

Introducing a ‘stochastic movement simulator’ for estimating habitat connectivity

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Summary

1. Estimating and improving landscape connectivity has become a key topic in conservation biology. While a range of connectivity indices exist and are widely used to inform spatial planning, they have potentially serious limitations.

2. We introduce a new method for modelling animals moving between habitat patches across a heterogeneous matrix. Our approach integrates features of least cost path analysis with stochastic movement modelling. Importantly, it relaxes assumptions that are implicit in the least cost path algorithm: our method does not assume omniscience nor does it assume that an individual has a planned destination when it leaves a habitat patch. The algorithm incorporates resistance values for matrix elements and parameters that relate to both perceptual range and to the degree of correlation in movement. By simulating sets of movements for individuals emigrating from habitat patches, relative connectivities between habitat patches are estimated.

3. Using an already published stylised landscape, we demonstrate that the connectivities estimated using our new method can differ considerably from those provided by structural methods and by least cost path analysis. Further, our results emphasise the sensitivity of the relative connectivities to an organism's perceptual range and the degree of correlation between movement steps.

4. We believe that using stochastic movement modelling can improve estimates of connectivity and also provide a method for determining how robust the indices derived from simpler methods are likely to be for different types of organisms.

Key-words: dispersal, habitat fragmentation, individual-based model, perceptual range

Introduction

Movement of organisms is a key process maintaining connectivity between subpopulations in fragmented landscapes and is thus of critical importance in the design and maintenance of reserve networks to conserve threatened species (e.g. Crooks & Sanjayan 2006; Hilty, Lidicker, & Merenlender 2006). Moreover, as environmental and climatic conditions change, species may need to undergo range-shifts to track the conditions to which they are adapted (e.g. Hanski 1999; Kokko & Lopez-Sepulcre 2006; Reusch & Wood 2007; Ronce 2007), and they will only be able to do so if at least some individuals are capable of dispersing to suitable habitat beyond their current range limit. To assess whether threatened and endangered species will be able to do this, conservation managers need

reliable and accurate methods for determining the degree of connectivity within fragmented habitat networks. The simplest measure of connectivity between any two patches, the Euclidean distance, will frequently be inadequate for this purpose, as dispersing individuals do not necessarily move in straight lines through a heterogeneous and often hostile landscape (e.g. Wiens 2001).

The least cost path (LCP) approach aims to improve upon Euclidean distance as a measure of connectivity by taking account of the character of landscape elements lying between isolated habitat patches. This method traditionally determines, for a pair of patches within a heterogeneous landscape, the optimum route between the patches incurring the least cumulative cost according to a cost grid (Adriaensen *et al.* 2003; Chardon, Adriaensen, & Matthysen 2003; Driezen *et al.* 2007). The approach may be extended by summing cost distance maps for the different potential sources of dispersers to evaluate cumulative and synoptic connectivity (e.g. Compton

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et al. 2007) or by evaluating LCPs among networks of points for species which view the landscape as a gradient of habitat quality rather than discrete patches (e.g. Cushman, McKelvey, & Schwartz 2009). The cost has been taken to represent the estimated resistance to movement (e.g. Sutcliffe *et al.* 2003; Vignieri 2005; Broquet *et al.* 2006; Finn *et al.* 2006; Lada *et al.* 2008; Koscinski *et al.* 2009; Hokit *et al.* 2010), the time taken to move through a habitat (e.g. Stevens *et al.* 2006) or an index representing some combination of more than one cost (e.g. Stevens *et al.* 2006; Nichol *et al.* 2010). Further possible costs could be the energetic demands of moving through a habitat or the risk of mortality, although we know of no examples in the literature of their use. The relative connectivity between different pairs of patches is then estimated by comparing the lengths and/or the costs of the LCPs among all possible pairs of patches.

Whatever the cost metric employed, however, the underlying assumption of the LCP approach is that of perfect knowledge of the entire landscape (omniscience) on the part of the moving individual. Although animals may indeed have excellent knowledge of a territory or home range, this assumption is presumed to be highly unrealistic for most animals during dispersal, and especially so for long-distance dispersal (LDD) and/or post-natal dispersal. Thus, animals presumably have to make frequent movement decisions during dispersal based on the limited information they have about the surrounding habitat types within their perceptual range (be that visual, olfactory or a combination of sensory mechanisms) (Zollner & Lima 1999; Conradt *et al.* 2000; Merckx & Van Dyck 2007), and which may be context-dependent (Olden *et al.* 2004). Even if an animal has a fundamental tendency to follow a highly correlated (i.e. fairly straight) dispersal path, it may still change its direction of movement based on choices that relate to the composition of habitat in the proximity of its route. Thus, animals may follow routes through inhospitable habitat which differ considerably from the optimum (in terms of least distance or cost), and as a result the effective (functional) connectivity between habitat patches may differ substantially from the LCP connectivity. Moreover, we predict that the smaller a species' perceptual range in relation to the grain of the landscape, the more the functional connectivity will deviate from the LCP connectivity, i.e. the correlation between LCP and functional connectivity will itself be positively correlated with perceptual range. For these reasons, the legitimacy of LCP-based decisions in land management has been questioned (Fahrig 2007; Baguette & Van Dyck 2007).

