A raster-based technique for analysing habitat configuration: The cost–benefit approach

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ABSTRACT

Advances continue to be made in modelling the spatial pattern of habitat. However, for models to be more useful, spatial pattern needs to be integrated with dynamic ecological processes. Existing modelling techniques often struggle to integrate faunal movement abilities or are impractical for routine application. We present here the cost–benefit approach (CBA), a modelling approach that integrates the costs of movement to organisms with the benefits of access to habitat. The approach brings together landscape ecology’s interest in realistically complex landscapes with fundamental theory from metapopulation ecology. CBA employs continuously variable spatial surfaces representing habitat quality and habitat permeability that reflect species’ habitat preferences and movement abilities respectively. Inter-site distance measurement is derived using the accumulated permeability along least cost paths. CBA provides both ecological rigour and tractability for real-world habitat modelling applications involving large, spatially complex datasets. The approach has been incorporated into simple geographic information systems based tools using raster (grid) data structures, and has been successfully employed in a variety of applications ranging from the measurement of local neighbourhood habitat context through to the estimation of metapopulation capacity for entire regions.

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1. Introduction

In the context of ever diminishing and increasingly fragmented habitat (Bennett, 1998), various forms of habitat modelling are attracting attention as tools to inform land-use planning and management and ultimately to promote the persistence of biodiversity. Fauna survival relies on species-specific movement behaviour across the landscape for such processes as habitat complementation, habitat supplementation, source–sink dynamics, neighbourhood effect (Addicott et al., 1987; Dunning et al., 1992), dispersal (Hanski, 1999a; Hanski and Ovaskainen, 2000) and migration. The efficacy of these processes is linked to habitat pattern: the composition and the physiognomic arrangement of habitat, as well as species, movement abilities in relation to a range of habitat conditions. Advances have been made in the modelling of spatial pattern (Guisan and Zimmermann, 2000). However, to understand how species survival relates to landscape, pattern and process need to be effectively integrated (Turner, 1989; Li and Wu, 2004).

With et al. (1997) have defined landscape connectivity as "the functional relationship among habitat patches", thereby highlighting the "process- as well as landscape-specific nature of connectivity". Increasing recognition of the impor-
stance of spatial processes to the survival of organisms has focused attention on finding ecologically meaningful ways of incorporating these processes into habitat modelling (Tischendorf and Fahrig, 2000b; Fischer and Lindenmayer, 2006).

The conceptual frameworks upon which models are based vary widely in terms of their complexity. Loehle (2004) identified six dimensions of complexity in ecology: spatial, temporal, structural, process, behavioural and geometric. For inherently simple processes, very simple models may be sufficient for any purpose. More complex models may yield more realistic and reliable results but this will not always justify the extra effort, overheads and expense required. For routine applications in conservation assessment and land-use planning requiring consideration of large numbers of species, there is a need for modelling techniques that are ecologically rigorous, yet simple and tractable.

1.1. Existing approaches to addressing connectivity in spatial habitat modelling

A number of measures and approaches has been developed to incorporate connectivity considerations into spatial modelling. These range from readily applied landscape metrics (Turner, 1989; Shumaker, 1996; Bender et al., 2003) through to complex individual-based simulations of movement throughout a landscape (Shumaker, 1996; Tischendorf and Fahrig, 2000b) and spatially explicit metapopulation models (Hanski, 1999a; Hanski and Ovaskainen, 2000).

Numerous landscape metrics have been developed that attempt to measure particular attributes of habitat configuration such as composition, fragmentation, contagion, isolation, patch shape and patch area (Flather and Sauer, 1996). These have been used as explanatory variables for predicting the distribution of habitat for particular species (Turner, 1989; New South Wales National Parks and Wildlife Service, 1994; Turner et al., 1995; Shumaker, 1996; Ferrier et al., 2002; Bender et al., 2003; Tischendorf et al., 2003). However, each of these metrics provide only partial insights into the functionality of species. They are, however, relatively complex and computationally demanding (Tischendorf and Fahrig, 2000b) and therefore of limited value for many large-scaled applications such as regional land-use planning exercises. They may nevertheless play an important role by serving as a benchmark with which to evaluate, and possibly calibrate, simpler models (Adler and Nuernberger, 1994).

