



How should we measure landscape connectivity?

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Abstract

The methods for measuring landscape connectivity have never been compared or tested for their responses to habitat fragmentation. We simulated movement, mortality and boundary reactions across a wide range of landscape structures to analyze the response of landscape connectivity measures to habitat fragmentation. Landscape connectivity was measured as either dispersal success or search time, based on immigration into all habitat patches in the landscape. Both measures indicated higher connectivity in more fragmented landscapes, a potential for problematic conclusions for conservation plans. We introduce cell immigration as a new measure for landscape connectivity. Cell immigration is the rate of immigration into equal-sized habitat cells in the landscape. It includes both within- and between-patch movement, and shows a negative response to habitat fragmentation. This complies with intuition and existing theoretical work. This method for measuring connectivity is highly robust to reductions in sample size (i.e., number of habitat cells included in the estimate), and we hypothesize that it therefore should be amenable to use in empirical studies. The connectivity measures were weakly correlated to each other and are therefore generally not comparable. We also tested immigration into a single patch as an index of connectivity by comparing it to cell immigration over the landscape. This is essentially a comparison between patch-scale and landscape-scale measurement, and revealed some potential for patch immigration to predict connectivity at the landscape scale. However, this relationship depends on the size of the single patch, the dispersal characteristics of the species, and the amount of habitat in the landscape. We conclude that the response of connectivity measures to habitat fragmentation should be understood before deriving conclusions for conservation management.

Introduction

Landscape connectivity is 'the degree to which the landscape facilitates or impedes movement among resource patches' (Taylor et al. 1993), or 'the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure' (With et al. 1997). Connectivity is therefore a feature of a whole landscape, where the scale of the landscape is determined by the habitat use and movement scales of the organism in question (e.g., Goodwin and Fahrig 1998). Connectivity has been measured in simulation models by counting the number of successful immigrants into all habitat patches or territories in a landscape – dispersal success – (Demers et al. 1995; Schippers et al. 1996; Schumaker 1996), or by counting the number of movement steps between all pairs of habitat patches

in a landscape – search time – (Doak et al. 1992; Ruckelshaus et al. 1997). In empirical studies, connectivity has been estimated by comparing movement frequencies among different observation points in a landscape (Pither and Taylor 1998) or by weighting distances between points in a landscape with observed movement frequencies and mortality rates in different habitat types (Petit and Burel 1998a,b).

Measures of connectivity based on immigration into habitat patches suffer from the problem that connectivity is predicted to be zero in any landscape containing just one habitat patch, even if that habitat patch covers the whole landscape. This is counter to our intuitive understanding of connectivity, which would associate a landscape completely covered with habitat with maximum connectivity. Note this intuition is reflected in the somewhat different concept of connectivity derived from percolation theory (Gardner et al.

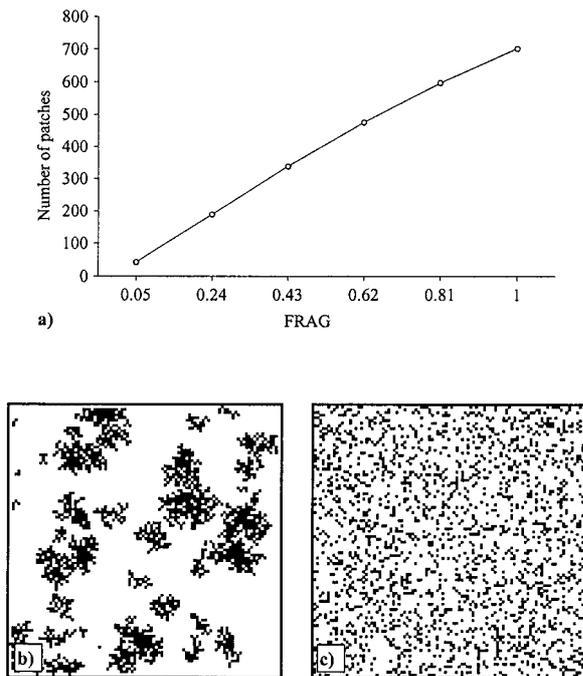


Figure 1. (a) Relationship between the fragmentation parameter FRAG and the number of patches on a grid of 200×200 cells and 40% of a cover type (e.g. habitat). The fragmentation parameter FRAG is linearly related to the number of patches. Higher values of FRAG split a cover type into more patches, which corresponds to higher fragmentation. (b) Spatial pattern of a cover type at FRAG = 0.05 and COV = 0.2 and (c) at FRAG = 1 and COV = 0.2.

1987; Green 1994; Keitt et al. 1997; Metzger and Dé-camps 1997; Wiens et al. 1997; With and King 1997; With et al. 1997; With 1997) (reviewed in Tischendorf and Fahrig in press). The contradiction between our intuition and this prediction from the quantitative measures of connectivity questions progress in our understanding of how landscape structure affects connectivity.