Stochastic modelling of organism movement has a long history much of which builds on early work using random walk models (e.g. Skellam 1951). In these first models, Brownian motion was assumed where the direction of movement in one step is completely independent of that in the previous step. For most organisms, it is more realistic to incorporate correlation between steps (Codling & Hill 2005) and such correlated random walks have become widely used in modelling animal movement (e.g. Bovet & Benhamou 1988; Byers 2001). Importantly in the context of our work, landscape ecology theory highlights that the degree of correlation in a movement

trajectory is key in determining the likelihood that an emigrating individual successfully arrives at a non-natal habitat patch (Zollner & Lima 1999). More recently, some studies have begun to incorporate biased movement either towards the centre of a home range (Morales *et al.* 2005) or towards a habitat patch (Bartoń *et al.* 2009). However, these models tend to assume movement in a largely homogenous environment with, at any one point in time, a positive bias towards a single point (but see Vuilleumier & Metzger 2006 for an alternative object-oriented approach to representing landscape features). In reality, an individual will frequently be moving through a complex landscape surrounded by a variety of matrix elements imposing different biases. By integrating concepts from LCP modelling with recent progress in modelling movement, we believe it should be possible to construct a relatively simple model that captures much of the complexity in terms of both the rules that an individual follows and the structure of the landscape.

Here, we demonstrate how we may model the dispersal of animals through a heterogeneous landscape, in which different components are associated with different costs of movement, in such a way that the path taken depends on a sequential series of movement decisions each based on the information about the landscape within the animal's perceptual range. We also aim to show how the perceptual range, the way in which an animal evaluates habitat quality and its tendency to move in a particular direction correlated with its previous direction interact to govern the efficiency with which it is able to locate suitable habitat patches, and hence how the functional connectivity of landscape patches is governed by these movement parameters.

Materials and methods

GENERAL PRESENTATION OF THE MODEL

The model is a stochastic individual-based model (IBM) in which virtual animals disperse from a source habitat patch and move independently through a landscape according to simple, but realistic (for many animal species) rules until they reach a target habitat patch, emigrate from the landscape or die after a given number of time-steps (fixed at 2000). We run the model, implemented in C++, for a series of combinations of three key parameters: the animal's perceptual range (PR), the method it uses to evaluate the habitat within its PR and its tendency to move in a straight line (i.e. to follow a correlated random walk). For each parameter combination, we calculate the functional connectivity of the source patch to each target patch as the proportion of dispersing individuals which reach the target patch. We compare this metric with the LCP lengths and costs calculated for the landscape using standard geographical information system algorithms.

THE LANDSCAPE

We derived our example virtual landscape from that used by Chardon, Adriaenssen, & Matthysen (2003), in which the source patch is located at the centre of the square landscape, and four target patches are located in the four cardinal directions, each separated from the source patch by a landscape feature which is either beneficial (a corridor or a series of stepping stones) or inhibitory (a barrier or an area of

poor habitat) to movement. We rescaled the landscape to a grid of 300×300 cells and replaced the central patch by a single source cell, but otherwise retained the original landscape characteristics, including the relative cost values of the various landscape features (Fig. 1). We recalculated the LCP distances between the source and the four target patches using standard methods in ArcGIS v9.2 (ESRI, Redlands, CA, USA).

ANIMAL MOVEMENT

PR was varied incrementally from 1 to 10 cells, and then in steps of five cells up to a maximum of 30 cells (i.e. 10% of the landscape dimension). Each animal moved through the landscape by choosing to move at each step from its current cell to one of the eight neighbouring cells. The probability that a cell was chosen depended on its cost value, the cost of neighbouring cells lying beyond it within the PR and the direction which the animal had taken to reach its current location.

If the PR was one cell, then the cost value of a neighbouring cell was simply its cost as determined by the landscape grid. When the PR was greater than one cell, the animal still had to make a choice between the eight neighbouring cells, but their effective cost had also to take into account the cost of potential future moves from the chosen cell on the basis of information available from all cells within the PR. We achieved this by taking as the effective cost of a neighbouring cell the mean of its own cost and of the costs of its own neighbours surrounding it in an array which extended to the edge of the perceptual range (Fig. 2). Three alternative methods were used for evaluat-

ing the effective cost: the (unweighted) arithmetic mean, the harmonic mean¹ and a weighted arithmetic mean (in which the contribution of each cell within the PR towards the effective cost was weighted by the inverse distance of the cell to the current cell).

There is good evidence from theoretical studies (Zollner & Lima 1999; Heinz & Strand 2006; Bartoń *et al.* 2009) and from empirical observations (Schultz & Crone 2001; Fahrig 2007 and citations therein; Schtickzelle *et al.* 2007; del Mar Delgado & Penteriani 2008) that dispersing animals tend to follow a highly correlated path, i.e. they make few large turns. We implemented this constraint within our model by increasing the probability of selection for cells in the direction of the animal's movement and decreasing it for those in the direction from which it had come. Specifically, we applied a weighting to the effective costs of neighbouring cells (prior to calculating cell probabilities), which was lowest in the direction taken in the previous step and highest in the opposite direction (i.e. a 180° turn). The weighting was controlled by a single parameter (hereafter 'directional bias'), which was raised to the power zero in the direction of previous travel, and to powers increasing from 1 to 4 in the direction of turns from 45° through to 180° ; larger values of the parameter reduce the tendency for the path to deviate from a straight line.²

Finally, the reciprocals of the weighted effective costs were taken and scaled to sum to unity to yield selection probabilities for the eight neighbouring cells (Fig. 2); the next cell in the path was chosen stochastically in proportion to these selection probabilities. Thus, our model bears strong similarities to the self-avoiding random walk of Gustafson & Gardner (1996), but with a non-zero probability of returning to the previous cell and, critically, with increased PR and directional bias. Example paths generated using our movement rules are shown in Fig. 3. The accumulated cost of the path taken was then incremented by the cost of the chosen move (i.e. the mean cost of the original cell and the chosen destination cell, weighted by $\sqrt{2}$ for diagonal moves). This is exactly the same method as the LCP algorithm uses to calculate the cost of movement between adjacent cells. No special recognition of the targets was implemented, but because they each comprised a block of low-cost cells, animals tended to move towards a target once it was within the individual's PR.

