Title Ecological relevance of least cost path analysis An easy implementation method for landscape urban planning

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Abstract

Landscape connectivity promotes dispersal and other types of movement, including foraging activity; consequently, the inclusion of connectivity concept is a priority in conservation and landscape planning in response to fragmentation. Urban planners expect the scientific community to provide them with an easy, but scientifically rigorous, method to identify highly connecting contexts in landscapes. The least-cost paths (LCP) method is one of the simplest resistance-based models that could be a good candidate to spatially identify areas where movement is potentially favored in a given landscape. We tested the efficiency of LCP predictions to detect highly connecting landscape contexts facilitating individual movements compared to those performed in un-connecting landscape contexts. We used a landscape-level behavioral experiment based on a translocation protocol and individual repeated measures. In the city of Rennes (France), 30 male hedgehogs *(Erinaceus europaeus)* were translocated and radio-tracked in both highly connecting and un-connecting contexts, respectively, which were determined by the presence and absence of modelled LCPs. Individual movement patterns were compared between the two predicted contexts. Individuals travelled longer distances, moved faster, and were more active in the highly connecting contexts compared to the un-connecting contexts**.** Moreover, in highly connecting contexts, hedgehog movement followed LCP orientation, with individuals using more wooded habitats than other land cover class. By using a rigorous experimental design, this study validated the ecological relevance of LCP analysis to identify highly connecting areas, and could be easily implemented by urban landscape planners.

Key words: least cost paths; city; ground-dwelling mammal; resistance based model; fragmentation; translocation; green infrastructure; hedgehog

1. Introduction

Urban areas are growing at an unprecedented scale around the world (United Nations, 2018). These ecosystems exhibit similar structures, functions and constraints throughout large spatial scales (Savard et al., 2000). They are all heterogonous, densely populated and dominated by artificial surfaces (Cadenasso et al., 2007). In urban landscapes, vegetated patches are extremely fragmented because impervious surfaces are prevalent (Forman, 2014). This fragmentation limits the ability of individual animals to access resources, leading to the isolation of populations. This phenomenon, in combination with high levels of disturbance and high risk to movement, negatively affect urban wildlife (Grimm et al., 2008; Beninde et al., 2015; LaPoint et al., 2015). Landscape connectivity is defined as the degree to which the landscape facilitates (or impedes) movement among resource patches (Taylor et al., 1993). Consequently, ensuring landscape connectivity has become a global conservation priority in response to landscape fragmentation (Beier and Noss, 1998; Crooks and Sanjayan, 2006; Aronson et al., 2017). According to this definition, landscape connectivity promotes both dispersal and other types of movement expressed at different spatio-temporal scales, such as foraging activity (LaPoint et al., 2015; Reichert et al., 2016; Abrahms et al., 2017). This connectivity concept, coupled with the ecological corridor concept (Beier et al., 1998), has been rapidly included in environmental policies (under the terms greenways, green infrastructures, among others) to mitigate the biodiversity crisis (e.g., Simberloff et al., 1992). Consequently, urban planners must establish greenways to address both ecological issues on conservation of biodiversity and ecosystems services, as well as the growing social demand for nature in cities. Faced with this legal obligation, urban planners regularly question the scientific community about the tools that would enable them to put ‘functional’ greenways into practice, along with associated methodologies that are easy to use, but remain scientifically rigorous (Ahern, 2013; LaPoint et al., 2015). Greenways are considered functional when they allow the movement of organisms to access to the resources they need, despite their habitats being fragmented.

Functional connectivity is organism-orientated, and reflects the ease with which an organism is able to access different locations within its environment depending on its mobility and the suitability of landscape elements (Taylor et al., 1993; Tischendorf and Fahrig, 2000; Kadoya, 2009). Functional connectivity is usually predicted using modeling techniques, such as resistance-based models (Fagan and Calabrese, 2006; Kool et al., 2013). These types of connectivity models are based on landscape resistance values that reflect the energetic costs for an individual to move, its willingness to move, and/or the risk of moving across each type of land cover type (Zeller et al., 2012). Complex connectivity models, such as the circuit theory (McRae et al., 2008), and individual-based models (Palmer et al., 2011) are available but they often require the input of accurate and numerous ecological and spatial data (Kool et al., 2013), as well as some modeling expertise and large computational power. Consequently, they are difficult to implement for landscape planners. Least-cost path (LCP) analysis is known to be a simpler resistance-based models to grasp and compute (Adriaensen et al., 2003; Sawyer et al., 2011). LCP analysis identifies routes between habitat patches that minimize the cumulative resistance to movement (i.e., the cost of movement) and correspond to paths of higher movement probability. Thus, LCP analysis could allow areas where movements are potentially favored in a given landscape to be spatially identified. LCP analysis assumes that individuals have perfect knowledge of the landscape, leading them to follow one optimal path. Although the biological realism of LCP analysis could be questioned, this method may be used when limited input data are available (Fagan and Calabrese, 2006) and is easily accessible to landscape planners (Coulon et al., 2015). However, few studies have validated the functionality of modelled LCP using field experiments (e.g. LaPoint et al., 2013; Abrahms et al., 2017). It is necessary to fill this gap to test whether LCP is an easy and relevant method for use by urban landscape planners.

