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Stepping stones: assessing the permeability of urban greenspaces to climate-driven migration of trees

Han, Q., & Keeffe, G. (2019). Stepping stones: assessing the permeability of urban greenspaces to climate-driven migration of trees. *Smart and Sustainable Built Environment*. <https://doi.org/10.1108/SASBE-12-2018-0065>

Published in:
Smart and Sustainable Built Environment

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

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Journal:	<i>Smart and Sustainable Built Environment</i>
Manuscript ID	SASBE-12-2018-0065
Manuscript Type:	Original Research Paper
Keywords:	forest migration, landscape permeability, stepping stones, seed dispersal, climate change, landscape accessibility

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Abstract

Large-scale urbanisation has become a significant barrier to the natural migration of tree species, which is being exacerbated by accelerated climate change. Within this context, improving the permeability of urban landscapes is expected to be an effective strategy to facilitate the process of forest migration through cities. This study develops a method to assess the permeability of urban green spaces as stepping stones for forest migration, from the perspective of seed dispersal. The proposed method combines a least-cost path model and a graph theory-based approach. The least-cost path model is applied to map the potential pathways of seed dispersal at multiple spatial and temporal scales, based on which graph theory-based indices are used to quantify the accessibility of urban landscapes for seed dispersal agents. This method is demonstrated by a case study in the Greater Manchester area, UK. Eurasian jay, Eurasian siskin, coal tit and grey squirrel are selected as the main seed dispersal agents in the study area. The results provide a comparison of the landscape permeability maps generated from different seed dispersal agents and identify key areas likely to facilitate the process of forest migration. Recommendations regarding landscape management for improving permeability are also discussed.

1. Introduction

As a response to global climate change, many tree species are moving to higher latitudes or elevations with more suitable climate conditions (Hampe, 2011). However, increased urbanisation means that they will have to overcome substantial anthropogenic barriers (e.g., agricultural land, buildings, and highways), which may impede their ability to keep pace with the rapidly warming climate or even modify their migration patterns (Tomolo and Ward, 2018). Within this context, assessing and improving the permeability of urban landscapes are expected to be an effective strategy to facilitate this ecological process. Here, “permeability” refers to the capacity of a landscape to support species’ movements.

Several methods have been proposed for assessing landscape permeability. Most of them focused on specific landscape features related to habitat quality or human modification, for example, land cover type, road density, and housing density (e.g., Gray et al., 2016, Littlefield et al., 2017). Other studies estimated landscape permeability by modelling or experiments (e.g., Shimazaki et al., 2016, Gastón et al., 2016, Cline et al., 2014, Caryl et al., 2013). Additionally, Anderson et al. (2015) utilised genetic data to infer the permeability of landscape features to animal movement.

Although these methods provide spatially explicit estimates of landscape permeability, they may be less useful for the study of forest migration. On one hand, they focus on the movements of active dispersers (animals) and thus may be unsuitable for the migration of trees that depend on passive seed dispersal. Successful forest migration depends on effective seed dispersal between forest fragments, which is affected by the ways in which seed dispersal agents move and interact with the landscape (Clobert et al., 2012). Therefore, the movement of seed dispersal agents should be considered in the efforts to assess landscape permeability. It should be noted that this study mainly focuses on animal-dispersed tree species, as water- or wind-dispersed tree species can be carried for long distances and therefore have a better chance of survival (Dyer, 1995, Casper, 2010). Therefore, the term “seed dispersers” hereafter refers to animals. Since different animals may respond very differently to the landscape (Saunders et al., 1991), a consideration of their dispersal abilities is also required. On the other hand, in human-dominated environments where landscapes are highly modified and fragmented, the main function of urban green spaces is acting as a series of stepping stones (functional connections) that form dispersal pathways and transmit ecological flows, rather than providing permanent habitats (Boscolo and Metzger, 2011). In this respect, the accessibility of urban landscapes might be of great importance because it directly influences the occurrence and abundance of seed dispersers, whereas landscape features related to habitat quality or human modification might be of limited value.