For each combination of PR, evaluation method and directional bias, we released sequentially a sample of 1000 animals into the landscape from the point source. An animal's path was terminated as soon as it entered any one of the cells of a target patch, and the animal was then classed as a successful disperser. We treated the landscape as a torus for the purpose of evaluating the effective cost if the animal was within its PR of the boundary, but once an animal made a move which took it beyond the boundary, its path was terminated and it was classed as an emigrant. If neither successful dispersal nor emigration occurred within 2000 steps, the animal was regarded as having

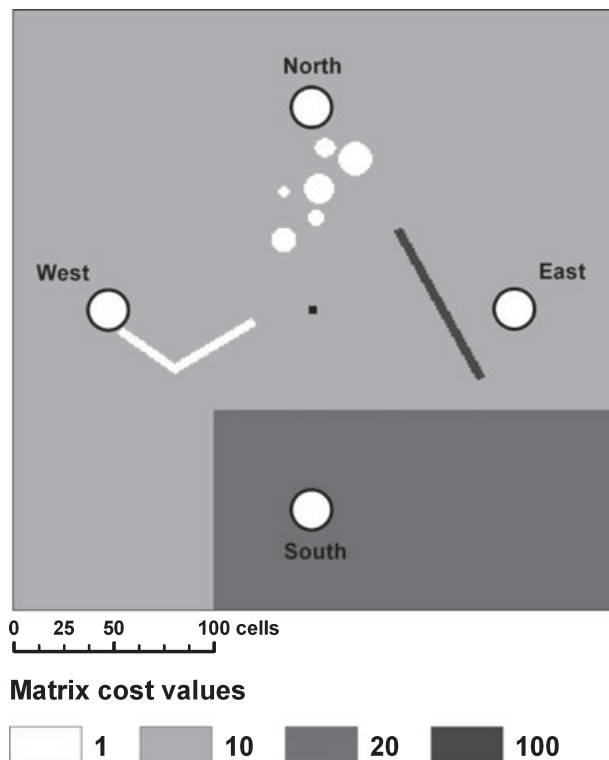


Fig. 1. The artificial landscape, following Chardon, Adriaenssen, & Matthysen (2003). Animals were released from the central source cell (here shown enlarged for clarity), and the four target patches are delimited by black circles.

¹The harmonic mean is the reciprocal of the arithmetic mean of the reciprocals of the observations. Consider a 3×3 array of cells, each having value 10 (the background matrix cost). The arithmetic mean is 10. Now, if we change the cost of just one of the nine cells to 1 (e.g. a target cell in the far corner of the array), the arithmetic mean is reduced to 9, a slightly lower effective cost, and thus slightly more likely to be the chosen direction, but not by much. However, the harmonic mean becomes five, halving the effective cost and thus doubling the chance of this particular direction being taken. Thus, the harmonic mean method is a simple way of increasing the detectability of good (low cost) habitat. Conversely, the harmonic mean method is less effective than the arithmetic mean method at detecting very costly habitat (e.g. a partial barrier).

²For example, if the directional bias parameter value is 2, then a 180° turn is 16 times (2 to the power 4) less likely than continuing in the same direction, all other factors (i.e. effective costs) being equal, but if the parameter is raised to 4, the 180° turn becomes 256 times less likely than continuing in the same direction.

Fig. 2. Examples of the calculation of cell selection probability dependent on cell cost and perceptual range (PR). For simplicity, we illustrate the method here with the directional bias parameter set to 1, i.e. there is no tendency to continue in the previous direction. In both (a) and (b), the animal starts in the centre cell, which has zero cost (in this case it is the source cell). In (a), the animal's PR is one cell: the effective cost of moving to a neighbouring cell is the neighbouring cell's cost, weighted by the length of the cell diagonal ($\sqrt{2}$) for diagonal moves. In (b), the PR is two cells: the effective cost of each neighbouring cell is given by the (arithmetic) mean of its cost plus the costs of its own neighbours up to the PR (as highlighted for the NW neighbour by a bold margin). For an orthogonal move, a rectangular block is assessed to retain symmetry (dashed margin to S). In both (a) and (b), the probabilities of selection are inversely proportional to the effective costs. The effect of greater PR in (b) is to increase the probability of moving SW or S owing to the presence of low-cost habitat in the SW corner of the PR.

(a) Cell costs within PR = 1 cell

	2	1	1	
	1	0	2	
	4	3	1	

(a) Effective cost

	$2 \times \sqrt{2}$	1	$\sqrt{2}$	
	1		2	
	$4 \times \sqrt{2}$	3	$\sqrt{2}$	

(a) Probability of cell selection

	0.074	0.209	0.148	
	0.209		0.105	
	0.037	0.070	0.148	

(b) Cell costs within PR = 2 cells

2	3	4	4	4
2	2	1	1	3
2	1	0	2	4
2	4	3	1	4
1	1	2	3	4

(b) Effective cost

	$\frac{9 \times \sqrt{2}}{4}$	$\frac{15}{6}$	$\frac{12 \times \sqrt{2}}{4}$	
	$\frac{13}{6}$		$\frac{15}{6}$	
	$\frac{8 \times \sqrt{2}}{4}$	$\frac{14}{6}$	$\frac{12 \times \sqrt{2}}{4}$	

(b) Probability of cell selection

	0.111	0.141	0.083	
	0.163		0.141	
	0.125	0.151	0.083	

run out of time and classed as dead. For each animal, its fate, the path length (number of steps), incurred total cost, target patch reached (if any) and number of steps spent in each of the four landscape feature types were recorded for subsequent analysis.