In this paper we address some of the problems that hinder progress in landscape connectivity research. Based on simulated dispersal across heterogeneous landscapes we (1) compare the responses of three connectivity measures – dispersal success, search time and cell immigration (defined below) – to habitat fragmentation, (2) test whether immigration into a single central patch is a sufficient index of landscape connectivity (i.e., comparison between patch-scale and landscape-scale measurement), and (3) compare connectivity values based on cell immigration in varying fractions of cells of a sample grid (i.e., effect of sample size). We conclude by advocating use of consistent, paradox-free connectivity measures.

Table 1. Landscape parameters and their factorial combinations.

Parameter name	Range	Step	Variations
H_COV	0.1–0.8	0.1	8
H_FRAG	0.05–1	0.19	6
HM_COV	$0-(1-H_COV)$	0.1	10, 9, ..., 3
HM_FRAG	0.05–1	0.19	6

H_COV is the proportion of the grid in habitat while HM_COV is the proportion in hospitable matrix. HM_COV can not exceed the difference between the total area and habitat amount. The factorial variation therefore depends on the actual habitat amount, i.e., $1-H_COV$. Fragmentation of habitat and hospitable matrix is controlled by H_FRAG and HM_FRAG respectively. All factorial combinations make up 1632 landscapes.

Methods

Landscape model

We created artificial landscapes on a grid of 40,000 cells (200×200). Each cell represents one of three cover types: Habitat (H), Hospitable Matrix (HM) or Inhospitable Matrix (IM). Initially, IM is assigned to all cells of the grid. A placement algorithm assigns first H and subsequently HM to cells of the grid (see also Fahrig 1997; Fahrig 1998). Two parameters COV and FRAG (see Table 1 and Figure 1) control the assignment of cells. COV stands for coverage and defines the number of cells assigned to either H or HM. The parameter FRAG controls fragmentation by shifting cell selection from pure random (FRAG = 1) to neighborhood-dependent (FRAG near 0). The placement algorithm works as follows. Two steps are repeatedly executed until the number of assigned cells is equal to the proportion of the grid as defined by COV. In step one a not-yet assigned cell of the grid is randomly selected. During step two the algorithm decides whether or not this cell will be assigned to a cover type. This decision depends on the cover type of its eight neighbor cells and the parameter FRAG. A random number between 0 and 1 is compared to the squared value of FRAG. If the random number is smaller than $FRAG^2$, the selected cell will be assigned to the cover type (H or HM). If the random number is larger than $FRAG^2$, at least one of the eight neighbor cells must hold the same cover type for the selected cell to be assigned. Note that squaring FRAG internally (within the algorithm) results in a linear relationship between FRAG and the number of patches of a cover type (Figure 1a). High values of

FRAG result in random assignment of cells (i.e., random distribution of a cover type), while small values of FRAG give higher priority to selecting cells contiguous to cells of the same cover type (Figure 1b, c). Consequently, lower values of FRAG result in larger coherent cell clusters of a cover type, which corresponds to less fragmentation, i.e., fewer patches and less edge (Figure 1). The placement algorithm works in the same way for assigning H and HM. However, since H is assigned first, HM cannot exceed the remaining, unassigned area (i.e., $HM \leq 40\%$, if H already covers 60% of the total grid).

After assigning cover types, a topology is built by combining adjacent (orthogonal and diagonal) cells of the same cover type to patches. In the final landscape model each cell of the grid belongs to a patch. Each patch is defined by its cover type and an identification number. This topology allows us to measure immigration into both patches and single cells of the grid.

Dispersal

Our dispersal model comprises movement, mortality and boundary crossing of individuals. All dispersal parameters are related to and vary between cover or boundary types of the landscape model (see Table 2). The actual value of a parameter therefore depends on the individual's position within the landscape (see also Tischendorf 1997).

Each individual has a pair of x , y coordinates to allow for a vector-based movement definition. Two parameters, step angle and step length (see Table 2), are drawn from random distributions and define successive values of the x , y coordinates for that individual. Before the individual is moved, a random number between 0 and 1 is selected and compared to the step-adjusted mortality parameter value (i.e., the parameter value in Table 2 divided by the total number of movement steps) for the corresponding cover type. If the random number is smaller than the mortality parameter value, the individual 'dies' and is deleted. When an individual encounters a boundary between two cover types, a random number is compared to the corresponding boundary crossing parameter (see Table 2), to determine whether the individual proceeds or returns into the previous patch. Individuals perceive the landscape model as a torus with no edges. Individuals move independently from each other, i.e. no density effects (e.g., Gaines and McGlenaghan 1980; Krohne and Dubbs 1984; Krohne and Miner 1985) or inter-

actions between them are considered. Habitat patches are always accessible and are not blocked for further immigrants by previous immigration or carrying capacity.

