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Comparison between three landscape analysis tools to aid conservation efforts

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Master thesis, 30 credits, in *Geomatics*

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Abstract

Habitat loss is a major threat to biodiversity, and often causes decreased connectivity between habitats. Geographical Information System (GIS) tools for spatially analysing landscape connectivity for different species have become increasingly common with the expansion of the field of landscape connectivity. Today several software tools are available, but few studies have compared their differences and how they might best be utilised in conservation planning. In this study three software tools were compared: Circuitscape, Linkage Mapper and Graphab. The goal was to link differences to the theory and algorithms behind each tool. Four different species varying in dispersal range and habitat preferences were chosen as model organisms in the analysis. These were hermit beetle (*Osmoderma eremita*), great crested newt (*Triturus cristatus*), red deer (*Cervus elaphus*) and spruce bark beetle (*Ips typographus*). We find that Circuitscape is better for general dispersal patterns, while Graphab and Linkage Mapper are more suited for showing connectivity among habitats and potential corridors. A suggested approach is to use Graphab at larger spatial scales to identify areas of constrained connectivity, and at smaller spatial scale use Linkage Mapper to model corridors, while Circuitscape can show patterns of dispersal inside the corridor to find areas where connectivity can be improved.

Keywords: *connectivity, landscape analysis, habitat fragmentation, conservation, GIS algorithms, graph theory, circuit theory, network theory, least cost path*

Sammanfattning

Habitatminskning är ett stort hot mot den biologiska mångfalden, som ofta orsakar sämre spridning mellan habitat. I och med att kunskapen om landskapssamband har växt, har GIS-verktyg för att rumsligt analysera landskapssamband för olika arter blivit allt vanligare. Idag finns flera programvaruverktyg, men få studier har jämfört deras skillnader och hur de kan användas inom naturvårdsplanering. I denna studie jämfördes tre programvaror: Circuitscape, Linkage Mapper och Graphab. Målet var att knyta skillnaderna mellan dem till teorin och algoritmerna bakom varje verktyg. Fyra olika arter med varierande spridningsavstånd och habitatpreferenser valdes som modellorganismer i analysen. Dessa var läderbagge (*Osmoderma eremita*), större vattensalamander (*Triturus cristatus*), kronhjort (*Cervus elaphus*) och granbarkborre (*Ips typographus*). Circuitscape är bättre för att visa arters generella spridningsmönster, medan Graphab och Linkage Mapper är mer lämpade för att visa länkade eller isolerade habitat samt potentiella korridorer. Ett tillvägagångssätt som föreslås är att använda Graphab i större skalor för att identifiera områden med sämre samband och i mindre skalor kan Linkage Mapper användas för att modellera korridorer, medan Circuitscape kan visa spridningsmönster inuti korridorer för att hitta områden där samband kan förbättras.

Nyckelord: *landskapssamband, landskapsanalys, fragmenterade habitat, naturvård, GIS-algoritmer, grafteori, kretsteori, nätverksteori*

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Glossary

Friction value	*An estimation of the difficulty for a species to cross a certain type of land cover, the higher friction the more difficult it is to cross. Friction value is a type of cost used in landscape connectivity analysis.*	Zeller at al. (2012)
Habitat	*All land cover with friction value 1, potential core habitat.*	Used in this study
Core habitat	*The home range of a species, covering all stages in a species life cycle, and are large enough to sustain an individual. It differs from habitat because it has a combination of necessary conditions which makes the core habitat essential to the species.*	Used in this study
Least cost path	*The path from one core habitat to another that generates the lowest cumulative cost or cost distance.*	Urban et al. (2009)
Cumulative cost	*The sum of all friction values in one least cost path.*	Clauzel et al. (2016)
Cost distance	*The cost-weighted distance; each cost distance unit equals to each metric unit times the friction value. Where a species crosses an area of friction value 5, each meter equals to 5*1=5 cost distance units.*	ESRI (2016)
Least cost path distance	*The route of the least cost path measured in metric unit (actual distance).*	Clauzel et al. (2016)
Graph	*A set of nodes, connected with links.*	Urban and Keitt (2001)
Spatial graph	*A type of graph with shape and geographical location of nodes and links – used in landscape ecology where nodes represent core habitats and links potential dispersal between them. Links can be in Euclidean distance or least cost paths.*	Fall et al. (2007)
Planar graph	*A graph where only nodes that are adjacent will be connected, no links cross each other.*	Fall et al. (2007)
Complete path	*A graph where all nodes are connected with each other.*	Fall et al. (2007)
Graph theory	*The mathematical field concerned with statistical measures of graphs.*	Proulx et al. (2005)
Network theory	*A collection name of landscape analysis tools and measures that originate from graph theory and use spatial graphs. Some are only concerned with the construction of a graph (e.g. Linkage Mapper), while others are also calculating different statistical measures on graphs (e.g. Graphab).*	Rayfield et al. (2011)
Circuit theory	*Based on graph theory but enhanced with theories from the field of electricity, such as Ohm's and Kirchhoff's laws. It was first used in Circuitscape, but the concept is now incorporated in many tools.*	Rayfield et al. (2011), McRae et al. (2008)

1. Introduction

Landscape ecology is a multi-disciplinary field which encompasses the dynamics of a landscape, its influence on biotic and abiotic processes, and also its management (Turner 1989). Landscape ecology is often concerned with changes in landscapes caused by disturbance – natural or anthropogenic (Turner 1989). One example of anthropogenic disturbance is habitat fragmentation and the effect this has on species dispersal.

Habitat loss caused by human disturbance is a major threat to biodiversity, and habitat loss is often connected to fragmentation and isolation of continuous habitat (Fahrig 2003). The connectivity of a landscape is dependent on the effect the surrounding landscape structure has on the facilitation or impedance of animal movement between their habitat patches (Tischendorf and Fahrig 2000). A landscape can be perceived as a mosaic of habitat and non-habitat, where for example hedgerows in an agriculture landscape can facilitate dispersal between habitat patches, whereas roads work as barriers (Turner 1989). Facilitation of animal movement between protected areas through the construction of corridors and stepping stones is frequently used in conservation planning (Worboys et al. 2010).

As the field of landscape ecology has grown, attempts have been made to model connectivity or species dispersal. The use of graph theory to model landscape connectivity for ecology and conservation has increased considerably in popularity since 2000 (Moilanen 2011; Rayfield et al. 2011). Graph theory is a branch of mathematics concerned with statistical description of graphs (Proulx et al. 2005). A graph consists of a set of nodes in which some are connected with links (Urban and Keitt 2001; Rayfield et al. 2011). In landscape ecology, the nodes represent habitats of a species, and the links represent the ability of individuals to spread between habitats (Urban and Keitt 2001).

Fall et al. (2007) used the term spatial graphs to separate it from conventional graphs. In spatial graphs, the graph theory is combined with Geographical Information Systems (GIS), by taking into account the shape and geographical location of the habitat and dispersal links, and sometimes also a species' response to the surrounding landscape structure (Fall et al. 2007). Because of this, spatial graphs are often useful when planning for corridors and protecting land in conservation (Fall et al. 2007).

Today a number of software tools are used for modelling landscape connectivity by using over 60 different graph-based measures (Rayfield et al. 2011). The question arises whether the different tools are comparable, or if some methods work better in some situations.

Therefore, the aim of this project is to see differences and similarities between three different landscape analysis tool that are commonly used. Studies have shown that more robust outcomes can be achieved by bringing together several models, termed the ensemble approach (Araújo and New 2006). Therefore, another goal is to evaluate which of the tools perform better in different scenarios and if they can complement each other to best aid conservation planning. The tools will be compared by using four species; hermit beetle (*Osmoderma eremita*), great crested newt (*Triturus cristatus*), red deer (*Cervus elaphus*) and spruce bark beetle (*Ips typographus*); which differ in habitat preference and dispersal distance. I chose to compare the three landscape connectivity analysis tools Circuitscape (Version 4.0; McRae et al. 2013a), Linkage Mapper (Version 1.0; McRae and Kavanagh 2011) and Graphab (Version 2.0; Foltête et al. 2012). These tools were chosen based on their popularity and because they use different approaches to estimate landscape connectivity, and have different theories.

My hypothesis is that the tools will differ depending on the theory and algorithm behind them, and that this difference will not be uniform across species.

2. Background

2.1 Applied use of landscape analysis tools

This study is carried out in collaboration with Calluna, an environmental consultancy company which uses Linkage Mapper and Circuitscape to model habitat connectivity. Calluna uses these tools for identifying sensitive links in a species' network, to locate in which areas measures could be taken to improve resilience of the network, to determine the functionality of a network depending on its degree of connectivity (Koffman 2014; Koffman 2015), and to estimate if new development will disrupt connectivity (Koffman and Bovin 2014).

2.2 Theoretical background

A whole branch of ecological and conservation measures and software have originated from graph theory, and the terms used for describing them are often inconsistent (Rayfield et al. 2011). Here they are broadly categorised in network theory (Graphab and Linkage Mapper), and circuit theory (Circuitscape) after Rayfield et al. (2011), see Fig. 1.1. Network theory loosely bundles all tools creating spatial graphs (Rayfield et al. 2011). In circuit theory, habitats are connected with multiple paths and based on both graph theory and on resistance analogous with laws of electricity (Rayfield et al. 2011).

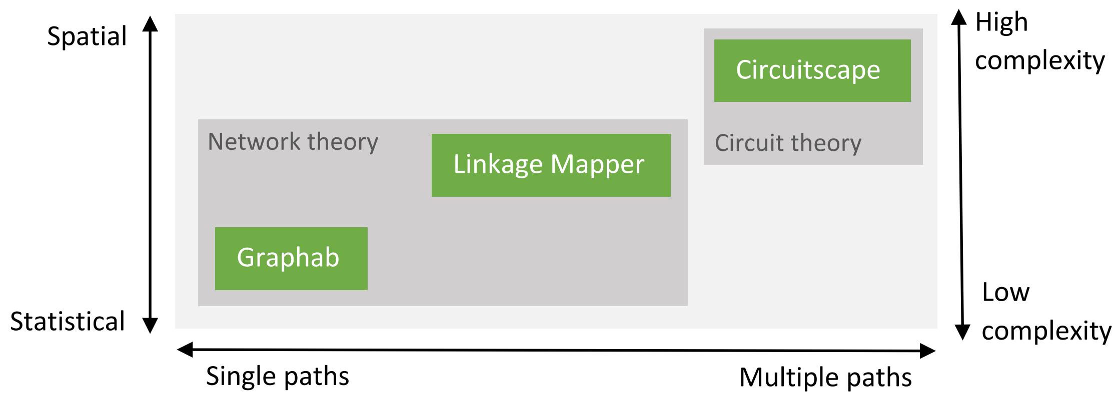


Fig. 1.1. The difference between Graphab, Linkage Mapper and Circuitscape in terms of spatial or statistical graph analysis, modelling of single or multiple paths, computational complexity and origin of theory.

The three tools can be placed along three different axes: spatial – statistical, number of paths and computational complexity (Fig. 1.1). Many early tools constructed graphs where habitats were represented as circles, connected through links in Euclidean distance (Rayfield et al. 2011). Later, graphs became more sophisticated and the link was based on movement costs, or so called friction value, of different land cover types – the least cost path (Rayfield et al. 2011). The least cost path is the route with the least cost from one habitat to another over a surface of friction values, showing the most likely dispersal link between habitats (Urban et al. 2009; Rayfield et al. 2011). Since a least cost path, contrary to a Euclidean path, has a certain spatial location depending on the land cover, it is possible to simulate multiple alternative paths between the same nodes (Fall et al. 2007). The habitat network at first primarily used statistical measures to describe connectivity, as for example number of links passing through each habitat patch as an estimation of its importance of connecting the network. Later this was extended with the geographical location and shape of the network, making way for its use in conservation planning of e.g. corridors (Fall et al. 2007). However, the use of multiple paths will often lead to higher computational complexity of the tools, mainly having the drawback of longer run time.

2.3 Technical background

Landscape analysis software has three main data inputs: the core habitats, dispersal distance of each species, and a raster file with friction values. The core habitats are patches between which dispersal is modelled, they are defined in this study as the essential habitat of a species. This means they contain all types of habitats necessary for all life stages of a species, and are large enough to sustain an individual.

A core habitat can be connected to all other core habitats, creating a complete graph, or to adjacent core habitats only, creating a planar graph (Fig. 1.2) (Fall et al. 2007). A complete graph might seem more realistic, but is both more difficult to visualise and requires longer computational time, therefore planar graphs are more often used (Fall et al. 2007). Each species' dispersal distance is used to remove links that connects core habitats above this limit, so that the graph show which core habitats are connected and which are isolated (Urban and Keitt 2001).

The friction value is an estimation of the difficulty for a species to move through a land cover type, higher value means more difficulty, and each cell in the friction raster is assigned a friction value. The raster can function as a graph, so that each raster cell centre is a node that can be linked to their four or eight neighbouring cell centres (Fig. 1.3) (Urban et al. 2009).