DATA ANALYSIS

The effects of the model parameters in determining realised path characteristics were examined by fitting the generated path data to statistical models having PR, evaluation method, directional bias (log-transformed to account for a curvilinear relationship) and all possible interactions between them as explanatory variables. The proportion of all paths which successfully reached a target patch was fitted to a generalised linear model incorporating a logit link function and a binomial error term. Similar general linear models were fitted to the total path length (log-transformed) and to the total cost incurred (log-transformed) by all successful dispersers (i.e. those which

reached a target patch). The relative importance of model parameters and their interactions was assessed by their type III Wald χ^2 values for the model of probability of success, and type III F statistics for the path length and cost models.

Results

DISPERSAL SUCCESS

Directional bias ($\chi^2 = 28713$) and PR ($\chi^2 = 9501$) had the greatest effect on the probability of successful dispersal, and there was also a substantial interaction between PR and evaluation method ($\chi^2 = 1202$). At low PR and low directional bias, very few individuals located a target patch within the prescribed number of steps, whereas at high values of these parameters, almost all did so (Fig. 4). At all but the

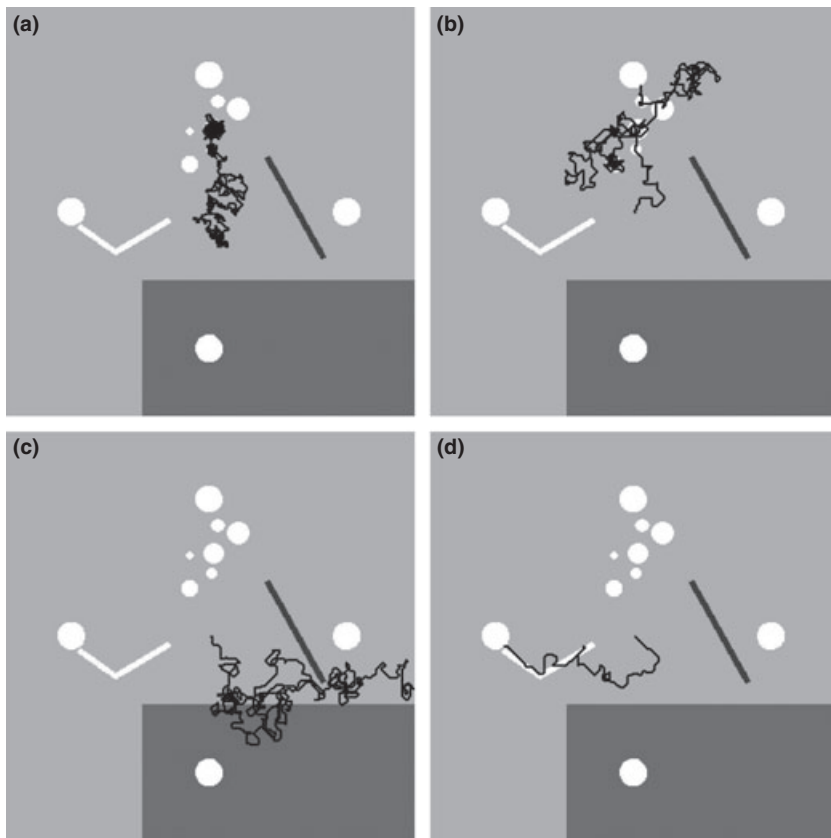


Fig. 3. Examples of individual movement paths generated by the model. Source location and landscape costs are as in Fig. 1. (a) Low perceptual range ($PR = 5$), low directional bias (2.0), harmonic mean method: the animal wanders aimlessly, becomes trapped in a stepping-stone patch and dies after 2000 time-steps. (b) Low PR (5), high directional bias (4.0), harmonic mean method: the path is less tortuous, and the stepping stones are used to reach the northern target patch. (c) Low PR (5), high directional bias (4.0), arithmetic mean method: the animal avoids the costly barrier, but fails to find the target patch beyond it owing to its low PR, and emigrates from the landscape. (d) High PR (20), high directional bias (4.0), harmonic mean method: efficient use is made of the corridor to reach the western target patch.

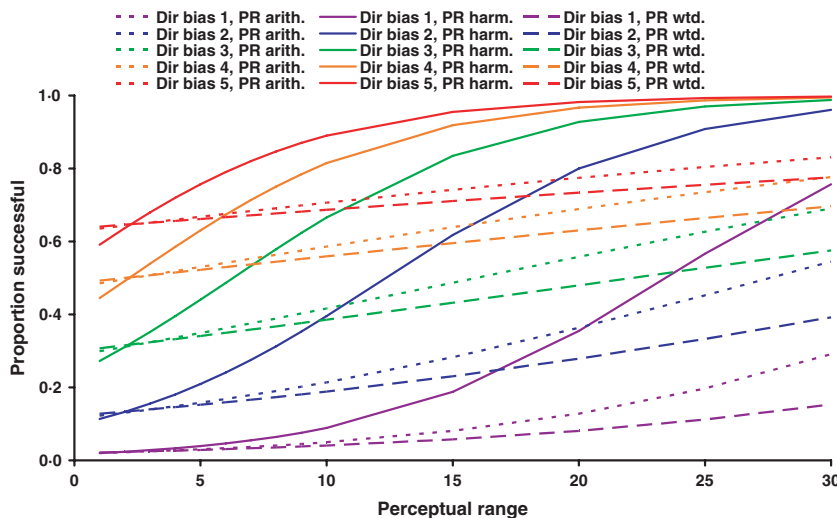


Fig. 4. Proportion of individuals which successfully located a target patch as a function of perceptual range, directional bias and perceptual range evaluation method (arith. = arithmetic mean, harm. = harmonic mean, wtd. = weighted arithmetic mean). Lines show fitted relationships; $n = 1000$ per parameter combination.