Accordingly, this study proposes a method for assessing landscape permeability to forest migration based on a measure of landscape accessibility for seed dispersers, assuming that landscapes with higher accessibility might have a higher probability of seed dispersal and therefore are more permeable to the migration of trees. Since the focus of this study is on seed dispersal, the movement of seed dispersers is mainly considered; other biotic or abiotic factors such as soil type, habitat quality, plant diversity, or interspecific competition are excluded. In addition, the activities of seed dispersers at both habitat and home-range scales are analysed in this study to account for the multi-scale behaviour of frugivores. Frugivores experience their landscapes as a mosaic of patches at multiple spatial and temporal scales and make different decisions at each scale (Holling, 1992). As a result, the occurrence and abundance of seed dispersers at a given location are based on their activities at multiple scales (Boscolo and Metzger, 2009).

The proposed method combines a least-cost path (LCP) model and a graph theory-based approach. The LCP model is applied to map potential movement pathways of seed dispersers, based on which graph theory-based indices are used to quantify landscape accessibility. The Greater Manchester area, UK, is used as a case study to demonstrate this method. Eurasian jay, Eurasian siskin, coal tit and grey squirrel are selected as the main seed dispersers in the study area.

2. Method

2.1 Data

We use the 2010 topography layer in Ordnance Survey Master Map as land-cover data, which can be downloaded from Digimap (<http://digimap.edina.ac.uk/>). This vector map gives a comprehensive view of 13 land-cover types in the study area. At the same time, to compare the degree of permeability with the intensity of human modification, the greenspace layer (with detailed land use categories which captures the major aspects of human modification) in the Ordnance Survey Master Map is used to classify urban green spaces as (1) natural, with a low intensity of human modification (e.g. natural woodland); (2) semi-natural, with an intermediate intensity of human modification (e.g. camping park, cemetery, golf course, public park or garden); and (3) manmade, with a high intensity of human modification (e.g. transport, bowling green, sports facility).

According to a research by the Forestry Commission (<https://www.forestry.gov.uk/fr/infid-837f9j>), there are a number of tree species that need to migrate through Greater Manchester in this century, including European larch (*Larix decidua*), Sitka spruce (*Picea sitchensis*), sweet chestnut (*Castanea sativa*), lodgepole pine (*Pinus contorta*), Scots pine (*Pinus sylvestris*), sessile oak (*Quercus petraea*), and beech (*Fagus*). Most of them are dispersed by frugivorous birds. The acorns and nuts of lodgepole pine, sweet chestnut, sessile oak, beech, and Scots pine can be moved by Eurasian jay (*Garrulus glandarius*), while Eurasian siskin (*Spinus spinus*) and coal tit (*Periparus ater*) are the principal seed dispersers for European larch and Sitka spruce. Besides, the grey squirrel (*Sciurus carolinensis*) is also considered as a main seed disperser in the study area, given that this small mammal is highly mobile and can disperse chestnut and acorn readily through fragmented urban landscapes (Rushton et al., 1997).

Spatial records of the four seed dispersers are obtained from the UK's NBN Atlas (<https://nbnatlas.org>). For Eurasian jay and grey squirrel, their dispersal distances as well as other key parameters are obtained from the literature (see Table 1). However, for the remaining two species, a direct observation of their daily dispersal is not available. Therefore, we use the model developed by Sutherland et al. (2000) to estimate their daily dispersal distances based on their body masses. The minimum home-range sizes of these species are then derived from the estimate of dispersal distance (Jenkins et al., 2007).

2.2 Landscape Accessibility at Habitat Scale

2.2.1 Identify Landscape Networks

The assessment of landscape accessibility starts from an identification of landscape networks for seed dispersers. Landscape networks at habitat scale (hereafter simply referred to as habitat networks) provide animals access to food resources (habitat patches) on a daily basis (Holling, 1992). In highly fragmented landscapes, animals that cannot find habitats large enough to support their survival may be able to overcome short distances and include neighbouring habitat patches within their range of movement to supply their resource requirements (Boscolo and Metzger, 2011, Kang et al., 2012, Galpern et al., 2011).

