

# How does landscape structure influence landscape connectivity?

Brett J. Goodwin and Lenore Fahrig

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We investigated the impact of landscape structure on landscape connectivity using a combination of simulation and empirical experiments. In a previous study we documented the movement behaviour of a specialized goldenrod beetle (*Trirhabda borealis* Blake) in three kinds of patches: habitat (goldenrod) patches and two types of matrix patch (cut vegetation and cut vegetation containing camouflage netting as an impediment to movement). In the current study, we used this information to construct simulation and experimental landscapes consisting of mosaics of these three patch types, to study the effect of landscape structure on landscape connectivity, using the *T. borealis* beetle as a model system. In the simulation studies, landscape connectivity was based on movements of individual beetles, and was measured in six different ways. The simulations revealed that the six measures of landscape connectivity were influenced by different aspects of landscape structure, suggesting that: (1) landscape connectivity is a poorly defined concept, and (2) the same landscape may have different landscape connectivity values when different measures of landscape connectivity are used. There were two general predictions that held over all measures of landscape connectivity: (1) increasing interpatch distance significantly decreased landscape connectivity and (2) the influence of matrix elements on landscape connectivity was small in comparison to the influence of habitat elements. Empirical mark-release-resight experiments using *Trirhabda* beetles in experimental landscapes supported the simulation results.

B. J. Goodwin and L. Fahrig, *Ottawa-Carleton Inst. of Biology, Carleton Univ., 1125 Colonel By Drive, Ottawa, Ontario, CANADA K1S 5B6 (present address of BJG, Inst. of Ecosystem Studies, Box AB (65 Sharon Turnpike), Millbrook, NY 12545-0129, USA [GoodwinB@ecostudies.org]).*

Rates of anthropogenic landscape change have increased markedly in the last century (Wilcove et al. 1986, Groom and Schumaker 1993). Persistence of wildlife populations in the face of these changes depends, at least in part, on their ability to move through modified landscapes. Such movements allow individuals to forage over multiple habitat patches (Kozakiewicz 1995), rescue local populations from extinction (Brown and Kodric-Brown 1977), or recolonize local populations after extinction (Henderson et al. 1985, McCauley 1989, Thomas 1994). The interaction between animal movement (set by physiology and behaviour) and landscape structure (set by landscape composition and configuration) will determine the ability of an animal to move through a landscape. Merriam (1984) referred to

the landscape property resulting from this interaction as “connectivity”. Landscape connectivity was later defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). Understanding the impact of landscape change on landscape connectivity is essential for predicting the impact of landscape change on a species.

Generally, landscape change negatively affects a species when its habitat is lost due to conversion into other patch types (e.g. forest into agriculture). Habitat loss tends to increase habitat interpatch distances and decrease habitat patch sizes (Turner and Ruscher 1988, Saunders et al. 1993). Both effects will tend to decrease landscape connectivity, as greater interpatch distances are harder to cross (Laan and Verboom 1990, Sjögren

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1991, Vos and Stumpel 1995, Matter 1996) and smaller habitat patches are harder to find (Kareiva 1985, Capman et al. 1990, Matter 1996). Additionally, the novel patch types generated during habitat loss (matrix patch types) can influence movement behaviour (Baars 1979, Crist et al. 1992, Johnson et al. 1992, Matthysen et al. 1995, Charrier et al. 1997, Pither and Taylor 1998, Jonsen and Taylor 2000, Goodwin and Fahrig 2002) and movement risk (Charrier et al. 1997, Sakai and Noon 1997, St Clair et al. 1998, Zollner and Lima 1999, Hanski et al. 2000). The effect of the matrix on landscape connectivity will depend on the composition and configuration of the matrix patches. Landscapes dominated by matrix patches that facilitate movement will have high connectivity while landscapes dominated by matrix patches that impede movement will have low connectivity. Similarly, certain configurations of matrix patches might reduce landscape connectivity (e.g. when impassable patches encircle all habitat patches) or increase landscape connectivity (e.g. when impassable patches are clumped and far from habitat).

General relationships between landscape connectivity and landscape structure, necessary for predicting the impact of landscape change on landscape connectivity, are lacking. This is, in part, due to the use of many connectivity metrics (Tischendorf and Fahrig 2000a, b), some focused on habitat structure (e.g. Green 1994, With et al. 1997, Metzger and Décamps 1997, Keitt et al. 1997, Tiebout and Anderson 1997) and others focused on organism movement (Doak et al. 1992, Demers et al. 1995, Gustafson and Gardner 1996, Schumaker 1996, Schippers et al. 1996, Ruckelshaus et al. 1997, Pither and Taylor 1998). Structural measures of connectivity often have no link to movement behaviour (Green 1994, With et al. 1997, Metzger and Décamps 1997, Collinge 2000) and as such merely describe landscape pattern and not connectivity (see definition in Taylor et al. 1993). Measures of connectivity based upon organism movements provide for the interaction between movement behaviour and landscape structure. Such measures of connectivity can be divided into two broad categories based on the approach to measuring animal movement: direct measures of individual movement such as search time, displacement distances, path tortuosity, or searching success based on tracking individuals (e.g. radio or GPS telemetry) and indirect measures of movement such as immigration rates based on mark-recapture/resight data. The nature of the system under study will dictate which approach is feasible. Finally, simulation and empirical approaches tend to use different connectivity metrics. For example, connectivity based on organism movements has been measured as mean probability of moving between pairs of patches (referred to as emigration success by Gustafson and Gardner 1996), dispersal success (Gustafson and Gardner 1996, Schumaker 1996, Schippers et al. 1996, Ruckelshaus et al. 1997,

Tischendorf and Fahrig 2000a, Tischendorf 2001), search time (Doak et al. 1992, Tischendorf and Fahrig 2000a, Tischendorf 2001), and cell immigration (Tischendorf and Fahrig 2000a, Tischendorf 2001) in simulation studies, and as dispersal success (Andreassen et al. 1996) and re-observation after displacement (Pither and Taylor 1998) in empirical work. Determining the relationships between different connectivity metrics will allow the results from different studies of landscape connectivity to be compared, which in turn should help generate general theories of landscape connectivity.

Our first goal in this study was to assess the influence of different aspects of landscape structure on landscape connectivity. Specifically, we used simulations to test how the spatial structure of habitat (amount of habitat, number of patches, patch size distribution, distance between patches, and patch shape) and matrix (relative coverage of different matrix patch types, matrix patch dispersion, matrix patch size distribution, matrix patch edge to area ratio) influence landscape connectivity. The simulations also allowed us to test the relative importance of various aspects of landscape structure on landscape connectivity. (i.e. Is habitat amount more important than arrangement? Are matrix patches more or less important than habitat patches?)

Simulations are always an abstraction and simulation predictions should be empirically tested. This is rarely done with landscape connectivity simulations (but see Fahrig and Merriam 1985, With and Crist 1995, Brooker et al. 1999, With et al. 1999). Accordingly, our second goal was to test the simulation predictions in the field. The field system consisted of a goldenrod specialist beetle, *Trirhabda borealis* (Blake), in mosaic landscapes of goldenrod patches (habitat), patches of cut vegetation (matrix), and cut patches containing camouflage netting to impede movement (also matrix).

Our third goal was to compare the response of multiple landscape connectivity metrics to variation in landscape structure. Work in landscape connectivity usually focuses on a single metric and different metrics are rarely compared (but see Tischendorf and Fahrig 2000a). However, due to the variety of landscape connectivity metrics in the literature, comparisons between simulation and empirical approaches or among results from different empirical systems will depend on the relationships between the different landscape connectivity metrics. Since our field system constrained us to estimate beetle movements in the landscapes through mark-resight methods, we focused on metrics of connectivity that could be used in such a situation in this paper. A comparison of metrics more appropriate for telemetry type studies is beyond the scope of this paper.

We measured connectivity in six different ways, transition probabilities between habitat patches, transition probabilities between habitat cells, mean number of habitat patches visited per individual, mean number of habitat cells visited per individual, habitat patch immi-

gration, and habitat cell immigration (Table 1). We measured landscape connectivity at both the cell and patch level for all our metrics of connectivity because earlier modeling work had suggested that cell immigration may avoid an artefactual increase connectivity with increasing habitat fragmentation that can occur with patch level metrics (Tischendorf and Fahrig 2000a, b). Immigration rates and the related measure, dispersal success, are the most common functional measures of connectivity (Goodwin 2000). Both patch and cell immigration should increase in landscapes with higher connectivity. Mean immigration rates may be sensitive to particular patches that are either easy or difficult for dispersing organisms to reach. An alternative approach is to average dispersal success across individuals instead of across habitat patches or cells, that is to average the number of habitat patches or cells visited per individual as they move through the landscape. The number of patches or cells visited by an individual should increase as landscape connectivity increases. Finally, though transition probabilities have rarely been used to measure connectivity (Gustafson and Gardner 1996, Hof and Flather 1996, Hof and Raphael 1997) they represent the most direct measure of connectivity as defined by Merriam (1984) and Taylor et al. (1993). Increases in the mean chance of moving between pairs of habitat patches or cells should indicate increased landscape connectivity.