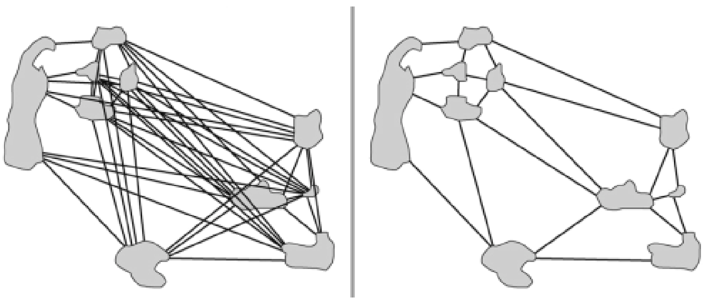


Fig. 1.2. The difference between a complete graph (left), where all core habitats are connected and planar graph (right), where only adjacent core habitats are connected. From Foltête et al. (2012).

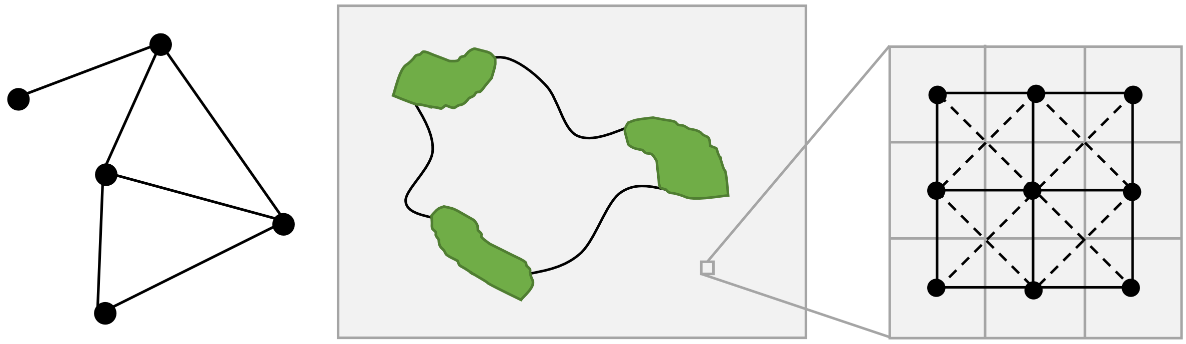


Fig. 1.3. A graph with links of Euclidean distance (left), a spatial graph with least cost paths connecting core habitats (middle), and the graph structure of the underlying friction raster cells (right) with connection of four neighbours (solid line) and eight neighbours (dashed line).

Dijkstra's algorithm (Dijkstra 1959) is commonly used in graph theory to find the shortest path between a start and end node. In the algorithm, the graph is stored in two matrices. The adjacency matrix stores distances between nodes that are connected, nodes that are not connected have zero distance (Worboys 1995). The state matrix is a dynamic matrix that is continuously updated with information about which nodes are visited, the current shortest distance from the start node, and which nodes this path goes through (Worboys 1995). When the end node is visited, the algorithm stops, and the shortest path from the start node to the end node can be derived from the state matrix (Worboys 1995).

On the friction raster graph, Dijkstra's algorithm is used to calculate the least cost path in cost distance or cumulative cost (Urban et al. 2009). The cost distance from cell A to cell B is calculated by *((friction of cell A* cell resolution) + (friction of cell B * cell resolution)) / 2* (ESRI 2016). When the path passes diagonally through two cells, the formula is multiplied by square root of 2 to compensate for the longer distance (ESRI 2016). For cumulative cost, the actual metric distance is not included, and the cumulative cost from cell A to cell B is calculated by *(friction of cell A + friction of cell B) / 2*, and this is the same for diagonal distances (Clauzel et al. 2016; ESRI 2016). The least cost path is calculated between all pairs of connected core habitats, with start and end nodes of the path located either on edges or centres of core habitats (Urban et al. 2009).

2.4 Graphab

Graphab was created by Jean-Christophe Foltête, Céline Clauzel and Gilles Vuidel in 2012 as a tool for integrating the visualisation of networks with calculation of connectivity measures (Foltête et al. 2012). The tool either creates a complete graph, connecting all core habitats or a planar graph (Clauzel et al. 2016). In a planar graph, Voronoi polygons (Fig. 1.4a) are created around the core habitats, defined by the distance from the core habitat edges in Euclidean distance (Clauzel et al. 2016). Any position inside the Voronoi polygon have to be closer to its generating object, in this case the core habitat edge, than to any other object, i.e. the edge of another core habitat (Fall et al. 2007).

The links connecting core habitats can be in either Euclidean distance or a least cost path, where the least cost path is calculated as a cumulative cost (Foltête et al. 2012). A link can later be removed if it is longer than the dispersal distance of a species (Foltête et al. 2012). Graphab is written in the programming language Java (Foltête et al. 2012).

2.5 Linkage Mapper

Linkage Mapper was developed by Brad McRae and Darren Kavanagh for the Washington Habitat Connectivity Working Group in a project concerning connectivity analyses over Washington State in 2010 (WHCWG 2010). The analyses were made at a large scale and included mainly mammals, many of which have long dispersal range.

Linkage Mapper is a toolbox in ArcGIS, written in the programming language Python, and uses mostly ArcGIS tools to create least cost paths and least cost corridors, which consists of multiple least cost paths. The options for construction a graph is either to connect all core habitats (a complete graph), or to only connect core habitats that are adjacent in Euclidean distance or in cost distance (a planar graph), by using ArcGIS tools "Euclidean allocation" and "Cost allocation" (Fig. 1.4b, c) (WHCWG 2010). "Euclidean allocation" allocates the landscape into polygons around each core habitat. The border of the polygons is the halfway distance between core habitats, so that all locations inside the polygon surrounding a core habitat are closer to that habitat than to any other, thus making it equivalent to Voronoi

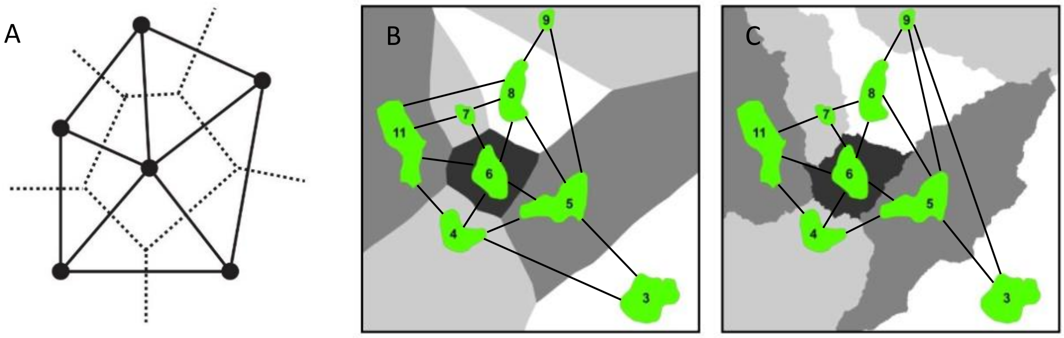


Fig. 1.4. A) A planar graph (solid lines) with connecting core habitats (dots), defined by Voronoi polygons (dashed lines). Only core habitats with Voronoi polygons adjacent to each other will be connected by a line. Figure from Urban et al. (2009). B) & C) Adjacency of core habitats by Euclidean distance (B) and cost distance (C). The grey areas surrounding habitats are used in the same way as Voronoi polygons, and adjacent habitats are connected with black lines. Modified from WHCWG (2010).

polygons used in Graphab. “Cost allocation” works in the same way, with the only difference that it uses cost distances instead of Euclidean distances.

Least cost paths and least cost corridors are created by first calculating the cost distance from all connected core habitats using the ArcGIS tool “Cost distance” (WHCWG 2010). The “Cost distance” tool creates a raster surface of the whole landscape, with a gradient of increasing cost distance starting from the edge of a core habitat. Least cost paths are first created with the help of the cost distance surface (WHCWG 2010). To find the least cost corridor between two core habitats, the cost distance raster of each of the two core habitats are added together, and then the least cost path length in cost distance is subtracted from all cells in the raster (WHCWG 2010). This creates a gradient raster surface with cost distance values ranging from 0 (the least cost path) and upwards (WHCWG 2010). Least cost corridors are created between all connected core habitats and are added together with the ArcGIS mosaic function (WHCWG 2010).

2.6 Circuitscape

Circuitscape was created by Brad McRae and Viral Shah in 2008 as an alternative to the common least cost approach. It is written in the programming language Python, first as a stand-alone software but later also available as a toolbox in ArcGIS (Shah and McRae 2008; McRae et al. 2013b). The theory was first set out to predict gene flow of species (McRae 2006), but has since been proposed also for conservation (McRae et al. 2008).

In the same way as when least cost paths are created, the friction raster in Circuitscape functions as a graph, where each cell centre is a node connected to neighbouring nodes with links (Shah and McRae 2008). But the difference is that the graph is interpreted as a circuit, and links have a friction value that combines the laws of electricity to estimate flow of animals (McRae et al. 2008; Shah and McRae 2008). In Ohm’s law, voltage V applied to a resistor R gives the current I through $I = V/R$, and correspondingly, a lower resistance in the landscape will give higher flow of animals (McRae et al. 2008). Kirchhoff’s law deals with effective resistance; when nodes are connected to several resistors the effective resistance will be the sum of the resistances: $\hat{R} = R_1 + R_2$ (McRae et al. 2008). In cases with parallel links, the effective resistance will be related to the number of links (Fig. 1.5), which means that the availability of multiple paths decreases the current (McRae et al. 2008).

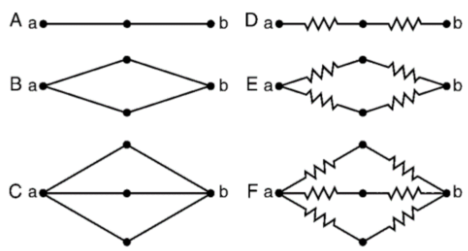


Fig. 1.5. If each link has the distance 1, the distance from node a to b in A, B and C will be 2 in all cases. If in D, E and F the resistance of each link is 1, the effective resistance from a to b in D is 2, in E 1 and in F 2/3. From McRae et al. (2008).

In each pair of core habitats, one core habitat is given a current source of 1 ampere and the other is connected to the ground (McRae et al. 2008). Effective resistance, voltage and current is then calculated over the landscape between the core habitats with Ohm's and Kirchhoff's laws (McRae et al. 2008). This is repeated between all habitat pairs, and the final map is produced by summing current values calculated between all pairs (McRae et al. 2013b).

2.7 Species background

The four species chosen as model organisms for the tools were hermit beetle (*Osmoderma eremita*), great crested newt (*Triturus cristatus*), red deer (*Cervus elaphus*) and spruce bark beetle (*Ips typographus*) (Tab. 1.1). Dispersal distance here refers to an individual's maximum capacity to spread to a new habitat, considering the area travelled between habitats are inhospitable except for shorter stops.

Tab. 1.1. The four species selected based on their varying dispersal range and habitat preferences.

Species	**Dispersal distance**	**Habitat preference**	**Type**
Spruce bark beetle *Ips typographus*	40 000 m	Stressed or wind-felled spruce trees	Specialist Long dispersing
Hermit beetle *Osmoderma eremita*	200 m	Old hollow trees, mainly oak	Specialist Short dispersing
Red deer *Cervus elaphus*	25 000 m	Dry deciduous forests	Generalist Long dispersing
Great crested newt *Triturus cristatus*	1300 m	Small ponds and wetlands connected to forests	Generalist Short dispersing

The hermit beetle lives in old hollow trees, mainly oak trees (*Quercus* spp.), and the larvae develops inside the tree consuming the trunk wall (Antonsson and Karlsson 2014). The beetle occurs in the south of Sweden, often in pasture woodlands; a type that is now declining significantly since the 19th century and becoming increasingly fragmented (Antonsson and

Karlsson 2014). The beetle is short dispersing, and few individuals leave the tree where they hatched (Antonsson and Karlsson 2014). The longest measured dispersal in Sweden is 500 m, but a majority of the dispersing individuals migrate between 50-100 m (Antonsson and Karlsson 2014). The hermit beetle is classified as near threatened by the IUCN, and its specific environment is also home to several other red listed species, making it an indicator species (Antonsson and Karlsson 2014).

The great crested newt inhabits most of Europe, including large parts of Sweden, but although widespread it is seldom common, and populations are declining (Malmgren 2007). The main habitat for the species is agricultural or cultural landscapes that are characterised by a mosaic of pasture, deciduous forest, and fish free wetlands and ponds (Malmgren 2007). The newt lives on land for most of the year, but need access to water during breeding (Malmgren 2007). Individuals can disperse as long as 1300 m from their pond, but more commonly they search for land habitat within a range of 50-200 m (Malmgren 2007). Since the great crested newt needs both water and land habitat that is beneficial for many species, it is considered an umbrella species and might also be used as an indicator of high biodiversity (Malmgren 2002; Malmgren 2007).

The red deer population in Sweden is scattered across the country, but with a concentration in the south (Naturvårdsverket 2015). The species prefers open land for foraging, and shelter forests during daytime (Jarnemo 2014). Females are, contrary to males, reluctant to leave their home range, and the species is therefore relatively stationary (Naturvårdsverket 2015). Female home range sizes in Scania, south Sweden, vary from 815 to 3391 ha (Jarnemo 2014), although studies in other places in Europe have shown home ranges as small as 80 ha (Kropil et al. 2014). The large differences regarding home range size are partly due to the type of landscape studied, and in some cases the animal shifts between more than one separate habitat patch (Jarnemo 2014). The red deer disperse seasonally between rutting areas and summer or winter habitat, and a study in Scania by Jarnemo (2008) shows that the majority of the dear dispersed 25 km or less, with a mean distance of 13.9 km.