To identify habitat patches, the vector map of land cover is converted to a raster-format habitat map (10 m cell size), in which land cover types are reclassified as either habitat or non-habitat area for seed dispersers. For the aim of this study, broadleaved, coniferous and mixed forests are selected as suitable for habitat. After that, we use the minimum habitat size (see Table 1) as grain size to change the resolution of the habitat map for each seed disperser, aggregating small, scattered habitat fragments into large, contiguous habitat patches. This is because animals utilise landscapes with species-specific grain size and may occupy habitat patches which contain non-habitat fragments (Holling, 1992). Cells are assigned to the habitat class when at least 30% area inside the cell is habitat area (Andrn, 1994, Freemark and Collins, 1992). Specifically, hexagonal grids are used to represent habitat maps for the birds, rather than frequently-used rectangular grids, considering their advantages in modelling movement paths (Birch et al., 2007). ArcGIS is used for the identification of patches.

Since dispersal probability is inversely related to the least-cost distance between habitats (de la Pena-Domene et al., 2016), a least-cost path (LCP) model is applied to map the dispersal pathways between habitat patches (as shown in Figure 1a). The LCP model uses a raster-based optimisation algorithm to identify the optimum path between patches, in terms of cumulative land-cover resistance (e.g., energetic cost, difficulty, or perceived risk) (Watts et al., 2010), based on an assumption that animals have accurate cognitive maps of their home ranges (Hovestadt et al., 2012). In the study of Greater Manchester, the resistance values of individual land-cover types are obtained by habitat suitability.

Habitat suitability modelling provides a more objective approach for evaluating resistance values than commonly-used expert-based approaches (Milanesi et al., 2017). It calculates the habitat suitability index (HSI) scores of non-habitat areas to infer land-cover resistance values, given that the spatial records of a species in non-habitat areas are related to its preference in movements (Stevenson-Holt et al., 2014). We use the MaxEnt software to conduct the habitat suitability modelling (Phillips et al., 2017). The spatial records of each seed disperser from 2005 to 2015 and the 2010 land cover raster map (with the same resolution as the spatial accuracy of the species' records) are used as input data. For the purpose of this study, habitat areas (woodlands) are removed from the land cover map. Particularly, in the modelling for grey squirrels, rocks and buildings are removed from the map as well, considering their high impermeability to small mammals. Moreover, in order to correct sampling bias towards accessible areas, all areas over 500 m from roads are also removed (Warton et al., 2013). This leaves a total of 148 records for Eurasian jays, 42 Eurasian siskins, 130 coal tits, and 163 grey squirrels that are within the remaining areas for the habitat suitability modelling. The output HSI scores (in a logistic format) from MaxEnt indicate the probability of a species' occurrence within each land cover type, ranging from 0—1. To obtain land-cover resistance values, HSI scores are reversed to a range of 0—100 by using $(1 - \text{HSI}) * 100$. Woodlands are given a value of 1 for all the seed dispersers. In the case of grey squirrels, particularly, a resistance value of 1000 is assigned to both rocks and buildings.

Based on obtained resistance values, the LCP tool in Graphab software (Foltête et al., 2012) is applied to create dispersal pathways between habitat patches for each seed disperser. The distance threshold of the pathways is determined by the maximum daily dispersal distance of the animal (see Table 1). For the following estimate of landscape accessibility, each set of interconnected patches is defined as a component (an isolated patch constitutes a component itself).

