

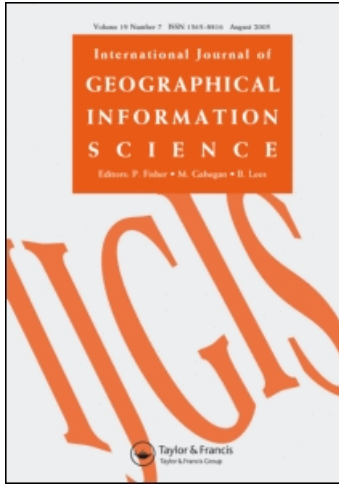
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Modelling the effect of intersections in linear habitat on spatial distribution and local population density

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Many species in human-dominated landscapes find their habitat in linear elements, such as road verges, hedgerows and ditches. Local concentrations of species have been observed in the intersections of linear elements, but their spatial distribution and local population density in this linear habitat are not well captured by existing theory. Using a simple, spatially explicit individual-based GIS-model simulating hedgerow bird species with different movement abilities, local high population density of our model species in intersections and their reduced density or absence in linear habitat could be explained by limited movement. We hypothesise that, for species with low movement ability, intersections of linearly shaped habitat could contain several local populations. We argue that these predictions are valid for organisms occurring in linear habitat with limited movement relative to the dimensions of their habitat, and whose movement is directed by their habitat. Our findings support the importance of intersections for biodiversity in human-dominated landscapes, as they may serve as refuges from which individuals can (re-)colonise unoccupied habitat.

Keywords: spatially explicit model; animal movement constraints; hedgerow birds; linear habitat; habitat geometry

1. Introduction

A large body of theory has been developed over the last few decades for the spatial dynamics of plant and animal populations in human-dominated landscapes (Forman and Godron 1986, Tilman and Kareiva 1997, Hanski 1999). In these landscapes, the habitat of species is often found in linear elements, such as networks of field margins (Kleijn and Van Langevelde 2006), road verges (Forman and Alexander 1998), hedgerows (Baudry *et al.* 2000), ditches (Van Dorp *et al.* 1997) and streams (Fagan 2002, Koizumi and Maekawa 2004). For example, the presence of many species within agricultural landscapes is restricted to such non-cropped, linear elements (Grashof-Bokdam and Van Langevelde 2005, Kleijn and Van Langevelde 2006), especially when agricultural land use is intensive (Kleijn *et al.* 2001, Weibull *et al.* 2000). These linear elements may act as corridors as well as habitat for many species, including plants, small mammals and birds (Fitzgibbon 1997, Hinsley and Bellamy 2000, Haddad *et al.* 2003, Whittingham *et al.* 2005, 2009, Gelling *et al.* 2007, Wehling and Diekmann 2008).

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Although fragmentation of habitat in human-dominated landscapes causes a decline in biodiversity, the factors explaining the spatial distribution and local population density (i.e. the number of individuals per unit area) of species found in linearly shaped habitat have only recently been studied (Petit and Burel 1998, Joyce *et al.* 1999, Baudry *et al.* 2000, Fagan 2002, Grashof-Bokdam and Van Langevelde 2005, Campbell Grant *et al.* 2006, Gelling *et al.* 2007). Yet, knowledge about the role of this linear habitat and their intersections is crucial in managing agricultural landscapes for biodiversity (Grashof-Bokdam and Van Langevelde 2005). These elements can vary substantially in structure and quality, which affects the presence and abundance of animals (Gelling *et al.* 2007). For example, a high level of connectivity between adjoining hedgerows typically maintains a high density of small mammals (Fitzgibbon 1997, Gelling *et al.* 2007), and increasing hedgerow width and length is related to increasing abundance of birds (Green *et al.* 1994, Hinsley and Bellamy 2000, Némethová and Tirinda 2005, Lindenmayer *et al.* 2007) and small mammals (Gelling *et al.* 2007, Michel *et al.* 2007). Many plant, bird and mammal species are found to be concentrated in the intersections of linear elements (Forman and Godron 1986, Lack 1988, Riffell and Gutzwiller 1996, Lindenmayer *et al.* 2007), which is attributed to higher habitat quality in these intersections compared with linear elements (Forman and Godron 1986, Lack 1988) or their width and higher structural diversity (Gutzwiller and Anderson 1987). However, spatial structure is also thought to play a role in determining these concentrations, that is, high local density of individuals (Lindenmayer *et al.* 2007). For example, Riffell and Gutzwiller (1996) found a higher diversity of plant species that are dispersed by birds or mammals in intersections, especially in intersections with many linkages (T- and X-shaped intersections). This pattern was attributed to the edge-following behaviour of birds that serve as the tree's primary seed dispersal vector. For several hedgerow birds, a higher local density was found in the intersections of hedgerows, for example, Common Redstart (*Phoenicurus phoenicurus*), Common Chiffchaff (*Phylloscopus collybita*), Icterine Warbler (*Hippolais icterina*), Wren (*Troglodytes troglodytes*), Blue Tit (*Parus caeruleus*) and Great Tit (*Parus major*) (Lack 1988, Oostenbrink *et al.* 1994, Némethová and Tirinda 2005). Despite observed intersection effects, the dynamics of populations in linearly shaped habitat are not well captured by existing spatial population theory (Campbell Grant *et al.* 2006).

