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The application of 'least-cost' modelling as a functional landscape model

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Abstract

The growing awareness of the adverse effects of habitat fragmentation on natural systems has resulted in a rapidly increasing number of actions to reduce current fragmentation of natural systems as well as a growing demand for tools to predict and evaluate the effect of changes in the landscape on connectivity in the natural world. Recent studies used 'least-cost' modelling (available as a toolbox in GIS-systems) to calculate 'effective distance', a measure for distance modified with the cost to move between habitat patches based on detailed geographical information on the landscape as well as behavioural aspects of the organisms studied. We applied the method to a virtual landscape and a small scaled agricultural system subject to different scenarios in a land re-allotment project. We discuss the importance of technical aspects and ecological assumption underlying this modelling method. The model is shown to be a flexible tool to model functional connectivity in the study of the relation between landscape and mobility of organisms as well as in scenario building and evaluation in wild life protection projects and applied land management projects. Since 'effective distance' has the same units as Euclidean distance (m), this effective distance may be a straightforward way to include landscape and behavioural aspects in other models which include distance as a measure for isolation. We show the importance of the 'ecological' quality of the input maps and the choice of relevant landscape features and resistance values.

Keywords: Landscape model; Effective distance; Cost-distance; Connectivity; Isolation; Environmental planning

1. Introduction

Fragmentation of natural habitats, and its consequences, are widely recognised as one of the most important threats to the survival of many species world-wide (Harris, 1984; Ehrlich and Wheye, 1986; Lovejoy et al., 1986, etc.). The growing awareness of the adverse effects of habitat fragmentation on natural systems has resulted in a rapidly increasing number of projects and plans to reduce current fragmentation of natural systems as well as a growing demand for tools to predict and evaluate the effect of land management projects and major infrastructural works on connectivity in the natural world. Scenario-testing

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is considered as a tool for exploring possible future developments. It can be considered as a means for forecasting in the sense that it may help to find the probable long-term consequences of decisions to be made. For this reason, there is a wide interest in making the concept of habitat connectivity operational for use by setting explicit goals for nature conservation (Van Apeldoorn et al., 1998).

Landscape connectivity “is the degree to which the landscape facilitates or impedes movement of organisms among source patches” (Taylor et al., 1993; Tischendorf and Fahrig, 2000). This definition emphasises that connectivity not only depends on characteristics of the landscape (structural connectivity), but also on aspects of the mobility of the organism (functional connectivity, Tischendorf and Fahrig, 2000, 2001; Moilanen and Hanski, 2001). This does not only make this measure species specific but, within the species, also specific for the process under consideration. For instance, a different set of rules may be needed to describe small scale dispersal within local populations and long distance dispersal between local populations of the badger (Wiens et al., 1997; Van Apeldoorn et al., 1998; see also Moilanen and Hanski, 2001; Ricketts, 2001).

Patch connectivity is usually calculated as a more or less complex function of the cost to move between patches (and thus the number of individuals in a patch or its presence/absence) (Moilanen and Hanski, 2001; Tischendorf and Fahrig, 2001 and references therein). This cost is usually assumed to be a function of the distance between patches. A simple and often used measure is the shortest (Euclidean) distance from a patch to its nearest neighbour (Moilanen and Hanski, 2001). Other studies use more complex measures, e.g. where all surrounding patches within dispersal distance of a patch contribute to its connectivity (Whitcomb et al., 1981; Hanski, 1994). But in most of these approaches only structural measures are used, and the characteristics of the landscape between the habitat patches (matrix) are not incorporated (Villalba et al., 1998). Nevertheless, there is growing awareness that in a landscape mosaic the matrix in between habitat patches (corridors, barriers, stepping stones, land cover, etc.) is an important factor in determining movement of organisms among patches (e.g. Wiens, 1997; Burel and Baudry, 2000; Tischendorf and Fahrig, 2000, 2001; Moilanen and Hanski, 2001; Ricketts, 2001; Schadt et al., 2002).

Including aspects of the landscape matrix other than measures for the presence of habitat requires a shift from a structural to a functional connectivity measure because the effect of different landscape elements on dispersal is species and process specific. Many studies used actual landscape information for their species incidence analysis, also including for instance hindering landscape elements (barriers) (e.g. Verboom and van Apeldoorn, 1990; Vos and Chardon, 1998). But in these studies only the area/length of specific elements in the landscape was used. The spatial configuration and directionality of these elements, were not included. An important reason for not including more precise landscape characteristics (and behavioural characteristics) in connectivity measures is the complexity of this process (Moilanen and Hanski, 2001; Ricketts, 2001) and the required calculation power.

However, the spatial configuration and orientation of smaller landscape elements may play a crucial role in the movements of organisms outside habitat patches (e.g. Bélisle and St. Clair, 2001). Since at present, most measures for connectivity are not suitable to incorporate detailed spatially explicit landscape information and its effect on species-specific (dispersal) movement, a different connectivity measure is needed (Knaapen et al., 1992; Gustafson and Gardner, 1996; Hanski, 1999).

Recently, some studies used ‘least-cost’ modelling as an approach to incorporate detailed geographical information as well as behavioural aspects in a measure for connectivity (e.g. Walker and Craighead, 1997; Villalba et al., 1998; Halpin and Bunn, 2000; Ferreras, 2001; Graham, 2001; Michels et al., 2001; Schadt et al., 2002). This modelling tool, originating from graph theory, is receiving growing attention in applied land- and species-management projects as well as in research, not in the least because tool boxes based on this algorithm are available in the most current GIS packages (e.g. ArcView-ArcInfo, this study; Idrisi (Michels et al., 2001 and references therein)) as well as in some specialised programs (e.g. CONNEC Gulinck et al., 1993; Villalba et al., 1998). The algorithm underlying this approach is similar to the method proposed by Knaapen (Knaapen et al., 1992) (see also Harms et al., 1989). In the latter model, every landscape unit (grid cell) was assigned a friction value according to its facilitating/hindering effects on the considered movement process. This value was used to calculate the connectivity between a source cell and a target cell, by adding the values of all cells crossed. In the model grid cells consist of complexes of landscape characteristics (habitat patches and corridors as well as barriers) and the friction value is a combination of the values of facilitating and hindering elements. Efficient algorithms and compact data structures developed in graph theory, and applied in GIS environment, now make it possible to consider relatively large landscapes and reduce the grid cell size to a level well below the size of relevant landscape elements (Bunn et al., 2000). As a result cells can be attributed one single land cover type instead of complexes (at the scale considered), and landscape elements can get their precise position and orientation.