We defined four generalized disperser types for our simulations. Each disperser type corresponds to one set of dispersal parameter values (Table 2). The four disperser types express a range from extreme specialist to extreme generalist dispersal behavior. We associate specialist dispersal behavior with (i) faster movement and higher interstep correlation in matrix (Baars 1979; Rijnsdorp 1980; Wallin and Ekbom 1988; Hansson 1991; Diffendorfer et al. 1995; Andreassen et al. 1996; Matter 1996; Charrier et al. 1997; Collins and Barrett 1997), (ii) higher mortality in matrix (Lidicker 1975; Gaines and McGlenaghan 1980; Krohne and Burgin 1987; Henein and Merriam 1990; Schippers et al. 1996; Charrier et al. 1997; Poole 1997; Ruckelshaus et al. 1997; Sakai and Noon 1997), and (iii) lower probability of crossing boundaries from habitat to matrix (Rijnsdorp 1980; Mader 1984; Merriam et al. 1989; Mader et al. 1990; Frampton et al. 1995; Charrier et al. 1997; Holmquist 1998). The extreme specialist (es, see Table 2) expresses very different movement patterns on different cover types, whereas the extreme generalist's movement and mortality are relatively similar across cover types (see Table 2).

Simulation

We conducted a factorial design by (i) varying the four landscape parameters over a wide range (see Table 1), and (ii) combining all resulting 1632 landscape models with each of the four disperser types (set of dispersal parameters, see Table 2). We simulated dispersal on each of these landscape patterns over 1000 movement steps after initially distributing 800 individuals randomly over the habitat area of the landscapes. Each simulation run was repeated ten times for the same landscape model. The whole experiment therefore comprised 6528 independent simulations and 65,280 simulation runs. Note that we optimized the fixed simulation settings (e.g., grid size, number of individuals and repetitions) by analyzing the statistical variance of the response variables in preliminary, exploratory simulations. The results are representative for larger grid sizes.

The response variables we measured were: dispersal success into all patches in the landscape, search time averaged across all individuals and patches, cell immigration into all habitat cells in the landscape, and

Table 2. Each disperser type is defined by a set of parameters defining its dispersal characteristics in each of the three cover types in the landscape model.

Disperser type	Parameters	Cover type		
		Habitat (H)	Hospitable matrix (HM)	Inhospitable matrix (IM)
Extreme specialist 'es'	Mortality (rate per 1000 movement steps)	0.1	0.5	1
	Step length	1	3	5
	Step angle	$\pm 180^\circ$	$\pm 45^\circ$	$\pm 5^\circ$
	Boundary crossing probability	H \rightarrow HM: 0.3	HM \rightarrow H: 1	IM \rightarrow H: 1
		H \rightarrow IM: 0.1	HM \rightarrow IM: 0.2	IM \rightarrow HM: 1
Moderate specialist 'ms'	Mortality (rate per 1000 movement steps)	0.1	0.4	0.8
	Step length	1	2	4
	Step angle	$\pm 180^\circ$	$\pm 90^\circ$	$\pm 45^\circ$
	Boundary crossing probability	H \rightarrow HM: 0.5	HM \rightarrow H: 1	IM \rightarrow H: 1
		H \rightarrow IM: 0.3	HM \rightarrow IM: 0.3	IM \rightarrow HM: 1
Moderate generalist 'mg'	Mortality (rate per 1000 movement steps)	0.1	0.3	0.6
	Step length	1	1	3
	Step angle	$\pm 180^\circ$	$\pm 135^\circ$	$\pm 45^\circ$
	Boundary crossing probability	H \rightarrow HM: 0.7	HM \rightarrow H: 1	IM \rightarrow H: 1
		H \rightarrow IM: 0.5	HM \rightarrow IM: 0.5	IM \rightarrow HM: 1
Extreme generalist 'eg'	Mortality (rate per 1000 movement steps)	0.1	0.2	0.5
	Step length	1	1	2
	Step angle	$\pm 180^\circ$	$\pm 180^\circ$	$\pm 135^\circ$
	Boundary crossing probability	H \rightarrow HM: 0.9	HM \rightarrow H: 1	IM \rightarrow H: 1
		H \rightarrow IM: 0.7	HM \rightarrow IM: 0.7	IM \rightarrow HM: 1

Step length is the expected value of a negative exponential distribution. Step angle is drawn from a uniform probability distribution. Boundary crossing probability defines the probability that an individual crosses that boundary type on each encounter.

immigration into a single selected habitat patch per landscape model (see Figure 2). This patch was randomly selected, and ranged in size from 20 to 6000 cells. Because of the torus topology, each selected habitat patch had a central position within its landscape model. All connectivity measures were averaged over the ten simulation runs.