lowest PR, individuals were more likely to locate a target patch if employing the harmonic mean method of evaluating landscape cost rather than either of the arithmetic mean methods. Moreover, as directional bias ($F = 7384$) and/or PR ($F = 613$) increased, the length of the path followed by successful dispersers decreased (Fig. 5a). The length of the path was also lower if using the harmonic mean method rather than either of the arithmetic mean methods at all but very low PR. Similarly, as directional bias ($F = 1018$) increased, the total path cost incurred by successful dispersers decreased, but the

decrease was substantial only if the harmonic evaluation method were used ($PR \times \text{method}$ interaction $F = 39.5$) and especially if there were high directional bias ($PR \times \text{bias}$ interaction $F = 273$) (Fig. 5b).

The increase in successful dispersal with increasing PR and directional bias was largely accounted for by increasing numbers of dispersers reaching the western and northern target patches lying beyond the corridor and stepping stones, respectively (supplementary material Fig. S1). These numbers reached asymptotes at high levels of directional bias

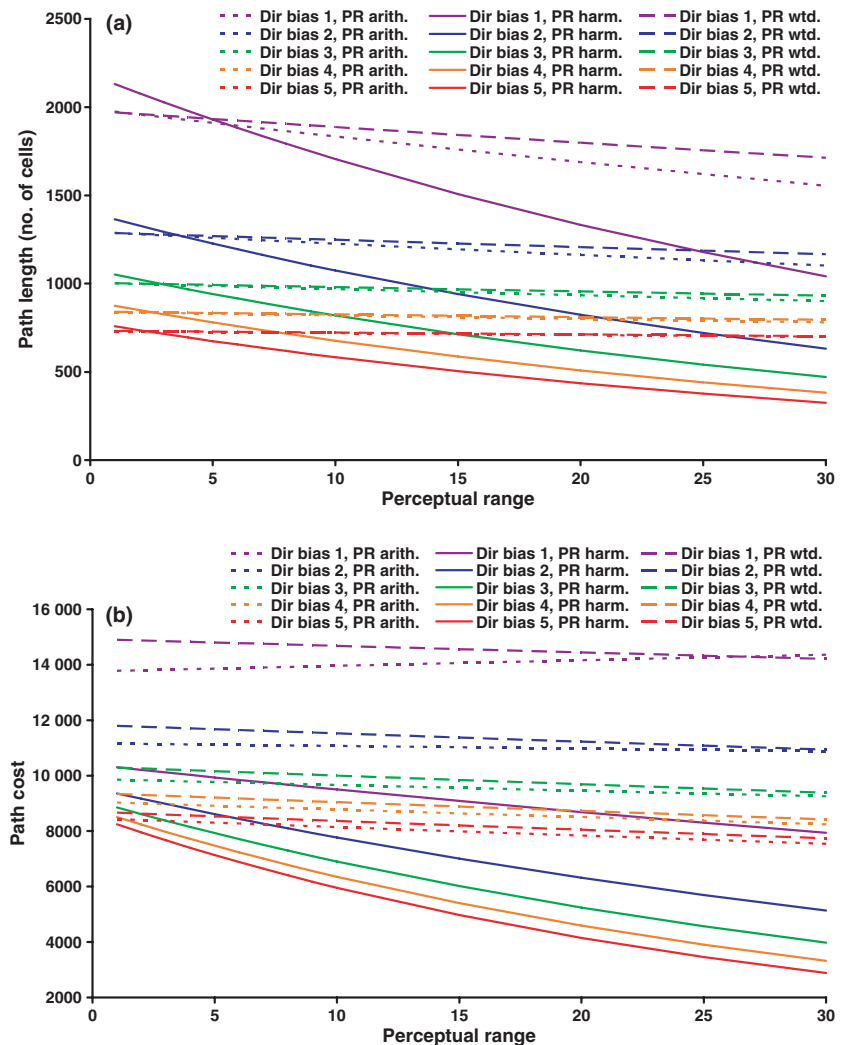


Fig. 5. (a) Length and (b) total accumulated cost of paths followed by individuals which successfully located a target patch as a function of perceptual range, directional bias and perceptual range evaluation method (arith. = arithmetic mean, harm. = harmonic mean, wtd. = weighted arithmetic mean). Lines show fitted relationships; $n = 1000$ per parameter combination.

(above 3.5), but continued to increase as PR was increased up to its maximum value. In contrast, as PR increased, the numbers reaching the eastern and southern patches decreased, which is attributed to individuals turning round on encountering inhibitory landscape features and thereby increasing their chance of subsequently locating the beneficial features and the patches to which they led. However, despite the increased efficiency afforded by high PR and directional bias, some successful dispersers incurred relatively high costs, which could be more than an order of magnitude greater than the LCP cost to the same patch (e.g. Fig. 6).