The spruce bark beetle is native to Europe and Siberia, and a major pest in spruce forest, since it infests the bark of the spruce tree – however it is a keystone species in natural ecosystems, since it is part of the degradation of dead trees (Wermelinger 2004). Spruce bark beetles attack sun-exposed, stressed trees, for example after a drought or wind-fell (Wermelinger 2004). The infestations are often small areas spread across the landscape (Kärvemo et al.

2014). Outbreaks can occur after large disturbances, for example a storm event (Wermelinger 2004). In outbreaks, new attacks are commonly spread 0-500 m from old attacks (Wichmann and Ravn 2001), and the high population enables the species to infest healthy stands nearby, that normally resist attacks (Wichmann and Ravn 2001; Wermelinger 2004; Kärvemo et al. 2014). The maximum flight of the spruce bark beetle is not well known, but when tested in a wind tunnel, about 90% could fly up to 20 km, and the longest flight recorded was 45 km (Forsse and Solbreck 1985; Byers 1996).

3. Methods

3.1 Selection of species and study area

Species were chosen based on their dispersal distance and habitat preference, with one long and one short dispersing generalist, and one long and one short dispersing specialist. Based on the available expert knowledge and previously used friction values the species chosen were spruce bark beetle, *Ips typographus* (long dispersing specialist), hermit beetle, *Osmoderma eremita* (short dispersing specialist), red deer, *Cervus elaphus* (long dispersing generalist) and great crested newt, *Triturus cristatus* (short dispersing generalist) (see Tab. 1.1).

The study area is situated in the south of Sweden, mainly in Sjöbo municipality (Fig. 2.1). It was chosen because of its varied landscape with lakes, urban areas, roads and several vegetation types, including potential habitat for each species. All species were found present in the area based on reports of the red deer, hermit beetle and great crested newt through the web site Artportalen (Artportalen 2016) and spruce bark beetle monitoring in the region (Lindelöw 2010).

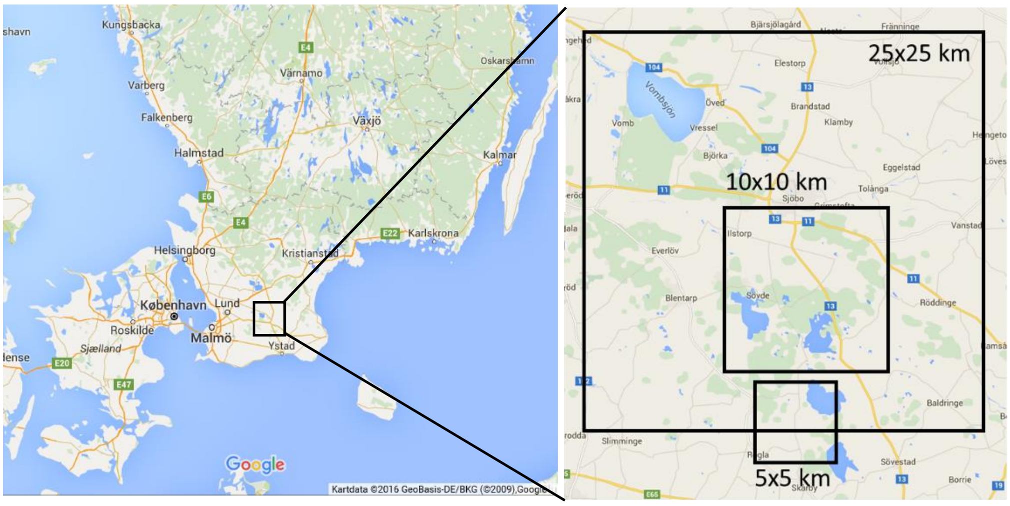


Fig. 2.1. The study area, in south of Sweden, including the three different sized landscapes that were used. Maps from Google Maps.

3.2 Data sources

The GIS layers data were obtained from four sources. The land cover was received from Metria's land cover classification over Sweden which was used to create maps of vegetation types in nature reserves in Sweden (Jönsson 2009). Water surfaces and watercourses used were from the Swedish Meteorological and Hydrological Institute (SMHI 2012), and in addition small ponds were derived from the Swedish Land Survey (Lantmäteriet 2016). Road data were acquired from the Swedish Transport Administration (Trafikverket 2016).

All GIS data were either converted to or originally in Sweref 99 TM projection. Since the land cover data were in a 10x10 m resolution, this resolution was kept for all analyses. The raster format used was GeoTIFF, since this format was accepted by all three tools in this study. All preparations of GIS data were carried out in ArcGIS (Version 10.2; ESRI 2011).

3.3 Creating friction raster

Friction values for all species except the spruce bark beetle were derived from values used by Calluna. The eight friction classes used for the great crested newt and hermit beetle were chosen as standard values: 1 (habitat), 2, 5, 9, 15, 20, 100 and 1000 (barrier). Fiction values for the red deer were higher than for other species, and were therefore adopted to corresponding values in the eight classes mentioned above. Friction values were not available from Calluna for the spruce bark beetle so new values were based on literature findings and expert opinion (Jönsson, pers. comm.) to fit into the same eight friction classes. All friction values can be seen in Tab. 2.1.

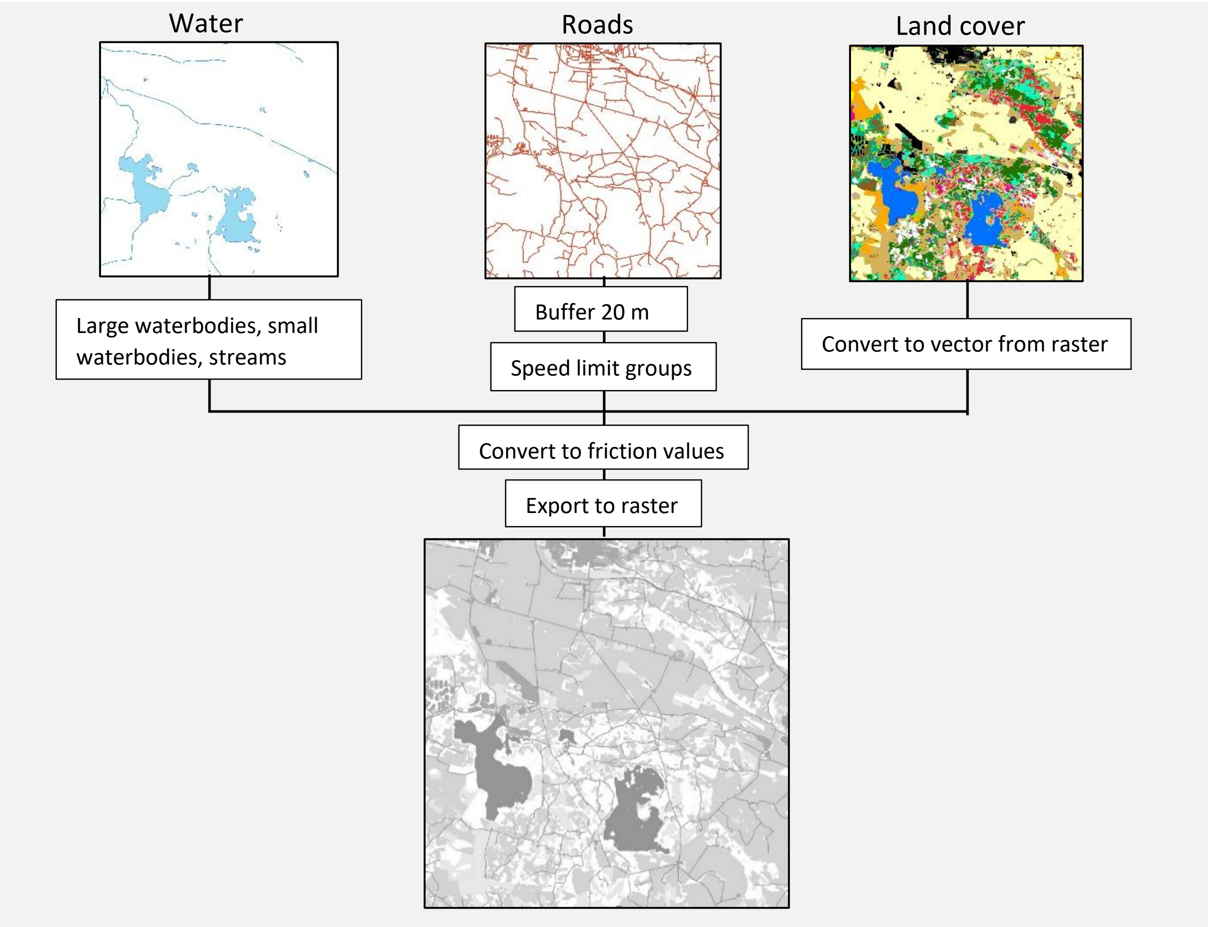
To create the friction raster (Fig. 2.2), all GIS layers were first clipped to fit the study area. The freshwater was separated into three categories, large waterbodies, streams and small waterbodies, and these were given different friction values due to their different functions. Large waterbodies will often function as a barrier, while small waterbodies are habitat for the great crested newt. Since the land cover data did not distinguish between different freshwater, vector data of lakes from SMHI were used as a reference to select and separate lakes in the land cover data and from other freshwater. Streams were then manually selected from the land cover data to separate them from other freshwater. Streams that were not present in the land cover data were added from vector data of streams from SMHI, with a buffer of 6 m. The remaining freshwater in the land cover data made up the group of small waterbodies, together with small ponds from the Swedish Land Survey map that were not recorded in the land cover data.

All roads were buffered to a width of 20 m. The roads were separated into groups depending on the speed limit, since roads with higher speed limit lead to higher mortality for crossing animals, these are given a higher friction value. The speed limit groups were 50-60 km/h, 70-80 km/h and over 80 km/h. Roads below 50 km/h were not included, since they were only present in urban areas, and all roads in urban areas were removed. The different parts were merged together, assigned a species specific friction value depending on group and exported to raster format for each species.

Tab. 2.1. Friction values for all species. 1) Sand and rocky areas, 2) Only water bodies from land use data and the Swedish Land Survey, 3) Only water bodies from SMHI data, 4) Only water courses: streams and rivers.

Land cover	**Red deer**	**Hermit beetle**	**Great crested newt**	**Spruce bark beetle**
Pine forest	2	9	5	5
Spruce forest	2	9	5	1
Mixed coniferous forest	2	9	2	2
Wet coniferous forest	2	9	1	2
Mixed forest (coniferous and deciduous)	2	9	1	5
Deciduous forest	1	9	1	9
Valuable deciduous forest	1	1	1	9
Deciduous forest with valuable deciduous forest	1	1	1	9
Wet deciduous forest	1	9	1	9
Young forests and clear cuts	1	9	5	9
Low production or sparse forests	5	2	1	9
Wet low production forests	9	2	1	9
Low production forests, sparse forests, young forests and/or clear cuts	2	2	5	9
Wetland	9	2	1	9
Peat mining	15	9	20	9
Agricultural land	9	2	5	9
Meadow	2	1	1	9
Pasture	9	1	1	9
Barren land[1]	15	2	5	9
Open areas excluding meadows and pasture	15	1	2	9
Exploited area	100	15	15	15
Recreation facility	15	2	9	9
Freshwater, small water bodies[2]	2	2	1	9
Freshwater, large water bodies[3]	20	15	20	9
Freshwater, watercourses[4]	2	2	5	excluded
Road >80 km/h	1000	15	1000	9
Road 70-80 km/h	15	9	20	excluded
Road 50-60 km/h	9	9	15	excluded

Fig. 2.2. The different steps in the process of making the friction raster.



3.4 Identifying core habitats

Core habitats are set to represent a species home range, and will typically encompass species requirements in all stages of their life cycle. In some cases, this has been simplified to reduce computer processing time. The core habitats of generalist species (red deer and great crested newt) were based on land cover, while the habitat requirements of the specialist species (hermit beetle and spruce bark beetle) needed additional data to be captured (Tab. 2.2).

The habitat (all land cover with friction value 1) of the great crested newt was separated into land and water habitat. Wetlands and freshwater, excluding watercourses or larger lakes were regarded as water habitat. All water habitat within 50 m of any of the land habitat was used as core habitat, since water is vital for the reproduction of the species. Areas sharing a border were merged into one, and since the species is unlikely to colonise ponds smaller than 10 m in diameter (Malmgren 2002), areas with the size of one pixel (10x10 m) were removed. The species also avoids ponds with predatory fish (Malmgren 2002), therefore water habitat in close proximity to larger lakes was removed since they were likely to contain predatory fish.

For the red deer all land cover with friction value 1 was used, but this generated a large number of polygons (>5000 in the largest scale, see Tab. 2.3), which would not be possible to run with the software. Many of the polygons were situated in clusters, and therefore polygons were aggregated within a distance of 50 m to generate larger connected areas. Areas with friction values of 100 and 1000 were set as a barrier over which polygons would not be joined, to avoid core areas containing barriers. Home ranges of red deer vary widely depending on region, and in lowland areas with few predators, as is the case with this study area, home ranges tend to be small (Kropil et al. 2014). A collection of home range sizes from different studies shows that the smallest home range of red deer was 80 ha (Kropil et al. 2014), therefore polygons smaller than this were removed.