## Methods

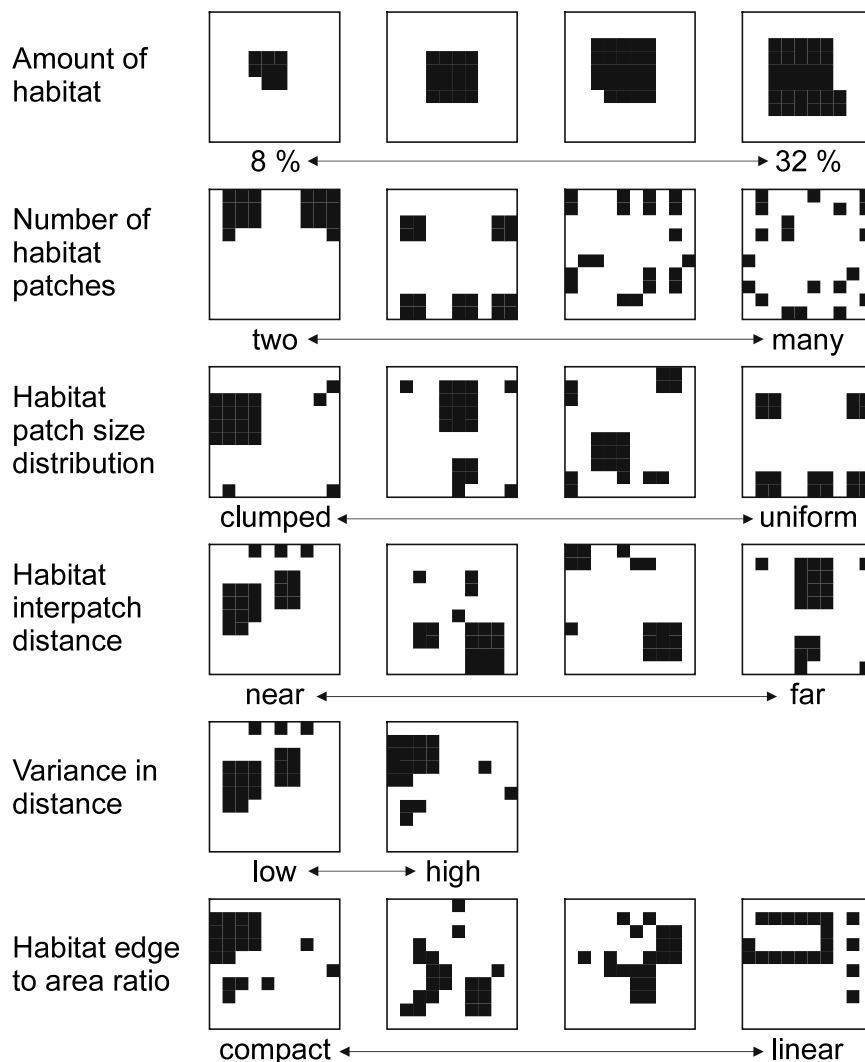
We assessed the influence of landscape structure on landscape connectivity using three experiments. The first was a simulation experiment assessing the influence of habitat amount and configuration on landscape connectivity (Fig. 1). The second was a simulation experiment primarily assessing the influence of matrix composition and configuration on landscape connectivity, but also including aspects of habitat structure the first experiment deemed important (Fig. 2). It was necessary to examine the influence of habitat and matrix structure with two experiments because the model runs would have taken too long if habitat and matrix variables were varied together. The third experiment was a combination of simulation and empirical experiments that tested the main predictions from the first two experiments (Fig. 3). Since we could not test as many aspects of landscape structure in the field as we could using simulations, we identified the most important aspects of landscape structure from the first two experiments, performed simulations focused on the identified landscape attributes, and then tested the hypotheses generated by that set of simulations with mark-release-resight experiments in the field.

All three sets of experiments involved two stages: the generation of landscapes and the tracking of individuals to determine connectivity within the landscapes. All

Table 1. Landscape connectivity metrics investigated.  $n_p$ ,  $n_c$ , and  $n_b$  are number of patches, cells, or beetles in the landscape, respectively.  $p_{ij}^p$  is the probability of moving from patch  $i$  to patch  $j$  and is estimated by dividing the number of beetles moving from patch  $i$  to patch  $j$  by the number available to move.  $p_{ij}^c$  is the probability of moving from cell  $i$  to cell  $j$  and is calculated similarly to  $p_{ij}^p$ .  $v_i^p$  and  $v_i^c$  are the number of patches or cells visited by beetle  $i$ , respectively.  $m_i^p$  and  $m_i^c$  are the number of immigrants into patch  $i$  or cell  $i$ , respectively.

Landscape connectivity metric	Description	Computation
Patch transition probability	Mean patch transition probability, averaged across all pairs of patches in the landscape	$\frac{\sum_{i=1}^{n_p} \sum_{j=1}^{n_p} p_{ij}^p}{n_p(n_p-1)}, i \neq j$
Cell transition probability	Mean cell transition probability, averaged across all pairs of cells in the landscape	$\frac{\sum_{i=1}^{n_c} \sum_{j=1}^{n_c} p_{ij}^c}{n_c(n_c-1)}, i \neq j$
Patch visits	Mean number of visits to a new patch per individual	$\frac{\sum_{i=1}^{n_b} v_i^p}{n_b}$
Cell visits	Mean number of visits to a new cell per individual	$\frac{\sum_{i=1}^{n_b} v_i^c}{n_b}$
Patch immigration	Mean number of immigrants per patch	$\frac{\sum_{i=1}^{n_p} m_i^p}{n_p}$
Cell immigration	Mean number of immigrants per cell	$\frac{\sum_{i=1}^{n_c} m_i^c}{n_c}$

Fig. 1. Variation in habitat spatial structure in the landscapes for simulation experiment 1: habitat. Each panel shows how one aspect of landscape structure was varied. The panel for amount of habitat is missing examples for 12, 20 and 28%. In simulations landscapes with all combinations of variables were created. The different patch types are ■ = habitat and □ = cut.



landscapes (both in the simulations and in the field) were  $5 \times 5$  m and were divided into a 10 by 10 cell grid. Each cell in the grid was assigned to one of three patch types: 1) goldenrod (habitat); 2) cut (matrix) where all vegetation was cut to 2 cm; and 3) netting (matrix) where camouflage netting was suspended in cut patches to emulate vegetation and thereby impede movement. Landscapes were created in the field by cutting natural vegetation to a height of 2 cm and leaving goldenrod patches uncut. Netting patches were created in the cut areas by stringing camouflage netting within each netting cell, such that the top of the netting was suspended approximately 50 cm above the ground. As the netting was 1 to 1.3 m in width this created a vertical panel of suspended netting (emulating the structure of standing vegetation) with the rest of the netting piled in the cell (emulating the structure of plant litter and ground-cover vegetation). Previous work (Goodwin and Fahrig 2002) demonstrated that these patch types influence *T.*

*borealis* movement behaviour and the empirically determined distributions describing those behaviours (Table 2) were used in the simulations.

### Simulation experiment 1. Habitat

The virtual landscapes for the habitat simulation experiment were created as follows (parameters and algorithms are described in Table 3). 1) The amount of habitat was set. 2) The number of habitat patches was set. 3) The size distribution of the habitat patches was determined. 4) The location for the first cell of the first habitat patch was chosen randomly. 5) The habitat patch was placed on the landscape by choosing cells using a self-avoiding random walk, which could only enter empty cells. The shape of the habitat patch was determined during this process by a) the number of steps in the random walk (set by the patch size) and b) the chance of the random walk turning, which was

varied to give more or less edge by having less or more turning, respectively. 6) To ensure that habitat patches did not coalesce, a 1-cell buffer inaccessible to the random walk was placed around the completed patch. 7) After the habitat patch was placed, the random walk jumped a set distance, determined by a distance parameter and distance variance parameter, in a random direction, to select the first cell of the next patch. If a habitat patch could not be placed at this location then the program systematically searched for another suitable location at the appropriate distance. Steps 5) through 7) were repeated, jumping from completed patch to the next new patch, until all the habitat

patches were placed in the landscape. If at any time a habitat patch could not be fit into the landscape the program would backtrack (removing habitat patches) until all of the patches fit. 8) Any part of the landscape not filled with habitat patches was filled with cut patches. This approach to generating landscapes produced slightly different values for indices of landscape structure (e.g. coefficient of variation [CV] for patch sizes, edge to area ratios, mean interpatch distance, CV of interpatch distance) even given the same algorithm parameters, so landscape structure indices were measured and these measures of landscape structure were used in subsequent analyses.