To validate if individual movement is facilitated by predictions made using connectivity models, two complementary approaches may be used. First, a Eulerian approach describes movement by its spatial location (Turchin, 1998). Movement is facilitated when spatial trajectories of individuals are consistent with predicted modelled corridors (i.e., if the movement of individuals was influenced by predicted LCP; Pullinger and Johnson, 2010; McClure et al., 2016; Abrahms et al., 2017). For example, Abrahms et al. (2017) showed that corridors predicted by LCP analysis overlap with a large majority of African wild dog (*Lycaon pictus*) GPS locations. A second approach (Lagrangian approach; Turchin, 1998, Bélisle, 2005) focuses on how animal movement is associated with movement costs. In this approach, a facilitated movement (i.e., when associated energy and risk for individuals are weak) leads to particular trajectory characteristics. Simulation and empirical studies show that movement in favorable habitats should be tortuous and slow (characterizing foraging or explorative movements; Zollner and Lima, 1999; Van Dyck and Baguette, 2005; Baguette and Van Dyck, 2007; Fahrig, 2007; Eycott et al., 2012). In contrast, movements in an unfavorable habitat should be straight and fast, to minimize risks and the time required to reach the next patch of favorable habitat. As a result, the term “facilitated”, which comes from the definition of connectivity, is not associated with fast and directed movements, which may seem counterintuitive. For example, Brown et al. (2017) showed that butterfly movements were shorter and more tortuous within habitat land cover types than in matrix land cover types (with variations within matrix subclasses). Similarly, Doncaster et al. (2001) showed that hedgehogs move more often and faster in unfavorable compared to favorable sites.

Both observational and experimental methods may be used to validate connectivity models (Knowlton and Graham, 2010; Kool et al., 2013). Observation-based studies have the advantage of being able to focus on the movements of organisms in their "real" environment, without the intervention of experimenters (e.g., McClure et al., 2016; Abrahms et al., 2017). However, such methods require sufficient sampling, with a large number of individuals being monitored over large time and spatial scales. These requirements are needed to: i) reduce the influence of inter-individual variability (controlled by differences in individual physiological state, behavioral plasticity, and motivation; Betts et al., 2015), and ii) to discriminate the behavioral states of individuals (migrants versus dispersers for the two examples in McClure et al., 2016). Indeed, individual and behavioral variability impact movement patterns (Bélisle, 2005; Van Dyck and Baguette 2005; Soulsbury et al., 2011; Abrahms et al., 2017; Keeley et al., 2017). As an alternative, experimental methods allow to control inter-individual variation in behavioral and physiological state. One such example is repeated-measure translocation experiments (Betts and al., 2015). This method allows researchers to: i) control for issues that are associated with observational studies, which allows sampling effort to be reduced, and ii) to standardize for behavioral state and motivation for movement (Bélisle et al., 2001; Knowlton and Graham, 2010; Betts et al., 2015).

To validate whether LCP analysis could be used by urban planners as an efficient tool for establishing greenways, the present study aimed to test whether the LCP allows areas where movements are facilitated to be identified. To achieve this aim, we confronted the landscape contexts in which LCPs were modelled as highly connecting contexts (movement facilitated) and landscape contexts in which LCPs were absent as un-connecting contexts (movement hindered). We conducted our experiment on the European hedgehog *(Erinaceus europaeus).*

This ground-dwelling mammal is common in urban environments, and represents a good model species to explore the effects of anthropogenic fragmentation and connectivity (Braaker et al., 2014). We analyzed the patterns of individual hedgehog movements after translocation from their home range into the two contrasting connectivity contexts. Each hedgehog was confronted with a highly connecting context and an un-connecting context in a repeated-measure design. We tested the efficiency of LCP predictions to detect highly connecting landscape contexts facilitating individual movements compared to movements performed in un-connecting contexts. Specifically, in order to study the relevance of LCP modelling in urban landscape planning, we tested the following hypotheses:

(1) Hedgehog trajectories are positioned according to the LCP direction when released in connecting contexts, and exhibit no preferred direction in un-connecting contexts.
(2) Hedgehogs move faster and through longer steps in un-connecting contexts compared to connecting contexts.
(3) Regardless of the release location, individuals select land cover with low resistance values and express nonrandom habitat use.

2. Materials and Methods

2.1. Model species and study area

The European hedgehog is a nocturnal, solitary, and small crawling mammal. It is an opportunistic species that mainly feeds on a wide range of invertebrates. Hedgehogs spend most of the night foraging (Riber, 2006), and rest during the day in one of their multiple nests that are mainly located in forested and semi-natural habitats (Rautio et al., 2013). In urban environments, individuals tend to move less, and their non-territorial overlapping home ranges are smaller compared to those found in rural environments (Doncaster et al., 2001).

They have also developed behavioral strategies to minimize risks associated with human activities. For instance, individuals avoid foraging near roads and are more active after midnight when road and foot traffic are low (Dowding et al., 2010). Males are more mobile than females (larger home ranges and longer traveling distances inside their home range). However, the pattern of habitat use is similar in both sexes (Rondinini and Doncaster, 2002). Finally, the European hedgehog is a species for which movements are not easily classified into different behavioral states. They disperse mainly through routine movements, rather than specific movement behavior (Van Dyck and Baguette, 2005; Braaker et al., 2014).

The current study was conducted across the urban agglomeration of Rennes (48° 06′ N–1° 40′ W, Brittany, France – Long Term Ecological Research site [LTER] Zone Atelier Armorique, Fig. 1). This urban study site covers 50 sq.km, is densely populated (around 4000 inhabitants per sq.km; INSEE, 2012), and is built up (proportion of artificial surfaces: 59%). However, the city contains a significant amount of green infrastructure (39%), ranging from isolated trees to major urban parks. We used a high resolution (5 m x 5 m) land cover map developed with a combination of GIS data from the National Geographic Institute of France (BD TOPO (c) IGN, 2010) and a classification of Worldview II remote sensing data (Digitale Globe (c) - 2011). This classification discriminates vegetated and impervious surfaces by using an object-based methodology (Definiens (c) Trimble) with an overall accuracy of 94%. Nine land cover classes were defined based on: i) their relevance for hedgehogs (Rondinini and Doncaster, 2002; Driezen et al., 2007; Braaker et al., 2014) and ii) their ease of acquisition by urban planners. The land cover classes were: building, large street, small street, highway, water, railway, impervious (all other asphalt surfaces, e.g., parking lots, sidewalks), wooded, and herbaceous areas (detailed in Supp. Table 1). Wooded land cover included trees, bushes, groves, and hedgerows. Herbaceous land cover encompassed grasslands, lawns, and ruderal areas.