Simpler models, that can be effective at integrating landscape structure with species’ movement abilities, have been developed within metapopulation ecology (Adler and Nuernberger, 1994; Hanski, 1999a,b; Hanski and Ovaskainen, 2000). This modelling relies on a patch-based view of landscapes, in which patches of habitat are arranged into relatively large discrete homogeneous units, forming a binary mosaic (Wiens, 1995; With et al., 1997). Such an arrangement may fail to capture the real complexity of habitat pattern exhibited by many species (Fischer and Lindenmayer, 2006). Inter-patch distances are measured, problematically, as the Euclidean (linear) distance between the closest edges of patches or the centres of patches (centroids). Patch shape and intra-patch variability is ignored, and no consideration is given to variation in the suitability or permeability within patches or within the matrix separating patches (Taylor et al., 1993; Bunn et al., 2000). While the potential of applying metapopulation models to continuously variable habitat surfaces has been demonstrated recently (Ovaskainen et al., 2002), applications of metapopulation ecology to real-world conservation planning have so far been wedded to a patch-based view of landscape structure.

1.2. The cost–benefit approach

We have formulated the cost–benefit approach (CBA) in order to provide a basis for undertaking ecologically rigorous, yet computationally tractable and data lean, spatial habitat modelling over complex landscapes. CBA utilises existing habitat suitability mapping – derived in any of a number of ways (Guisan and Zimmermann, 2000) – considered here as defining the benefits to an organism in the landscape such as food resources, or potential colonisation sites. These benefits are integrated with the costs of movement to organisms in a simple computationally efficient manner.

Essentially, CBA adopts Hanski’s (1999a,b) definitions of the connectivity of a patch and colonisation potential, which have been extensively applied within patch-based metapopulation approaches, and applies these to continuously varying raster data structures (Fischer and Lindenmayer, 2006). The CBA thereby combines landscape ecology’s interest in realistically complex landscapes, with rigorous theory from metapopulation ecology for modelling population processes at a landscape scale. Added to this, CBA employs an efficient organism-centric and landscape sensitive distance measurement based on graph theory (Dijkstra, 1959; Berry, 1993; Bunn et al., 2000). By representing habitat as raster data, at an appropriate resolution, the problematic and arbitrary distinction between intra-patch and inter-patch processes becomes unnecessary (Tischendorf and Fahrig, 2000b).

CBA is likely to improve and simplify modelling in applications involving processes that are sensitive to landscape connectivity, where the spatial configuration of habitat is complex or highly variegated or where habitat quality and permeability changes along a gradient (Fischer and Lindenmayer, 2006).

CBA has already been applied as:

- An approach to refining statistical models of habitat distribution (Ferrier et al., 2002);
• a site based isolation measure (neighbourhood effect) (Ferrier et al., 2002; Scotts and Drielsma, 2003);
• a measure of edge effect (Hoole, 2002);
• a predictor for modelling vegetation condition (Zerger et al., 2006);
• a measure of landscape capacity (Resource and Conservation Assessment Council, 2004);
• a basis for identifying potential wildlife corridors (Scotts and Drielsma, 2003; Drielsma et al., 2007).

CBA has also been incorporated into conservation prioritisation techniques (Scotts and Drielsma, 2003; Resource and Conservation Assessment Council, 2004; Department of Environment and Conservation (NSW), 2004).

In this paper, we first describe the underlying model that underpins the CBA—its recognition of landscape variability, the unique relationship between species and landscape, and the interplay between benefits and costs (from a biological perspective) that govern ecological processes upon which the survival of individuals and populations depend. We then describe how we have approached the computational implementation of CBA: the use of habitat quality and permeability grids; how least cost paths can be used to improve distance measurement, and how computation speed has been optimised.