However, little is published on the fundamentals and ecological assumptions underlying the use of least-cost analysis for modelling functional landscape connectivity, which may be crucial for the reliability of the conclusions drawn from such an analysis. In this paper, we present the application of least-cost modelling based on the spatial analyst 'cost-distance' extension of ArcView (3.2, ESRI 1996). We applied the model on a virtual landscape as well as on a Belgian landscape, subject to different scenarios in a land re-allotment project. We will discuss some technical aspects and underlying biological assumptions and aspects which may strongly influence the ecological relevance of the output, as well as some possibilities of the method in the evaluation of different landscape scenarios.

2. Material and methods

2.1. The least-cost algorithm

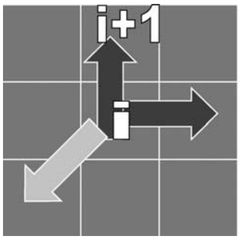
The method is based on a simple algorithm (ESRI 1996, Fig. 1): for any given movement from cell N_i to cell N_{i+1}, the cumulative cost is calculated as the cost to reach cell N_i plus the average cost to move through cell N_i and N_{i+1}. Taking the average makes the relationship symmetrical (Fig. 1). The model is based on an eight-neighbour-cell algorithm which also allows for movements along the diagonals. In case of diagonal directions, the cost is multiplied by the square root of two to compensate for the longer distance. Based on the same algorithm also a negative growth model can be designed (Villalba et al., 1998; Adriaensen et al., 2000). In this case, the model starts with a maximal starting value and for each step the cost (calculated in the same way as above) is subtracted.

2.2. Cost-distance analysis

Two GIS layers, a source layer and a friction/resistance layer form the input of the model. The source layer indicates the habitat patches from which the connectivity is calculated (or individuals are expected to emigrate). This may be a single patch, or a complex of patches. The resistance layer indicates both the resistance value and the geographical position and orientation of all relevant landscape elements. The resistance value of each cell in the grid is based on the resistance value of the land cover type attributed, but can be refined in many different ways if necessary (e.g. to include the effect of altitude, flow rate (Michels et al., 2001), ocean currents (Halpin and Bunn, 2000), etc., see also discussion). For habitat, the resistance value is set to 1, assuming that this land use type has a minimum cost of movement (see also Walker and Craighead, 1997). Optionally, a maximum cost value can be set. When the maximum cost value is reached calculations are stopped, and cells with higher values than this maximum cannot be reached (maximum dispersal limit).

The outcome of a cost-distance analysis is a "cost" layer around a given source. The cost value in each cell represents the distance to the source, measured as the least effort (lowest cost) in moving over the resistance layer. The cost is calculated from edge to edge (Villalba et al., 1998). The unit of measurement is "grid cell equivalents" which is also equal to the number of time steps (Villalba et al., 1998). A cost value of n indicates the cost of moving through n cells with a resistance value of 1, or through one cell with a resistance value of n, etc. Cost values can be converted into an equivalent distance measure by multiplying the cost by the cell size (Ferreras, 2001, see also below).

Many different terms are in use for describing the cost for an organism to move between habitat patches: landscape connectivity (or its inverse: landscape resistance or isolation), effective distance, functional distance, etc. Some recent studies, applying



$$N_{i+1} = N_i + (r_i + r_{i+1})/2$$
or
$$N_{I+1} = N_i + 2^{**}0.5 * (r_i + r_{i+1})/2$$

N_i = accumulated cost in cell i
r_i = resistance value in cell I
i: source cell
i+1: target cell

Fig. 1. Algorithm underlying 'least-cost' modelling (see text).

least-cost models, agree on the term 'effective distance' (Ferreras, 2001; Verbeylen et al., submitted for publication) or 'effective geographical distance' (Michels et al., 2001) for Euclidean distance modified for the effect of landscape and behaviour. To avoid further confusion, in this study we will also use the term 'effective distance' for the ecological translation of the calculated cost-value.

2.3. Landscapes studied

In this study, the model will be applied to two landscapes: a virtual landscape and a Belgian landscape, recently subject to a land re-allotment project.

2.3.1. The virtual landscape

The virtual landscape (1 km × 1 km, Fig. 2A) has a central source patch and, at equal (Euclidean) distance, four target patches embedded in a landscape matrix. In the landscape matrix, we find different landscape elements situated between source and target patches. Elements may belong to different land cover classes. Depending on the land cover class, each cell in the grid has its own resistance value towards a movement process of an organism (see below). As the narrowest element in the map was 10 m wide, cell size for the grid was set to 1 m × 1 m, but for instance 2 m × 2 m would have resulted in very similar results.

2.3.2. The Belgian landscape

We selected a small scaled agricultural landscape 'Hoge en Lage Rielen' in Belgium (Lichtaart-Kasterlee, province of Antwerp; Fig. 3). Because the site was part of a recently conducted land re-allotment project, different landscape scenarios were available. To the northwest, this landscape is bordered by a forest and a valley rich in woody vegetation, to the south by a forest complex on higher ground. Scattered in the agricultural area, we find small forested patches (especially in the northwest and south) and many tree rows, hedgerows, natural road sides, rough field edges and ditches. In the central part, there is a built-up area, and many farmhouses lay scattered in the landscape.