2.2. Connectivity modeling

Landscape connectivity context was assessed by LCP analysis (Adriaensen et al., 2003). This method requires: i) the identification of habitat patches for hedgehogs, and ii) the setting of a resistance map based on resistance values of land cover. Habitat patches, a priori defined as the favorable resting and foraging sites for hedgehogs (La Point et al., 2013; Rautio et al., 2013) were continuous wooded areas >3 ha, corresponding to major urban parks that were dominated by trees and rich in vegetation structures (e.g., grove, scrubs, tall herbs, see Fig. 1). Because of our purpose of validating a usable method for urban planners, we deliberately selected resistance values using existing biological knowledge of the studied species based on published information (Braaker et al., 2014) The resistance values (RV) were assigned after ordering land cover from less resistant to more resistant, as follows: wooded RV=1), herbaceous (RV=2.5), impervious and small street (RV=6.8), large street and railway (RV=18.4, building, highway and water (RV=50) (Braaker et al., 2014; detailed in Supp. Table 1). The resistance map was built by using a sliding window analysis (using Chloé2012; Boussard and Baudry, 2014), in which the resistance value of each pixel was weighted by the mean of the resistance of the neighboring cells that have a diameter of a specific size (Supp. Fig. 3). To test the sensitivity of LCP predictions to landscape resolution, we generated several resistant maps, each corresponding to a different sizes of sliding windows: 15, 25, 35, 55, and 75 m in diameter. These sliding windows sizes were selected according to the perceptual range (i.e., 'the distance from which a particular element can be perceived as such (or detected) by a given animal' (Lima and Zollner, 1996)) of hedgehogs (Moorhouse et al., 2014). For the rest of the analyses, all pixels for which resistance values were equal to 50 were considered to be barriers and were excluded from the resistance maps (i.e., buildings, highways and water). LCPs were then computed from each of the five resistance maps, linking all habitat patches to one another, using ArcMap 10.3 (ESRI, USA) and Graphab (Foltête and al., 2012). Two modalities of landscapes contexts were categorized, based on the predicted connectivity by LCP maps. The highly connecting contexts (HCC) were defined as areas where LCPs, calculated from the five different resistance maps, overlapped. Thus, HCC was consistent regardless of landscape scale. In comparison, un-connecting contexts (UCC) were areas characterized by high resistance values and where no LCP was predicted, regardless of the scale of the resistance map used (Fig.2 and Supp. Table 2). The whole procedure was summarized in a flowchart (Supp. Fig 1). Thirty landscape contexts of each modality (HCC and UCC) were selected as release points for the translocation experiment (see below).

2.3. Data collection and statistical analyses

From April to July 2015, hedgehogs were found across the city by searching for them at night with a torch. Captured individuals were sexed and weighed. Females were immediately released to avoid disturbing breeding females. Thirty males were tagged with radio-transmitters (Biotrack, Dorset, U.K, 10 g) fixed to spines on their lower back, after shortening the spines. To control for inter-individual variation, each individual was successively translocated to two contrasting connectivity contexts (30 release points in HCC and 30 release points in UCC) in a random order (Fig. 1, Fig. 2 and Supp. Table 2). Whatever the connectivity context, the hedgehog release points were mainly small herbaceous areas such as bases of trees, lawns. HCC and UCC were selected beyond the limits of species home range (a release point was located, on average, 2.25 km from the capture site; diameter of urban home range: around 460 m; Braaker et al., 2014). In this way, all individuals had to explore a new environment. Tracking lasted for two nights in each connectivity context (Fig. 2). Individual locations were recorded every 30 min from 22:00 to 02:30. In total, 18 h of radio-tracking data was obtained per individual. After tracking sessions, all hedgehogs were recaptured, their transmitters were removed, and they were released at their original capture site.

We studied path orientations to determine whether individual movement followed the predicted LCP in highly connecting contexts (HCC). The overall orientation (i.e., between the first and last locations) of each observed exploratory path was compared to the orientation of the predicted LCP. The angle between these two paths (Supp. Fig. 2) was analyzed using Rayleigh's test of uniformity (after an axial transformation: by doubling the angles), in which the null hypothesis is a uniform distribution (Jammalamadaka and Sengupta, 2001; R package Circular – Agostinelli and Lund, 2011). If the movement of individuals followed predicted LCPs, the angle between the orientations of the observed exploratory path and the LCP should be close to zero, and H0 would be rejected. In parallel, to avoid bias caused by other potential orientations mechanisms, we also tested if the observed exploratory paths in both HCC and UCC had a preferential orientation. Thus, we conducted the same test between observed exploratory paths and an arbitrary orientation (we used north). If the angle measured between the observed exploratory path and an arbitrary orientation was not zero, hedgehogs moved with a random orientation.

To characterize hedgehog movement patterns, we extracted four movement variables for each night from each observed exploratory path (i.e., trajectory travelled by an individual over one night of radio-tracking; Fig.2); namely, Minimal distance: the sum of Euclidean distances between successive locations; Effective distance: the Euclidean distance between the first and the last locations; Mean speed: the mean length of displacement for each 30 min step (m/h) excluding null length displacement; Activity ratio: the number of records followed by movement divided by the total number of records. Path analysis was performed in the Tracking Analyst extension of ArcMap 10.3. Each of the four movement variables was analyzed separately with linear mixed models and was transformed where assumptions were not met (minimal distance and effective distance were square-root transformed and mean speed was log-transformed). Connectivity context (HCC or UCC) was considered to be a fixed factor. It was associated in an additive model with individuals and nights (first and second night), which were considered as random factors (with random intercepts) to control for inter-individual and inter-night variation, respectively (R 3.4.3 (R Core Team 2017) and lme4 package (Bates and al., 2014)). We used a likelihood ratio test to assess the effect of connectivity contexts on movement variables.