Dispersal success was measured as the total number of immigration events into all habitat patches in the landscape, divided by the initial number of individuals (800). Only the first time an individual entered a habitat patch was counted as an immigration event for that individual (Figure 2).

Search time was measured as the average number of movement steps between all pairs of habitat patches in the landscape. The average was calculated over all

successful movements of all individuals between any two different habitat patches (Figure 2).

The calculation of cell immigration was similar to dispersal success but based on habitat grid cells (rather than on patches) (see Figure 2). Cell immigration was measured as the total number of immigration events into all habitat cells in the landscape, divided by the initial number of individuals (800). As for patches, only the first entry of an individual into a habitat grid cell was counted as immigration for that individual. Hence, movement within a habitat patch contributes to this measure of connectivity, since a habitat patch is composed of habitat grid cells.

Immigration into a single habitat patch, as a patch-scale index of landscape connectivity, was measured as the total number of immigrations recorded for this

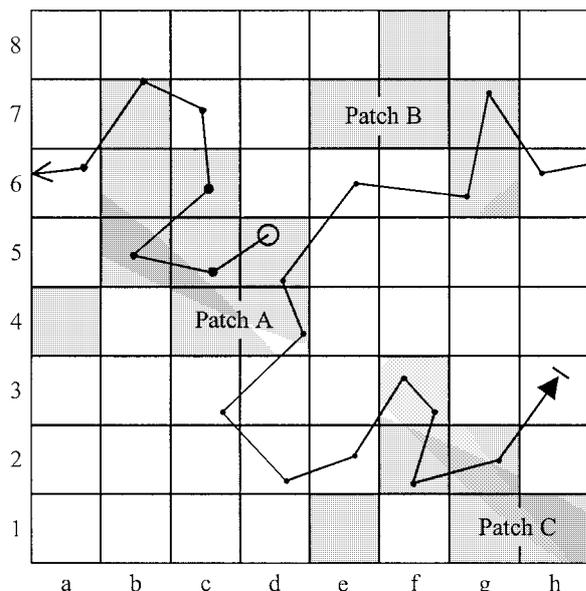


Figure 2. Sample movement path of an individual. Gray cells represent habitat and white cells are inhospitable matrix. The movement path starts in cell d5 and ends in cell h3. The moving individual perceives the landscape model as a torus and therefore moves from cell a6 to cell h6. If the individual encounters a horizontal border of the landscape, e.g., at d8, it exits and reenters at cell d1. Contiguous cells (orthogonal and diagonal) form patches. At the end of the movement the connectivity measures (for this individual only) have the following values: (i) dispersal success = 2 (immigration into patch B and patch C; return to patch A is not immigration); (ii) search time = 5 = (3+7)/2 (3 movement steps between patch A and patch B, and 7 steps between patch B and patch C); (iii) cell immigration = 10 (only the first immigration into a cell is recorded, e.g., c5, b5, c6, b7, ...).

patch divided by the initial number of individuals (800).

We also measured immigration into various fractions of the total amount of habitat cells on the landscape, to examine effects of varying sample size. The lowest fraction was 1 out of 81 cells, which corresponds to 1.23% of the total landscape area. We obtained this fraction by first subdividing the whole grid into blocks of 9×9 cells. During a simulation we sampled only the central cell of each block, i.e., 1 out of 81, and only if this cell was assigned to habitat. The obtained sample is representative, since the underlying landscape structure was generated by a random process.

Table 3. All Pearson correlation coefficients are significant at $p < 0.001$.

	Dispersal success	Search time	Cell immigration
Dispersal success	–	–	–
Search time	–0.12	–	–
Cell immigration	0.32	0.17	–
MNN	–0.14	0.76	0.58
NP	0.9	–0.08	0.05

MNN = mean nearest neighbor distance between habitat patches. NP = number of habitat patches. Connectivity measures are weakly correlated. Dispersal success is strongly dependent on the number of habitat patches while search time is mainly affected by the mean nearest neighbor distance.

Results

Figures 3a–c show the responses of dispersal success, search time and cell immigration to habitat fragmentation. Dispersal success was almost zero in the least fragmented landscapes and reached its maximum in highly fragmented landscapes. Search time is inversely related to connectivity. The decline of search time with increasing habitat fragmentation corresponds therefore to higher connectivity in more fragmented landscapes. On the contrary, connectivity decreased with habitat fragmentation when measured as immigration into equal sized habitat cells, i.e., cell immigration. The different responses of the connectivity measures to habitat fragmentation is supported by their correlations to the number of and the mean nearest-neighbor distance between habitat patches (Table 3), calculated using Fragstats (McGarigal and Marks 1995). Correlation analysis also suggests an overall weak relationship among the three measures of connectivity (Table 3).