The main goal of the land re-allotment project was to enhance efficiency (connectivity) for agricultural activities (e.g. parcel size and form). A final plan for the re-allotment project was approved in 1994. Because of the high nature value of the forest rich sites around this area, the plans paid special attention to the connecting role of the agricultural site for forest inhabiting organisms. Changes in land use (and its distribution) and the number, type and location of small landscape elements as well as roads may play an important role in this connectivity. In the new plan, three forested stands were removed and replaced by new ones situated elsewhere. In some parts, most of the ditches, shrub and tree rows between the plots were removed to optimise farming efficiency. To compensate for this loss of higher vegetation, new tree rows were planned along some of the roads. Total length of all linear woody elements remained about equal: 63 versus 64 km in the new situation. Except for ditches, which dropped to about 60% in length, all other landscape elements remained more or less stable in terms of surface area/length.

In this study, we compared the original situation scenario (A) with the approved scenario (B). To allow for an evaluation of the observed differences, we added one extreme scenario (C): the original landscape stripped of all tree rows, hedgerows and natural edges.

Landscape information on the site was available in GIS vector format from the Vlaamse Landmaatschappij (VLM): polygons for the land cover information and lines for the linear elements (without any data on

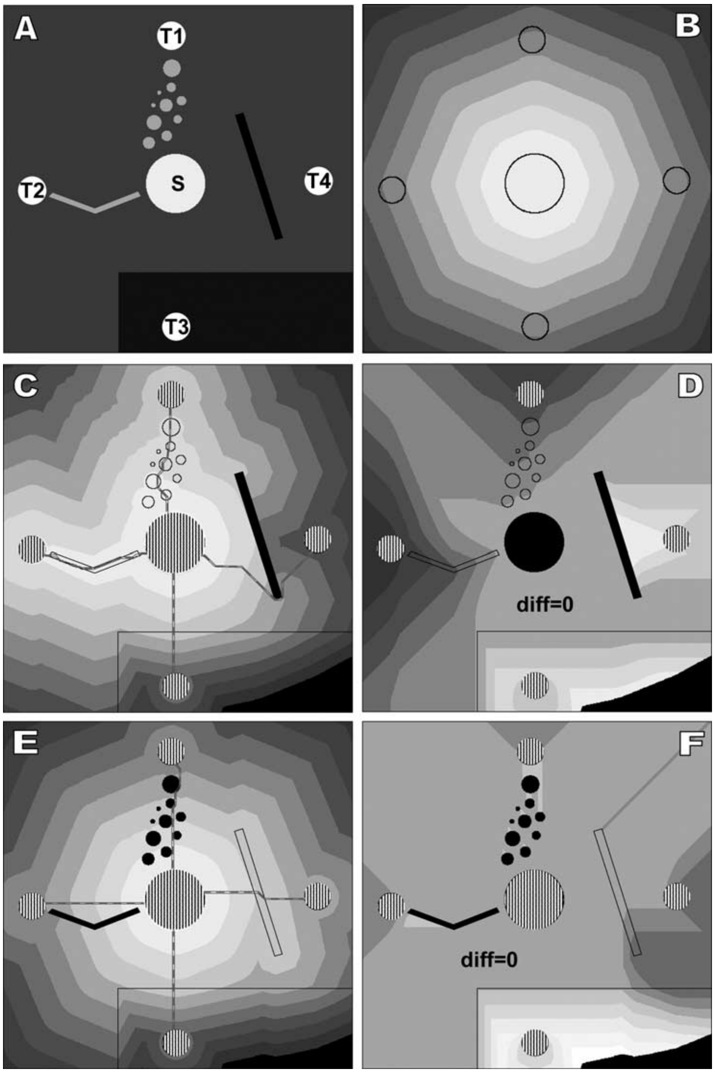


Fig. 2. Effective distance in a virtual landscape (1 km × 1 km, cell size 1 m) with four target patches at equal (Euclidean) distance from a central source patch (see text). (A) Land cover/friction map. In the matrix (resistance $R = 20$) different landscape elements are: source patch (S, $R = 1$), target patches (T1–T4, $R = 1$), to the east a relative barrier ($R = 200$), to the north small habitat patches ($R = 5$), to the west a corridor ($R = 5$) and to the south land cover resistance is higher ($R = 40$). (B) Cost map for a landscape with homogenous resistance (all landscape elements $R = 20$, equivalent to Euclidean distance). The banding pattern indicates cells with effective distance in the same class (8 classes). (C) Cost map for the landscape and resistance set in map A. For equal Euclidean distance each target patch now has a different effective distance. Double lines indicate least-cost paths to target patches. (D) Cost shadow map C–B. For each grid cell this map shows the difference between the cost in the differentiated landscape (C) and the cost in the homogeneous landscape (B). Darker/lighter colours: lower/higher relative effective distance in the differentiated landscape (zone for which effective distance is equal in both landscapes indicated with 'diff = 0'). Figures (E) and (F) show similar maps as in (C) and (D) but resistance values for barriers and corridors/habitat patches were swapped (east: corridor ($R = 5$), west: barrier ($R = 200$), north: hindering patches ($R = 200$)). Note equal effective distances for target patches to the east, north and west, which are also equal to distance in map B.