2.2.2 Evaluate Landscape Accessibility

This study applies graph theory-based indices to evaluate landscape accessibility. Graph analysis has been shown to be an effective way of representing complex landscape structures (e.g., Kong et al., 2010), performing connectivity evaluations (e.g., Galpern et al., 2011, Urban and Keitt, 2001), and modelling species occurrence (e.g., Awade et al., 2011). It transforms the landscape network into a planar graph, in which patches are represented as nodes and dispersal paths are expressed as links between the nodes (Figure 2b). In general, the area of each patch is taken as the attribute of its corresponding node, and the distance of each path is assigned to the link's attribute as well.

The probability of connectivity (PC) index (Saura and Pascual-Hortal, 2007) is used to calculate landscape accessibility at habitat scale. The PC index is a probabilistic index that integrates both patch area and inter-patch distance in one measure and has been shown to relate well to actual species movement and occurrence patterns (Awade et al., 2011, Pereira et al., 2017). We evaluate the accessibility of each patch based on a quantification of its contribution to the overall PC value of the component that the patch belongs to. Patches with a high contribution are key stepping stones for dispersal and therefore have a high frequency of visitation by seed dispersers. The calculation of the PC index is conducted with Graphab software, in which a few parameters are set to obtain a 5% probability of dispersal corresponding to maximum daily dispersal distances of animals (Table 1).

2.3 Landscape Accessibility at Home-range Scale

2.3.1 Identify Landscape Networks

While the inter-patch movements at habitat scale directly contribute to daily seed dispersal, movements at the annual home-range scale result in long-distance (> 1 km) seed dispersal (Rayfield et al., 2016), which is considered of great importance for the climate-driven migration of trees (McCarthy-Neumann and Ibáñez, 2012).

In order to map landscape networks at home-range scale, habitat components that are bigger than the minimum home-range size of the animal (see Table 1) are connected by least-cost paths, based on the land-

cover resistance values previously obtained (Figure 1c). The distance threshold of the paths is determined by the maximum distance that the animal could move in its search for new home ranges.

2.3.2 Evaluate Landscape Accessibility

Similar to the assessment conducted at the habitat scale, we transform the habitat components and the least-cost paths between them into a node-link graph to evaluate landscape accessibility at the home-range scale. The integral index of connectivity (IIC) (Pascual-Hortal and Saura, 2006) is applied for the assessment rather than the PC index because it has been shown to better relate to the functional connectivity at home-range scale (Decout et al., 2012). The main difference between PC and IIC is that the former takes into account the length of each dispersal path, whereas the latter only focuses on the topological distances (in terms of the number of paths) between nodes, thereby providing a rough description of accessibility.

The accessibility of each habitat component is evaluated by a measurement of its contribution to the overall connectivity (IIC value) of the landscape network, using the Graphab software (Figure 1d). To do this, we first calculate the IIC index for the whole landscape network, and then systematically remove each node to recalculate the IIC index without that node. The percentage of connectivity loss indicates the individual contribution of each node to the overall landscape connectivity and can be interpreted as the relative probability of long-distance dispersal from or to that node.

2.4 Landscape Permeability to Forest Migration

For the purpose of this study, the measurement of landscape accessibility at both habitat and home-range scales are combined to infer landscape permeability, based on the assumption that the permeability of a landscape to forest migration would be proportional to its accessibility for seed dispersers. We calculate the permeability of each habitat area by multiplying the accessibility results of section 2.2 and 2.3, considering the interactions between different scales (Figure 1e). Habitat areas are then classified into three categories, high-, medium-, and low-permeable, using the method of natural breaks in ArcGIS. Finally, we combine the resulting permeability map with the map of human modification to identify areas for improvement.

3. Results

As shown in Table 2 and Figure 2, the aggregation of habitat areas yields 498, 498, 1677, and 7240 habitat patches for Eurasian jays, Eurasian siskins, coal tits, and grey squirrels, respectively. After that, the dispersal paths between habitat patches are identified using the LCP model, based on the land-cover resistance values derived from habitat suitability modelling (Table 3). The interconnected habitat patches are then divided into 91, 171, 248, and 1255 components for the four seed dispersers, respectively.