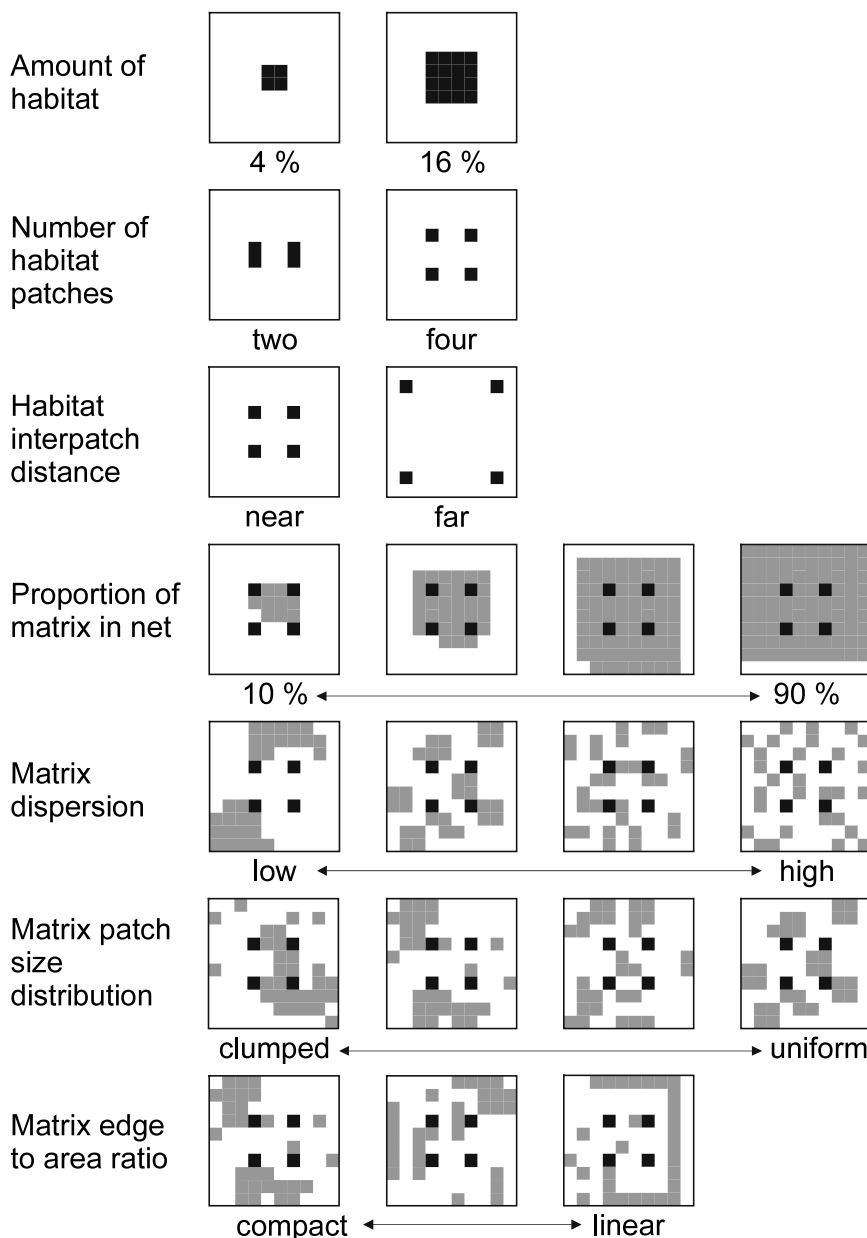
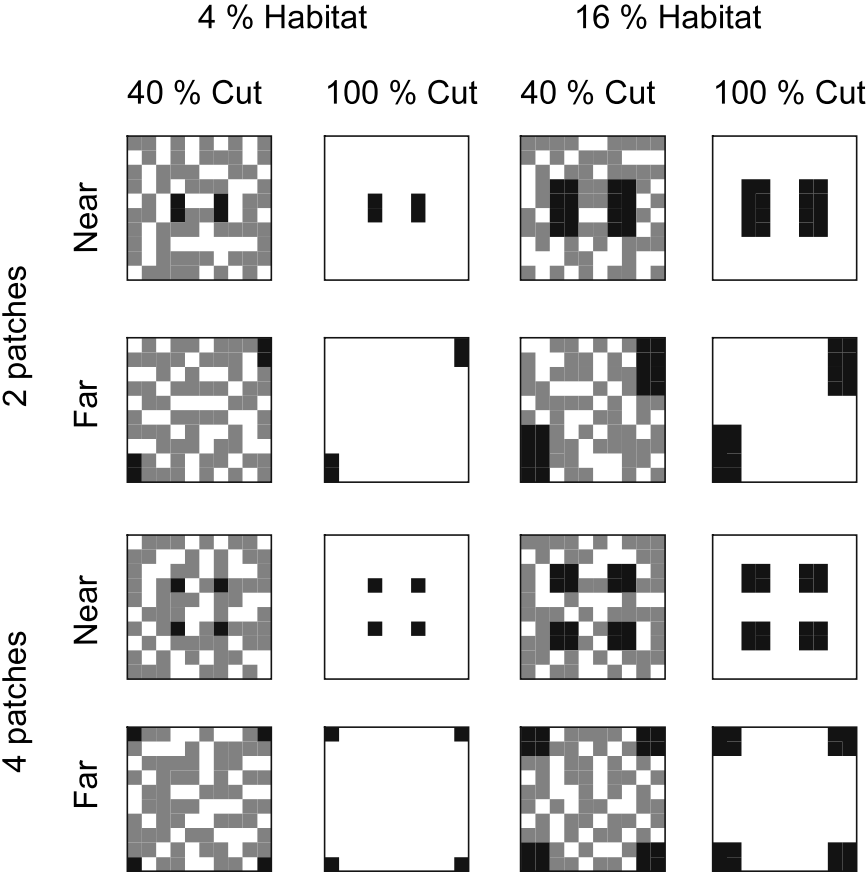


Fig. 2. Variation in habitat and matrix spatial structure in the landscapes for simulation experiment 2: matrix. Each panel shows how one aspect of landscape structure was varied. The panel for proportion of matrix in net is missing examples for 20, 40, 60 and 80%. In simulations landscapes with all combinations of variables were created. The different landscape elements are ■ = habitat, ▨ = camouflage netting, and □ = cut.

Fig. 3. Design of landscapes for experiment 3  
(■ = habitat, ▨ = camouflage netting, □ = cut).



To determine landscape connectivity one hundred virtual beetles were randomly placed in the goldenrod patches. Movements were modeled using empirically determined, patch-type specific, movement parameter distributions (see Table 2 for a summary) in a vector-based, stochastic movement model. The movement model kept track of movement state (moving or not) and kept an individual in that state for a duration drawn from the empirically determined distribution. If the individual was moving, a turning angle and step-

length were randomly chosen from the appropriate distribution. Movements were modeled using a 30 second time step. Each model run lasted 5800 time steps, approximately equivalent to four 12-hour days in the empirical system. During movements each individual was tracked and data for calculating the six landscape connectivity indices were tabulated (see Table 1 for computational details). Landscape edges were tiled, so the surrounding landscape was like the focal landscape, and individuals were allowed to move beyond and

Table 2. Summary of *T. borealis* movement behaviour in the three patch types (see Goodwin and Fahrig 2002 for details).

Patch type	Movement parameter		
	Probability of moving <sup>1</sup>	Step length <sup>2</sup>	Turning angle <sup>3</sup>
Goldenrod	Short bouts of mobility (0.5, 0.5, 3.0) Long bouts of immobility (0.5, 2.0, 49.0)	Short (1, 8, 28)	Uniform distribution ( $K = 0$ )
Cut	Long bouts of mobility (0.5, 0.5, 9.0) Short bouts of immobility (0.5, 1.0, 27.5)	Short (1, 6, 30)	Forward concentration ( $K = 0.4$ )
Netting	Short bouts of mobility (0.5, 0.5, 2.5) Intermediate bouts of immobility (0.5, 1.0, 42.0)	Long (1, 8, 63)	Uniform distribution ( $K = 0$ )

<sup>1</sup> Duration of bouts of mobility or immobility in minutes; minimum, median, and maximum values are presented.

<sup>2</sup> Step lengths in centimetres per 30 second time step; minimum, median, and maximum values are presented.

<sup>3</sup> Shape of turning angle distribution as described by a von Mises distribution (Batschelet 1981); concentration parameter  $K$  is provided.

Table 3. Description of the landscape variables for the habitat simulations. The generating algorithm is described as well as the minimum and maximum values attained. Units of measure are indicated.