Finally, we studied how resistance values and habitat type (land cover classes) were selected by hedgehogs according to connectivity contexts. The resistance values and habitats used by hedgehogs were compared to simulated locations. Simulations were based on null models, assuming the random use of resistance values and habitats (e.g., Rondinini and Doncaster, 2002; Martin and al., 2008). For each observed exploratory path (group of 10 consecutive locations), we simulated 500 paths, starting at the same first location and maintaining the same distances between consecutive locations (to preserve the ability of each individual to move), as the observed exploratory path. The order of consecutive distances and step orientations, however, varied randomly. Simulated locations that ended on inaccessible land cover classes (i.e., where hedgehogs were never observed, such as buildings, highways, and water) were removed from the analysis (Braaker et al., 2014). For each observed and simulated location, respectively (10 locations per path), we extracted the resistance value of the corresponding pixels from the resistance maps of 15, 35, and 75 m (extreme and average sliding window sizes).We also extracted the land cover class of all these locations. Only wooded, herbaceous, and impervious habitats were considered. Large and small streets land cover classes were not statistically tested because not enough locations were observed in these classes. The extracted variables (three average resistance values and percentage of three land cover class per path) were examined separately by linear mixed models with fixed factors; specifically, location origin (predicted vs observed) and connectivity contexts (HCC vs UCC) were used, with individual and night representing random factors (random intercept). A post-hoc test of contrasts was added when the interaction of the fixed factors was significant, to test the effect of origin for different contexts of connectivity (R package phia - Rosario-Martinez et al., 2015).

3. Results

3.1. Path orientation

Thirty male hedgehogs were successively translocated to two contrasting connectivity contexts (30 release points in HCC and 30 release points in UCC) in a random order.
The hedgehog path orientation in relation to predicted LCPs was characterized. Rayleigh's test was only significant for the distribution of angles relative to LCP in HCC (Statistics = 0.22, p = 0.0077; Table 1). In other words, the difference between the orientations of observed exploratory paths and LCPs was not uniform, but followed a unimodal distribution centered on 0 (mean direction = -0.29; mean resultant length = 0.23). Thus, individuals tended to follow the direction of LCP. In contrast, the distribution of angles that were measured with arbitrary orientations (such as North, for both HCC and UCC) were uniform (the statistical test did not reject H0; Table 1).

3.2. Movement patterns

Hedgehog movement patterns were then quantified. Movement metrics differed between the two connectivity contexts. Individuals moved significantly more in the highly connecting contexts, covering longer distances (minimal and effective, Table 2). Specifically, both distance metrics were 1.58 times higher in HCC compared to UCC. The minimal distance travelled was, on average, 425 m +/- 39 (Mean +/- Standard Error) in HCC and 266 m +/- 32 in UCC. The mean effective distance was 194 m +/- 26 in HCC and 122 m +/- 19 in UCC. Hedgehogs moved faster (increase of 36 m/h in HCC compared to UCC), and were more active (74% of activity ratio in HCC versus 63% in UCC), in HCC (Table 2). No homing behavior was detected; individuals were, on average, recorded at the same distance from their original capture site at the end of tracking compared to the release time (permutation test for paired data, 1000 permutations, $p = 0.31$).

3.3. Resistance and habitat selections

Finally, the selection of resistance values and habitat type by hedgehogs was studied according to connectivity contexts. Hedgehogs were found more often than expected by chance on less resistant cells for the lowest window size (15 m diameter) and in the highly connecting context (HCC, Table 3). With higher sliding window sizes (35 and 75 m diameter), or in the UCC, observed and simulated locations had similar resistance (non-significant post-hoc interaction test).Concerning land cover classes, hedgehogs avoided impervious surfaces and roads (large and small streets): radio-tracked individuals used 27% of impervious surfaces for their movement versus 30% in random simulations in HCC, these figures were 35% versus 42% in UCC respectively (Fig. 3). Conversely, individuals preferentially selected wooded areas in both connectivity contexts: they routes were made of 42% of wooded areas versus 28% in random simulations in HCC, these figures were 27% versus 19% in UCC, respectively. Herbaceous habitats were visited more often than expected by chance in the UCC (29% versus 21% in random simulations). In comparison, in the HCC, herbaceous habitats were visited at a similar frequency in observed and simulated locations (respectively 28% and 29%; (Fig. 3).

4. Discussion

4.1. Hedgehog movement patterns in urban landscapes

Different hedgehog movement patterns were detected depending to the degree of predicted connectivity in urban landscapes.

In highly connecting contexts, hedgehogs followed predicted corridors and their exploratory movements were similar to those described for non-translocated (i.e., intra-home range) urban hedgehogs. The distance traveled and speed of travel were 425 ± 35 m and 117 ± 9 m/h, respectively. This result was consistent with that of Rondinini and Doncaster (2002), who recorded mean distance of 380 ± 30m and mean speed of 111 ± 7 m/h. Moreover, hedgehog movements appeared to be sensitive to fine scale variation in resistance. Non-random movement occurred in highly connecting contexts when resistance was computed using a sliding window of 15 m diameter, but not when it was computed for sliding windows of 35 or 75 m diameter. This range was consistent with the perceptual range of this species of hedgehog (the distance over which individuals perceive and respond to landscape connectivity; Moorhouse and al., 2014). Finally, hedgehogs selected less resistant areas and preferentially exploited wooded areas, while avoiding impervious area and roads. Although out of the home range, these results support similar habitat selection detected by previous studies realized inside the home range of individuals (Driezen et al., 2007; Braaker et al., 2014).