The result of graph analysis is an understanding of which habitat area in the landscape network are more accessible for seed dispersers. Figure 3 illustrates the relative accessibility of individual habitat patches and components. Habitats with high values are critical for maintaining landscape connectivity and therefore can be regarded as key stepping stones for seed dispersal. As shown in the figure, for all the four seed dispersers, only a handful of habitat components are responsible for a disproportionate share of seed dispersal events in the landscape network.

After the calculation of permeability in section 2.4, each habitat area is assigned a value representing its permeability to forest migration, with higher values indicating greater ease of movement. The permeability values are categorised into four classes: high-permeable, medium-permeable, low-permeable, and impermeable. The impermeable class is the areas that are suitable for habitat but cannot be identified as patches for dispersal agents. Table 4 shows the range of permeability values for each class. The percentage of each class regarding both patch number and habitat area is presented in Figure 4. The percentage of habitat patches with high or medium permeability is higher for Eurasian jays and siskins than for the other two dispersal agents. Nevertheless, the total percentage of the high and medium class between the four dispersal agents is not very different, in terms of habitat area. This is because most of the low-permeable and impermeable areas are small patches. Figure 5 shows the spatial distribution of the four permeability classes for different seed dispersers. The differences in spatial distribution indicating that landscape permeability to forest migration is influenced by the dispersal capabilities of local species.

We integrate the results from the four dispersal agents to obtain a permeability map of Greater Manchester (Figure 6a). In summary, around 13% of the total habitat area are very permeable to forest migration when all the four seed dispersers are considered, while the areas corresponding to the medium-permeable class account for 24%. Those low-permeable and impermeable areas cover more than 60% of the total habitat area, although most of them (95%) are smaller than 1 ha.

Figure 6(b) describes the percentages of permeable areas in natural, semi-natural and manmade green spaces in Greater Manchester. Landscapes showing high- or medium- permeability occupy 30% of natural, 34% of semi-natural, and 19% of manmade greenspaces. These relatively permeable natural and semi-natural greenspaces are very important for forest migration because they can support both seed dispersal and plant establishment, whereas the manmade greenspaces are potential locations where habitat quality should be improved to increase their contributions to forest migration. At the same time, 69% of natural and 65% of semi-natural greenspaces appear low permeable to forest migration, indicating that they are isolated habitats where the permeability could be improved by adding new stepping stones to increase their accessibility.

4. Conclusion

This study develops a new method to assess the permeability of urban green spaces to forest migration. Rather than focusing on habitat quality, the developed method utilises landscape accessibility for seed dispersers as a measure of permeability. It combines an LCP model that identifies landscape networks and a graph theory-based approach which evaluates landscape accessibility at multiple scales. This allows designers to re-visualise highly modified and fragmented urban landscapes as stepping stones for seed dispersal, which in turn allows for a more piecemeal form of landscape design to optimise urban landscapes for climate adaptation.

The proposed method is demonstrated in the Greater Manchester area, UK. The results identify urban green spaces with the potential to facilitate the climate-driven migration of trees through the city and provide a comparison of the permeability maps generated from different seed dispersers. Moreover, this study combines the map of permeability with the map of human modification to illustrate the application of the proposed method to incorporate other considerations and analytical possibilities. It is believed that this method would be particularly useful for landscapes where human activity is concentrated and implementing large continuous corridors or reserves is not feasible. Future research should explore how to add new stepping stones in the landscape matrix to favour the movements of seed dispersers and thereby to improve the permeability of cities to forest migration.

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Figure 1. Illustration of The Mapping Method. (a) Identify Habitat Networks, (b) Evaluate Landscape Accessibility at Habitat Scale, (c) Identify Home-range Network, (d) Evaluate Landscape Accessibility at Home-range Scale, and (e) Assess Landscape Permeability.

197x109mm (300 x 300 DPI)

Figure 2. Example of Habitat Patches Identified for Different Dispersal Agents: (a) Eurasian Jays and Siskins, (b) Coal Tits, and (c) Grey Squirrels.