2. CBA’s underlying habitat model

Combining measures of cost and benefits to help guide decision-making is familiar to economics (Pearse, 1983; Samuelson, 1983) and parallels can be drawn to ecological theory (Jones and Krummel, 1985). Accessing resources across the landscape provides benefits to an organism while imposing energy costs and risks. Movement behaviour by organisms

![Graph](image-url)

**Fig. 1** – The decay in link permeability as link length increases. Hypothetical decay curves are shown for a link through homogenous conditions (effective distance per metre is constant) and for a link through a mosaic where the effective distance per metre is influenced by the variable conditions (effective distance is greater than or equal to geographic distance) (panel a). Corresponding potential and actual marginal connected habitat accumulation as radius increases. The disproportionately high increase in area as radius increases means that for radii less than $1/\alpha$ the rate of habitat connectivity can potentially increase despite diminishing link permeabilities; but must then fall (panel b). Link length is measured in geographic distance units. $1/\alpha = 1000$ m.
Fig. 2 – The calculation of the neighbourhood effect for an example focal cell with a neighbourhood of $5 \times 5$ cells. Permeabilities are calculated between the centres of adjoining cells. The permeability between diagonally adjoining cells equals the orthogonal permeability raised to the power of root 2. The process can be repeated for all cells in a region by moving systematically through the grid one cell at a time. In each case the total neighbourhood effect is stored at the cell location of the focal cell in a new output grid. A suite of variations to this measure such as colonisation potential (see Hanski, 1999a,b) can also be derived using this approach.

$$\Gamma_i = \sum_j H_j w_{ij} = 1100.2$$
can often be assumed to be rational at least in part, aimed at maximising the chance of survival (Lindenmayer, 1998).

2.1. Analysis units—a case for raster

We assume a landscape in which habitat quality and habitat permeability can vary continuously across space and in which habitat data can be aggregated into spatial units of a scale appropriate to any ecological process under consideration (Parody and Milne, 2004).

Habitat models can be constructed using raster or polygonal data structures—the spatial units can be grid-cells or patches. The quantity of habitat can vary for each spatial unit, either due to variation in area, as would be the case with polygons, or with variation in habitat quality, which is more applicable to cells. However, grid-cells offer the following advantages:

- Data storage, retrieval and computation is more efficient since spatial units are of regular size and shape and are regularly arranged.
- Using grid-cells overcomes the problem of choosing appropriate source and destination points from which to measure distance (of most concern when patches have complex or elongated shapes)—the centre of the cell can be used.
- The vagaries of size and shape of individual spatial units is removed.
- Raster spatial units can be treated as fluid objects that can readily be re-sampled to coarser granularity without damaging the integrity of the data.

2.2. Permeability—links through space

The level of connectivity between habitat in a landscape depends on the nature of the intervening environment. For practical purposes point-to-point connectivity is often calculated on the basis of a single path between a pair of points: either a direct (straight line) path or, as we suggest here, a least cost path. We use the concept of permeability to describe the degree to which ecological processes can be conducted between two points. Permeability may be thought of as either the probability of movement success, or the ease of movement in terms of energy expenditure, or a combination of the two. Permeability is a property both of individual grid-cells and of whole habitat links or paths consisting of strings of adjacent grid-cells.

The manner in which the permeability, \( w_{ij} \), of a link decays with distance can be described with a dispersal kernel typically, but not necessarily, of the form:

\[
 w_{ij} = e^{-\alpha d_{ij}}, \tag{1}
\]

where \( d_{ij} \) is the effective distance between sites \( i \) and \( j \) (estimated here in terms of a least cost path) and \( 1/\alpha \) is the average movement ability for a given spatial process (Hanski, 1994). The parameter \( 1/\alpha \) can be estimated from empirical observation or from expert knowledge. For example, experts have estimated \( 1/\alpha \) for the white-browed tree creeper of South-Eastern Australia (Climacteris affinis) to range from 45 m across the most inhospitable land to 900 m through the most suitable habitat for day-to-day movement, and from 330 to 3300 m, respectively, for dispersing juveniles (Ellis et al., in press). The value of \( 1/\alpha \) represents a theoretical soft limit to how far a species will travel. However, it is expected that individuals will not always achieve this distance, and may occasionally exceed this distance in accordance with Eq. (1). Permeability has values between zero and one, where a permeability equal to one represents perfect conductivity and a value of zero represents an absolute barrier.