Immigration into a central patch of a landscape is related to connectivity at the landscape scale, measured as cell immigration (Figure 4a). We conducted one-way ANCOVA's using Statistica (StatSoft, Inc. 1995) to test separately for effects of habitat amount, habitat fragmentation, patch size and disperser type (class variables) on the relationship between patch immigration and cell immigration. We converted patch size into a class variable by combining values of patch sizes within ranges of 200 cells into one value of the corresponding class variable (see Figure 4d). We found significant effects for habitat amount ($F = 1454$, $p < 0.001$, $df=4$), habitat fragmentation (1372.6 , $p < 0.001$, $df=5$), patch

size ($F=247.3$, $p<0.001$, $df=5$) and disperser type ($F=679.1$, $p<0.001$, $df=3$). ANOVA assumptions were met. Figures 4b-e show correlation coefficients for each level of each of the four class variables. The relationship between patch immigration and cell immigration is weaker in landscapes containing more habitat (Figure 4b) and when habitat is highly fragmented (Figure 4c). The size of the patch into which immigration is measured has a substantial effect on the correlation between patch immigration and cell immigration. Correlation values are generally lower when immigration is measured into larger central patches of a landscape (Figure 4d). The results in figure 4e suggest that the relationship between patch-scale and landscape-scale measure strongly depends on a species' dispersal behavior.

We also measured cell immigration into varying fractions of all habitat cells. The lowest fraction was 1 out of 81 cells, which corresponds to 1.23% of the total landscape area. Cell immigration into this fraction was still highly correlated to immigration into all habitat cells (Figure 5a). Correlations were significantly affected by habitat amount ($F=9.08$, $p<0.001$, $df=7$), habitat fragmentation ($F=151.7$, $p<0.001$, $df=5$) and disperser types ($F=40.4$, $p<0.001$, $df=3$), based on one-way ANCOVA's (Figures 5b-d).

Discussion

The two most common measures of landscape connectivity, dispersal success and search time, predict that landscape connectivity increases with increasing habitat fragmentation. This is problematical for conservation, as it suggests we should advocate fragmentation to improve connectivity. Both measures are based on immigration into habitat patches and are therefore strongly tied to the number of and mean nearest neighbor distance between habitat patches in the landscape (Table 3). In contrast, measuring immigration into equal sized areas of habitat (habitat grid cells) does not depend on the number of habitat patches (Table 3) in the landscape, and incorporates both within- as well as between-patch movement. Cell immigration over the landscape is high when habitat fragmentation is low and vice versa (Figure 3c). Conclusions drawn from this measure will therefore not advocate increasing fragmentation to enhance landscape connectivity.

The three connectivity measures were weakly correlated to each other (Table 3), indicating that these measures are not interchangeable, and that results

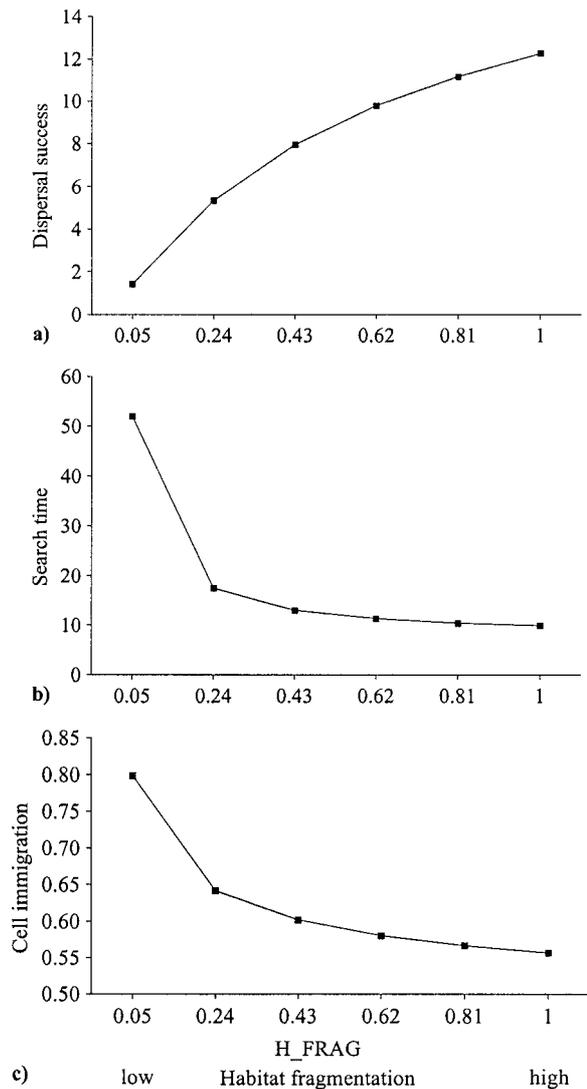


Figure 3. Effect of habitat fragmentation on landscape connectivity measures. Data points are means over all landscape configurations at the corresponding H_FRAG value (see Table 1) and over all disperser types (see Table 2). Dispersal success (a) and search time (b) indicate higher connectivity in more fragmented landscapes (note that longer search time corresponds with lower connectivity). When measured as cell immigration (c), connectivity decreases with increasing habitat fragmentation.

based on different connectivity measures are not directly comparable. We therefore recommend careful choice and justification of connectivity measures in future studies, to ease comparisons and potential generalizations.