In un-connecting contexts, the movements of hedgehogs were isotropic and characterized by a lower traveled distance (266 ± 32 m) and lower speed of travel (83 ± 8m/h). Habitat selection was similar to that observed in highly connecting contexts, except for the herbaceous land cover class. This result suggests that herbaceous land cover becomes attractive when favorable habitats, such as wooded land cover, are scarce. When the degree of fragmentation increases, this type of land cover represents secondary habitat, allowing the movement of individuals (concept of landscape supplementation; Dunning et al., 1992). Thus, the level of resistance of each habitat class varies depending on local landscape contexts. These elements are important for parameterizing connectivity models, but also realistic movement rules, when implementing individual based simulations. This study presents the first observation obtained in an urban matrix predicted to be unfavorable to individual movements.

Experimental studies (such as translocation) reveal how individual movement is influenced over large ranges of land cover and landscape configurations, in which observational studies might under-represent some modalities (Knowlton and Graham, 2010; Betts et al., 2015).

4.2. Importance of landscape permeability matrix for movement patterns

Contrary to our expectations, we demonstrated that the studied hedgehogs: i) moved less, were slower, and exhibited high pausing rates in un-connecting contexts that were dominated by impervious surfaces when compared to highly connecting contexts; and ii) only selected low resistance values in highly connecting contexts. This limited movements in unfavorable landscape contrasted with general assumptions of the published literature. Existing studies suggest that individual movement is quick and directional in unfavorable areas because of the tradeoff between dispersal and mortality risk (Knowlton and Graham, 2010), based on optimal search behavior models (Zollner and Lima, 1999). These predictions have been supported by observations made on different species when comparing movements made by individuals in habitats that were characteristic of their home ranges with habitats considered unsuitable for establishing home ranges, but suitable for movement. Examples of such studies include a study on our focal species in an agricultural landscape (the meadow brown butterfly *Maniola jurtina*, Delattre et al., 2010; the European hedgehog, Doncaster et al., 2001; the Siberian flying squirrel, *Pteromys volans*: Mäkeläinen and al., 2016). These classical predictions were not met in our study, probably because of the specificities of the urban landscape, and because we compared two types of matrix. Movements made between habitat patches indeed depend on the type of matrix that is passed through (Bakker and Van Vuren 2004; Brown et al., 2017). The main contrast between unfavorable agricultural and urban landscapes is the lack of vegetation cover for urban landscapes. The urban matrix might also be perceived as highly costly in terms of predation risk and energy expenditure, supporting the proposal of Bakker and Van Vuren (2004). The authors hypothesized that the red squirrel shows reduced travel speed and higher pausing rates in forest clearcuts to avoid predation risk. In addition to differences in movement patterns, hedgehogs selected less resistant areas in highly connecting contexts only. Less resistant areas were not accessible or were not detected by hedgehogs when predicted connectivity was low.

Overall, our results suggest that predicted movement patterns at the landscape scale depend on landscape matrix permeability. This result reasserts the observation that matrix properties must be considered in movement ecology (Stevens et al., 2004; Bender and Fahrig, 2005). In particular, the reluctance of individuals to move on specific substrates has been advocated by Baguette and Van Dyck (2007) as an important driver of movement patterns in the landscape matrix.

4.3. LCP analyses: a feasible method for urban landscape planning

Our results supported the relevance of resistance-based models for predicting efficient corridors where movement is truly facilitated. LCP modeling assumes individual landscape omniscience, optimal movement, and known desired destination (Palmer et al., 2011; Coulon et al., 2015). Such assumptions appear unrealistic, and their relevance is subject to discussion (LaPoint et al., 2015). However, our study indicated that these hypotheses are not an obstacle for predicting paths of actual high facilitated movement in urban environments. LCP predictions seem more efficient in urban landscapes compared to agricultural or forested landscapes, which are usually studied to discuss LCP performances (Coulon et al., 2015; McClure et al., 2016). Urban landscapes are extremely fragmented and contrasted, with few alternative routes being available for movements. These specificities may make the urban landscape particularly compatible with LCP models. Because urban ecosystems are recognized to be similar to each other in terms of structures, functions and constraints (Savard, Clergeau, & Mennechez, 2000), this method, tested here in a medium-sized city in Western France, could prove efficient across cities, especially in Europe. Nevertheless, predictions of urban corridors based on LCPs must be validated in other biological models, especially for species with other habitat requirements and/or dispersal abilities.

5. Conclusions

Ecologically relevant tools are needed for urban planning to establish, restore, and/or maintain corridors and greenways (Kettunen and al., 2007). In this study, we proposed a rigorous field experimental design to validate the ecological relevance of LCP, which is a method that could be easily used by urban landscape planners. Contrasted degrees of connectivity predicted by this simple resistance-based model revealed different movement patterns in hedgehogs. LCP is already a tool that is widely used in research (Sawyer et al., 2011), and our results confirm that it is also a good candidate for use by stakeholders. Indeed, the predictions of LCP models reflected field-based movement. Even though this approach shares basic data requirements (resistance maps) with other modeling tools, it is both simpler in its principle and lighter in computation (computation times are short and GIS integrated tools are available). Through validating LCP modelling for urban contexts, our results highlight shortcomings in animal movement models that do not consider the quality of the matrix in which movement occurs.

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Table 1. Descriptive statistics, Rayleigh's test results and distribution diagram of angles between observed exploratory paths and LCP direction (Θ_{LCP}) or north direction (Θ_{N}) in HCC (highly connecting context), and UCC (un-connecting context).