Assuming that a landscape provides less than perfect conductivity, permeability approaches zero as the effective length of a link or path increases. The reduction in link permeability with distance is rapid if the permeability of individual cells along the path is low, or more gradual in the case of high permeability cells (see Fig. 1a).

Across more realistic habitat mosaics, links may consist of a string of habitat units of varying permeability. The permeability of each habitat unit can be calculated by substituting the effective distance across the habitat unit (Berry, 1993) for \( d_{ij} \) in Eq. (1). For the sake of convention, for each habitat unit the value of \( d_{ij} \) can be allocated effective habitat values greater than or equal to the actual width of the habitat unit. The permeability of a link between sites \( i \) and \( j \) that comprises habitat units indexed by \( n \) can then be derived alternatively as the product of the component permeabilities:

\[
 w_{ij} = \prod_{n} w_{n}. \tag{2}
\]

2.3. Metapopulation analysis

Where basic information on habitat preferences and movement behaviour is available, simple metapopulation models can be constructed that provide valuable insights into the

\[\text{Fig. 3 – Contour representation of link permeability between a focal cell and its neighbourhood based on the least cost paths algorithm. Areas shown as grey represent regions of high permeability; white represents regions of low permeability. The focal cell is represented by the black dot. Each contour line represents points of equal link permeability back to the focal cell. The intervals between each successive contour are equal.}\]
likely occupancy patterns and likely persistence of populations subject to habitat scenarios (Hanski, 1999a; Hanski and Ovaskainen, 2000). Essentially, these models rely on spatial information at two scales: habitat availability at a site, often associated with nesting and foraging, calculated at the scale of a home range; and colonisation potential of a site calculated at the scale of dispersal (Hanski, 1999a).

The neighbourhood effect of site $i$, denoted $\Gamma_i$, can be calculated using a slight variant of the patch connectivity measure (Hanski, 1999a):

$$\Gamma_i = \sum_j H_j w_{ij},$$

where $H_j$ is the habitat value of site $j$ and where all spatial units in the region are indexed by $j$. Fig. 1b illustrates how the rate at which the patch connectivity (Marginal Connected Habitat, MCH) accumulates with increasing radius across homogeneous and variegated landscapes. For a homogeneous landscape, MCH increases for radii less than $1/\alpha$ from the focal site, peaks where the radius equates to $1/\alpha$, then falls for radii greater than $1/\alpha$.

The colonisation potential of site $i$, denoted $R_i$, can be calculated as (Hanski, 1999a):

$$R_i = H_i / \Gamma_i$$

It is likely that the value of $1/\alpha$ will differ for neighbourhood effect and colonisation since these processes tend to operate at different scales (Addicott et al., 1987) making it necessary to undertake separate analysis, each with $1/\alpha$ set to an appropriate value. Landscape-scale measures

![Fig. 4](image-url) - Mapped representation of variable habitat quality (panel a), neighbourhood effect (panel b) and colonisation potential (panel c) for the same region. In each case high values are represented by darker shading. Neighbourhood effect and colonisation potential are derived using habitat quality as the 'benefit' grid. In this example the permeability grid was derived by range transforming the habitat quality data. $1/\alpha = 1000$ m. Grid-cells have effective orthogonal cell widths ranging from 100 m (the cell width) for high permeability cells, to 200 m for the lowest permeability cells.
can be calculated by summing site-based measures across a region.

Neighbourhood effect and colonisation potential calculations can form the basis of analysis leading to predictions of species occupancy across a landscape and the likelihood of regional persistence, either using a patch-based approach (Hanski and Ovaskainen, 2000), or a raster approach (Drielsma and Ferrier, in preparation).