Landscape variable	Description Generating Algorithm; (Min., Max.)
Amount of habitat	Amount of habitat in the landscape (proportion of landscape) Set levels: 0.08, 0.12, 0.16, 0.20, 0.24, 0.28, 0.32; (0.08, 0.32)
Number of habitat patches	Number of habitat patches Set levels: 2, amount/4, amount/2, 3*amount/4; (2, 24)
Habitat patch size distribution	Coefficient of variation (CV) of the habitat patch sizes Every patch gets one cell of habitat, start putting the remaining habitat in the first patch, probability of moving on to a new patch set at 4 levels: 0, 0.1, 0.25, 1; (0.00, 1.98)
Habitat edge to area ratio	Ratio of total edge to total area for all habitat patches Patches are placed as self-avoiding random walks with 4 levels for the probability of turning: 0.75, 0.5, 0.25, 0.05; (0.88, 3.75)
Interpatch distance	Mean distance between habitat patch edges (cells) The base step distance from one patch to the next as they are placed in the landscape is set at 4 levels: 2, 4, 6, 8 cells; (0.00, 7.07)
Variance in interpatch distance	CV of distances between habitat patch edges Two levels of variance: first level: no change in step distance; second level: randomly changed the step distance from -2 to +2 cells; (0.00, 1.41)
Intercell distance	Mean distance between habitat cell centres (cells) Set by placing patches; (1.84, 7.49)
Variance in intercell distance	CV of habitat cell distances Set by placing patches; (0.37, 0.95)

possibly back into the focal landscape. Only movements in the focal landscape were counted in landscape connectivity measures.

## Simulation experiment 2. Matrix

Based on their relative importance in the first simulation experiment (see results below) we included amount of habitat, number of habitat patches, and interpatch distance in the matrix simulation experiments. Habitat

edge to area ratio was also a candidate but habitat amount had to be relatively low to allow for manipulation of matrix structure, precluding any reasonable manipulation of habitat edge to area ratios. For these landscapes habitat patches were placed in predetermined patterns (Fig. 2) and then patches of the least common matrix patch type were placed in a similar manner as the habitat patches were in the first simulation experiment (parameters and algorithms are described in Table 4), but distances between matrix patches were random (as opposed to the set distances in

Table 4. Description of the landscape indices for the matrix simulations. The generating algorithm is described as well as the minimum and maximum values attained. Units of measure are indicated.

Descriptor	Description Generating Algorithm; (Min., Max.)
Amount of habitat	Amount of habitat in the landscape (proportion of landscape) Set levels: 0.04, 0.16; (0.04, 0.16)
Number of habitat patches	Number of habitat patches Set levels: 2, 4; (2, 4)
Habitat interpatch distance	Mean distance between habitat patch edges (cells) Set levels: near, far; (2, 10)
Proportion of matrix as net	Proportion of the non-habitat landscape taken up by the netting Set levels: 0.1, 0.2, 0.3, 0.4, 0.6, 0.7, 0.8, 0.9; (0.1, 0.9)
Matrix dispersion	Number of matrix patches Set levels based on the number of cells of the least common matrix element (LCM): 2, LCM/4, LCM/2, 3*LCM/4; (2, 28)
Matrix patch size distribution	Coefficient of variation (CV) of the least common matrix type patch sizes Every patch gets one cell of the least common matrix type, start putting the remaining matrix in the first patch, probability of moving on to a new patch set at 4 levels: 0, 0.1, 0.25, 1; (0.00, 0.22)
Matrix edge to area ratio	Ratio of total edge to total area for all patches of least common matrix type Patches are placed as self-avoiding random walks with 4 levels for the probability of turning: 0.75, 0.5, 0.25, 0.05; (1.0, 3.6)

the habitat simulations). After all of the least common matrix patches were placed the rest of the landscape was filled with the more common matrix patch type. Modeling of movement and calculation of landscape connectivity indices were performed exactly as in the first simulation experiment.

### Simulation experiment 3 and field test

For the third simulation experiment amount of habitat, number of habitat patches, placement of habitat patches, and matrix composition were all set (Fig. 3) and matrix cells were randomly assigned to patch type. All of the area outside the focal landscape was the cut patch-type to emulate the buffer strips in the field tests (see below). Modeling of movement was performed exactly as in the first two simulation experiments. Landscape connectivity in these simulations was calculated in a manner that matched the limitations faced in the field (see below).

We ran the model a second time to determine both the average displacement from release point over time and confidence intervals around that average. This second run was required because we needed more runs to construct the confidence envelope around the average displacement. In this second run the model was set up the same as it was for the runs that determined landscape connectivity. Displacement was calculated as the distance from the centre of the cell the individual was released in to the centre of the cell the individual was observed in for both the simulations and the field releases. For the simulations, a 90% confidence envelope was constructed around the mean displacement by determining the 5th and 95th percentiles from 1000 simulation runs.

For the field tests 4 landscapes were constructed at each of 4 sites in an old field south of Ottawa, Canada. Over the course of the field season (July 28 to September 9, 1997) each unique type of landscape (Fig. 3) was replicated 4 times ( $n = 64$ ). To do this we ran 2 sequential replicates, 16 landscapes per replicate, at 16% goldenrod and then cut the goldenrod back to 4% and ran two more replicates. At each site all the natural vegetation between landscapes (minimum 1 m separation) and a buffer around the 4 landscapes (minimum 1 m width) was also cut. Between releases of beetles, any re-growth of vegetation in the cut or netting patches was trimmed back. When *T. borealis* populations in the surrounding fields had finished pre-ovipositional long-distance dispersal (Messina 1982) and were only engaged in short-distance, "trivial" movement, individuals were captured and marked by dusting with fluorescent powder. Twenty-five of these marked beetles were released into a single goldenrod patch in each of the experimental landscapes. We used a different colour of powder for each landscape at a site, so immigration from a neigh-

bouring landscape could be detected and not influence measures of movement within a particular landscape. The 4 sites were separated by a minimum of 50 m of old field vegetation, so the chance of beetles moving between sites was extremely low. Beetles were released in a small paper bag and allowed to find their own way out to allow any effect due to handling to have a minimal influence on their movements. Any beetles that had not left the paper bag by the first night of searching were removed at night when they were sluggish and unresponsive. Movements of the marked beetles were monitored for four nights following release by searching the goldenrod patches using a hand-held UV lamp. The numbers of beetles in each patch or cell were recorded.

Since we could not obtain the information necessary to calculate all landscape connectivity metrics in the field (e.g. differentiate between individual beetles to determine the number of patches visited), we were restricted to calculating landscape connectivity as either cell or patch immigration rates. For both simulations and field tests there was an initial release followed by four subsequent observations of patch or cell occupancy, spaced a day apart. These observations allowed us to estimate immigration rates (either into cells or patches). Since the beetles could potentially visit multiple cells or even patches in a day this approach will consistently detect fewer immigration events than occurred in the first two simulation experiments where we knew the locations of all individuals all the time.

## Results

### Simulation experiment 1. Habitat

Based on multiple regressions, landscape connectivity was strongly influenced by overall landscape structure ( $R^2$  ranged from 0.85 to 0.94 for all landscape connectivity measures, except for patch immigration where  $R^2 = 0.58$ ; Table 5). However, ranking landscape variables by partial correlation indicate that the landscape connectivity metrics respond to different aspects of landscape structure as four different landscape variables were ranked highest for at least one landscape connectivity metric (amount of habitat, number of habitat patches, distance, habitat edge to area ratio; Table 5). Furthermore, landscape variable rankings could vary dramatically among landscape connectivity metrics (e.g. number of habitat patches was ranked first for patch visits and sixth for patch immigration). Relationships among landscape connectivity metrics were not clear-cut, ranging from no relationship (Fig. 4a) to linear (Fig. 4b) and curvilinear (Fig. 4c) relationships that depended on the state of the landscape (e.g. amount of habitat, number of habitat patches).



Table 5. Multiple regression results for simulation experiment 1: habitat.  $R^2$  values for the overall model and partial correlations for each of the landscape variables are presented for six regression models, one for each landscape connectivity metric ( $n = 3584$  for each model). Additionally, the partial correlations are ranked within each model (column) and significant terms in the model ( $\alpha = 0.05$ ) are indicated with the ranking in **bold**.