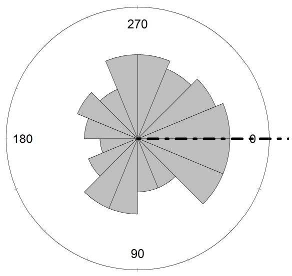
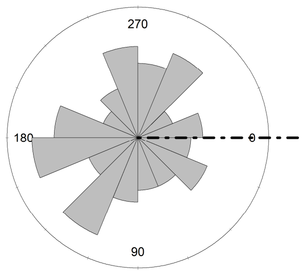
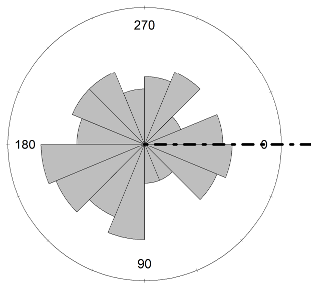
Angle referential	Θ_{LCP}	Θ_{N}	
Connectivity contexts	**HCC**	HCC	UCC
Mean direction	**-0.29**	-3.06	2.66
Mean resultant length	**0.23**	0.136	0.16
Statistics	**0.22**	-0.13	-0.14
p-value	**0.0077**	0.92	0.94
Angle distributions			

Table 2: Movement data (Mean +/- Standard Error (SE)) and how they differ between the highly connecting context (HCC), and un-connecting context (UCC). The P-values result from likelihood ratio tests based on linear mixed models. **: $p < 0.01$; ***: $p < 0.001$

	Minimal distance (m)	Effective distance (m)	Mean speed (m/h)	Activity ratio (%)
HCC –				
Mean +/- SE	425 +/- 39	194 +/- 26	117 +/- 9	73.9 +/- 2.8
range	*8; 1339*	*6; 953*	*13; 348*	*0; 100*
UCC –				
mean +/- SE	266 +/- 32	122 +/- 19	83 +/- 8	62.8 +/- 3.4
range	*5; 1117*	*5; 678*	*16; 279*	*0; 100*
Difference (HCC –UCC)				
mean +/- SE	160*** +/- 58	70**+/- 33	36** +/- 14	11.1** +/- 4.5
range	*-433; 1007*	*-326; 554*	*-99; 217*	*-39; 56*

Table 3. Mean +/- Standard Error (SE) resistance values of locations (weighted by 15 m diameter sliding window analysis) according to the connectivity context (HCC: highly connecting context, UCC: un-connecting context) and the location origin (Observed, Simulated). Post-hoc contrast test associated.

	Mean +/- SE resistance by location origin		Post-hoc interaction test		
	Observed	Simulated	Chisq	df	p-value
HCC	5.4 +/- 0.4	6.8 +/- 0.3	13.1	1	0.0006
UCC	9.5 +/- 0.6	9.4 +/-0.3	0.37	1	0.54

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Figure 1. Geographic location of the study area (Rennes, Brittany in the north-west France) (left). Map of resistance values of the study area, location of habitat patches (continuous wooded areas >3 ha) and least cost paths (LCP) (right). Representation of hedgehog release points in highly connecting contexts (HCC) and un-connecting contexts (UCC).

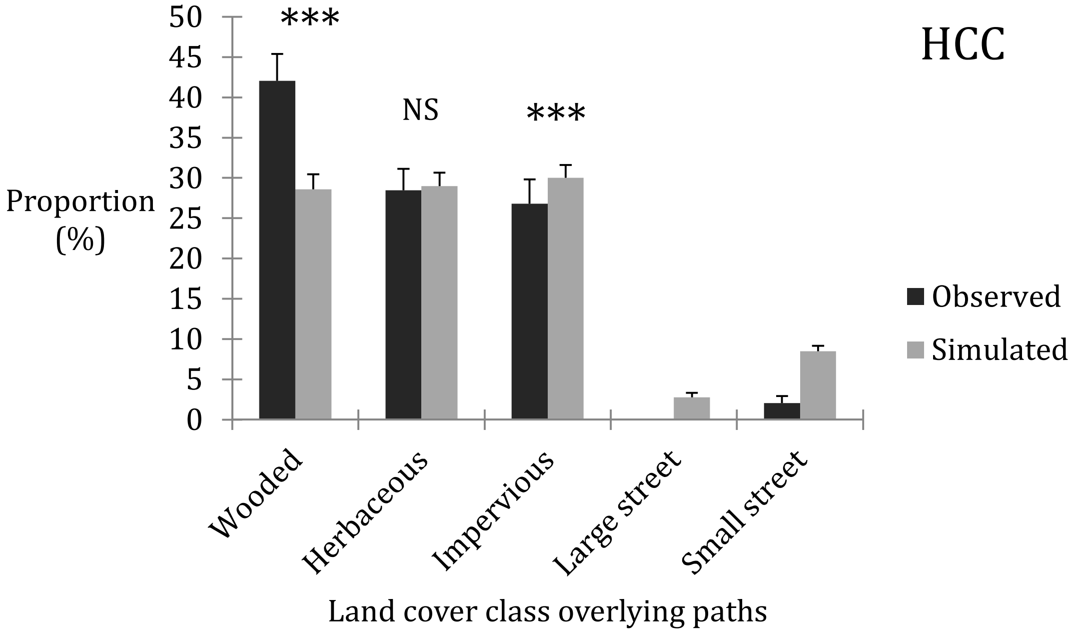
Figure 2. Example of observed exploratory paths (the recorded locations are white dots and virtually linked by black lines) over two nights of radio-tracking (paths of the two nights are virtually linked by dotted lines) in both tested connectivity contexts: a. highly connecting contexts (HCC) correspond to areas where least cost paths (green lines) were modeled over different sliding window sizes are redundant and b. un-connecting contexts (UCC) correspond to areas were none least cost paths were modelled. Background is the resistance map (light grey indicates low resistance, dark grey high resistance, and black infinite resistance).

Figure 3. Percentage (mean and standard error) of each land cover class overlying observed and simulated paths (set of locations) in each connectivity context (HCC: Highly Connecting context, UCC: Un-connecting Context). Each land cover class was analyzed separately. See text for details on the statistical analyses. *: $p < 0.1$; ***: $p < 0.001$. Large and small streets habitat classes were not statistically tested because not enough locations were observed in these classes.