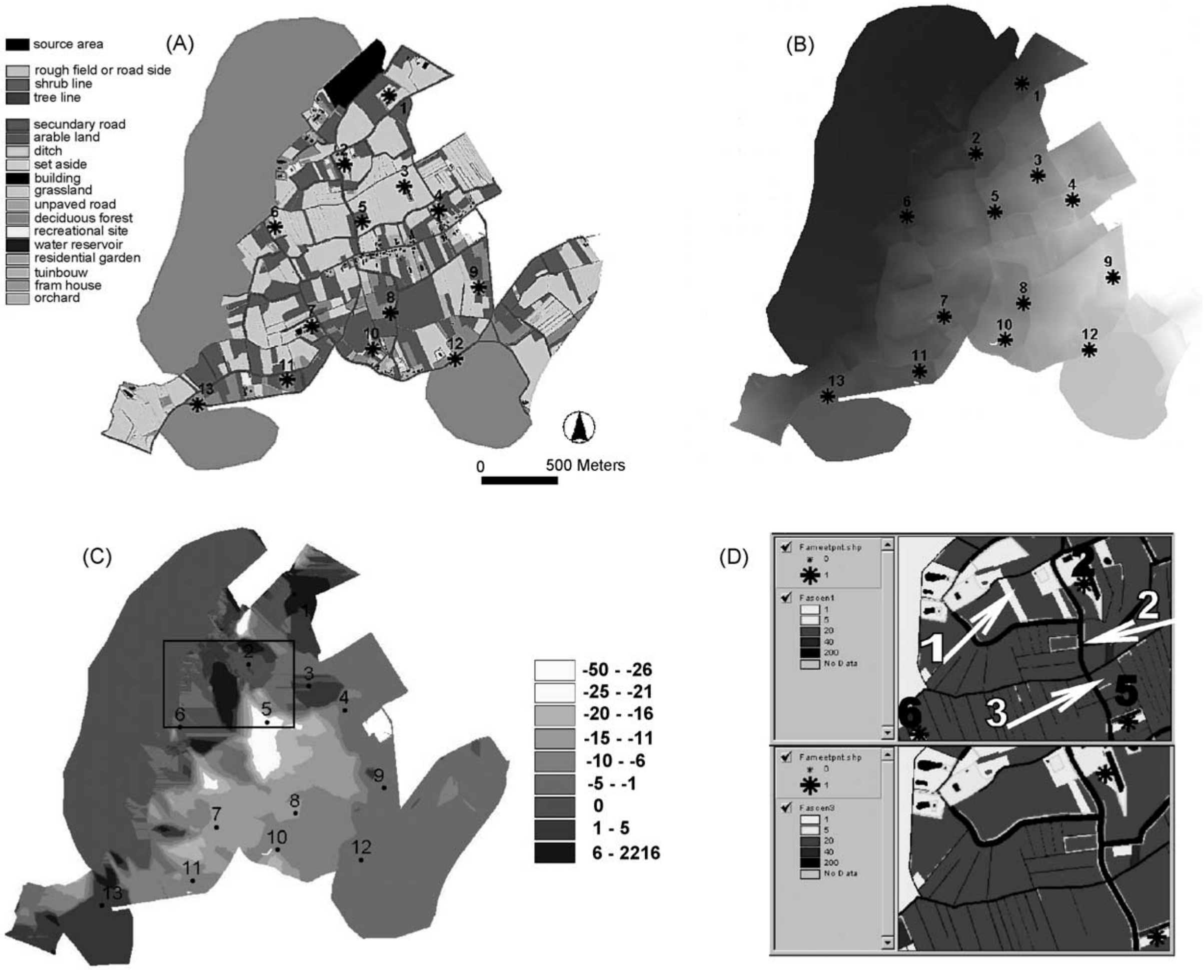


Fig. 3. Belgian landscape 'Hoge en Lage Rielen'. (A) Land cover map: source indicated as dark area to the northwest, plots 1–13 (✱) were used as sampling points (see text). (B) Resulting cost map for scenario B in greyscale. Each pixel has its own grey-value relative to the effective distance associated, scaled from 0 (lowest effective distance) to 255 (highest effective distance). (C) Difference map (scenario B−scenario A). Darker colours represent higher effective distances in scenario B. (D) Details from the friction layers for scenario A (top) and B (bottom), see rectangle in C (see text).

the width). Before these maps could be converted to a grid (1 m × 1 m), the exact relative position of elements in the line maps and polygon maps had to be checked carefully, and adjusted in several places (see also O'Neill et al., 2000). Exact positioning of, e.g. a tree line on one side of a road, and not on top of the road or crossing it at one point, may have a profound effect on the resulting cost map (see above). According to the vegetation type, lines were buffered to a total width of 2 m for natural road and field edges, 3 m for hedgerows and 4 m for tree rows.

2.4. The setting of resistance values and maximum cost

In this study, we used a resistance set for a virtual organism. However, resistance values are based on our experience with testing and validating cost-distance models for terrestrial, forest inhabiting animals (Adriaensen et al., 2000; Verbeylen et al., submitted for publication; Chardon et al., submitted for publication). It could be a useful starting point, for example, for a small forest inhabiting mammal in a more open matrix with scattered woody vegetation and ditches or roads. The same resistance set was used for both landscapes. Resistance values (integer values) for different land cover classes were chosen in such a way that resistance for the matrix ($R = 20$) was clearly higher than for habitat patches (by default $R = 1$, see above) and smaller habitat-like patches (including corridors; $R = 5$), but clearly lower than for hindering landscape elements ($R = 40$ for a different, more hostile, land use and $R = 200$ for a relative barrier). Relative barriers impede (restrict, but not prevent) movement, while absolute barriers totally prevent (or deflect) movement. Resistance values for absolute barriers should be coded as 'no data' (ESRI 1996) or set equal to or higher than the maximum cost value.

Maximum cost value was set to 13,000 units in the virtual landscape. This is about the minimum value to allow for all the cells to be reached through the matrix. Maximum dispersal distance in the matrix ($R = 20$) is then 650 grid cells (equal to meter in this study with $1\,\mathrm{m} \times 1\,\mathrm{m}$ grid cells), while in a barrier ($R = 200$) the maximum cost will be reached after 65 m and in a corridor ($R = 5$) after 2600 m. No maximum was set in the Belgian landscape because we wanted all cells to be reached under all circumstances to allow for quantitative comparison.