Empirical studies often focus on individual habitat patches, while modeling studies usually operate on the whole landscape (Tischendorf and Fahrig in press). It

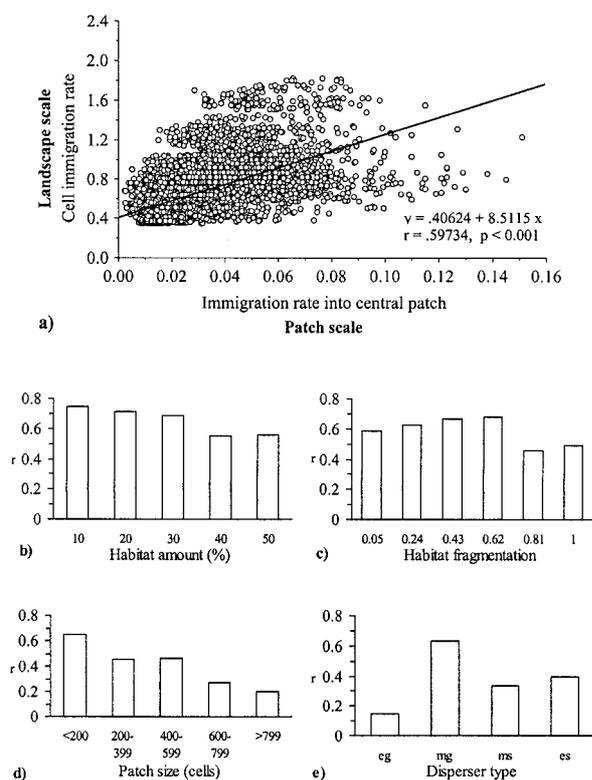


Figure 4. (a) Relationship between single-patch immigration and cell immigration (measured over the whole landscape). The values of the Pearson product-moment correlation coefficients between single-patch immigration and cell immigration depend on (b) habitat amount, (c) habitat fragmentation, (d) size of the patch into which immigration is measured and (e) disperser types (see Table 2). All correlation coefficients are significant at $p < 0.001$.

is therefore important to determine whether we can use patch-scale measures, i.e., immigration into a single patch, to predict landscape-scale connectivity. To answer this, we measured both single-patch immigration and landscape connectivity. Our results showed an overall moderate correlation between single-patch immigration and cell immigration (over the whole landscape) (Figure 4a). Further analysis revealed that the strength of the correlation depends on the amount of habitat in the landscape, the size of the sampled patch, and dispersal attributes of the organism (Figure 4b,d,e). Our result suggests that a larger amount of habitat in a landscape leads to a weaker relationship between single-patch immigration and cell immigration. We assume that this effect is related to the result in Figure 4d, because larger habitat patches are more likely to occur in landscapes containing more habitat. The reason for the effect of patch size on the relationship between single-patch immigration and cell

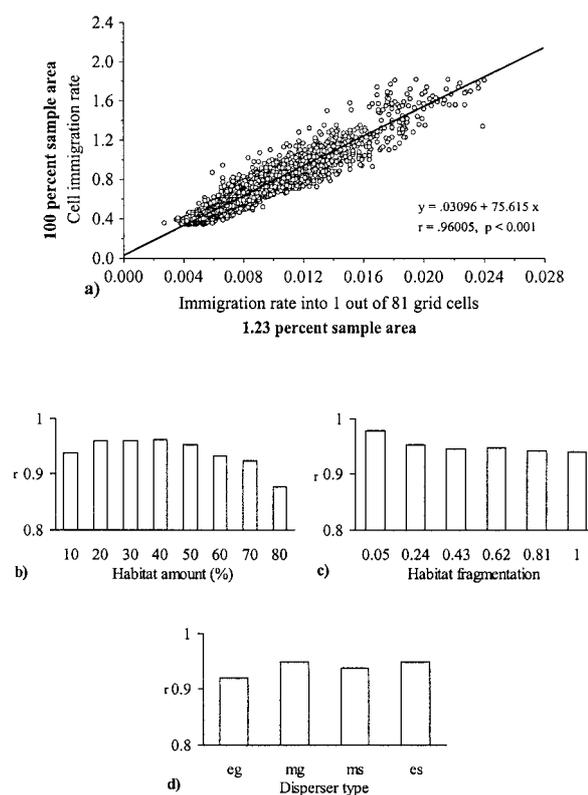


Figure 5. (a) Relationship between cell immigration obtained from a thinned vs. complete sample grid (see text). Correlation values depend on (b) habitat amount, (c) habitat fragmentation and (d) disperser types (see Table 2). All correlation coefficients are significant at $p < 0.001$.