The core habitat of the hermit beetle was based on coordinate points at locations of hollow old oak trees registered in the Tree portal (Trädportalen 2016). The coordinates were imported as a GIS point layer and buffered to 20 m in diameter to represent the area of a tree.

It was difficult to find spatial data over wind felled spruce trees in the study area that could be used as core habitat for the spruce bark beetle, instead the core habitat was estimated based on a large storm over parts of south Sweden in 2005 (Fridh 2006). Information on volume spruce trees damaged in the storm in Skåne from Fridh (2006) was used to estimate the amount of wind felled spruce in hectares. The percentage wind felled spruce during a large storm was estimated by dividing the hectare wind felled spruce in Skåne with the total hectare spruce forest in Skåne in 2005. This percentage, 5%, was used to calculate total hectares of wind felled spruce forest in the study area. The total hectare spruce forest in the study area was calculated in ArcGIS and 5% of this, 57.5 ha, was the wind felled forest, i.e. the total core habitat area. “Random point” tool in ArcGIS was used to generate 50 random points in the areas with spruce forest in the study area. The points were buffered until their collective area was approximately 57.5 ha.

Tab. 2.2. Methods used to identify core habitats for the different species.

Species	Method of identifying core habitat
Great crested newt	Water with friction 1 within 50 m of land with friction 1 Remove habitat with size of 1 pixel ($100 m^2$) Remove water close to large waterbodies
Red deer	Land cover with friction 1 Aggregate habitats within 50 m of each other Remove habitats smaller than 80 ha
Hermit beetle	Hollow oak trees (points) buffered 20 m in diameter
Spruce bark beetle	50 random points in spruce forest Buffer points until total area is equal to estimated wind fell during a large storm

3.5 Landscape connectivity modelling

Three different scales were used in the modelling: 5x5 km, 10x10 km and 25x25 km (Tab. 2.3). Since Circuitscape crashed at 25x25 km scale, only Linkage Mapper and Graphab were used at this scale. The 25x25 km scale was only used for the long range species, the 5x5 km scale only for the short range species, and the 10x10 km scale for all four species.

Tab. 2.3. Construction of the analyses by scale, species and software.

Scale		**5x5 km**	**10x10 km**	**25x25 km**
Short range	*Specialist*	Hermit beetle	Hermit beetle	N/A
	Generalist	Great crested newt	Great crested newt	N/A
Long range	*Specialist*	N/A	Spruce bark beetle	Spruce bark beetle
	Generalist	N/A	Red deer	Red deer
Software		Linkage Mapper, Graphab, Circuitscape		Linkage Mapper, Graphab

Depending on software the input file formats were different (Tab. 2.4). All software used a friction raster (GeoTIFF format), but in Graphab a single raster file containing both information about friction values and core habitats was required as input. The cells in the raster file that represented core habitats were given value 0 to separate them from other areas. In Circuitscape the core habitats were in raster format, while in Linkage Mapper the core habitats were in vector format (ESRI shapefile). As required by Linkage Mapper, Conefor input toolbar (Jenness 2016) in ArcGIS was used to calculate distances between core habitat edges, with each species' dispersal distance as the threshold, before Linkage Mapper could run. After each tool run, the time it took was noted.

In this study, the software options were selected to generate comparable outputs from the three tools (Tab. 2.4). In both Linkage Mapper and Graphab, the links between core habitats were constructed as a planar graph with Euclidean adjacency between connected core habitats. Link distances were always measured from core habitat edges, and the calculation of the least cost paths were done by connecting all eight neighbours of a cell in the friction raster. In Linkage Mapper and Graphab, links that cross a core habitat were removed, this is often done since a link crossing a core habitat is the same as a link going to and from the core habitat.

Graphab does not distinguish between different core habitats with an ID as in Linkage Mapper and Circuitscape, but instead the program defines core habitats from a "landscape map", in which a certain landscape type can be selected as the species' habitat (Clauzel et al. 2016). The habitat patch can then be constrained by choosing a minimum area, include diagonal cells (8-connexity) or not (4-connexity) as part of a habitat patch, and the patch shape can also be simplified (Clauzel et al. 2016). To keep the core habitats as similar as possible to the original file, 8-connexity of the habitat was chosen (so that cells situated diagonally will be included in the same core habitat), with a minimum patch area of zero (to include all core habitats), and the option to simplify the habitat was left unchecked. Graphab also uses cumulative cost instead of cost distance, but the friction value was multiplied by 10 to estimate the cost distance, since the resolution of the friction raster was 10x10 m. The option of using bounding circles buffer in Linkage Mapper reduces run time, since the least cost corridor raster output is cut to a specified buffer area calculated from the centre of all core areas (McRae and Kavanagh 2014). Bounding buffer was chosen at the same distance as each species' dispersal distance.

In Circuitscape, the modelling mode chosen was one-to-all, in which one core habitat is connected to a current source of 1 ampere and the rest are connected to the ground, which is then iterated through all core habitats (McRae et al. 2013b). In pairwise mode, all pairs of core habitats are calculated separately; this is similar to calculating least cost path, but one-to-all is much faster (McRae et al. 2013b). Current maps were chosen as output with log transformed values to enhance the visibility.

Tab. 2.4. Different options of each software, the options chosen in the analyses are underlined.

Type of option	Graphab	Linkage Mapper	Circuitscape
Input	*Habitat and friction*: raster file	*Habitat*: vector file *Friction*: raster file *Distance file*	*Habitat*: raster file *Friction*: raster file
Unit	Cumulative cost / Least cost path distance / Euclidean distance	Cost distance	Current / Voltage
Thresholding	Cumulative cost / Least cost path distance / Euclidean distance	Cost distance / Euclidean distance	N/A
Graph topology	Planar / Complete	Planar / Complete	N/A
Core habitat adjacency	Euclidean	Cost-weighted / Euclidean / Cost-Weighted & Euclidean	N/A
Measured from	Edge	Centre / Edge	Edge
Neighbours	8	8 / 4	8 / 4
Modelling mode	N/A	N/A	Pairwise / one-to-all / all-to-one / advanced
More options	- Remove links crossing core habitat - Patch connexity: 4/8 - Minimum patch area - Simplify patch	- Remove links crossing core habitat - Bounding buffer	- Log-transform values

3.6 Sensitivity analysis

Graphab and Linkage Mapper were compared in a sensitivity analysis by counting the number of links generated depending on different parameter settings. The original settings of dispersal distance, one where the distance was increased by 20% to represent the best case in terms of species dispersal abilities, and one where it was decreased by 20% to represent worst case (Tab. 2.5). The difference of ±20% of values represent a reasonable variation and gives a uniform comparison between all species. The same was done with friction values, with one worst case scenario (higher than usual friction values) and one best case scenario (lower than usual friction values) (Tab. 2.6).

Tab. 2.5. Sensitivity analysis of dispersal distance in meters, best case with 20% increase in dispersal length and worst case with 20% decrease in dispersal length.

Species	Best estimate	Best case	Worst case
Hermit beetle	200	240	160
Great crested newt	1300	1560	1040
Spruce bark beetle	40 000	48 000	32 000
Red deer	25 000	30 000	20 000

Tab. 2.6. Sensitivity analysis of friction values, in the best case friction values were lower and in the worst case friction values were higher than original values.

Friction class	Best case	Worst case
1	1	1
2	1	5
5	2	9
9	5	15
15	9	20
20	15	100
100	20	1000
1000	100	10000

In Circuitscape, pinch points are areas with high current. The pinch points are used to identify areas with high flow of animals, as these could be areas that are important for connectivity (McRae et al. 2008). The concept of pinch points was used in this study to compare Linkage Mapper and Circuitscape, by finding out how much of the pinch points was covered by the least cost corridor created in Linkage Mapper, as has previously been done by Rose (2013). Since Circuitscape models have unlimited dispersal distance, to be able to compare the two tools, corridors in Linkage Mapper were used without a limit in dispersal distance, i.e. all core habitats were connected.

There is no standard threshold that defines a pinch point, therefore 25% of the upper current values were used as pinch points, as suggested by Rose (2013). Values above zero cover core habitats, and by excluding these, only the currents flowing from and to core habitats were visualised. To account for differences in histogram distribution of values in the raster image, ±2.58 standard deviations (99% of all values) were used to create a window where most of the values were located (Fig 2.3). Inside of this window, a threshold value was created at 25% of the upper limit.

The least cost corridor generated in Linkage Mapper is a raster image with a gradient of cost distance above the least cost path (McRae and Kavanagh 2014). By using different cut-offs, the width of the corridor can be modified. A cut-off of zero cost distance will give all possible least cost paths. Since the corridor is affected by the friction values, this means that with the same cut-off value the width of the corridor will be different for different species, and it will also become narrower when passing areas of high friction and wider when passing areas of low friction (WHCWG 2010). A corridor cut-off value of 250 cost distance was chosen as a standard, since this gave a reasonable corridor width for all species.

Tab. 2.7. Combinations of thresholds of pinch point in Circuitscape and corridor cut-off in Linkage Mapper.

Pinch point & corridor thresholds	200	250	300
20%	20% & 200	20% & 250	20% & 300
25%	25% & 200	25% & 250	25 % & 300
30%	30% & 200	30% & 250	30% & 300

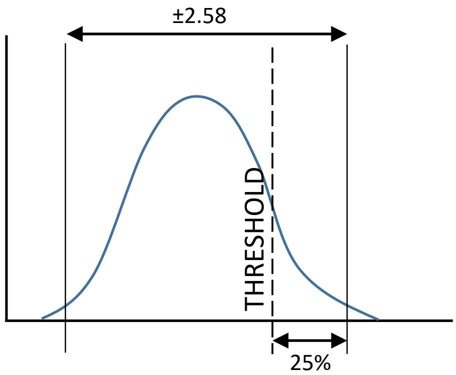


Fig. 2.3. The construction of the threshold of pinch points in Circuitscape from the raster image histogram.

The raster images from Circuitscape were reclassified so that all cells with a value above the pinch point threshold were set to 1 and all cells with a value below the threshold were set to 0. The least cost corridors from Linkage Mapper were reclassified so that all values below 250 were set to 1, and the values above were set to 0. “Zonal Statistics” in ArcGIS were used to calculate the percentage of the pinch point in Circuitscape located inside Linkage Mapper’s least cost corridor.

The same procedure was done using pinch points at a threshold value and corridor cut-off at 20% less and more. All nine combinations with a corridor threshold of 200, 250 or 300 and a pinch point threshold of 20%, 25% or 30% were calculated with “Zonal statistics” (Tab. 2.7).

In both sensitivity analyses, mean over the three scenarios was used, and to find the variation a confidence interval of 95% was calculated on the mean. The mean was used to give a better estimation of differences between different tools and species than a single value would have done. The variation shows how sensitive a tool is to changes in parameter settings, a larger variation means a tool is more sensitive.

4. Results

Circuitscape creates a surface of current, Linkage Mapper creates links and corridors, and Graphab creates links (Fig. 3.1). Links between short dispersing species were difficult to see at larger scales, and long dispersing species at scales smaller than their dispersal distance connected all habitats. The different analyses show similar patterns of connectivity, although Linkage Mapper (Fig. 3.1b), compared to Graphab (Fig. 3.1a), shows possible passages between habitats that are not linked by a least cost path. In Circuitscape (Fig 3.1c) it is even clearer where possible paths are located between unconnected habitats, and these areas could for example be improved by reserving and restoring land.