RELATIVE CONNECTIVITY

If the relative connectivity of the source patch to the four target patches were determined on the basis of the reciprocal of Euclidean distance, then all target patches would be equal as they were equidistant from the source (Fig. 7a). Replacing Euclidean distance by the LCP length made little difference (roughly 10% increases to the northern and southern patches and similar decreases to the other two patches; data not shown), as the LCPs did not deviate very far from straight

lines. Replacing Euclidean distance by the LCP cost increased the relative connectivity to the northern and western patches as the stepping stones and corridor (especially) provide relatively low-cost paths (Fig. 7b). In contrast to this deterministic method, connectivity estimated by the simulation of individual movement depended on the parameters controlling the movement. Here, we use the relative numbers of successful dispersers to each target patch under a particular scenario as the measure of connectivity and illustrate this for four examples of combinations of parameters. An example of a simulation with low PR and low directional bias shows the western patch linked by the corridor being favoured, but the stepping stones to the north provided poor connectivity as individuals tended to become trapped within them (Fig. 7c). Increasing the directional bias could counteract the trapping problem, leading to improved relative connectivity to the northern patch (Fig. 7d). In an example where PR was high but directional bias was low, no individuals located the southern patch in the poor matrix habitat, and very few the eastern patch behind the barrier (Fig. 7e), whereas high directional bias combined with high PR enabled more dispersers to either pass around or break through the barrier to the east and to locate and move towards

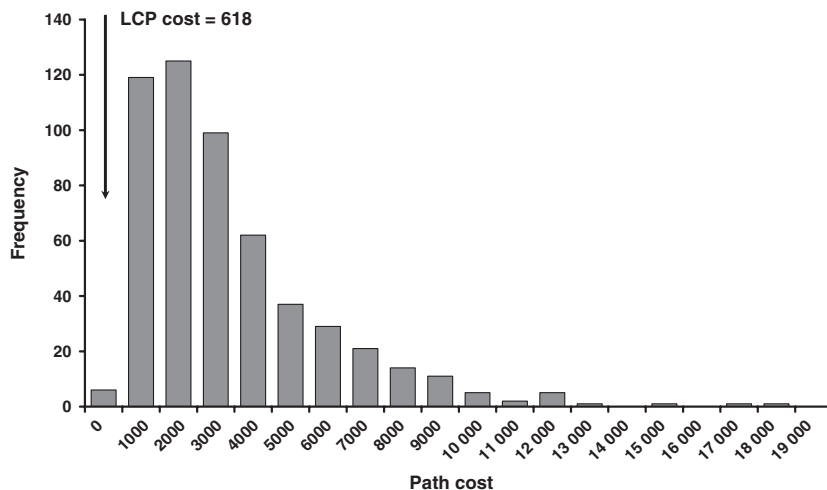


Fig. 6. Frequency distribution of path costs incurred by successful dispersers reaching the northern target patch under the conditions $PR = 30$, directional bias = 5.0, harmonic mean method ($n = 539$). The minimum incurred cost was 871 and the mean was 3872, whereas the least cost path incurs a cost of 618.

the southern patch even though higher cost matrix cells have to be crossed (Fig. 7f). Further examples of how the relative connectivity changed in relation to changing directional bias and PR are presented in the supplementary material (Fig. S2).

In order to check that our results were unlikely to be artefacts of assumptions we had made in constructing the model, we ran a series of additional separate variants as follows: (i) the corridor and stepping stones had a cost of two units rather than 1 (i.e. to be more costly than the target patches), (ii) the maximum number of steps was increased from 2000 to 5000 and (iii) once a target patch was within the PR, the individual moved directly towards it. In all cases, there were trivial and expected effects, such as an overall change in the proportion of successful paths and their mean costs, but the patterns of interaction between PR, directional bias and evaluation method were, broadly speaking, unaltered. One point of note, though, is that variant (ii) was initially attempted with no step limit, in which case one individual finally completed a path of over 125 million steps, of which 99.98% were spent stuck in the stepping stones. This implies that the inclusion of some form of step-dependent mortality risk or resource loss will be crucial in more realistic versions of the IBM.

Discussion

There has been substantial recent progress in modelling animal movement (e.g. Zollner & Lima 1999; Morales 2002; Morales & Ellner 2002; Morales *et al.* 2004, 2005; Heinz & Strand 2006; Vuilleumier & Metzger 2006; Bartoń *et al.* 2009), much of which uses stochastic models incorporating correlation and bias in the movement rules. We believe that there is considerable potential in integrating these concepts and methods in landscape ecology, in particular for improving estimates of connectivity. Here, we have presented a deliberately simple method, which utilises the same landscape information as LCP modelling, i.e. resistance parameters for each of the matrix elements in the landscape, and models movement in discrete space (in this respect our model is distinct from many of the recent models of movement). Our method requires just two additional parameters to the standard LCP algorithm, one

specifying the PR and the other the strength of correlation in the movement. A third can be optionally used to specify the method employed to determine the mean effective cost within the PR. Later, we explain the key results generated from our model and highlight key future applications and further developments of the approach.

Our novel stochastic rule-based model simulates the inter-patch movement of individuals through a landscape matrix. It clearly demonstrates how the probability of successful dispersal depends on both the movement correlation of the path and on the perceptual range of the individual. Zollner & Lima (1999) have previously demonstrated the effect of movement correlation on success and shown how it interacts with the landscape configuration, the risk of mortality and the energy reserves of the disperser. Even if all these factors are the same for two different species, and even if they have the same habitat preferences and incur the same movement costs, their probability of successful dispersal will differ if their perceptual ranges differ. Thus, the functional connectivity of the habitat network will also differ for the two species.