immigration lies in the different responses of the two measures to patch size. While we found single-patch immigration to be correlated with patch size ($r = 0.55, p < 0.001$), cell immigration over the landscape was not ($r = 0.0064, p < 0.547$). Finally, the extreme generalist dispersal type was the least suitable disperser for predicting cell immigration by single-patch immigration. The differences among the four disperser types are difficult to explain, because of the combined effects of movement, mortality and boundary behavior. This suggests that knowledge of dispersal behavior is necessary when using immigration into a single patch to predict landscape connectivity.

We are aware that measuring immigration into all cells of a sample grid across all habitat in a landscape is not feasible for empirical studies. We therefore compared cell immigration into a fraction of the sample grid to the measurement obtained from sampling all cells or 100 percent of the habitat area. After thinning the sample grid to 1 out of 81 cells which corresponds

to 1.23 percent of the total landscape area, measured connectivity was still highly correlated to the reference measurement (Figure 5a). This indicates that we can predict landscape connectivity using only a small sample of the landscape. Note that cell immigration depends on the resolution of the sample grid, i.e., the size of the grid cells. Comparisons across different empirical studies must therefore be based on the same cell size for the sampling grids. We conclude that the best approach for measuring landscape connectivity is to determine the rate of immigration into several equal-sized habitat areas within each landscape, and average these values to produce a single connectivity value for that landscape.

Conclusion

1. Two common measures of landscape connectivity, dispersal success and search time, both averaged over all patches in the landscape, indicate higher connectivity in more fragmented landscapes. This is problematical for conservation plans.
2. Landscape connectivity measured as immigration into all habitat cells in the landscape predicts higher connectivity in less fragmented landscapes.
3. The three connectivity measurements respond differently to landscape structure and dispersal characteristics.
4. Immigration into a single central patch is related to connectivity at the landscape scale. The strength of this relationship depends, however, on the size of the central patch, the amount of habitat in the surrounding landscape and the dispersal behavior of the species under consideration.
5. Immigration into equal sized habitat areas (cells) is highly robust to reductions in sample size. We hypothesize that sampling as little as 1% of the total landscape is sufficient to measure landscape connectivity.
6. Consistent measurement of landscape connectivity is crucial to ease comparisons across different studies.

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References

- Andreassen, H.P., Ims, R.A. and Stenseth, N.C. 1996. Discontinuous habitat corridors: Effects on male root vole movements. *J Appl Ecol* 33: 555–560.
- Baars, M.A. 1979. Patterns of movement of radioactive carabid beetles. *Oecologia* 44: 125–140.
- Charrier, S., Petit, S. and Burel, F. 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agr Eco Enviro* 61: 133–144.
- Collins, R.J. and Barrett, G.W. 1997. Effects of habitat fragmentation on meadow vole (*Microtus pennsylvanicus*) population dynamics in experiment landscape patches. *Lands Ecol* 12: 63–76.
- Demers, M.N., Simpson, J.W., Boerner, R.E.J., Silva, A., Berns, L. and Artigas, F. (1995). Fencerows, edges, and implications of changing connectivity illustrated by two contiguous Ohio landscapes. *Cons Biol* 9: 1159–1168.
- Diffendorfer, J.E., Gaines, M.S. and Holt, R.D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmon, Microtus, and Peromyscus*). *Ecology* 76: 827–839.
- Doak, D.F., Marino, P.C. and Kareiva, P.M. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. *Theor Pop Biol* 41: 315–336.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *J Wildl Manag* 61: 603–610.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecol Model* 105: 273–292.
- Frampton, G.K., Cilgi, T., Fry, G.L.A. and Wratten, S.D. 1995. Effects of grassy banks on the dispersal of some carabid beetles (Coleoptera: Carabidae) on farmland. *Biol Cons* 71: 347–355.
- Gaines, M.S. and McGlenaghan, L.R. 1980. Dispersal in small mammals. *Ann Rev Ecol Syst* 11: 163–196.
- Gardner, R.H., Milne, B.T., Turner, M.G. and O'Neill, R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Lands Ecol* 1: 19–28.
- Goodwin, B.J. and Fahrig L. 1998. Spatial scaling and animal population dynamics. *In Ecological Scale: Theory and Application*. pp. 193–206. Edited by D. Peterson and V.T. Parker Columbia University Press, New York, NY.
- Green, D.G. 1994. Connectivity and complexity in landscapes and ecosystems. *Pac Conserv Biol* 1: 194–200.
- Hansson, L. 1991. Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42: 89–103.
- Henein, K. and Merriam, G. 1990. The elements of connectivity where corridor quality is variable. *Lands Ecol* 4: 157–170.
- Holmquist, J.G. 1998. Permeabilities of patch boundaries to benthic invertebrates - influences of boundary contrast, light level, and faunal density and mobility. *Oikos* 81: 558–566.
- Keitt, T.H., Urban, D.L. and Milne, B.T. 1997. Detecting critical scales in fragmented landscapes. *Conserv. Ecol*. [online]1: 4. Available from the Internet. URL: <http://www.consecol.org/vol1/iss1/art4>
- Krohne, D.T. and Burgin, A.B. 1987. Relative success of residents and immigrants in *Peromyscus leucopus*. *Holarctic Ecol* 10: 196–200.

