khakee, A. (2006). Urban comprehensive planning - Identifying barriers for the maintenance of functional habitat networks. *Landscape and Urban Planning, 75*(1–2), 43–57. https://doi.org/10.1016/j.landurbplan.2004.11.016.

Schneiberg, I., Boscolo, D., Devoto, M., Marcilio-Silva, V., Dalmaso, C. A., Ribeiro, J. W., … Varassin, I. G. (2020). Urbanization homogenizes the interactions of plant-frugivore bird networks. *Urban Ecosystems, 23*(3), 457–470. https://doi.org/10.1007/s11252-020-00927-1.

Sick, H. (1997). Ornitologia Brasileira. (J. F. Pacheco, Ed.) (Terceira). Rio de Janeiro: Nova Fronteira.

Silva, A. R., Pereira, J. A. A., De Barros, D. A., Borges, L. A. C., Teixeira, M. D., & Acerbi-Jr., F. W. (2015). Avaliação da cobertura florestal na paisagem de Mata Atlântica no ano de 2010, na região de Ouro Preto - MG. *Cerne, 21*(2), 301–309. https://doi.org/10.1590/01047760201521021539.

Simpkins, C. E., Dennis, T. E., Etherington, T. R., & Perry, G. L. W. (2017). Assessing the performance of common landscape connectivity metrics using a virtual ecologist approach. *Ecological Modelling, 38*, 1–11. https://doi.org/10.1016/j.ecoinf.2016.12.005.

Stotz, D. F., Fitzpatrick, J. W., III, T. A. P., Moskovits, D. K., & (eds.) (Eds.). (1996). Neotropical birds: ecology and conservation. Chicago, USA: University of Chicago Press.

Stratford, J. A., & Stouffer, P. C. (2015). Forest fragmentation alters microhabitat availability for Neotropical terrestrial insectivorous birds. *Biological Conservation, 188*, 109–115. https://doi.org/10.1016/j.biocon.2015.01.017.
Suter, W., Bollmann, K., & Holderegger, R. (2007). Landscape permeability: From individual dispersal topopulation persistence. In K. F., W. O., & G. S. (Eds.), A Changing World. Landscape Series (Vol 8, pp. 157–174). Springer, Dordrecht: Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-4436-6_11.
Teng, M., Wu, C., Zhou, Z., Lord, E., & Zheng, Z. (2011). Multipurpose greenway planning for changing cities: A framework integrating priorities and a least-cost path model. *Landscape and Urban Planning, 103*(1), 1–14. https://doi.org/10.1016/j.landurbplan.2011.05.007.
Tian, T., & Wang, M. (2016). Shanghai Zhangjiabang urban design and landscape master plan. *Landscape Architecture Frontiers, 4*(3), 70–85.
Tremblay, M. A., & St. Clair, C. C. (2009). Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *Journal of Applied Ecology, 46*(6), 1314–1322. https://doi.org/10.1111/j.1365-2664.2009.01717.x.
Tremblay, M. A., & St. Clair, C. C. (2011). Permeability of a heterogeneous urban landscape to the movements of forest songbirds. *Journal of Applied Ecology, 48*(3), 679–688. https://doi.org/10.1111/j.1365-2664.2011.01978.x.
Uezu, A., Metzger, J. P., & Vielliard, J. M. E. (2005). Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. *Biological Conservation, 123*(4), 507–519. https://doi.org/10.1016/j.biocon.2005.01.001.
UNESCO. (1980). Historic Town of Ouro Preto. Retrieved June 2, 2020, from http://whc.unesco.org/en/list/124.
United Nations. (1992). Agenda 21. Retrieved June 2, 2020, from https://sustainabledevelopment.un.org/.
United Nations. (2018). World Urbanization Prospects: The 2018 Revision. Retrieved June 2, 2020, from https://www.un.org/development/desa/publications/2018-revision-of-world-urbanization-prospects.html.
White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C., & White, C. (2014). Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos, 123*(4), 385–388. https://doi.org/10.1111/j.1600-0706.2013.01073.x.
Wood, E. M., & Esaian, S. (2020). The importance of street trees to urban avifauna. *Ecological Applications, 30*(7), Article e02149. https://doi.org/10.1002/eap.2149.
Wu, J. (2014). Urban ecology and sustainability: The state-of-the-science and future directions. *Landscape and Urban Planning, 125*, 209–221. https://doi.org/10.1016/j.landurbplan.2014.01.018.
Xun, B., Yu, D., & Wang, X. (2017). Prioritizing habitat conservation outside protected areas in rapidly urbanizing landscapes: A patch network approach. *Landscape and Urban Planning, 157*, 532–541. https://doi.org/10.1016/j.landurbplan.2016.09.013.
Zeller, K. A., McGarigal, K., & Whiteley, A. R. (2012). Estimating landscape resistance to movement: A review. *Landscape Ecology, 27*(6), 777–797. https://doi.org/10.1007/s10980-012-9737-0.