Figure 1

Figure 2

Figure 3


HCC
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15
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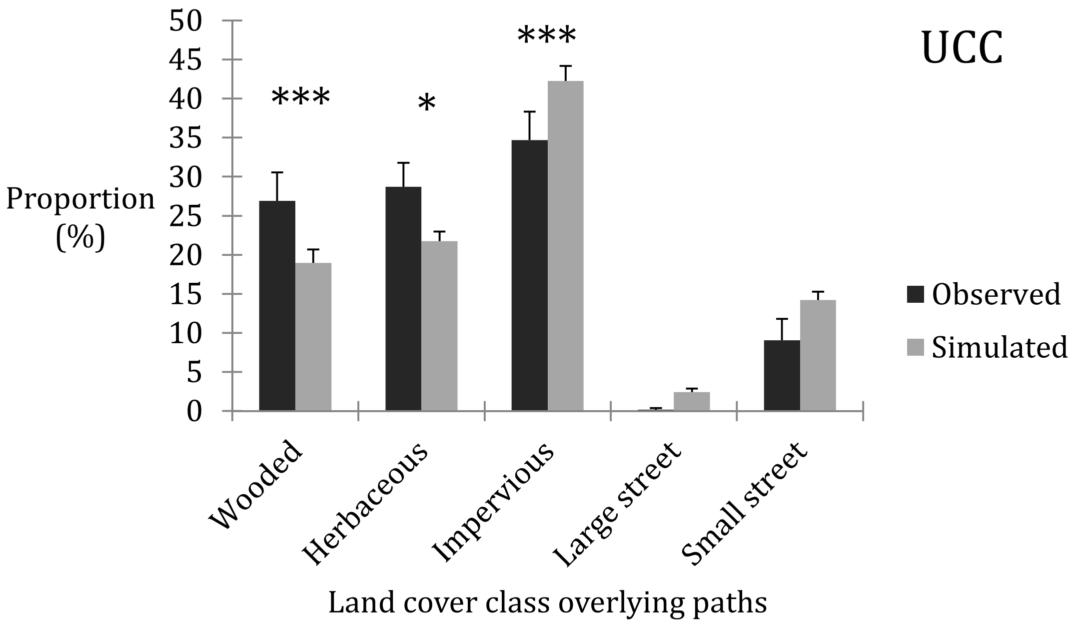
Proportion (%)
***
NS
***
Observed
Simulated
Wooded
Herbaceous
Impervious
Large street
Small street
Land cover class overlying paths


UCC
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Wooded
Herbaceous
Impervious
Large street
Small street
Land cover class overlying paths

SUPPLEMENTARY MATERIAL:

Supplementary Table 1. Hierarchy and resistance coefficients for each land cover. Resistance values were deliberately selected from existing biological knowledge of the studied species based on published information (adapted from Braaker et al., 2014) to validate a usable method for urban planners

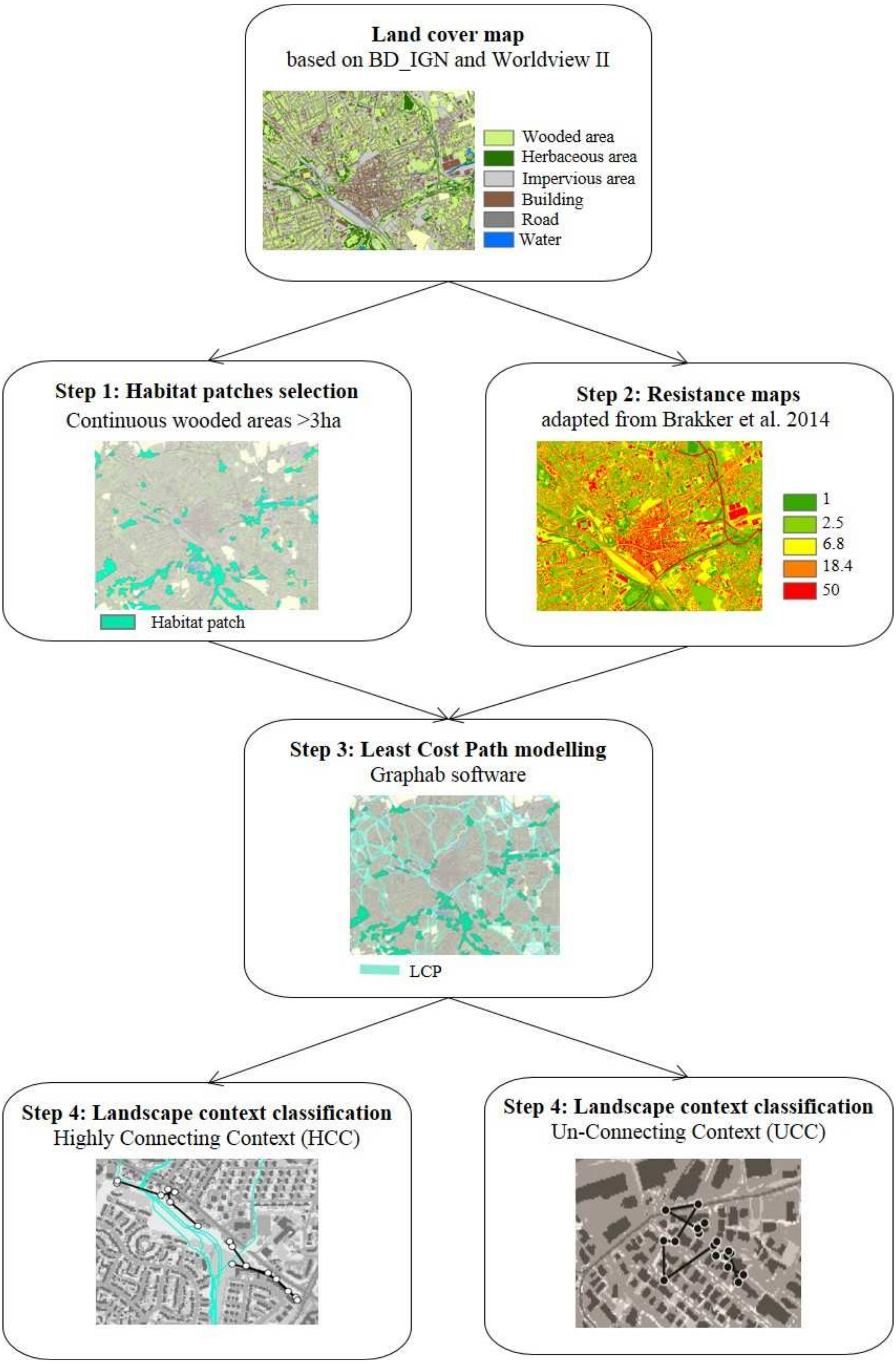
Land cover	Description	Hierarchy	Resistance values
Wooded surfaces	High vegetation layer, wood, hedge of trees and/ or shrubs, bush, grove, isolated tree, mainly public park, private garden	1	1
Herbaceous surfaces	Lawn, grassland, ruderal area, herbaceous plant, flower garden	2	2.5
Impervious surfaces	Asphalt surfaces other than roads, parking lots, sidewalk	3	6.8
Small street	Residential roads		
Large street	Main road with traffic	4	18.4
Railway	Railroad		
Building	Building, construction	5	50
Highway	Four-lines road with heavy traffic		
Water	Canal, ditch, pond		