	Patch transition probability	Cell transition probability	Patch visits	Cell visits	Patch immigration	Cell immigration
$R^2$	0.8680	0.8545	0.9418	0.9365	0.5802	0.9393
Amount of habitat	0.2107 (4)	-0.6046 (1)	0.0902 (5)	0.5714 (2)	0.2782 (4)	-0.6217 (3)
Number of habitat patches	-0.3013 (3)	-0.0706 (6)	0.8161 (1)	0.0021 (6)	-0.1238 (6)	0.4659 (4)
Habitat patch size distribution	0.0507 (6)	-0.2431 (3)	-0.2890 (4)	0.2955 (3)	-0.1971 (5)	0.0041 (6)
Distance <sup>a</sup>	-0.7255 (1)	-0.3407 (2)	-0.5446 (2)	-0.2934 (4)	-0.6485 (1)	-0.6898 (2)
Variance in distance	-0.6379 (2)	0.2427 (4)	0.3699 (3)	-0.1751 (5)	0.3322 (2)	0.2504 (5)
Habitat edge to area ratio	0.1808 (5)	0.1739 (5)	0.0682 (6)	-0.6657 (1)	0.2891 (3)	-0.7182 (1)

<sup>a</sup> Average interpatch distance for patch based measures and average intercell distance for cell based measures.

Distance was the only landscape variable that behaved consistently across all landscape connectivity measures, strongly and negatively influencing landscape connectivity (though the effect was stronger for patch level measures of landscape connectivity). The strength and direction of the relationships between the remaining landscape variables and landscape connectivity varied between connectivity metrics. Amount of habitat was relatively important for all the cell level metrics (magnitude of partial  $r$ 's of 0.57 to 0.62, Table 5) but not for patch level connectivity metrics (magnitude of partial  $r$ 's  $< 0.28$ , Table 5). However, landscapes with more habitat had more cell visits per individual but a lower cell transition probability and lower cell immigration. The number of habitat patches in the landscape had a strong, positive effect on patch visits but was relatively unimportant for the remaining landscape connectivity metrics (and effects were both positive and negative). Habitat edge to area ratio had strong, negative effects on the number of cell visits and cell immigration rate but weak, positive effects on the remaining landscape connectivity metrics. Variance in interpatch distance had a strong, negative effect on patch transition probability but had weaker, mixed effects on the remaining landscape connectivity metrics. Finally, habitat patch size distribution had a consistently low partial correlation across all landscape connectivity metrics though direction of the effect varied among metrics.

## Simulation experiment 2. Matrix

Matrix configuration (matrix dispersion, matrix patch size distribution, and matrix edge to area ratio) had no impact on any of the six measures of landscape connectivity (magnitude of all partial  $r$ 's  $< 0.02$ , Table 6). Matrix composition (proportion of matrix as net) was the only aspect of the matrix that had even a minimal impact on landscape connectivity. For all six measures of landscape connectivity increasing the amount of netting in the matrix decreased landscape connectivity, but this effect was weak in all cases (magnitude of all partial  $r$ 's  $< 0.2$ , Table 6), and with the exception of patch immigration was always less important than the habitat variables.

Habitat amount often affected landscape connectivity in a direction opposite to its effect in simulation experiment 1. For cell visits and cell immigration the number of habitat patches also had an opposite effect to their effect in simulation experiment 1. For the matrix simulations increasing the amount of habitat decreased the habitat edge to area ratio ( $r = -0.91$ ,  $n = 9216$ ) while increasing the number of habitat patches increased the edge to area ratio ( $r = 0.39$ ,  $n = 9216$ ). This allowed the effect of edge to area ratios to reverse the anticipated effect of habitat amount or number of patches. In fact, this hidden effect of habitat edge to area ratio was

Fig. 4. Examples of relationships between different connectivity metrics for simulation experiment 1: habitat.

a) Connectivity measured as cell immigration vs connectivity measured as patch immigration,

b) connectivity measured as cell visits vs connectivity measured as cell immigration, and

c) connectivity measured as patch transition probability vs connectivity measured as patch immigration.

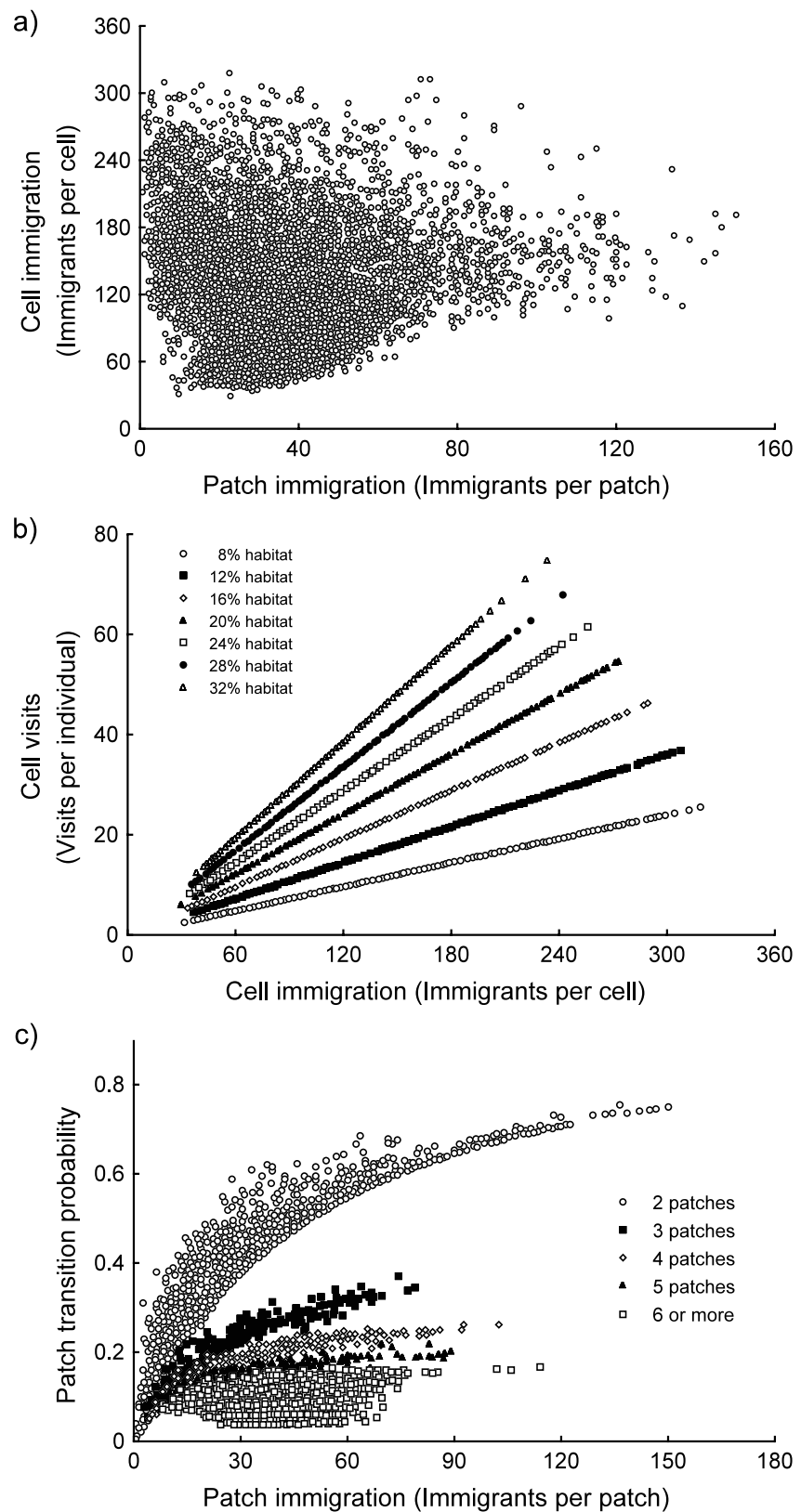


Table 6. Multiple regression results for simulation experiment 2: matrix.  $R^2$  values for the overall model and partial correlations for each of landscape variables are presented for six regression models, one for each landscape connectivity metric ( $n = 9216$  for each model). Additionally, the partial correlations are ranked within each model (column) and significant terms in the model ( $\alpha = 0.05$ ) are indicated with the ranking in **bold**.

	Patch transition probability	Cell transition probability	Patch visits	Cell visits	Patch immigration	Cell immigration
$R^2$	0.8563	0.7341	0.7910	0.9352	0.8789	0.8727
Amount of habitat	-0.2313 (3)	-0.8163 (1)	-0.2153 (3)	0.9613 (1)	-0.3014 (2)	0.8333 (2)
Number of habitat patches	-0.7312 (2)	-0.5915 (2)	0.5877 (2)	-0.7519 (2)	-0.1229 (4)	-0.8747 (1)
Distance <sup>a</sup>	-0.9163 (1)	-0.2646 (3)	-0.8634 (1)	-0.4880 (3)	-0.9369 (1)	-0.5577 (3)
Proportion of matrix as net	-0.1306 (4)	-0.0324 (4)	-0.1425 (4)	-0.1346 (4)	-0.1962 (3)	-0.1265 (4)
Matrix dispersion	0.0035 (5)	0.0057 (6)	0.0112 (5)	0.0012 (7)	0.0124 (5)	0.0045 (6)
Matrix patch size distribution	0.0012 (6)	0.0003 (7)	-0.0049 (6)	-0.0010 (6)	-0.0039 (7)	-0.0062 (5)
Matrix edge to area ratio	0.0003 (7)	-0.0074 (5)	-0.0044 (7)	0.0016 (5)	-0.0044 (6)	-0.0026 (7)

<sup>a</sup> Average interpatch distance for patch based measures and average intercell distance for cell based measures.