In this article, we analyse whether the spatial distribution and local population density of species in linearly shaped elements can be related to habitat geometry, focusing on hedgerow birds. Our objective is to show that the spatial structure of linearly shaped habitat containing highly connected intersections with linear elements in-between can lead to increased local population density of these bird species in intersections. We use a simple, spatially explicit individual-based GIS model for species with different movement abilities. This model does not aim to simulate an existing landscape or existing species but is used to generate hypotheses that can be tested in the field. We used a series of model landscapes and two model species.

2. The model

The model simulates reproduction, mortality and movement of individuals. It is based on the PCRaster Environmental Modelling language, which is a computer language for the construction of iterative spatio-temporal environmental models (<http://www.pcraster.nl/>). We first explain how we modelled the habitat, varying from linear to compact habitat, and how to quantify habitat geometry. Then the characteristics of our model species are given, followed by details about the simulations and the analysis of the results.

2.1. Habitat modelling

To analyse the spatial distribution and local population density in different habitat geometries, we used a series of 75 model landscapes of 32×32 grid cells. In each landscape, structurally connected habitat of 100 grid cells was generated (habitat covers around 10% of the model landscapes as found in many fragmented landscapes; Forman and Godron 1986), where each grid cell with habitat was connected to at least one other grid cell with habitat. To vary its geometry, that is, linear versus compact habitat, we applied the following rules. The first grid cell was assigned randomly in the landscape. The second grid cell was assigned adjacent to the first one, but in a random direction. Each next grid cell was assigned adjacent to the previous one based on a predefined probability distribution.

A series of 25 landscapes was generated based on the probability of 0.98 that the next grid cell was located adjacent to the previous one in the same direction as the previous one, and on the probabilities of 0.01 that it was located at either the left-hand side or the right-hand side of the previous one. This provided us with 25 landscapes with linear habitat. A more compact habitat, also in 25 landscapes, was generated with the probability of 0.8 for assigning each next grid cell in the forward direction, and the probability of 0.1 for each of the sideward directions. The most compact habitat, again in 25 landscapes, was generated with an equal probability of 0.33 for assigning the next grid cell in the forward or each of the sideward directions.

To distinguish between these different habitat geometries, we quantified the compactness of the habitat. We first measured the position of each habitat site i relative to all other sites j in a landscape. The relative position of each site i was approximated as the reciprocal of the shortest effective distances d_{ij} to all other sites j (distance from centre to centre; Van Langevelde *et al.* 1998, Van Langevelde 2000):

$$c_i = \sum_{j=1}^n \frac{1}{d_{ij}} \quad \forall i \text{ and } i \neq j$$

where n is the total number of habitat sites within the landscape (here, $n = 100$ cells). Low values of c_i imply that site i is at the periphery of the habitat, that is, long distances to other sites. The compactness C of the habitat was then measured by summing the values for the relative position of all sites as:

$$C = \sum_{i=1}^n c_i$$

Low values of C indicate linearly shaped habitat. The compactness C and the relative position c_i of site i can be used for comparison between the landscapes (Van Langevelde *et al.* 1998). Other parameters are available to quantify the compactness or linearity of patches, especially the perimeter–area ratio, the radius of gyration and the linearity index (all available in FRAGSTATS, McGarigal and Marks 1995). The perimeter–area ratio is a simple measure of shape complexity (an increasing value means a more complex shape, here interpreted as a more linear shape). The radius of gyration is a measure of patch extent (an increasing value means that the extent of the patch increases, here interpreted as more linear). The linearity index is based on the medial axis transformation of the patch (low values represent compact patches, and values close to 1 are patches which are all edge, i.e. linear patches). We calculated these parameters for our landscapes and correlated them with C to