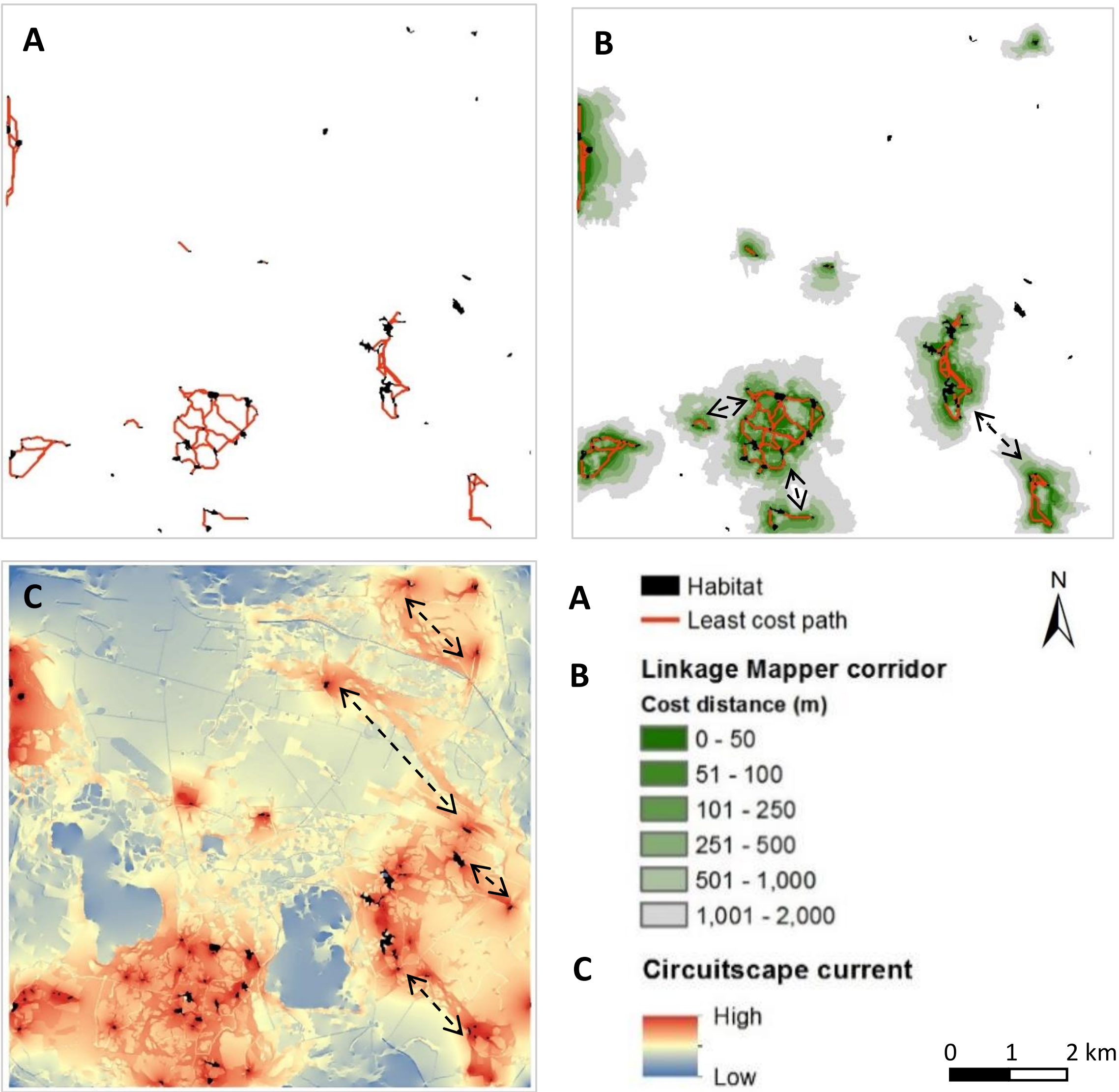


Fig. 3.1. Great crested newt at a scale of 10x10 km modelled in (A) Graphab, (B) Linkage Mapper and (C) Circuitscape. The dashed arrows highlight possible passages for the newt, between habitats that are not connected with least cost paths.

The least cost path of Graphab did not always coincide with Linkage Mapper's least cost path, but often overlapped with the least cost corridor at zero cost distance, which shows all possible least cost paths (Fig. 3.2). Resulting maps from all analyses with Linkage Mapper and Graphab can be seen in Supplemental Figures S1-S2, and analyses with Circuitscape in Supplemental Fig. S3.

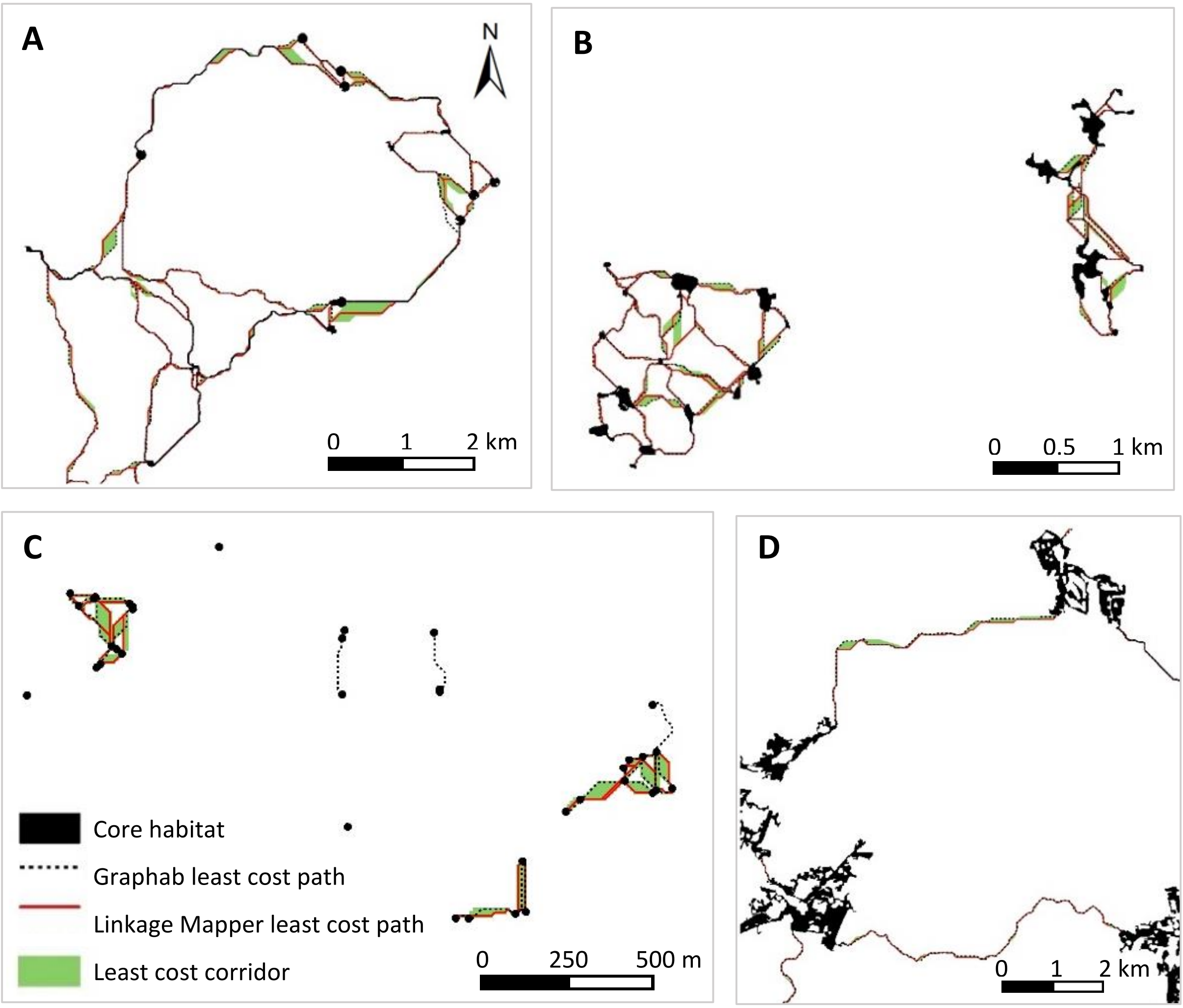


Fig. 3.2. Maps of A) spruce bark beetle, B) great crested newt, C) hermit beetle and D) red deer, with least cost paths from both Linkage Mapper (red) and Graphab (black dashed), and all possible least cost paths in green. The maps are details of complete analyses, at different scales.

4.1 Efficiency

The analyses showed a trend with longer run time at larger scales (larger number of cells), and also with more core habitats and links (Tab. 3.1). A resolution of 10x10 m resulted in 6.25 million cells in 25 km scale, 1 million cells in 10 km and 250 000 cells in 5 km. Number of links will partly depend on number of core habitats and partly the dispersal distance of a species; long range species will connect more core habitats and generate more links.

Tab. 3.1. Different run times of the programs. Note that run time increases with scale but also with number of core habitats and links.

Scale (cells)	**Species**	**No. core habitats**	**No. of links G/LM**	**Graphab**	**Linkage Mapper**	**Circuitscape**
5x5 km	Hermit Beetle	44	30/33	~ 1 s	7 min	6 min
(0.25 mil)	Great crested newt	12	6/6	~ 5 s	3 min	2 min
10x10 km	Hermit Beetle	76	50/63	~ 5 s	13 min	44 min
(1 mil)	Great crested newt	73	87/94	~ 10 s	18 min	44 min
	Spruce bark beetle	23	41/43	~ 5 s	12 min	11 min
	Red deer	3	10/2	~ 10 s	2 min	3 min
25x25 km	Spruce bark beetle	50	85/86	~ 30 s	46 min	N/A
(6.25 mil)	Red deer	20	42/29	2 min	25 min	N/A

The run time was longer at larger scales, especially Circuitscape was sensitive to large areas and would crash at 25x25 km scale. Graphab was much faster than the others, and seemed to be mainly affected by number of habitats. Linkage Mapper was probably also more affected by number of habitats than the extent of the area, but this was linked to whether dispersal distance and bounding buffers were used. Linkage Mapper was slower than Circuitscape at smaller scales, but faster at larger scales.

4.2 Least cost paths

Graphab and Linkage Mapper generated similar number of links, except in the case of red deer where Graphab consistently generated more links than Linkage Mapper (Fig. 3.3 and 3.4). The sensitivity analysis of altered dispersal distance, showed the most variation in analysis with the hermit beetle and great crested newt at 10x10 km scale (Fig. 3.3). When friction values were changed, great crested newt at 10x10 km scale and spruce bark beetle at 25x25 km scale showed the largest variation. Often the variation was larger when friction values were changed compared to when dispersal distances were changed (Fig 3.4). In general, it seemed like the variation became greater at larger scales. For the two long dispersing species at 10x10 km scale, all core habitats were connected, therefore no links could be added when friction values were reduced or when dispersal distances were extended.

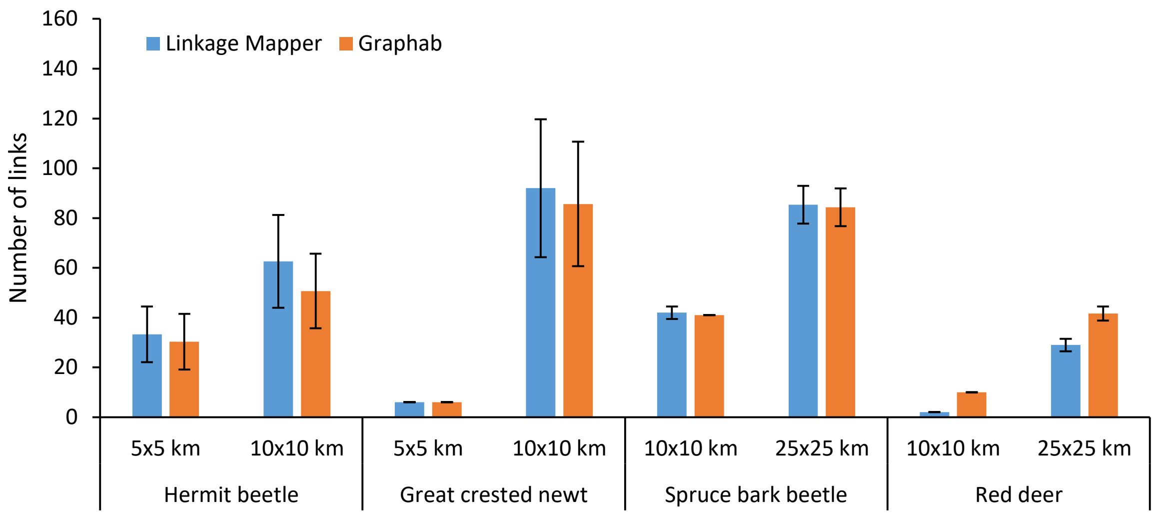


Fig. 3.3. Number of links, mean over 3 scenarios of different dispersal distances, with 95% confidence interval.

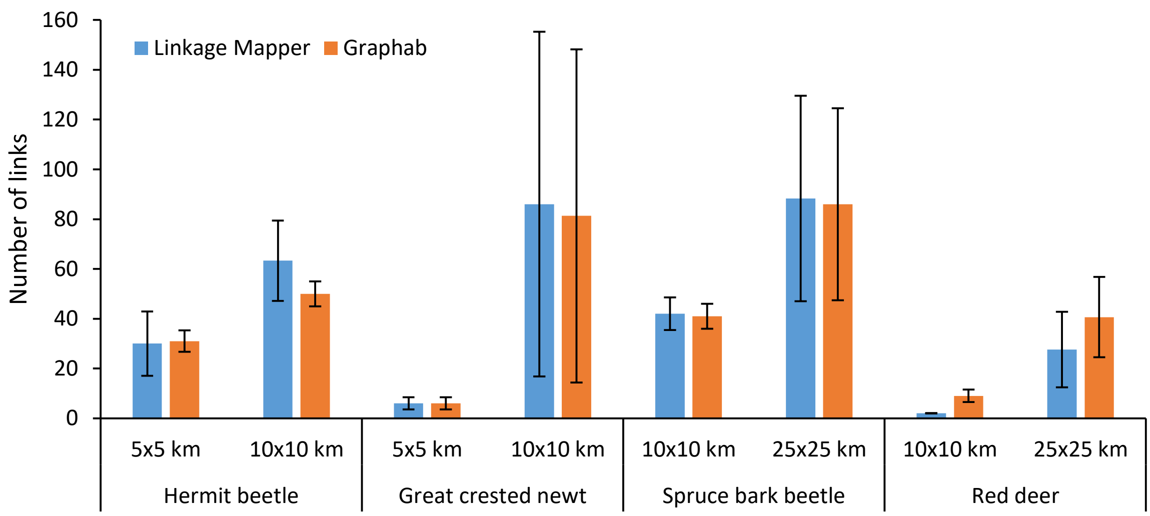


Fig. 3.4. Number of links, mean over 3 scenarios of different friction values, with 95% confidence interval.