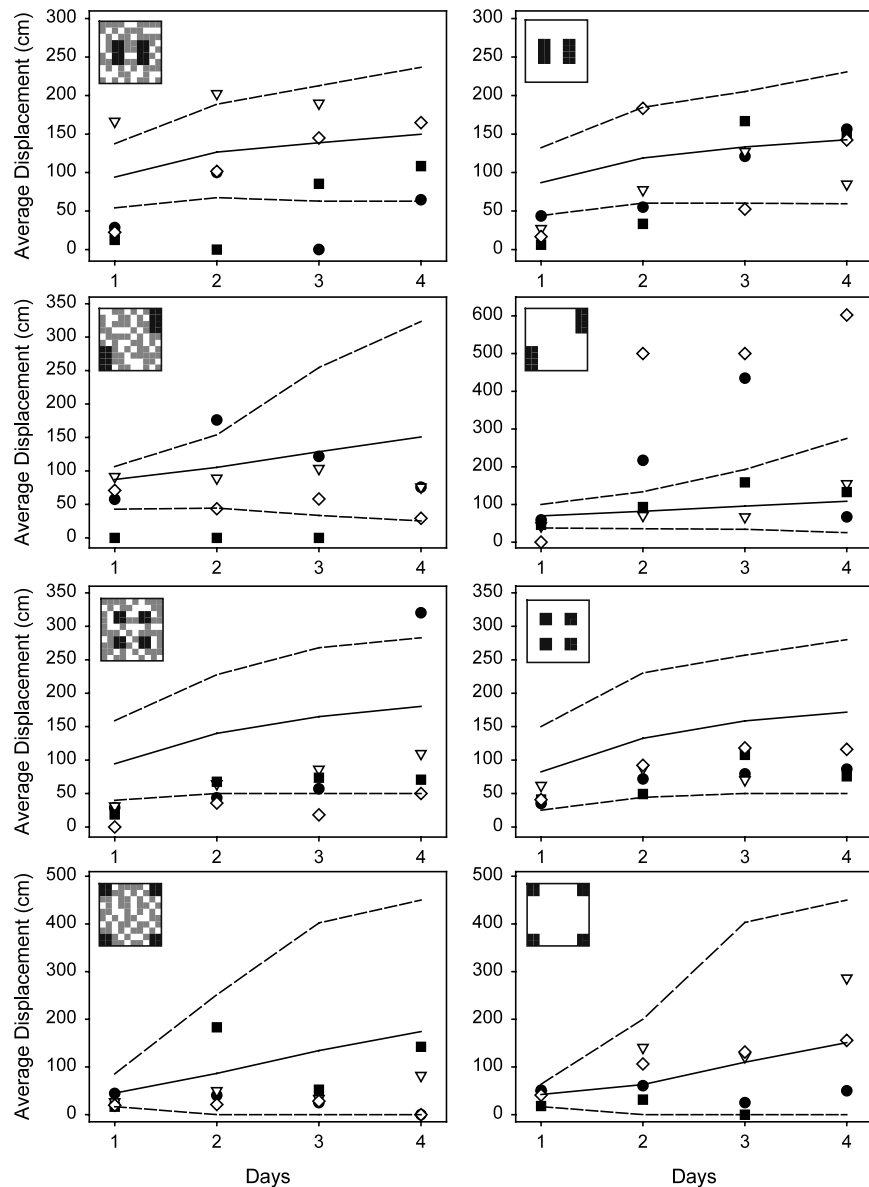
strongest in the two landscape connectivity metrics most sensitive to habitat edge to area ratios (cell visits and cell immigration).

### Simulation experiment 3 and field test

With 16% habitat, the model had a slight positive bias when predicting average beetle displacement over time, though most observed displacements in the field fell within a 90% confidence envelope for the model predictions (Fig. 5). Cases where the observed mean displacement fell outside the 90% envelope all had low resighting success, allowing for a few individuals that had either not moved very far from the release point or moved a long way from the release point to skew the average displacement. Similar patterns held for 4% habitat, though there were more cases of only a few individuals being resighted. Model predictions for patch immigration were significantly positively biased ( $\chi^2 = 896.7$ ,  $df = 63$ ,  $p < 0.0001$ ). However, standardizing predicted and observed patch immigration by the predicted or observed mean patch immigration, respectively, removed this bias ( $\chi^2 = 31.05$ ,  $df = 63$ ,  $p = 0.998$ ) suggesting that the model was correctly predicting the direction of the response of connectivity to landscape structure but not the absolute magnitude of the effect. Furthermore, patch immigration responded in the same direction in both the field and simulation experiment 3 to all four of the landscape variables (Fig. 6). A similar pattern was observed for cell immigration. This suggests that though detection of immigration in the field was somewhat limited this did not alter the observed pattern of response to landscape structure. Additionally, patch immigration in these simulations responded similarly to the landscape variables as in the other simulations (compare Table 7 with Tables 5 and 6). Together, this evidence suggests that the model represented the response of interpatch movements in *T. borealis* to landscape structure well, while overestimating the absolute magnitude of patch immigration. Alternatively, field measurements might have underestimated patch immigration.

Along with the independent effects of landscape variables on patch immigration, significant interaction terms in the simulation analysis suggest that patch immigration in landscapes with more habitat should be more strongly influenced by the number of habitat patches and more weakly influenced by interpatch distance while patch immigration in landscapes with more habitat patches should be more weakly influenced by interpatch distance (Table 7). For the field tests we first removed the effects of two significant covariates, site location and within-site landscape location, since all the southerly sites and all the landscapes that were southerly within their site had higher patch immigration. The ensuing ANOVA revealed the only significant

Fig. 5. Observed average beetle displacement from point of release (symbols) and expected average displacement (solid line) along with 90% confidence envelop (dashed lines). Expected values are based on 1000 model runs. Results have been grouped according to each unique landscape arrangement (inset figure, corresponding to Fig. 3). Unique symbols differentiate between replicate landscapes. Note different scales on the displacement axes.



aspects of landscape structure to be distance between habitat patches and number of habitat patches. However, with the exception of number of patches, all of the landscape variables influenced patch immigration in the same direction as they did in the simulation (Table 7). Only the interaction between habitat amount and number of patches acted in a different direction in the field tests than the simulation.

Similarly, along with the independent effects of landscape variables on cell immigration, significant interaction terms suggest that cell immigration in landscapes with more habitat should be less strongly influenced by intercell distance and number of habitat patches. As with patch immigration, in the empirical analysis we removed the effects of the significant covariates, site location and

within-site location, since the southerly sites had higher cell immigration and the southwest landscape at each site had higher cell immigration. The ensuing ANOVA revealed that number of habitat patches, distance between patches, amount of netting in the matrix, the interaction between amount of habitat and number of patches, and the interaction between amount of habitat and distance were significant and all of the landscape variables influenced cell immigration in the same direction as they did in the simulations (Table 8). The only discrepancy between the field tests and the simulations was a significant, negative effect of amount of netting on estimated cell immigration in the field, which was not significant in the simulations. However, in both cases netting had a negative effect on estimated cell immigration.