3. Results

3.1. The virtual landscape

In the first analysis, cost was calculated for a landscape scenario in which all landscape elements (including source and habitat patches) show equal resistance values (here $R = 20$). The resulting cost map (Fig. 2B) shows parallel bands of equal effective distance in an octahedral form. The width of the bands is the result of reclassification in eight categories for better visualisation, but each cell in the grid does have its own cost value. Given a cell size of $1\,\mathrm{m} \times 1\,\mathrm{m}$, effective distance is here equal to Euclidean distance multiplied by 20 (except for the deviation from the circular pattern due to the eight-neighbour-cell algorithm, see discussion).

Fig. 2C shows the cost map resulting from a cost-distance analysis using the resistance set for the virtual organism (see Section 2, Fig. 2A). The pattern of parallel bands is still present, but it is clearly distorted by the presence of landscape elements with deviating resistance values. The four target patches all have a different effective distance, even though they are at equal (Euclidean) distance from the source patch. For patches to the north and the west, movement was facilitated by habitat elements scattered in the matrix. Both now have a relatively low effective distance compared to the effective distance in the homogenous landscape (Fig. 2B) and compared to the effective distance of the patches to the south and east. For the latter, movement was impeded by hindering elements. To generate a clear picture of the effect of the landscape structure as such (corrected for the distance of each cell from the source), we constructed a 'cost shadow map' by subtracting layers C and B (Fig. 2D). In this map, the 'shadow' effect or the area of influence of landscape elements is clearly visible. Because of the positive effect of facilitating patches (north and west) an area much wider than the patches in itself can be reached at relatively low cost (lower than through an homogenous matrix). The opposite is true for hindering element (east) for which the effect is gradually reduced with distance beyond the element due to cost-paths 'flowing' around the linear patch. For the situation to the southeast this is not the case because the whole area has a higher resistance value, and no paths through lower resistance areas are possible within the given landscape. The black corner to the southeast indicates that the effective distance to these cells was higher than the maximum value set (13,000 cost units). Optionally the CD-extension can visualise the 'least-cost path' to reach a predefined target patch (to be defined in an extra layer). This 'path' represents the series of cells which resulted in the lowest cost value for that patch (Fig. 2C) (but, see discussion).

Fig. 2E and F show the results on a similar landscape as to the position of the landscape elements, but in this landscape the resistance values of the smaller landscape elements were swapped. As a result, the corridor to the west now became a barrier aligned with the main direction of movement instead of perpendicular to it (see Fig. 2C). And vice versa, the barrier became a corridor perpendicular to the direction of movement. Stepping stones were turned into small hostile patches (e.g. ponds for a forest inhabiting mammal). Because the algorithm is designed to calculate the lowest cost to reach a cell, and the path coinciding with it, the effect of orientation of linear elements is extremely important and opposite for barriers and corridors. Barriers in the direction of movement and corridors perpendicular to the direction have virtually no effect. This is clearly shown in Fig. 2E, where, in contrast to Fig. 2C, almost no places are detected that differ in effective distance from the default 'distance' map in Fig. 2B (including three out of four target patches), and cost paths are almost straight lines. Only a minor positive effect shows up at both ends of the corridor to the east.

3.2. The Belgian landscape

We defined a source area in the northern part of the adjacent valley (north-western corner of the map, Fig. 3A). To monitor the quantitative evolution of connectivity (cost) throughout the landscape, we located 13 sampling point in the landscape (all in wooded parcels, Fig. 3A–C) for which we collected cost values in the different scenarios. To monitor effective distance between the two sites adjacent to the actual study area (see above) two of these point were situated in the forested area to the south of the agricultural area, one in the east and one in the west.

Fig. 3B shows the resulting cost map for scenario B in greyscale (each pixel has its own grey-value relative to the cost value associated, 0–255). Increasing cost values (lighter colours) towards the southeast clearly show the effect of distance from the source patch in the north. The importance of low resistance values in the adjacent forested area to the northwest (outside the actual area under investigation) is revealed by the evolution of the cost values along a front line in parallel with the edge of this forest.

Table 1 summarizes, in a quantitative way, the effect of the landscape configuration on the connectivity in the 13 sampling points for the three scenarios (see Section 2). Removal of all linear woody vegetation (scenario C) resulted in a higher effective distance for all but one sampling point (a digitising error). On average effective distance increased by 8.5%. Both sampling points in the target area to the south (12, 13) increased by about 12%. In the newly planned situation (scenario B), effective distance is on average 6% lower compared to the original situation. Effective distance slightly decreased in sample point 12 (−4%), but increased in point 13 (+2.5%). The 'shadow' map, scaled as percent of the original cost-value (Fig. 3C), gives an overview of the change in cost values through the landscape. Darker colours show higher cost values in scenario B. A small number of very high values was caused by inconsistencies in the digitising. Comparison of the two friction layer maps (Fig. 3D) shows

Table 1
Effective distance (m) for 13 sampling points in the Belgian landscape

Sampling points	Scenario A	Scenario B		Scenario C	
	Effective distance (m)	Effective distance (m)	B−A	Effective distance (m)	C−A
1	1165	1384	219	1495	330
2	1590	1603	13	1576	−14
3	5370	5480	110	5412	42
4	6879	6575	−304	6929	50
5	4471	3383	−1088	4785	314
6	1456	1458	2	1456	0
7	5482	4836	−646	6429	947
8	6440	5792	−648	7561	1121
9	8855	8550	−305	8878	23
10	7830	7067	−763	8817	987
11	5426	5033	−393	5804	378
12	9117	8724	−393	10207	1090
13	3787	3892	105	4376	589
Average	4848	4556 (−6%)		5266 (+8.5%)	

Original situation (scenario A), approved final scenario (B), original landscape stripped of all linear woody vegetation (C). B−A, C−A: difference in effective distance with scenario A. Location of sampling points in Fig. 3A.

that the negative evolution in the triangle formed by sampling points 2–5–6 is caused by the removal of a long but narrow wooded parcel in the direction of the movement (arrow 1), and that the positive evolution around point 5 was the combined effect of an extra woodlot (arrow 2) and a new double tree row along the road (arrow 3).