4.3 Pinch points and corridors

For most species, the overlap of pinch points and corridors were over 50%, but the results from the red deer were always below 50% (Tab. 3.2). The highest coverage in percentage was found for the hermit beetle at 5x5 km scale. The shorter dispersing species had overall higher overlap. Percentages seem to be affected by scale, but not in a uniform way since the hermit beetle showed higher percentages in the smaller scale while the opposite was true for the great crested newt. The result can be seen as a map in Fig. 3.5, in which the corridor of the hermit beetle is wider than for other species, and the corridor for the red deer is very short. For maps for all species, see Supplemental Fig. S4.

Tab. 3.2. Sensitivity analysis of Circuitscape pinch point and Linkage Mapper corridor. The values represent the percentage of the pinch point area covered by a corridor.

Corridor cut off	Pinch point	Hermit beetle 5x5 km	Hermit beetle 10x10 km	Great Crested newt 5x5 km	Great Crested newt 10x10 km	Bark beetle 10x10 km	Red deer 10x10 km
	20%	96.8	79.1	81.7	90.1	64.1	19
200	25%	94.3	71.6	70.1	83.8	52.5	43.2
	30%	88.8	64.9	62.7	75.8	40.4	12.7
	20%	98.4	82.7	85.1	92.9	68	19
250	25%	96.6	75.6	74.3	87.7	56.2	45.9
	30%	92.4	69	67	80.7	43.7	13.9
	20%	99.3	85.8	87.8	94.9	71.3	19.5
300	25%	97.9	79.3	77.8	90.9	59.6	48.7
	30%	94.4	72.9	70.7	85	47.3	14.9

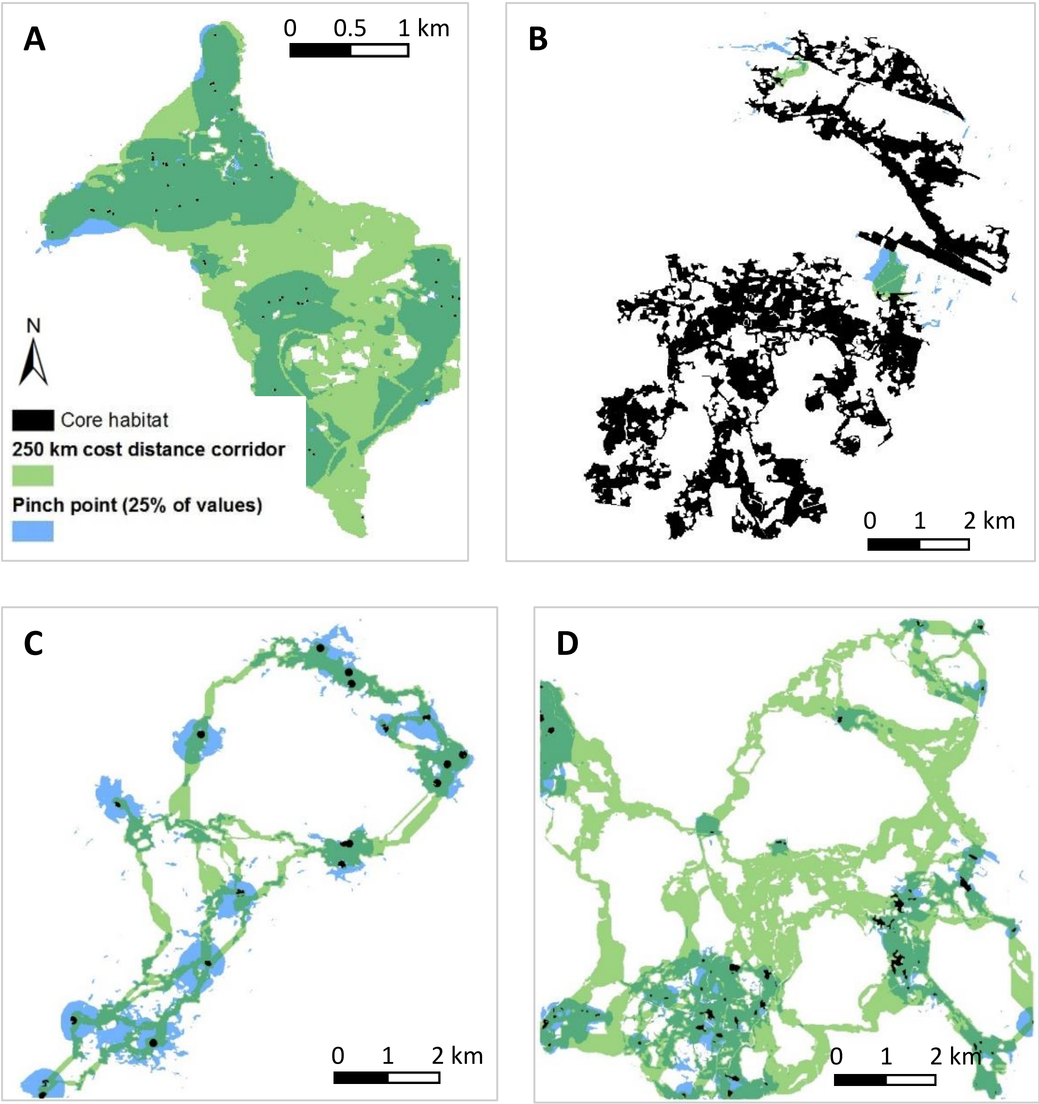


Fig. 3.5. Pinch points in blue (25% threshold) and corridors in green (cut off at 250 m), darker green are where the two overlap. Models show (A) hermit beetle, 5x5 km scale, (B) red deer, 10x10 km scale, (C) spruce bark beetle, 10x10 km scale and (D) great crested newt, 10x10 km scale.

When the corridor cut-off was kept fixed and the pinch point threshold was changed, there was a larger variation in percentage (Fig. 3.6) than if the pinch point threshold was kept fixed and the corridor cut-off was changed (Fig. 3.7). This means that a change in corridor cut-off (200, 250 or 300) only changed the width of the corridor very little. The area of high current representing pinch points on the other hand changed much more in size between its respective thresholds.

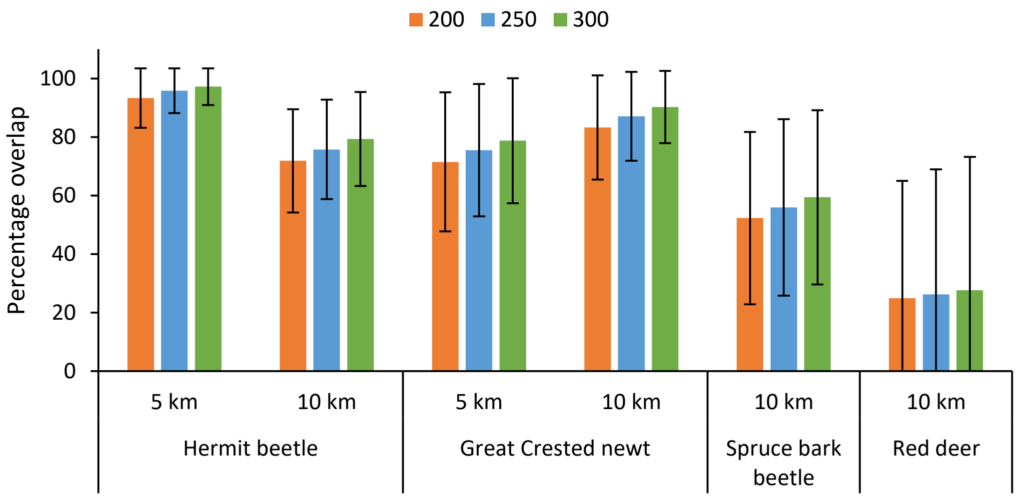


Fig. 3.6. The Linkage Mapper corridor is fixed at 200 (red), 250 (blue) and 300 (green), and the error bars show the 95% confidence interval with different pinch point thresholds (20%, 25%, 30%) at the same corridor width.

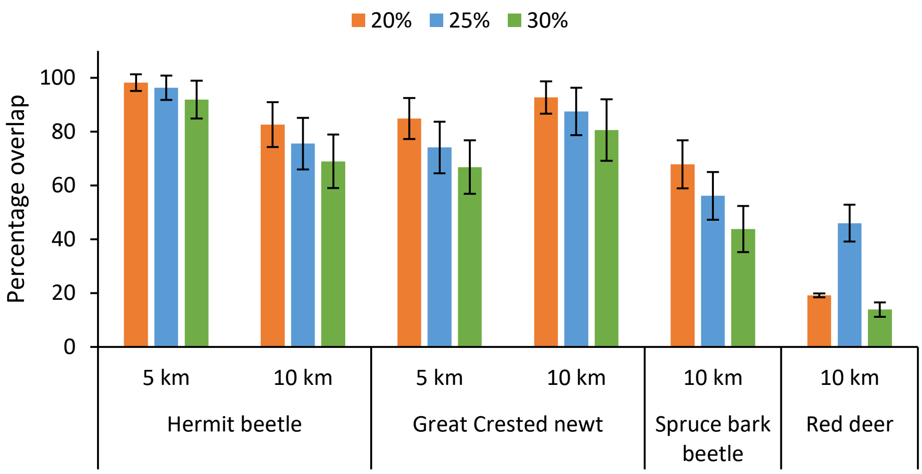


Fig. 3.7. The Circuitscape pinch point threshold is fixed at 20% (red), 25% (blue) and 30% (green), and the error bars show the 95% confidence interval with different corridor width (200, 250, 300) at the same pinch point threshold.

5. Discussion

5.1 Spatial and visual differences

The different programs will provide different results visually and spatially, and the differences are important to know when deciding which program to use. Both Graphab and Linkage Mapper are developed based on network theory, and are therefore similarly built. Dijkstra's algorithm is used to find the path with the least cost between connected habitats in both Linkage Mapper and Graphab, but the results in this study show that the location of the least cost paths was not always identical (e.g. Fig. 3.2). This is because there is often more than one path of equal cost, but only one of these paths will be selected, which is selected depends on in which order the paths are evaluated by the algorithm. Different methods have been proposed to incorporate all possible least cost paths, such as the Conditional Minimum Transit Cost and the Multiple Shortest Paths (Pinto and Keitt 2009). Linkage Mapper finds all possible paths and their cost over the landscape, and can therefore show all least cost paths if the cost distance cut-off is set to zero. The corridor provides a more robust result than the least cost path, since it shows alternative pathways. Circuitscape gives a completely different visual result, instead of mapping links or corridors between habitats it shows the flow of animals over the whole landscape.

5.2 Difference in run time

The performance of a tool is often crucial when choosing it, since a fast running tool will save money and allow for several runs where different parameters can be tested. In this study, it was clear that Graphab had the shortest run time, Circuitscape had shorter run time than Linkage Mapper at small scales but rapidly increasing run time at larger scales (Fig. 3.1). The run time is dependent on two main factors: the scale of the landscape (number of cells) and number of habitats. Scale influences run time because the least cost path is calculated on a graph where each node corresponds to a cell in the friction raster, and larger spatial scale generates more nodes, thus longer calculation time (Urban et al. 2009; McRae et al. 2008; Shah and McRae 2008).

In Linkage Mapper, the calculation of least cost corridors and the least cost paths is based on the calculation of cost weighted distance from habitats (McRae and Kavanagh 2014). The cost weighted distance finds the cost of travelling from the edge of the core habitat to each cell in the landscape and is therefore influenced by scale. Runtime can be reduced by using bounding circles, in which cost weighted distance is calculated only within a radius of a specified distance from the core habitat centre (McRae and Kavanagh 2014). The run time results (Tab. 3.2) show that the analysis from Linkage Mapper of the short dispersing hermit beetle at 10x10 scale took 13 minutes, while the long ranging spruce bark beetle in the same scale took 12 minutes for a third of the number of core habitats. The hermit beetle analysis was done using a bounding buffer of 200 m, while no bounding buffer was used for the spruce bark beetle.

Only the least cost path is calculated in Graphab; and Dijkstra's algorithm ends when the end node (a node at the edge of a core habitat) is visited and does not continue to calculate cost over all other nodes (Worboys 1995), and scale is therefore of less importance for the run time. The algorithm will find the least cost path between a start and end node, and with each new start or end node the process has to be repeated (Worboys 1995). Since least cost paths are calculated from the edge of the core habitat, longer edge generates more end and start nodes between core habitats, thus resulting in longer run time. This is evident when looking at the difference in run time for Graphab between spruce bark beetle and red deer, the red deer has less than half the number of habitats but four times as long run time (see Tab. 3.1).

The early version of Circuitscape, written in MATLAB programming language, could take three days to run on a moderate sized landscape with 1 million nodes (Shah 2007). This is linked with the complex set up of Circuitscape, where in each node, effective resistance, current and voltage is calculated (Shah and McRae 2008). The results from this study show that Circuitscape run time depends highly on the landscape scale, i.e. the number of nodes. The program crashed in a landscape of more than 6 million nodes on a standard desktop computer, and previous tests have shown that landscapes above 6 million nodes failed due to memory limitation (Shah and McRae 2008).