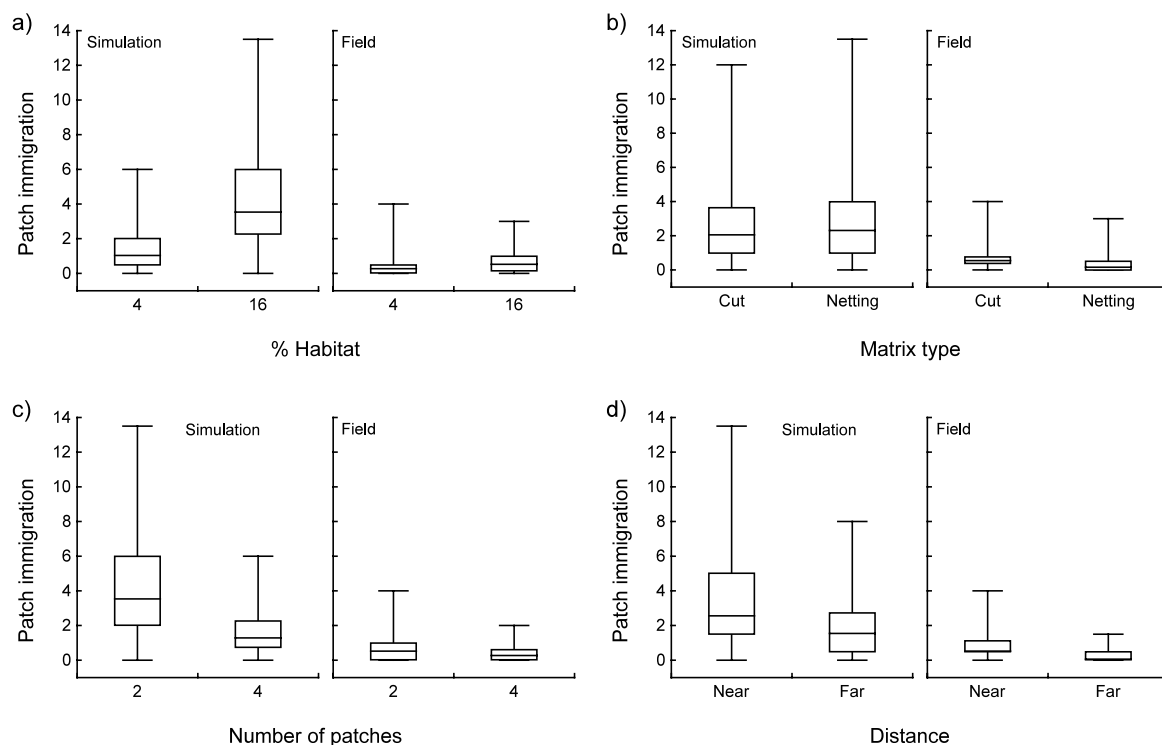


Fig. 6. Box-whisker plots of estimated patch immigration for the simulation results (left panel of each pair,  $n = 320$ ) and field tests (right panel of each pair,  $n = 64$ ). Plots have been classified by the four landscape variables: a) amount of habitat in the landscape, b) whether the matrix was predominately cut or netting, c) number of habitat patches, and d) distance between habitat patches. Whiskers represent the range, the boxes represent the interquartile range and the horizontal lines indicate the median value.

Table 7. Results of ANOVA (single factors and all 2-way interactions) for the influence of landscape structure (Fig. 3) on estimated patch immigration in simulated landscapes ( $n = 320$ ) and field tests ( $n = 64$ ). Effects for significant factors from either the simulation or the empirical results ( $\alpha = 0.05$ ) are described.

Variable	Simulations			Field tests <sup>a</sup>		
	<i>F</i>	<i>p</i> -level	Effect	<i>F</i>	<i>p</i> -level	Effect
Amount of habitat (PG)	408	0.0000	↑ PG ↑ immigration	1.77	0.19	↑ PG ↑ immigration
Number of patches (NP)	311	0.0000	↑ NP ↓ immigration	4.26	0.045	↑ NP ↓ immigration
Distance (DIST)	126	0.0000	↑ DIST ↓ immigration	15.5	0.0003	↑ DIST ↓ immigration
PG × NP	83.4	0.0000	↑ PG ↑ effect of NP	0.14	0.71	↑ PG ↓ effect of NP
PG × DIST	19.6	0.0000	↑ PG ↓ effect of DIST	0.23	0.64	↑ PG ↓ effect of DIST
NP × DIST	18.8	0.0000	↑ NP ↓ effect of DIST	2.96	0.092	↑ NP ↓ effect of DIST
PN × DIST	1.54	0.22		0.08	0.78	
Amount of netting (PN)	1.14	0.29		1.77	0.19	
PG × PN	0.80	0.37		1.77	0.19	
PN × NP	0.02	0.88		0.144	0.71	

<sup>a</sup> After the removal of 2 significant covariates, site location and landscape location within site.

## Discussion

### The influence of spatial patterning of habitat on landscape connectivity

Interpatch distance had the most consistent and, for patch-level measures, strongest influence on landscape connectivity. This is not a surprising finding, as other researchers have noted that interpatch distance has a strong effect on functional measures of connectivity

(Doak et al. 1992, Schippers et al. 1996, With and King 1999, Tischendorf and Fahrig 2000a). For the matrix simulations, amount of habitat, number of habitat patches (fragmentation), and interpatch distance (isolation) were varied essentially independently. Interpatch distance always had the strongest, negative effect on landscape connectivity; habitat amount and fragmentation were not always important and could affect landscape connectivity negatively or positively depending

Table 8. Results of ANOVA (single factors and all 2-way interactions) for the influence of landscape structure (Fig. 3) on estimated cell immigration in simulated landscapes ( $n = 320$ ) and field tests ( $n = 64$ ). Effects for significant factors from either the simulation or the empirical results ( $\alpha = 0.05$ ) are described.

Variable	Simulations			Field tests <sup>a</sup>		
	<i>F</i>	<i>p</i> -level	Effect	<i>F</i>	<i>p</i> -level	Effect
Distance (DIST)	110	0.0000	↑ DIST ↓ immigration	3.42	0.071	↑ DIST ↓ immigration
Number of patches (NP)	75.6	0.0000	↑ NP ↓ immigration	8.98	0.004	↑ NP ↓ immigration
PG × DIST	6.63	0.011	↑ PG ↓ effect of DIST	10.8	0.002	↑ PG ↓ effect of DIST
PG × NP	2.67	0.10	↑ PG ↓ effect of NP	21.1	0.0000	↑ PG ↓ effect of NP
PN × DIST	2.65	0.10		0.14	0.708	
Amount of habitat (PG)	2.26	0.13		1.46	0.234	
Amount of netting (PN)	2.20	0.14	↑ PN ↓ immigration	8.89	0.004	↑ PN ↓ immigration
PN × NP	0.20	0.66		1.50	0.280	
NP × DIST	0.07	0.79		1.38	0.246	
PG × PN	0.03	0.87		2.39	0.129	

<sup>a</sup> After the removal of 2 significant covariates, site location and landscape location within site.

on the connectivity metric. Ruckelshaus et al. (1997) found that dispersal success increased as habitat increased and decreased as fragmentation increased though both effects were weak. For search time and cell immigration, Tischendorf and Fahrig (2000a) found stronger correlations with mean nearest neighbour distance than the number of habitat patches, though they found the opposite for dispersal success.

The terms habitat loss (reducing the amount of habitat) and fragmentation (increasing the number of patches) have been used interchangeably in the literature, and many authors think of the two as being a single process (Wilcox and Murphy 1985, Wilcove et al. 1986, Herben et al. 1991, Robinson et al. 1992, Perry and Gonzalez-Andujar 1993, Diffendorfer et al. 1995, Holt et al. 1995, Schumaker 1996, Donovan and Flather 2002). It has been argued that the two should be separated (Fahrig 1997, 1998, McGarigal and Cushman 2002, Schmigelow and Mönkkönen 2002). Trzcinski et al. (1999) and McGarigal and McComb (1995) measured the independent effects of habitat (forest) fragmentation and loss in actual landscapes and both found that habitat loss had a much stronger effect than fragmentation on bird species presence or abundance. Using an individual-based, spatially explicit simulation model, which separated the effects of habitat amount and fragmentation, Fahrig (1997) found amount of habitat had a greater effect than fragmentation on extinction probability. Similarly, the landscape connectivity measures that we investigated responded differently to habitat loss and fragmentation, with most influenced more strongly by amount of habitat than habitat fragmentation, suggesting that the distinction between amount and fragmentation of habitat can be important.

Habitat fragmentation has two potential effects on connectivity. Fragmentation will reduce average patch size and increase the edge to area ratio. Smaller patches may be more difficult for moving organisms to find (Kareiva 1985, Capman et al. 1990, Matter 1996).

Alternatively, the increased amount of edge may make patches easier to find (Bowman et al. 2002). Additionally, fragmenting a fixed amount of habitat will tend to decrease interpatch distances, since the small fragments would be spread throughout the landscape, which in turn would increase connectivity. Using a simulation model Schumaker (1996) found that fragmentation measured as the number of patches in a landscape was only weakly correlated with dispersal success. After accounting for effects due to isolation, in our simulations most measures of landscape connectivity decreased as the number of patches increased, suggesting that for most measures of connectivity the response to habitat fragmentation was more sensitive to patch finding success than gap crossing ability. But patch visits and cell immigration increased with fragmentation, suggesting that these two measures of landscape connectivity were more sensitive to gap crossing ability than patch finding success. With and King (1999) found a similar effect where dispersal success was strongly linked to landscape lacunarity, a measure of the gaps in the landscape (Plotnick et al. 1993). This importance of gap crossing was particularly evident with patch visits, as number of patches was the landscape variable with the strongest effect on landscape connectivity. Patch visits increased with fragmentation because more patches offer more opportunities for individuals to visit new patches; fragmenting habitat therefore increases the mean number of patches visited per individual.

Landscapes with more habitat should have higher landscape connectivity because it will be easier for moving individuals to find the greater amount of habitat in the landscape. This is the inherent assumption in structural connectivity measures based on percolation theory (Gardner et al. 1987, Gardner and O'Neill 1991, Green 1994). Paradoxically, landscape connectivity metrics based on between-patch movements should decline at high habitat amount because habitat will tend to congeal into a single large patch precluding between-patch movements (Tischendorf and Fahrig 2000b).