4. Discussion

First, we will discuss the results of the application of least-cost modelling on both the virtual landscape and the Belgian landscape, followed by some more general discussion on the ecological consequences of different aspect of the method (algorithm, maps, land cover classes and their resistance values, least-cost paths).

4.1. The virtual landscape

Analyses on a virtual landscape demonstrated some important aspects of 'least-cost' as a modelling tool. The eight-neighbour-cell algorithm does generate some inaccuracies in the cost layer (octahedral deformation of circular pattern). However, in contrast to systems in which parameters are known far more accurately (e.g. fire propagation), it seems questionable if this could really influence the outcome of analyses on landscape connectivity for dispersing animals. Probably, in most ecological systems these deviations caused by the algorithm will be far less important than the inaccuracies in the estimation of the model parameters (resistance values, landscape classes, etc.). But, at least theoretically, alternative methods which allow for more directions are possible to improve calculation precision (e.g. Xu and Lathrop, 1994, 1995). The analyses also demonstrate the importance of orientation of linear landscape elements, and the asymmetrical effect in facilitating and hindering elements. As a consequence, for the outcome of an analysis the width of hindering elements is far more important than for facilitating linear elements.

4.2. The Belgian landscape

Even though there were no big differences in land use between the three scenarios, cost values clearly differed. Changes in connectivity were mainly due to changes in linear elements. When all tree rows and hedgerows are removed from the landscape, the average effective distance increased by about 8.5%. The reorganisation of these linear elements in scenario B, resulted in a improvement of the average connectivity (6% lower effective distance) as well as in most of the individual sampling points. This improvement must be due to the location and continuity of the new linear elements, since almost no extra length was added. Even though differences in outcome between scenarios are limited (maximum 25% in a small number of locations) the analyses do show that in the new situation connectivity did improve for this virtual organism.

We have to emphasize here that the analyses in this study do not enable a full picture to be obtained. We only depicted some scenarios to demonstrate the problems and possibilities of the method. An analysis, for example, for amphibians could give a completely different results since many ditches disappeared. Since functional connectivity is species and process specific, it will be important in every connectivity study to either set target patches and target ecological groups very consciously (e.g. forest species in this study), or to apply a multi-species approach and compare resulting maps. To give a more complete picture for this study, analyses should also include other locations of the source patch and/or an overall connectivity analysis for a complex of source patches. Because in scenario comparison within the same landscape nothing but the landscape changes, maybe details in the resistance set are less important than the choice of ecological group(s), or a multi-species approach. However, further studies are required to test this.

4.3. The algorithm

The simple algorithm and powerful calculation procedures make it possible to do analysis on very complex and extended landscapes. Association with graph theory may also have interesting applications for further functional analysis of landscapes. For instance, mathematical graphs can be used as an ecological construct with respect to habitat connectivity, and graph operations (node and edge removal) can be applied to study connectedness of a landscape (Bunn et al., 2000; Halpin and Bunn, 2000). The simplicity of the algorithm makes it relatively easy to judge the underlying biological assumption for the process studied.

Improvements in the algorithm are certainly possible (diagonal movements, number of neighbour cells (see above), distance function (Villalba et al., 1998), etc.). The cost value may be an interesting integrated measure for effective distance, but, because of the very strong correlation between Euclidean distance and effective distance, profound statistics are needed to study the effect of distance and the effect of the landscape structure independently (Verbeylen et al., submitted for publication).

Patch connectivity is usually calculated as a more or less complex function of the cost to move between patches (Moilanen and Hanski, 2001; Tischendorf and Fahrig, 2001 and references therein), and this cost usually is assumed to be a function of the distance between patches ('measured in any manner that is considered appropriate' Moilanen and Hanski, 2001). Since 'effective distance' is measured in the same units as is Euclidean distance (m), this effective distance may be a straightforward way to include landscape and behavioural aspects in other models which include distance as a measure for isolation (see also Verbeylen et al., submitted for publication).

4.4. The importance of the quality of the maps

As it stands, all GIS packages use grid maps as input for the least-cost model. This implies that a lot of GIS information available in vector format (e.g. linear infrastructures, field edges, etc.) has to be converted to grids and combined with other grid based information (e.g. satellite data on land cover) before application of the model. Since the grid map is the only input, its quality is decisive for the quality and reliability of the resulting cost map. This has important consequences for different aspects of the map. Relatively low resolution (large grid cells) may do for general land cover since parcels mostly have larger dimensions. However, resolution is crucial for smaller or narrower elements in the landscape (see below).

The scale of the map should be appropriate (e.g. well beyond dispersal capacity) for the species and process studied (see also Walker and Craighead, 1997; Brooker et al., 1999; O'Neill et al., 2000; Schadt et al., 2002). This may not always be easy to determine since in many species the range over which individuals use or experience (e.g. Zollner, 2000) the landscape is far from known (see also below). This study showed the importance of including the landscape surrounding a study site in the map. Especially facilitating elements and potential extra source patches (Verbeylen et al., submitted for publication) outside the study area, but within the area of influence for the species, may have important effects on the outcome of the analyses (see also Schadt et al., 2002).