check whether our parameter C agrees with the results obtained by these other parameters. For this correlation test, we calculated the non-parametric Spearman rank correlation coefficient (using SPSS 15.0). The advantage of using C in combination with c_i is that we quantify both the compactness of the habitat and the relative position of each grid cell with habitat relative to all others.

2.2. Modelling species

Our model species represent hedgerow bird species whose density is found to be higher in hedgerow intersections (Lack 1988, Oostenbrink *et al.* 1994, Némethová and Tirinda 2005). Each grid cell with habitat in our model landscapes represents a site that can be occupied by our model species. As we only focus on the effects of habitat geometry, all sites are assumed to have the same habitat quality (food availability) with similar reproduction or mortality probability. During simulations, we assume that the number, size and habitat quality of the sites remain constant. We differentiate between cells that are occupied by a breeding pair and cells with only one individual (unpaired individuals or ‘floaters’). The sum of all cells occupied by a pair is a measure for population density that can reproduce during the next year. Each simulation started with 50% randomly selected occupied sites with pairs. We did not find an effect of different starting values on the outcomes. Each time step (1 year) starts with all sites occupied by a pair. The model then determines which pairs produce juveniles, followed by the redistribution of these juveniles over unoccupied sites. Finally, it is determined whether animals will experience a severe or normal winter, which determines their survival. The surviving pairs can reproduce the next time step.

A pair of our model species in a habitat site has a probability P_j ($=0.6$, accounting for annual variation) that J juveniles ($=6$) are produced. Clutch sizes are generally between 3 and 7 for open nesting passerine birds (Slagsvold 1989; around 5 for Icterine Warblers, Weidinger 2001; and 6 for Common Redstarts, Rutila *et al.* 2002). After reproduction, the juveniles move away from their natal site and search for unoccupied sites. Each unpaired individual (Brown and Long 2007) and juvenile searches for an unoccupied site within a certain radius, that is, the maximum movement distance D that is defined as the maximum number of grid cells of an individual can move from its natal site. Two individuals in the same grid cell are assumed to form a breeding pair, where differences in sex are neglected for reasons of simplicity.

In the model, we assume that the probability that an unoccupied site within this radius will be selected depends on the distance to this site and the costs for movement (Hanski 1999). Therefore, we calculate the effective distance from the natal site to the unoccupied sites to conform Adriaensen *et al.* (2003). This effective distance is a measure for the distance modified with the costs to move based on the landscape to be crossed as well as behavioural aspects of the organism. In our simulations, we assumed that there are no costs for moving through habitat (resistance value = 1), whereas the non-habitat has high costs for movement (resistance value = 9). The result of this effective distance is that movement along the linear habitat occurs most often. The mean movement distances are relatively short for bird species found in hedgerows such as Wren, up to 500 m (Paradis *et al.* 1988), and areas without cover could further limit movement of these birds in open areas, for example, it has been found that the most foraging trips of hedgerow birds are made within 100 m of the nest site in the hedgerow (Morris *et al.* 2001). The probability of a bird crossing open area decreases sharply with increasing distance (Bélisle *et al.* 2001), which could lead to a ‘crowding effect’ in small and more isolated habitat patches (Debinski and Holt 2000). We assume that the further an unoccupied site is located from occupied ones, the lower the

probability that it will be selected. This probability decreases exponentially with the distance to an occupied site (Hanski 1999), as $P_m = 0.1^{d_{ij}/D}$, where d_{ij} is the shortest effective distance from site i to site j . For the maximum movement distance D , the probability to be selected is arbitrarily set to 0.1, and the probability for distances larger than D equals 0.

When non-habitat has high costs for movement, the movement of these hedgerow birds is directed by their habitat. These high costs also account for mortality (e.g. due to predation) during movement in open areas (Whittingham and Evans 2004): when sites are only located at large distances from the natal site, the probability of dying during movement equals $(1 - P_m)$. Individuals that do not find an unoccupied site within their movement radius are further neglected. No immigration occurs. In our simulations, we separately applied species with low and high movement ability relative to the size of the computer landscape ($D = 3$ and 30 cells, respectively).