Measuring landscape connectivity at the cell-level, particularly cell immigration, has been suggested as a potential solution to this paradox (Tischendorf and Fahrig 2000b). In our habitat simulations, cell immigration and cell transition probability strongly declined as habitat amount increased, for two reasons. First, cell immigration per habitat cell declined in landscapes with more habitat because the same total number of immigration events were spread across more habitat cells, therefore depressing the landscape-wide average. This is confirmed by the fact that the mean number of cell visits, which was not averaged over cells but individuals, increased as habitat amount increases. Second, in our simulations based on *T. borealis* behaviour, individuals in habitat patches moved infrequently in short bursts of slow movement producing tortuous paths (Table 1, Goodwin and Fahrig 2002). Landscapes with more habitat have more of such slow movements further reducing the ability of individuals to move between habitat cells. In the habitat simulation experiment, individuals in landscapes with more habitat actually spent less time moving ( $r = -0.96$ ,  $n = 9216$ ).

Changes to habitat configuration can also occur via changes to patch size distributions (O'Neill et al. 1988, Riitters et al. 1995, Gustafson 1998). Patch-based measures of landscape connectivity did not seem to respond to habitat patch size variability, but cell-based measures did. Number of cell visits and cell immigration rates declined as patches became more uniform. In these cases, when there were a few large patches individuals could move more easily among many cells in that large patch than they could move between habitat patches, despite being slowed by their movement behaviour in goldenrod. These within-patch movements increased both the average number of habitat cells visited per individual and the average number of immigrants per habitat cell, for a given amount of habitat. This suggests that maintaining heterogeneity in the landscape, especially regarding patch sizes, should increase landscape connectivity. In contrast, cell transition probability increased as patches became more uniform in size and shape. This difference is most likely due to the cell transition probability weighting each possible habitat cell to habitat cell movement equally, such that any isolated, single-cell habitat patch will contribute extremely low probabilities of exchanging individuals with all the other habitat cells. When there are many single cell habitat patches in the landscape they all contribute low probabilities to the mean habitat cell transition probability, thereby depressing the mean cell transition probability over the entire landscape. Higher cell transition probabilities in the few large habitat patches will not offset the effect of the single cell habitat patches as only the transition probabilities for pairs of habitat cells in the patch will be increased.

Anthropogenic habitat loss both decreases habitat amount and increases habitat isolation. Both of these

landscape changes decrease landscape connectivity. It has been suggested that the arrangement of habitat could offset detrimental effects of habitat loss (Kareiva and Wennergren 1995). The consistent negative response of all measures of landscape connectivity to interpatch distance suggests that measures decreasing isolation such as corridors (Merriam 1991, Noss 1993, Rosenberg et al. 1998), stepping-stones (Potter 1990, Arnold et al. 1993), relocation programs (McCullough et al. 1996) or habitat restoration (Holland et al. 1991, Fedorowick 1993), all have the potential to increase landscape connectivity. However, the relatively weak responses of the landscape connectivity measures to the remaining landscape variables suggest that other aspects of habitat arrangement (e.g. patch shape, degree of fragmentation) could not mitigate against detrimental effects of habitat loss. Furthermore, the fact that many of the landscape connectivity measures responded differently to some of the landscape variables suggests that a particular arrangement of habitat patches might have high landscape connectivity for some measures while having low landscape connectivity for others measures. This suggests that managing habitat arrangement to increase connectivity will not be straightforward and most likely will not be successful. This argues primarily for the preservation of habitat and secondarily for managing habitat loss to minimize patch isolation.

### The influence of spatial patterning of matrix elements on connectivity

To date there has been little work on the influence of matrix composition and, particularly, matrix configuration on movements among habitat patches. There are suggestions that matrix characteristics can be important since different matrix elements have been shown to function as barriers to movement (Mader 1984, Merriam et al. 1989, Baur 1990, Mader 1990, Kozakiewicz 1993), influence movement behaviour (Baars 1979, Crist et al. 1992, Johnson et al. 1992, Matthysen et al. 1995, Charrier et al. 1997, Pither and Taylor 1998, Jonsen and Taylor 2000, Goodwin and Fahrig 2002) and influence movement risk (Krohne and Burgin 1987, Fahrig et al. 1995, Schippers et al. 1996, Taylor and Merriam 1996, Charrier et al. 1997, Sakai and Noon 1997). It would seem reasonable to expect landscape matrix pattern to affect landscape connectivity. At a minimum, as the matrix becomes more difficult to move through, due to increasing proportions of impervious matrix elements, landscape connectivity should decline (Knaapen et al. 1992). In fact, theoretical formulations of the idea of landscape connectivity seem to focus almost exclusively on the influence of the matrix (Merriam 1984, Taylor et al. 1993). However, our simulations and field studies found little effect of matrix composition and

no effect of matrix configuration on landscape connectivity.

The simulations and field tests may have failed to find much effect of matrix structure on landscape connectivity because matrix structure might influence connectivity through means other than movement behaviour within matrix elements (Wiens et al. 1985). Matrix structure may influence landscape connectivity through its effects on edge crossing behaviour and/or mortality, components that were not present in the simulations or the *T. borealis* field test (earlier experiments found no response to edges; Goodwin and Fahrig 2002). The way an organism responds to edges influences patch residence times (Kareiva 1985, Turchin 1986, Buechner 1987, Stamps et al. 1987) and movement through corridors (Soulé and Gilpin 1991, Tischendorf and Wissel 1997), so one might expect that the pattern of matrix patches that influence edge crossing behaviour might affect landscape connectivity. Similarly, different risks of mortality in different matrix elements should change landscape connectivity, since movements will terminate with mortality events. While not investigating landscape connectivity per se, using a simulation experiment Fahrig (2001) found that varying mortality risk in the matrix had a stronger influence on extinction risk than habitat fragmentation, suggesting that the importance of the matrix can be increased by considering mortality. Further investigation of the necessary conditions for the landscape matrix to influence connectivity, such as differential matrix mortality and behavioural responses to patch edges, would be fruitful.

### How should landscape connectivity be measured?

Our simulation and empirical experiments demonstrated that different potential measures of landscape connectivity respond to different aspects of landscape structure, and in some cases respond differently to the same aspect of landscape structure. Currently there is no broadly accepted metric of landscape connectivity and many different metrics have been used in the literature. Based on the fact that the six measures of landscape connectivity we investigated responded to different aspects of landscape structure, were weakly correlated, and showed complex interactions, it is highly unlikely that all the connectivity results in the literature are directly comparable. The addition of more metrics of connectivity to our analysis would not change this conclusion.

This also suggests that landscape connectivity is a poorly defined concept. If the investigator is constrained to mark-recapture or mark-resight approaches, patch and cell immigration are the easiest to measure in the field. However, patch immigration increases as the number of patches increases. This increase is a reflection of how the metric is calculated and does not

indicate more movement in more fragmented landscapes. Also, the  $R^2$  value for patch immigration was the lowest, suggesting that patch immigration does not respond as strongly to landscape structure as the other measures of connectivity. Therefore, we recommend use of cell immigration as the most practical and consistent measure of landscape connectivity when using mark-recapture or mark-resight approaches. When using direct measures of movement such as telemetry other metrics of connectivity may be more appropriate.

It is worth mentioning, though, that in many cases researchers are constrained to mark-recapture/resight approaches. Many telemetry approaches are infeasible for smaller taxa (but see Mascanzoni and Wallin 1986). When they are feasible, most telemetry approaches are so effort intensive that only a few individuals can be followed. These restrictions make comparisons between landscapes with different structure difficult. Additionally, many of the connectivity metrics that might be applied to telemetry data have potential problems as well. For example, the relationship between distance travelled and landscape connectivity is not clear; short distances could either indicate high connectivity due to short traverses between habitat patches or poor connectivity due to individuals being unable to leave habitat patches. It would be interesting to see how potential connectivity metrics based on telemetry approaches would change as landscape structure changes and how such metrics would relate to the metrics we investigated in this paper.

### Conclusions

These results suggest three general points about the relationship between landscape structure and the measures of landscape connectivity we investigated. First, given that matrix patches differ only in their influence on movement behaviour as in our system, the influence of habitat spatial structure seems much more important than the influence of matrix spatial structure on landscape connectivity. Second, all measures of landscape connectivity declined when habitat patches were farther apart. This suggests that mitigation of the effects of landscape change on connectivity requires reduced interpatch distances. Overall, the general relationships between landscape structure and landscape connectivity warn that habitat loss should be avoided. Third, different measures of landscape connectivity respond differently to landscape structure. Based on what is easily measured in the field we recommend cell immigration as a good measure of landscape connectivity.

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