The way linear elements in the landscape are represented in the grid map will be crucial for the relevance of the resulting effective distances (see also Villalba et al., 1998). In order to convert linear and smaller elements in a reliable way, grid cell size must be clearly smaller than the width of the narrowest element in the landscape. If not, small items may disappear from the grid, and linear elements may become discontinuous (Sastre-Olmos et al., in preparation). The latter may have dramatic consequences for the resulting cost map because corridors may become intersected by high resistant cells, and, probably much more important, barriers may show 'holes'. Even a gap of one cell or just two cells touching by corners will allow cost paths to cross a barrier. This may completely remove or at least strongly reduce its effect on effective distance (Fig. 4). Line elements either have to be digitised using their actual width, or have to be converted to polygons through GIS manipulations (e.g. buffering). At least three important aspects have to be considered when applying the latter. (1) The width has to be limited not to cover other important landscape elements, e.g. roads bordering a tree row. (2) The width has to be wide enough relative to the cell size of the final grid (see above). (3) The actual width of facilitating linear elements (corridors) only has a limited effect on connectivity, since the algorithm will find the least-cost path through it, even if the corridor is only one cell wide or cells merely touch by corners. This is not so for hindering linear elements (barriers) for which the width as well as the structure is crucial (see above, Fig. 4). In many cases, it may be necessary to use general land cover maps and superimpose information on linear and point elements from other digital source layers (see also Schadt et al., 2002).

4.5. Defining land cover classes

Landscapes are complex associations of land cover classes. Which classes are recognized and included in the landscape map may play a very important

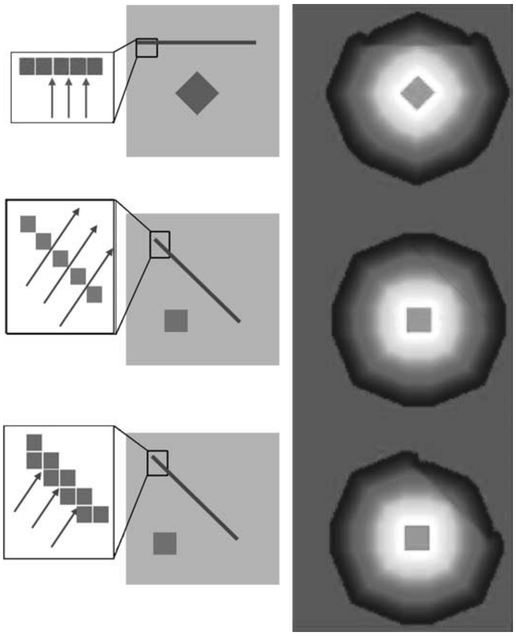


Fig. 4. Linear barriers and the grid effect on the calculation of effective distance (see text). Central column: resistance layers for virtual landscapes with one source patch in the centre and a barrier to the north (top) or to the northwest (middle and bottom). Left column: magnification of the barrier showing its grid structure (arrows = least-cost paths). Right column: cost maps for the three landscapes (dispersal to maximum cost value).

role in the process of least-cost modelling (Verbeylen et al., submitted for publication). This landscape classification represents, or should represent, the way the species experiences the environment (see also Schadt et al., 2002). If for instance parcel edges are important in butterfly movements (e.g. Fry and Robson, 1994), these edges have to be emphasised in the map. If a bird or squirrel only 'sees' trees in the landscape, the landscape classes should represent this view (Adriaensen et al., 2000; Verbeylen et al., submitted for publication). For zooplankton, the relevant features may be ponds, creeks and currents (Michels et al., 2001).

Currently available GIS information and calculation power make it often possible to distinguish in detail between different land cover types and landscape elements. We think it is important to avoid, as much as possible, the use of complex land use classes (e.g. agricultural area with hedgerows, forest with highway) at the relevant scale because it will be very difficult to judge resistance values and the orientation and exact location of sub-elements is lost. Quality of the calculated effective distance will profit by the precise location and orientation of linear elements (see above).

4.6. Setting the resistance values

The resistance is a value representing the permeability of a grid cell for the movement of an individual of a species (Villalba et al., 1998) within the framework of a certain process. Permeability stands for the fraction of individuals that would not be able, or willing, to cross the specific landscape element (Villalba et al., 1998). It is not a measure of speed, but rather a measure for the reluctance to use habitat for movement (Ferreras, 2001; Schadt et al., 2002). Together with the definition of the land cover classes, the setting of resistance values in the friction layer is biologically probably the most important step in the process of calculating effective distance. It is the link between the (non-ecological) GIS information and the ecological-behavioural aspects of the mobility of the organism or process under investigation. Besides the availability of sufficiently accurate map information, the development of a suitable set of resistance values is probably the most important bottle neck for applying least-cost analyses.

For most organisms setting the resistance values will be a difficult process in which expert judgement and data available in literature will play an important role (see also Walker and Craighead, 1997; Schadt et al., 2002). In some cases, actual field data can be used to estimate the resistance values. For instance, resistance values were calculated as inversely related to habitat preference in the Iberian lynx (Ferreras, 2001), or flows of individuals in zooplankton and butterflies (Michels et al., 2001; Ricketts, 2001). However, once a "starters kit" of resistance values is available, it is possible to study the sensitivity of effective distance for variation in the resistance values by running models with alternative resistance sets (e.g. Adriaensen et al., 2000; Schadt et al., 2002; Verbeylen et al., submitted for publication). Especially, when the purpose is to construct a predictive model for conservation or management, it is critical that the model (and thus resistance and connectivity measures) is rigorously parameterised using empirical data and validated in independent landscapes (see also Moilanen and Hanski, 2001; Schadt et al., 2002).

Resistance values (as well as the resulting cost values) are relative values (Villalba et al., 1998). In a set of resistance values it is the relative value for the different landscape elements (in combination with the maximum cost value) that will make the difference with a model based on Euclidian distance, not the absolute resistance values. Larger relative differences between land cover classes make it possible for least-cost paths to deviate further from the default straight line between source and target patches (see also Schadt et al., 2002).