For successful dispersers, the total path length and total cost incurred are also affected by the way in which the animal evaluates the landscape within its perceptual range. Undoubtedly, animals actually use some form of rule-based method to decide amongst the alternatives available at any point in their path, rather than the mathematical methods adopted here. The benefits gained by increasing PR in our model were greater using the harmonic mean method than under the unweighted or weighted arithmetic mean methods, as these diluted the influence of low-cost cells on the probability of movement. Weighting the arithmetic mean by inverse distance actually had only a very limited effect in our simulations (compared to the unweighted arithmetic mean), but in part this may have been because the matrix we used was largely homogeneous (except for the specific features) in terms of cost value. Further evaluation of the relative benefits of various potential weighting methods would undoubtedly be worthwhile, but, nevertheless, our results suggest that a rule-based method which gives a high weighting to beneficial landscape features, such as corridors or stepping stones, is likely to be the most efficient. For simplicity,

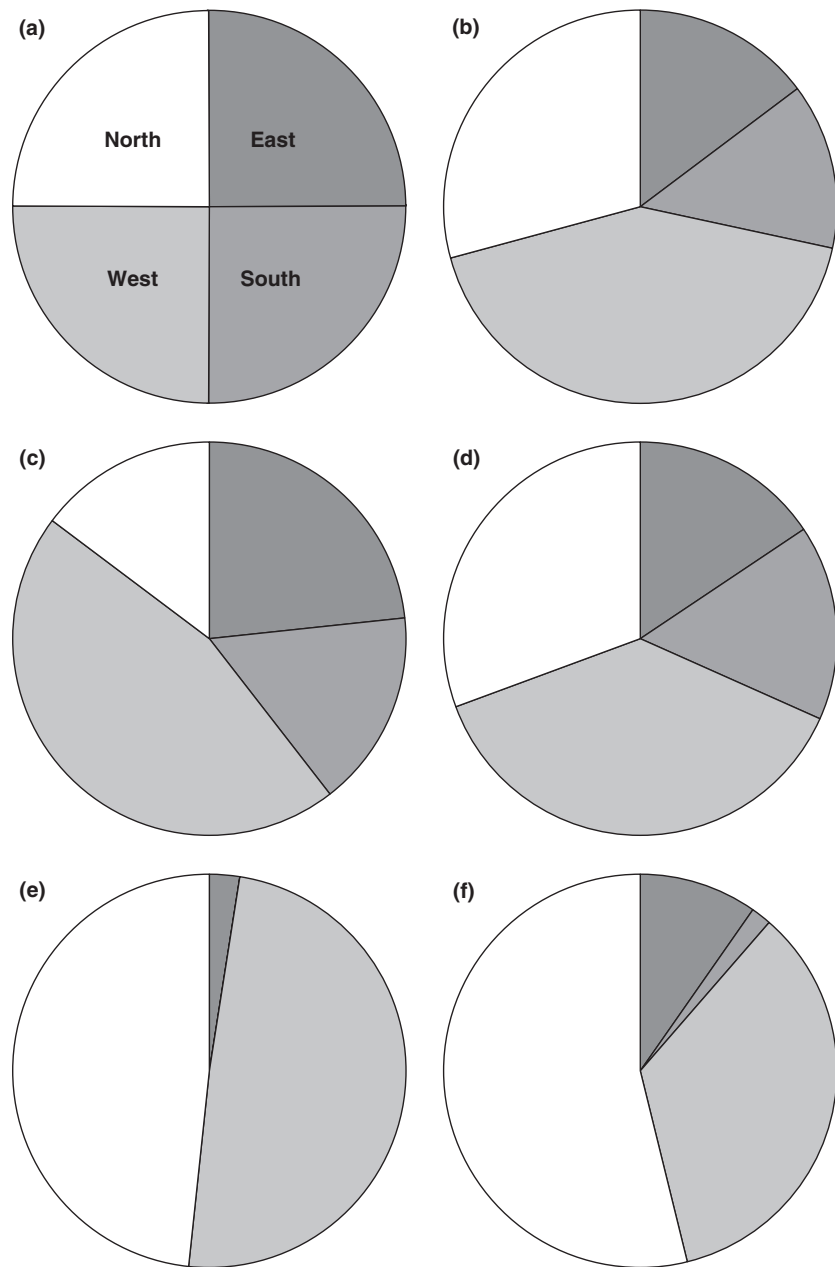


Fig. 7. The relative connectivity of the central source cell to each of the four target patches under different connectivity models. (a) Euclidean distance; (b) Least cost path (reciprocals of path cost); (c) Stochastic movement simulator (SMS) (relative numbers of successful dispersers), PR = 2, directional bias = 2.0, arithmetic mean method ($n = 150$ successful dispersers); (d) SMS, PR = 5, bias = 4.0, arithmetic mean method ($n = 551$); (e) SMS, PR = 20, bias = 1.5, harmonic mean method ($n = 629$); (f) SMS, PR = 25, bias = 5.0, harmonic mean method ($n = 987$).

we did not include energy reserves or mortality risk explicitly in our model, although we acknowledge that it would typically be more realistic to do so. However, it is intuitive that increasing the perceptual range will tend to lead to a more efficient path through the landscape and hence a reduced likelihood of mortality through exhaustion of energy reserves or predation.