During winter, the occupied sites have a probability that they will become unoccupied because of mortality, depending on the severity of a given winter (Gillings *et al.* 2005). We differentiated between the survival probability P_n for normal winters ($=0.8$) and P_s for severe winters ($=0.4$). Severe winters occur with probability P_w ($=0.2$). After winter, the remaining pairs can reproduce during the next year.

2.3. Simulation and analysis of results

Because of the stochastic character of the model, we conducted 10 simulations for each model landscape per model species. Each simulation ran for 100 time steps. We recorded for each time step whether a site was occupied by a pair or not. For each simulation, the mean number of occupied sites was only calculated for time steps 51–100 to avoid influences of the initial distribution.

To show that the spatial distribution of hedgerow bird species is mainly limited to highly connected intersections, we first tested whether the frequency of site occupation is related to the relative position of the sites (c_i) using logistic regression, separately for the two model species with low and high movement abilities. These values for the relative position of each site can be compared between the model landscapes (they all contain habitat structures of 100 cells; Van Langevelde *et al.* 1998). To test the occupation frequency as a function of c_i , we applied a Generalised Linear Model (GLM with a binomial distribution and logit link function in SPSS 15.0), with the occupation frequency (between 0 and 100) as dependent variable and 100 as the fixed value for the number of subjects. Second, the average population density for the two species was related to the compactness of the habitat C using ordinary least square (OLS) linear regression (in SPSS 15.0, after confirming that the residuals of the regression were normally distributed, tested with the Shapiro–Wilk test).

3. Results

Examples of different model landscapes and the generated occupation frequency of sites for species with different movement abilities are presented in Figure 1 (minimum value for C given 100 cells is 926.2 and maximum value is 2606.3). We found a high correlation between our compactness parameter C and the Fragstats parameters: Spearman rank correlation coefficient $r = -0.960$ ($P < 0.001$, $n = 75$) for the perimeter–area ratio, $r = -0.978$ ($P < 0.001$, $n = 75$) for the radius of gyration and $r = -0.759$ ($P < 0.001$, $n = 75$) for the linearity index. These correlations suggest that these parameters would provide similar results as our parameter C . For species with low movement ability, there is a large difference in the occupation frequencies between sites in linear habitat (Figure 1a), whereas there is less