The results also show that run time increases with more core habitats, since each calculation will be repeated between all pairs of core habitats that are connected. The connected core habitats are first determined based on criterions such as Euclidean adjacency (i.e. a planar graph), the least cost paths are then calculated between these connected pairs (WHCWG 2010; Foltête 2012). The links between connecting core habitats that are longer than the dispersal distance are removed afterwards (McRae and Kavanagh 2014; Clauzel et al. 2016). In Linkage Mapper, Conefor Input tool is used before the analysis to restrict the connected core habitats to those within the maximum dispersal in Euclidean distance (McRae and Kavanagh 2014), and this reduces the run time especially for short dispersing species since fewer least cost paths need to be calculated. In the results, this is shown by the run time of the great crested newt and the hermit beetle at 10x10 km scale, which have similar run time as the spruce bark beetle although the bark beetle has much less core habitats.

Circuitscape is influenced by number of core habitats in a similar way as Graphab and Linkage Mapper, but run time can be limited by using the modelling modes one-to-all (used in this study) or all-to-one instead of between each pair of core habitats (McRae et al. 2013b). In one-to-all mode each core habitat is successively connected to a current source of 1 ampere while all other core habitats are connected to the ground. The all-to-one mode works the same, but instead one core habitat is connected to the ground and all other are connected to a source of 1 ampere; both methods will reduce number of iterations needed (McRae et al. 2013b). For example, if the analysis is run with 4 core habitats, the pairwise modelling mode will need 6 iterations to calculate the current between all combinations of pairs (in each iteration one core habitat is connected to the ground and the other to a 1 ampere source), with 5 core habitats 10 combinations, and with 10 core habitats 45 combinations etc. In the all-to-one and one-to-all, each core habitat is only iterated once, so number of iterations is equal to number of core habitats, which makes the method much faster.

5.3 Number of least cost paths

In this study, the number of links generated by Linkage Mapper and Graphab were in most cases similar, except for the red deer where Graphab had more links than Linkage Mapper (Fig. 3.3-4). Since Graphab does not have a fixed core habitat like Linkage Mapper does (McRae and Kavanagh 2014), but instead forms core habitats based on a number of input parameters, the number of core habitats will be different compared to Linkage Mapper. Results from this study show this often occurred when core habitats were close together or had an irregular shape, like those of the red deer. A number of small areas that in Linkage Mapper belonged to the same core habitat of the red deer was in Graphab treated as separate habitats, and subsequently links were created between each of these core habitats (see Supplemental Figure S1c).

The sensitivity analysis of friction values generated a larger variation in number of links than the sensitivity analysis of dispersal distances. This could be due to the fact that a change in dispersal distance only changes the length of the link, but a changed friction value will be multiplied by every meter travelled. Several studies using sensitivity analysis on least cost path models showed that the least cost path is sensitive to changes in friction values (Rayfield et al. 2010; Sawyer et al. 2011). This stresses the importance of being as accurate as possible when determining friction values, and before accepting the output of the analysis it might be good to test more than one scenario of different friction values.

The variation in number of links generated was greater at larger scales (Fig. 3.3-4), indicating a higher uncertainty. This could be due to that larger spatial scales tend to cover more core habitats within different distances from each other, and the likelihood of a link to be added or removed because of changed friction values or dispersal distances is therefore higher.

5.4 Overlap of pinch points and least cost corridors

When pinch points and corridors were compared in this study, once more the red deer stood out by having an overlap of less than 50% in all cases (see Tab 3.2). The size of the corridor was more similar between different cut-off values compared to when the threshold of the pinch points was changed, probably due to the method used to extract pinch point threshold. This was especially visible in the case of the red deer. The histogram of current values from the red deer had a negatively skewed distribution, which generated a large difference in area of the pinch points depending on threshold (see methods of extracting threshold, Fig. 2.3). When the pinch point threshold was 20% of the highest current values, the pinch points were very small, while a threshold at 30% generated very large pinch points. A possible better way of extracting a pinch point threshold that will be less influenced by the shape of the histogram is to find a percentage of the area under the curve of the histogram. The short distances between the red deer's three core habitats could also be part of the explanation. A shorter corridor means a smaller area that can coincide with pinch points, and they would only coincide well with pinch points at 25% threshold (see Fig. 3.5b).

Even though the high current values in Circuitscape in most cases overlapped fairly well with the corridors in Linkage Mapper, there were some obvious spatial differences. The value of the current is relative, and will not, like the least cost corridor, be directly dependent on the friction values. In the results, the current decreased further away from the core habitat, leading to areas of high current concentrated around core habitats (see Fig. 3.5c, Supplemental Fig. S3). This could be because all core habitats are by default set to have a current of 1 ampere (McRae et al. 2013b), and when core habitats are small, this means the same amount of current will be divided on a smaller number of nodes than for larger habitats, which has been observed in previous studies (Dickson et al. 2013; Rose 2013).

The current will also depend on the configuration of the landscape. Due to Kirchhoff's law, current will decrease with multiple paths, since it is split between all links going out of the same node. For example, between two areas with the same friction value, the area that is narrow and surrounded by areas of higher friction will have the highest current. This means that a small city park will have much higher current compared to a large forest, which shows that current is a relative measure that is not directly related to habitat quality. The tendency of current to funnel through a checkered area with high and low friction was also found by Chambers (2015) and Rose (2013). This phenomenon could potentially be reduced by using gradual transition of friction values between different areas of land cover.

5.5 Uses in conservation planning

The idea of a landscape connectivity analysis tool is to model dispersal based on a friction raster representing dispersal impendence. The model can show dispersal of genes (McRae and Beier 2007; Schwartz et al. 2009; Pérez-Espona et al. 2012) or species (O'Brien et al. 2006; Dickson et al. 2013; Dutta et al. 2015; Su et al. 2015), and it has been used for both conservation (Carroll et al. 2012; Clauzel et al. 2013; Clauzel et al. 2015) and planning for climate change (Nuñez et al. 2013).

Linkage Mapper and Graphab are easier and more straightforward to interpret, since they use a maximum dispersal distance and least cost paths to illustrate movement between core habitats. They clearly show which core habitats are connected and which are isolated, and are easy to translate into conservation planning. The single least cost path varies slightly between Graphab and Linkage mapper, the least cost corridor in Linkage Mapper gives a more complete picture. The current in Circuitscape is a relative measure that is dependent on both the friction value and the number of paths available. Therefore, high current means that there are more animals travelling through the area, but it is not necessarily an area which is suited as a corridor. High current in Circuitscape shows paths where animals are likely to concentrate, while Linkage Mapper and Graphab gives the best route if the animals would have an overview of the landscape.

When it comes to usability, Graphab is a stand-alone software that uses file formats that easily transfers to ArcGIS or other GIS software such as QGIS, while Linkage Mapper is limited to users with ArcGIS. Circuitscape is available both as a toolbox in ArcGIS and as a stand-alone software, but the raster format needed, ASCII, is less commonly used than Graphab's GeoTIFF format.

Validation of landscape connectivity analysis has been done for a number of species. In a study looking at movement paths of caribou, it was found this was not explained by least cost paths (Pullinger and Johnson 2010), but another study looking at hedgehogs show least cost are better correlated with movement than random cost, but the correlation is relatively weak (Driezen et al. 2007). A study modelling elk migratory movements showed that Linkage Mapper's least cost corridor best explained movement of the tools tested, while Circuitscape performed second best (Chambers 2015). Another study looking at validation of Circuitscape maps showed a significant correlation of reptile and amphibian road mortality with areas of high current (Koen et al. 2014), showing that current do correspond to animal movement rates. One study of wolverine populations has showed that circuit theory predicts gene flow better than least cost path (McRae and Beier 2007), but the opposite was found in a study by Schwartz et al. (2009).

The varying results of landscape connectivity analysis showed in both this and other studies, suggest that models should be used with caution, and more studies comparing tools are needed. It could be important to include consideration of the theory behind the tool when choosing which to use; if the goal is to model connectivity, dispersal or to plan for conservation. This study shows that Circuitscape and Linkage Mapper will require longer run time in larger scales than Graphab, but on the other hand gives a more detailed model of connectivity. The study also shows that both scale and species will influence the outcome of the analysis. However, the tools are in most cases comparable, but outcomes can be improved by using several tools together, which have also been suggested by Sawyer et al. (2011).

One approach can be to use Graphab for large areas to give an overview of the network, since Graphab is less detailed but runs faster. Interesting areas of the network can be located through the Graphab analysis. These areas can be analysed by Linkage Mapper and Circuitscape, which are slower tools but gives a more detailed result, to for example evaluate the best corridors.

6. Conclusion

Graphab and Linkage Mapper are, with specific settings, comparable, but still have small variations that can be important to note. The least cost corridor is more robust since it includes all least cost paths, and also shows alternative paths with higher cost distance. Circuitscape will not give the same results as Graphab and Linkage Mapper, although high current values (pinch points) seemed in most cases to overlap with least cost corridors generated by Linkage Mapper. The main spatial difference is that high current in Circuitscape will be concentrated around core habitats, especially if they are small, and tend to increase when funnelled into narrow corridors of low friction surrounded by high friction.

Graphab have much shorter run time and is therefore better suited for larger spatial scales. Circuitscape is difficult to run in landscapes of above 6 million cells on a regular computer and will therefore be better suited for smaller spatial scales. However, if cell resolution is lowered, with the difference that the level of detail will be reduced, both Linkage Mapper and Circuitscape will decrease run time.

Graphab and Linkage Mapper can limit dispersal distance and are therefore useful for both short and long ranging species, while Circuitscape has no dispersal limit and might therefore overestimate dispersal for short ranging species. When it comes to generalist and specialist species, the larger and less defined core habitats of generalists like the red deer can be difficult to use in Graphab since habitats are not separated by an ID. Specialists with small core habitats are difficult to use in Circuitscape because of currents concentrating at small core habitats.

All the tools provide different perspectives; if the goal is to find the best location for a corridor, or finding the relative connectivity or isolation of core habitat patches, then it is better to choose Graphab or Linkage Mapper. If instead the dispersal pattern in the landscape is the focus, Circuitscape is more suitable. They can however be used together, a suggested approach is to use Graphab at large spatial scales to identify areas of constrained connectivity, and at a smaller spatial scale Linkage mapper can be used to model corridors, while Circuitscape can be used inside the corridor to show patterns of dispersal and areas where connectivity can be improved.

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Supplemental Figures

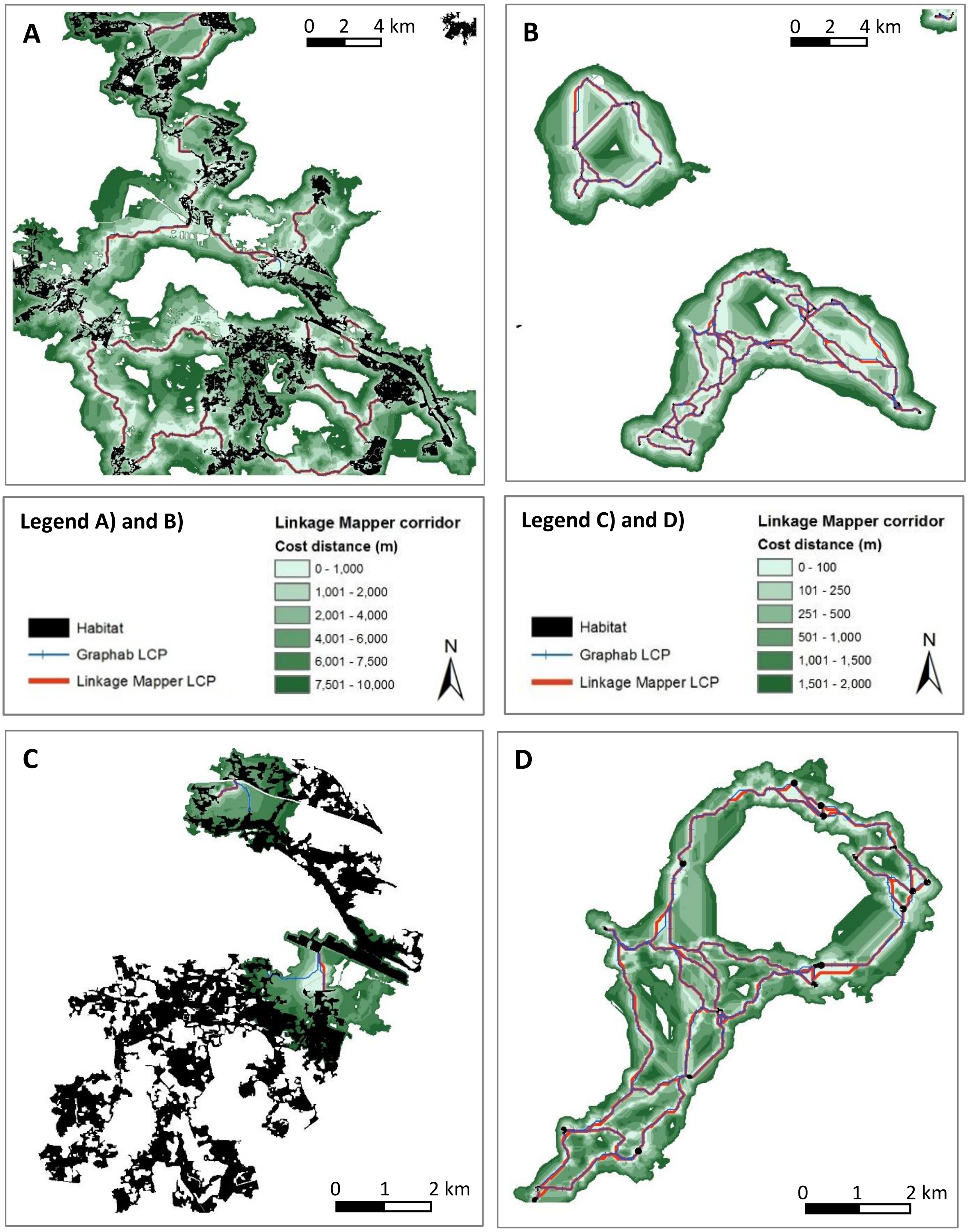

Fig. S1. Linkage Mapper and Graphab analysis of A) red deer 25x25 km, B) spruce bark beetle 25x25 km, C) red deer 10x10 km and D) spruce bark beetle 10x10 km.