209x54mm (300 x 300 DPI)

Figure 3 Landscape Accessibility for Four Seed dispersers

198x315mm (300 x 300 DPI)

Figure 4 Percentages of the Four Permeability Classes

209x59mm (300 x 300 DPI)

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Figure 5 Spatial Distribution of The Four Permeability Classes for (a) Eurasian Jays, (b) Eurasian Siskins, (c) Coal Tits, and (d) Grey Squirrels

264x152mm (300 x 300 DPI)

Figure 6 (a) Permeability Map of Greater Manchester Considering Four Dispersal Agents, (b) Percentages of Areas of Each Permeability class in Natural, Semi-natural and Manmade Greenspaces.

241x107mm (300 x 300 DPI)

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Table 1 Key parameters of the four seed dispersers in Greater Manchester Conway and Fuller (2010), Go´mez (2003), Dyer (1995), De Montis et al. (2016), Rolando (1998), Nupp and Swihart (2000), Pascual et al. (2014), (1992), and Sellers (2011).					
Seed Disperser	Habitat Size	Home-range Size	Daily dispersal Distance	Long-distance Dispersal	Body Mass
Eurasian Jay	≥ 4 ha	≥ 10.7 ha	≤ 1 km	1 km -5 km	161.7 g
Eurasian Siskin	≥ 4 ha	≥ 8 ha	≤ 0.5 km	0.5 km - 3 km	13.8 g
Coal Tit	≥ 1 ha	≥ 3 ha	≤ 0.4 km	0.4 km - 5 km	9.25 g
Grey Squirrel	≥ 0.0625 ha	≥ 0.5 ha	≤ 0.15 km	0.15 km - 2 km	510 g

Table 2 Landscape Elements for Dispersal Agents

Scale	Number	Eurasian Jay	Eurasian Siskin	Coal Tit	Grey Squirrel
Habitat	Patch	498	498	1677	7240
	Path	423	192	1726	6546
Home-range	Component	91	171	248	1255
	Path	182	273	1900	7938

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Table 3 HSI Scores Obtained from The MaxEnt Software and the Land-cover Resistance Values for The Four Seed Dispersers

Land Cover Type	Eurasian Jay		Eurasian Siskin		Coal Tit		Grey Squirrel	
	HIS	Resistance	HIS	Resistance	HIS	Resistance	HIS	Resistance
Buildings	0.46	54	0.45	55	0.51	49	N/A	1000
Health	0.43	57	0.45	55	0.43	57	0.2	80
Marsh	0.43	57	0.45	55	0.43	57	0.2	80
Residential	0.47	53	0.58	42	0.61	39	0.71	29
Agricultural	0.4	60	0.45	55	0.39	61	0.3	70
Orchard	0.43	57	0.45	55	0.43	57	0.2	80
Roads	0.69	31	0.45	55	0.43	57	0.63	37
Rock	0.5	50	0.45	55	0.43	57	N/A	1000
Grassland	0.41	59	0.58	42	0.43	57	0.2	80
Scrub	0.67	33	0.57	43	0.57	43	0.37	63
Urban	0.43	57	0.45	55	0.43	57	0.28	72
Water	0.85	15	0.78	22	0.86	14	0.35	65
Woodland	N/A	1	N/A	1	N/A	1	N/A	1

Table 4 Classification of Landscape Permeability

Permeability	Eurasian Jay	Eurasian Siskin	Coal Tit	Grey Squirrel
High-permeable	0 - 0.0039	0 - 0.0047	0 - 0.0017	0 - 0.0024
Medium-permeable	0.0040 - 0.0135	0.0048 - 0.0212	0.0018- 0.0081	0.0025 - 0.0108
Low-permeable	0.0136 - 0.0364	0.0213 - 0.0617	0.0082 - 0.0265	0.0109 - 0.0231
Impermeable	N/A	N/A	N/A	N/A