Supplementary Table 2. Description of the two connectivity contexts (HCC and UCC). Resistance and land cover percentages were extracted in100 m radius buffer around hedgehogs release points - Mean +/- Standard Error.

	Highly Connecting Context (HCC)	Un-connecting Context (UCC)
resistance	9.2 +/- 2.6	16.3 +/- 3.5
% wooded areas	27.0 +/- 15	13.1 +/- 6
% herbaceous areas	24.8 +/- 13	17.0 +/- 7
% impervious areas	25.0 +/- 12	32.1 +/- 7
% built-up areas	12.4 +/- 7	23.7 +/- 8
% roads	21.0 +/- 11	32.4 +/- 2

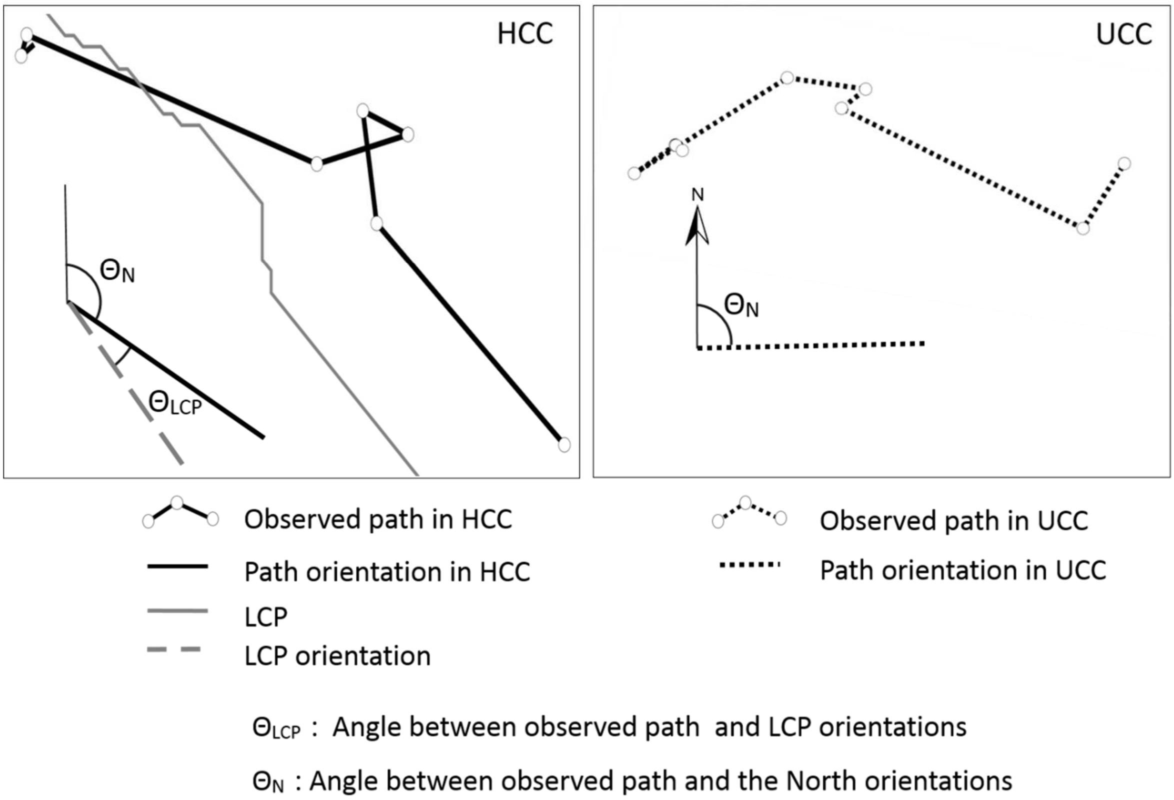
Mean resistance per land cover class differed between the two connectivity contexts (permutation test on paired sample, p-value < 0.0001).

Supplementary Figure 1. Flowchart of connectivity modelling procedure



Supplementary Figure 2. Observed exploratory path orientation compared to LCP and North orientations.

HCC: Highly Connecting context, UCC: Un-connecting Context



LCP orientation was extracted from the orientation of the LCP segment included in a circle of a 200 m radius centered on the individual release location.

Observed exploratory path orientation was extracted from the straight line linking the first and the last recorded locations.

Supplementary Figure 3. Schematic representation of sliding window analysis

The circular window size is defined by the number of cells constituting the circle diameter. This size is an unpaired number because the circle is centered on a cell. The circular window embedded all cells whose the center is included in the circle area.

In this study, the cells size was 5 x 5 m.