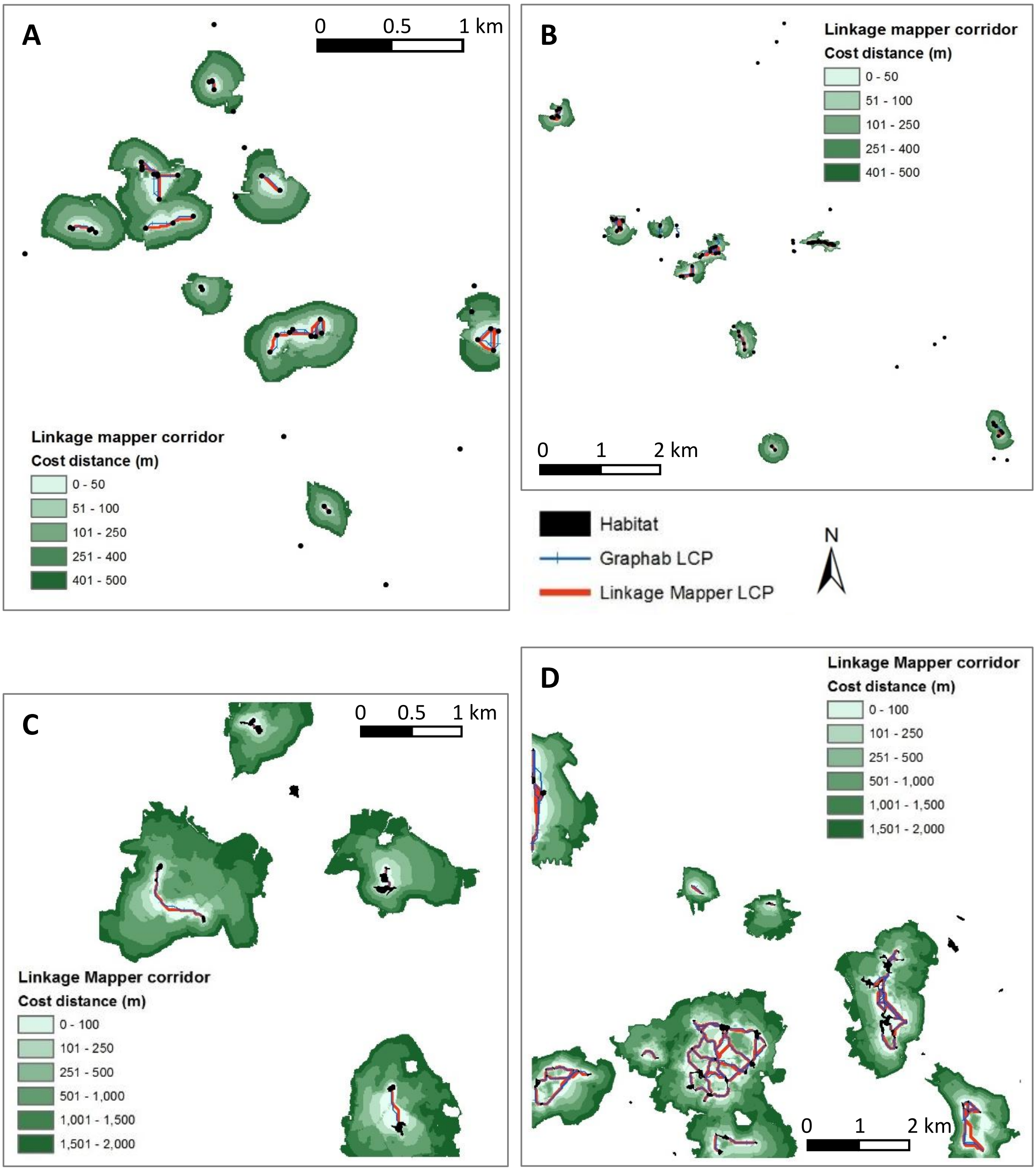

Fig. S2. Linkage Mapper and Graphab analysis of A) hermit beetle 5x5 km, B) hermit beetle 10x10 km, C) great crested newt 5x5 km and D) great crested newt 10x10 km.

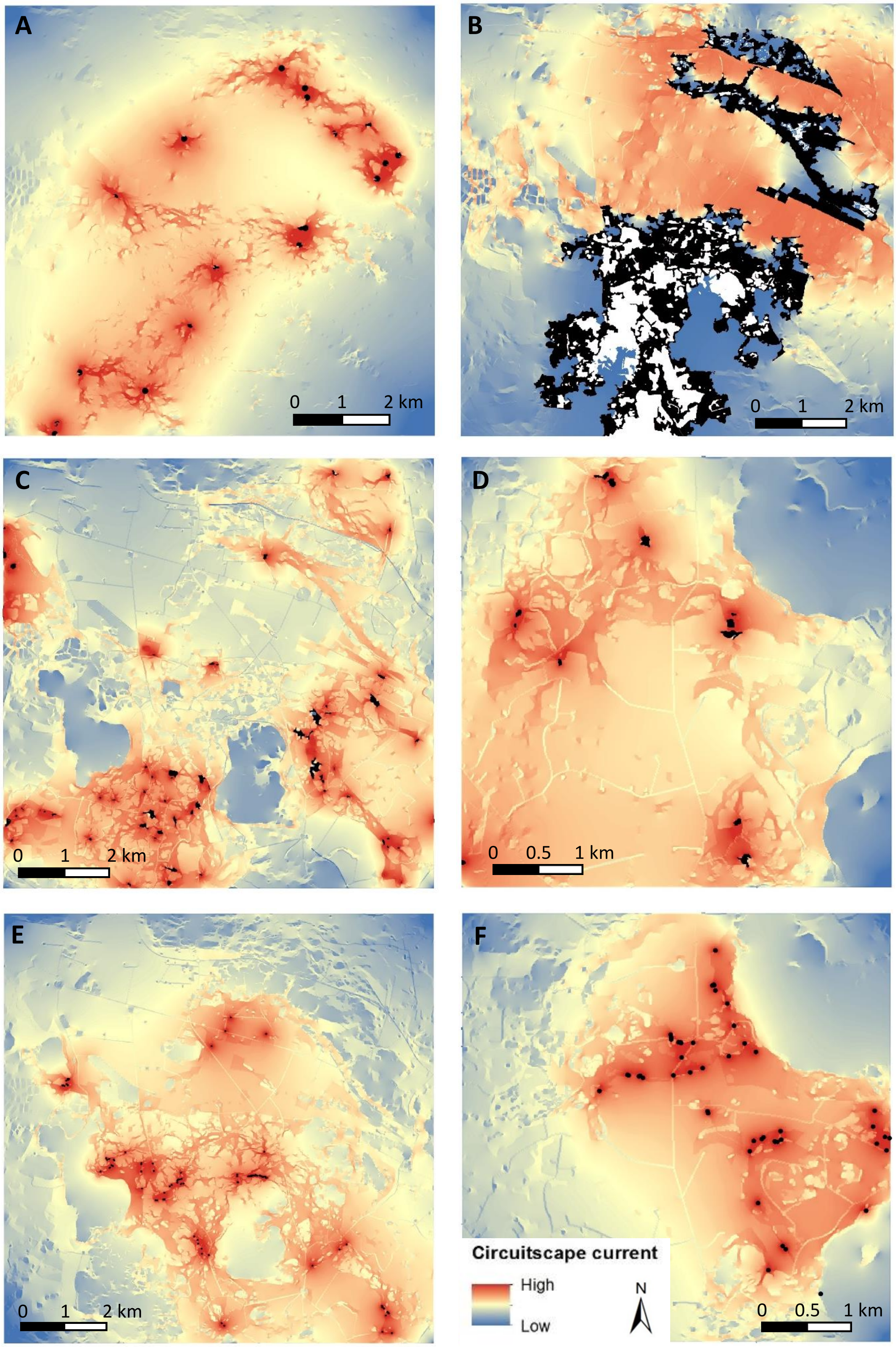

Fig. S3. Circuitscape analysis of A) spruce bark beetle 10x10 km, B) red deer 10x10 km, C) great crested newt 10x10 km, D) great crested newt 5x5 km, E) hermit beetle 10x10 km and F) hermit beetle 5x5 km.

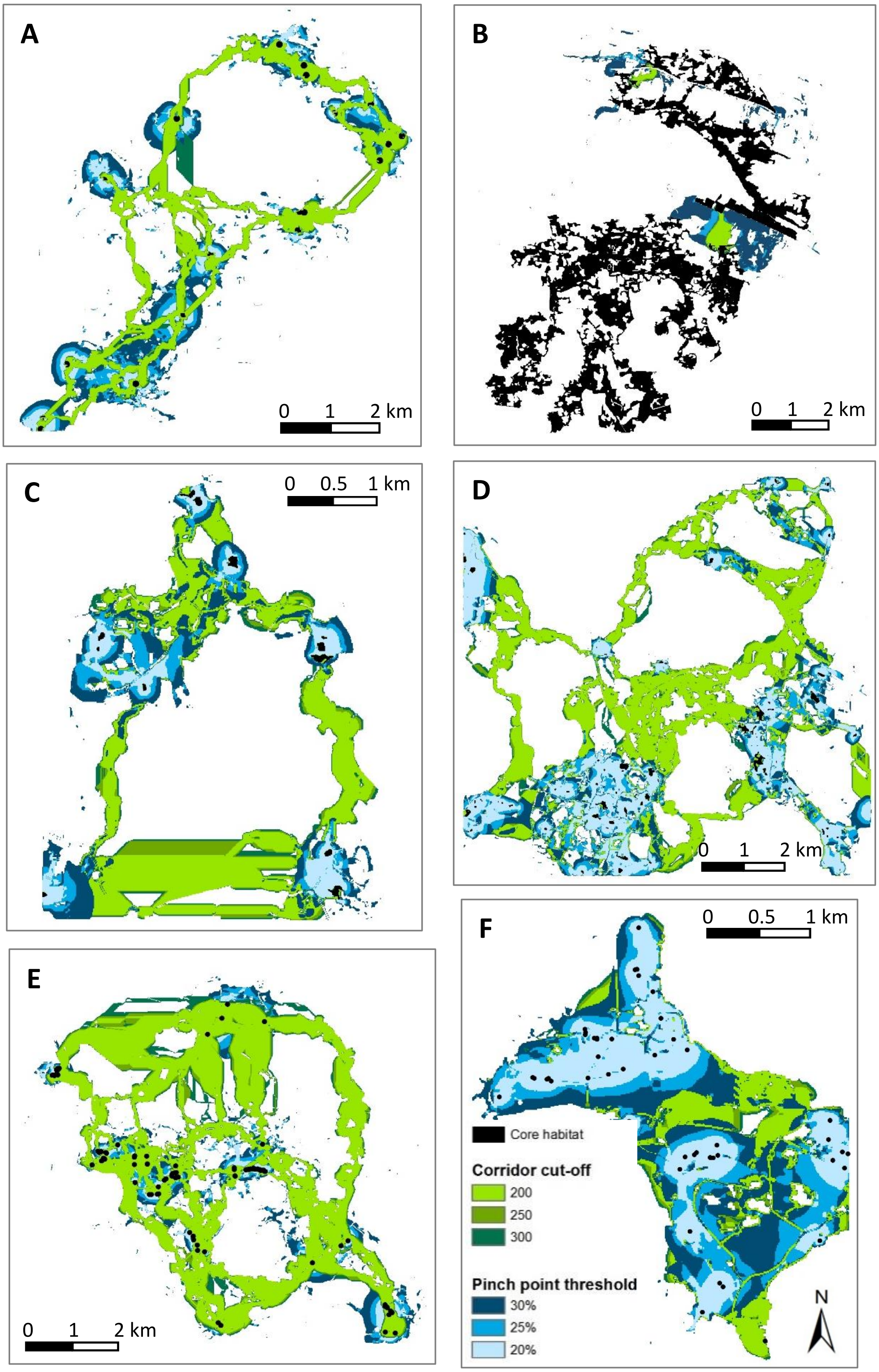

Fig. S4. Pinch point and corridor comparison of A) spruce bark beetle 10x10 km, B) red deer 10x10 km, C) great crested newt 5x5 km, D) great crested newt 10x10 km, E) hermit beetle 10x10 km and F) hermit beetle 5x5 km.

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