Because least-cost paths easily find their way around small elements in the landscape, point elements only have a limited impact on the resulting effective distance. This is especially so for small hindering patches. Numerous small facilitating elements may still have an impact. So, if in a given system point elements play a crucial role in the connectivity between landscape elements (e.g. Graham, 2001) special attention for the way these are represented in the resistance map will be necessary. It may be necessary to enhance their effect artificially by enlarging their surface to an 'area of attraction' or assigning for instance an alternative resistance value to the entire parcel in which the point element is located (e.g. 'pasture with tree' instead of 'pasture' and 'tree').

4.7. The interpretation of least-cost values and least-cost paths

The least-cost value may be an interesting tool to modify a distance parameter with aspects of landscape and behaviour into an effective distance. But, behaviour is only included in a very general way and especially behavioural aspects at the individual level are not included. Least-cost is a measure for the overall landscape resistance of the total trajectory between two spots in the landscape or the effort an individual has to exert to move between patches (Walker and Craighead, 1997; Michels et al., 2001). It does not say anything about the behavioural feasibility of it, and least-cost paths do not necessarily give a reliable picture of the most likely way to be followed (Walker and Craighead, 1997; Brooker et al., 1999; Schadt et al., 2002). Individual decisions during every step of the movement may be very important in the ultimate dispersal path (Brooker et al., 1999). For instance, at the start of dispersal, movements may be highly related to the habitat surrounding the source patch and subsequent movements may be conditioned by initial movements. During dispersal, landscape structure may determine the likelihood of finding a corridor, which may be strongly asymmetrical as to the direction of movement (Ferreras, 2001).

Although all source patches may be included in the source map, the least-cost value represented in the cost map is the cost to nearest patch only (in terms of effective distance). No extra effect of other patches at higher effective distances is included (see also Verbeylen et al., submitted for publication). Some models can also sum minimum cost values over all source patches automatically (e.g. CONNEC, see Villalba et al., 1998). However, to go from patch connectivity to entire landscape connectivity, for all patches, is not obvious (sum, average, etc.) (Moilanen and Hanski, 2001; Tischendorf and Fahrig, 2001 and references therein). Also the role of source patches when crossed by least-cost paths is a point open for debate, and probably strongly dependent on the species and process studied. As it stands, other source patches are merely modelled as low resistance land cover patches. However, depending on e.g. the social system and dispersal behaviour these habitat patches may have very different effects in the real world (e.g. Ferreras, 2001). Good places to settle may act as sponges—stopping further dispersal—or vice versa, these patches may be occupied by e.g. territorial con-specifics, which may enhance the probability of larger dispersal distances and reaching the next patch.

Least-cost values are also independent of the width of the least-cost path leading to the target patch. A corridor or gap of one grid cell will do for the model, but may be biologically irrelevant. When assigning resistance values to corridors or gaps through a barriers it may be necessary to adjust the resistance values based on land cover for the width of the corridor (e.g. when it is know that the system studied is sensitive to the width of the patch or to boundary effects). For gaps in discontinuous corridors in a highly resistant matrix it may be necessary to take into account the gap-crossing ability of the organism (e.g. Desrochers and Hannon, 1997; Brooker et al., 1999).

The least-cost path is the route that offers an organism (if it would use it, see above) the greatest probability of survival in traversing the entire distance between source and target patch (Walker and Craighead, 1997). However, least-cost paths in their simplest form are only representing the single series of cells which resulted in the lowest cost value. It is not possible to asses the stability of these paths in case of small changes in the input parameters. It is also not possible to judge the location of least-cost path for other grid cells in the same patch, or alternative paths for the same or very similar cost values.

However, extra GIS manipulations applying least-cost path algorithms in a iterative way (e.g. ArcInfo Grid function 'corridor') may allow to convert these least-cost paths into corridors for movement, which may be a useful tool to judge the biological usefulness of the least-cost paths (Walker and Craighead, 1997; Halpin and Bunn, 2000).

5. Conclusions

As already argued by other authors (Walker and Craighead, 1997; Bunn et al., 2000; Halpin and Bunn, 2000; Verbeylen et al., submitted for publication) this study showed that least-cost modelling is indeed an interesting tool for calculating inter-patch distances modified with landscape structure and movement behaviour (effective distance). The method is also a flexible research tool to obtain insights into the relation between dispersal and landscape characteristics, crucial to design conservation strategies, for example, for endangered species (Ferreras, 2001; Schadt et al., 2002). It is also an interesting toolbox for scenario building and improvement in land re-organisation projects and for predicting the effect of changes in the landscape on connectivity in a quantitative way. Since it can be applied as a standard GIS-application, in many studies extra information will be directly available, which also enables the use of the same maps and approach for the study of, e.g. change in connectivity for the farmers or traffic, spreading of noise, connectivity for recreational activities (bicycles, etc.), fire propagation, etc. However, this will require further investigation of resistance values and the required detail and accuracy in the maps (see above, O'Neill et al., 2000).

The method has a lot of potentials to study (and visualise) connectivity problems in many different ways (e.g. Figs. 2–4 of this study, see also Walker and Craighead, 1997; Villalba et al., 1998; Halpin and Bunn, 2000; Schadt et al., 2002). Scenarios can be compared in a quantitative way at the landscape level as well as for individual grid cells. Qualitative evaluation can be made at the landscape level using cost maps and differences between maps (cost in different scenarios of cost versus distance). Since resistance values and the resulting cost-values can be expressed as relative parameters, it may be possible to compare qualitative and quantitative results among species and sites (Villalba et al., 1998). Making use of the patch ID (the patch producing the lowest cost value) it is possible to construct areas of influence of patches in a complex landscape. Least-cost paths and corridor analysis may indicate priority locations for mitigating actions. Development of the GIS-environments may lead to many more tools in this toolbox.

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