3. Computational implementation of CBA

3.1. Habitat value and permeability (costs and benefits)

The CBA technique, as we have applied it, requires two input grids of equal dimensions and resolution: a benefit (habitat quality) grid and a cost (permeability) grid. In practice these two grids may be derived from the same spatial habitat data (as is the case in Fig. 4). The benefit grid represents the distribution of habitat resources across the region of interest, providing values for \( H_i \) in Eq. (3) and \( H_i \) in Eq. (4). The cost grid represents the ease of movement, providing values for \( w_n \) in Eq. (2). These permeabilities can be calculated from Eq. (1) by substituting the effective orthogonal cell width for \( d_i \). Permeability across the diagonal of a grid-cell equals the orthogonal permeability raised to the power of the square root of 2.

3.2. Distance measurement (least cost paths)

The measurement of inter-site distances is a core component of connectivity analysis and distance can be estimated in a variety of ways. With the CBA, the effective distance between sites is derived as a function of species’ movement abilities and the composition of the intervening landscape.

In CBA applications to date this has been achieved by employing the least cost path algorithm (LCPA) from graph theory (Dijkstra, 1959) to identify the route through connecting grid-cells that maximises the total permeability between two sites, i.e. \( w_n \) from Eqs. (1) and (2). The LCPA is particularly useful for modelling movement for species in which individual routes tend to follow landscape features that are advantageous in terms of such things as energy efficiency, resource access and the low risk of predation (Bunn et al., 2000). Even the (successful) displacements arising from a number of unintentional movements may reflect habitat pattern. For species in which movement is unrelated to landscape pattern alternative functions may need to be adopted.

Fig. 2 illustrates diagrammatically how the neighbourhood effect calculations can proceed using the LCMA for an example focal cell with a 5 x 5 window. Fig. 3 illustrates the pattern of link permeability between an ‘ecological neighbourhood’ and an example focal cell and Fig. 4 illustrates an example of CBA outputs mapped for a region.

3.3. Computational optimisation

Rapid approaches to habitat connectivity modelling are needed for many applications yet previous attempts to measure habitat connectivity using raster data have been limited by the computational challenges of applying such approaches (Tischendorf and Fahrig, 2000a). Rapid approaches are needed for applications in which numerous species or species groups need to be assessed in relation to multiple landscape scenarios, where study regions are extensive, where models of habitat connectivity need to be incorporated into iterative optimisation algorithms (e.g. simulated annealing, genetic algorithms) for generating optimal landscape configurations or for higher level metapopulation analysis (Drielsma and Ferrier, in preparation).

The CBA has been made operational as a highly optimised software function in the C++ programming language. The functions have been highly optimised for computational efficiency and they allow the balance between rigour and speed of computation to be adjusted to suit different applications.

Firstly, the analysis window is constrained to a radius beyond which functional connectivity is assumed to be trivial. This radius can be calculated as the distance beyond which the MCH (see Fig. 1b) cannot exceed a user-defined threshold (e.g. 0.05 of the maximum MCH, at a radius of 1/\( \sigma \)) even under conditions of maximum permeability.

Secondly, we have developed a new ‘petals’ technique for grid sampling that further reduces processing demands. This technique allows cells to be aggregated into temporary analysis units (petals) that decrease in spatial resolution as the distance from the focal cell increases (see Fig. 5). The degree of aggregation can be customised to suit any given species or species’ landscape process. The resulting reduced set of units, which we call petals, then becomes the basis for the simplified LCPA calculations. The habitat value for a petal is simply the sum of the habitat values of the member cells of the petal; the permeability of the petal is the average permeability of the member cells extrapolated over the average width of the petal. The size of the petals can increase with distance from the focal cell so that spatial precision is sacrificed where it...
has the least bearing on the outcome. The trade-off between ecological rigour and computation time is therefore achieved efficiently.

4. Conclusion

Many applications, such as regional-scale conservation planning exercises require relatively quick yet ecologically rigorous ways to assess the efficacy of landscape habitat configurations. Habitat modelling can be improved by recognizing within the modelling variability in landscape structure and by considering the response of faunal movement abilities to that variability. The approach to habitat connectivity modelling presented here offers a balance between computational demand and ecological rigour that is likely to be well suited to such applications.

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