- Krohne, D.T. and Dubbs, B.A. 1984. An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus*. *Am Midl Nat* 112: 146–156.
- Krohne, D.T. and Miner, M.S. 1985. Removal trapping studies of dispersal in *Peromyscus leucopus*. *Can Zool J* 63: 71–75.
- Lidicker, W.Z. 1975. The role of dispersal in the demography of small mammals. *In* Small mammals: their productivity and population dynamics. pp. 103–128. Edited by F.B. Golley, et al. Cambridge University Press, Cambridge.
- Mader, H.J. 1984. Animal habitat isolation by roads and agricultural fields. *Biol Conserv* 29: 81–96.
- Mader, H.J., Schell, C. and Kornacker, P. 1990. Linear barriers to arthropod movements in the landscape. *Biol Cons* 54: 209–222.
- Matter, S.F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: Individual responses to patch size and isolation. *Oecologia* 105: 447–453.
- McGarigal, K. and Marks, B.J. 1995. Fragstats: spatial pattern analysis program for quantifying landscape structure. U. S. Forest Service General Technical Report PNW 351.
- Merriam, G., Kozakiewicz, M., Tsuchiya, E. and Hawley, K. 1989. Barriers as boundaries for metapopulations and demes of *Peromyscus leucopus* in farm landscapes. *Lands Ecol* 2: 227–235.
- Metzger, J.P. and Décamps, H. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *Acta Ecol* 18: 1–12.
- Petit, S. and Burel, F. 1998a. Connectivity in fragmented populations – *Abax parallelepipedus* in a hedgerow network landscape. *Comptes Rendus de l' Academie des Sciences Serie III – Sciences de la vie – life Sciences* 321: 55–61.
- Petit, S. and Burel, F. 1998b. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agr Ecol Environ* 69: 243–252.
- Pither, J. and Taylor, P.D. 1998. An experimental assessment of landscape connectivity. *Oikos* 83: 166–174.
- Poole, K.G. 1997. Dispersal patterns of lynx in the northwest territories. *J Wildl Manag* 61: 497–505.
- Rijnsdorp, A.D. 1980. Pattern of movement in and dispersal from a Dutch forest of *Carabus problematicus* Hbst. (Coleoptera, Carabidae). *Oecologia* 45: 274–281.
- Ruckelshaus, M., Hartway, C. and Kareiva, P.M. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conserv Biol* 11: 1298–1306.
- Sakai, H.F. and Noon, B.R. 1997. Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *J Wildl Manag* 61: 343–350.
- Schippers, P., Verboom, J., Knaapen, P. and van Apeldoorn, R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: An analysis with a GIS-based random walk model. *Ecography* 19: 97–106.
- Schumaker, N.H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77: 1210–1225.
- StatSoft, Inc. 1995. STATISTICA for Windows [Computer program manual]. Tulsa, OK.
- Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571–572.
- Tischendorf, L. 1997. Modeling individual movements in heterogeneous landscapes: potentials of a new approach. *Ecol Model* 103: 33–42.
- Tischendorf, L. and Fahrig, L. On the usage and measurement of landscape connectivity. *Oikos*, in press.
- Wallin, H. and Ekbom, B.S. 1988. Movements of carabid beetles (Coleoptera Carabidae) inhabiting cereal fields: A field tracing study. *Oecologia* 77: 39–43.
- Wiens, J.A., Schooley, R.L. and Weeks, R.D. 1997. Patchy landscapes and animal movements: Do beetles percolate? *Oikos* 78: 257–264.
- With, K.A. 1997. The application of neutral landscape models in conservation biology. *Cons Biol* 11: 1069–1080.
- With, K.A., Gardner, R.H. and Turner, M.G. 1997. Landscape connectivity and population distributions in heterogeneous environments. *Oikos* 78: 151–169.
- With, K.A. and King, A.W. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79: 219–229.