Recent empirical studies have demonstrated a closer correlation with LCP connectivity than with Euclidean connectivity of genetic distance among populations or among individuals (e.g. Coulon *et al.* 2004; Cushman *et al.* 2006; Stevens *et al.* 2006; Hokit *et al.* 2010; but see Greenwald, Purrenhage, & Savage 2009). This suggests that differential resistance values of matrix elements do indeed influence gene flow across landscapes. However, the improvement in the correlation is often very limited. The fact is that, for most animal species, LCPs are

a poor representation of movement behaviours, especially when individuals are engaging in dispersal behaviour, as opposed to regular foraging activity. It is only if an individual knows its intended destination and has information on matrix quality for all potential routes to it that the individual is likely to take the LCP. Otherwise, the paths taken are substantially longer and less efficient than the LCP (Russell, Swihart, & Feng 2003; Driezen *et al.* 2007). Our results clearly illustrate this. Imagine that a real species moves according to the set of rules used in producing Fig. 7c. The relative connectivity of the four destination patches is poorly approximated by Euclidean distance (Fig. 7a) and is not much better approximated by LCP (Fig. 7b), which provides an improved estimate for the West patch, but a poor estimate for the East patch. In other cases, the relative connectivity obtained by Euclidean distance

and LCP are both very different to those obtained using simulations of movement rules (compare Fig 7e and f with 7a and b). An important next step will be to see how much better a fit to genetic distances can be obtained using a model of movement that incorporates not only different matrix resistance values but also correlation and bias. Another reason for the poor improvement provided by LCPs is that LCP distance can depend critically on (i) exactly how the landscape is represented in the form of discrete cells, especially with regard to beneficial or inhibitory linear features (Adriaensen *et al.* 2003) and (ii) on the attribution of cost values to the different landscape elements, which is more often based on expert opinions than on experiments or on field data (but see the approach of Verbeylen *et al.* 2003); note, though, that these two factors may be expected to influence the individual-based approach too. Recent theoretical attempts to improve on estimates of connectivity have included extending the LCP method stochastically to generate a set of possible paths forming a corridor of variable width between patches (Pinto & Keitt 2009) and combining the standard incidence function model (Hanski 1994) with the LCP distance between patches (Watts & Handley 2010). Another approach has been to draw a parallel between the flow of individuals and electrical current and hence borrow from electrical circuit theory to estimate landscape connectivity: sources of individuals are represented as nodes linked by electrical resistors of conductance proportional to the number of migrants between the sources. The main advantage of this method is that it allows incorporating multiple pathways (as several resistors can link the same two sources) and evaluating the relative importance of each of them for landscape connectivity (McRae 2006; McRae & Beier 2007; McRae *et al.* 2008). However, none of these methods allows for limited perceptual range. The method of Vuilleumier & Metzger (2006) incorporates perceptual range, and functional connectivity estimates derived from it correlated better than Euclidean distance with observed genetic distance (Vuilleumier & Fontanillas 2007). However, their model does not include any tendency to move in the same direction as previously, and therefore patch-location success was poor if perceptual range was limited, leading to a tendency to become trapped in the matrix (Vuilleumier & Perrin 2006), as we have also found in the present study.

Conservation managers desire simple connectivity indices that can inform their selection of sites for reserves. Clearly, although it remains relatively simple, the method proposed here is more complex than existing structural (e.g. Euclidean) or functional (LCP) estimates. Gaining estimates for the two additional parameters comes at a cost, and it is important to understand how much of an improvement our more complex method provides. Future work should establish for which types of species and for which types of landscapes we should invest the extra effort required to parameterise the more complex model. And, conversely, we should be able to recommend when the existing methods are likely to do a sufficiently good job that the extra investment of time and money is not worthwhile.

Future testing and development of the model can progress in several directions. In terms of model testing, an important

next step will be to evaluate the connectivities for a broad range of landscapes with different proportions and spatial arrangement of habitat and various compositions of matrix. The estimates of connectivity generated by our stochastic movement simulator for a range of different animal behaviours can then be compared against those produced by alternative structural and functional connectivity indices, with the objective being to establish whether there are particular types of landscapes, or particular types of species, for which the much-used existing methods are likely to be most erroneous. In terms of future model development, it is increasingly recognised that all individuals in a population, or belonging to a species, do not behave identically. Instead, there is often substantial inter-individual or inter-population variability in dispersal behaviour (e.g. Stevens, Turlure, & Baguette 2010). The distribution of behaviours is likely to be important in determining relative patch connectivity, spatial population dynamics and gene flow. A simple extension to the existing model would be to consider how variation in movement rules influences the connectivity between patches and to establish the degree to which relatively few individuals with 'rare' movement behaviours make the LDD events that are so important in terms of range expansion and genetic dynamics. Recent work has begun to consider how inter-patch movement rules should be expected to evolve (Heinz & Strand 2006; Bartoń *et al.* 2009). Both of these two models incorporate correlation, but only Bartoń *et al.* (2009) also incorporates bias towards habitat patches, and neither model includes a heterogeneous matrix. There is clearly scope to develop new theory related to the evolution of movement rules in complex landscapes by integrating the method presented here with dynamic evolutionary modelling.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. (a) Numbers of individuals successfully reaching each of the four target patches in relation to the strength of directional bias. (b) Numbers of individuals successfully reaching each of the four target patches in relation to the perceptual range.

Fig. S2. (a) Example of the effect of increasing directional bias on the number of individuals successfully reaching each of the target patches: perceptual range is low (2 cells) and evaluated using the arithmetic mean method. (b) Example of the effect of increasing directional bias on the number of individuals successfully reaching each of the target patches: perceptual range is high (25 cells) and evaluated using the harmonic mean method. (c) Example of the effect of increasing perceptual range on the number of individuals successfully reaching each of the target

patches: directional bias is intermediate (3.5), and the harmonic mean method was used to evaluate PR.

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