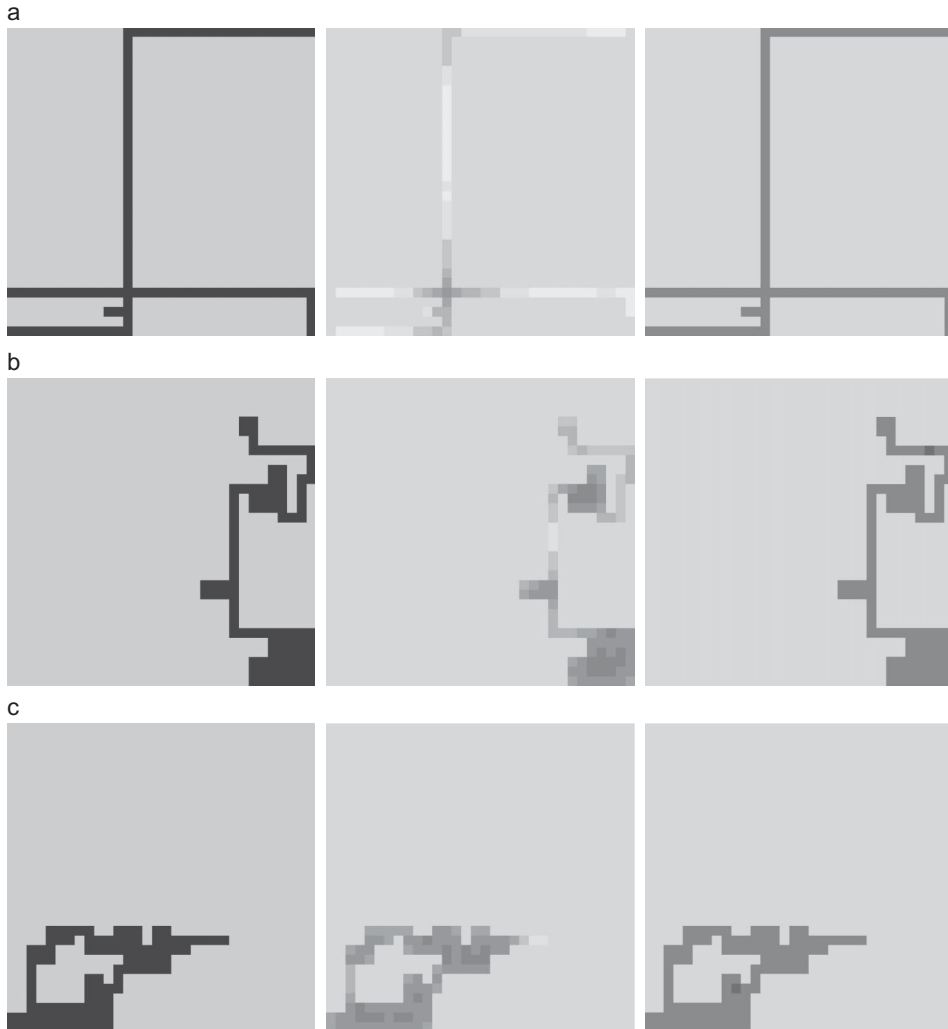


Figure 1. Examples of three model landscapes that vary in habitat geometry (left-hand panels) and the simulated frequency with which habitat sites are occupied by our model species, representing hedgerow birds. The panels in the middle represent the occupancy by species with low movement ability, and those at the right-hand side by species with high movement ability. The grey colour indicates the frequency that sites are occupied (over the last 50 time steps), where darker grey indicates a higher occupation frequency (0–100). Parameter values: maximum movement distance $D = 3$ for the species with low movement ability and $D = 30$ for the species with high movement ability, number of juveniles $J = 6$, probability to produce J juveniles $P_j = 0.6$, survival probability during normal winters $P_n = 0.8$, survival probability during severe winters $P_s = 0.4$, probability of a severe winter $P_w = 0.2$.

difference in more compact habitat (Figure 1b and c). In linearly shaped habitat (even in more compact habitat), individuals are locally absent, whereas they mainly concentrate in intersections. For species with high movement ability, local differences in occupation frequencies disappear. For species that show less aversion to the non-habitat (or matrix; VanderMeer and Carvajal 2001), differences in local distribution disappear for species with low movement ability (resistance value < 4 for the non-habitat, data not shown). Slight

changes in the mortality parameters (P_n, P_s, P_w) or reproduction parameters (P_j, J) did not yield qualitatively different patterns for both species.

The pattern of high occupation frequency in intersections and absence in linear habitat for species with low movement ability is shown by the relationship between the frequency of site occupation by species and the relative position of the sites (Figure 2a). Figure 2b shows the same relationship for species with high movement ability. Across all model landscapes, there was a gradient from sites that are at the periphery of the habitat, for example, in linear parts (low values for c_i), to sites that are in intersections and in the centre of compact habitat (high values for c_i). As expected, sites with high values for their relative position c_i have, on average, a higher occupation frequency than sites with low values. There is a relatively strong increase in occupation frequency with increasing value of the relative position of sites and then it levelled off. We found a significant positive effect of the relative position of sites on their occupation frequency (GLZ, $n = 7500$, Wald chi-square = 82017.9, $P < 0.001$). For species with high movement ability, the relationship between the occupation frequency and their relative position was absent (GLZ, $n = 7500$, Wald chi-square = 0.11, $P = 0.738$).

Figure 3 presents the average population density over the last 50 time steps for species with low and high movement ability as a function of the compactness of the habitat C . There was a non-linear increase in population density with an increase in the compactness of habitat for species with low movement ability. Linear regression analyses yielded a quadratic model: compactness + (compactness)² (OLS regression, $n = 75$, adjusted $R^2 = 93.5$, with $t = 9.927$ and $P < 0.001$ for compactness and $t = -6.661$ and $P < 0.001$ for (compactness)²). There was no such relationship between population density and compactness for species with high movement ability (OLS regression, $n = 75$, $t = 0.583$, $P = 0.562$ for compactness).

4. Discussion

In this article, we explored spatial discontinuity in distribution and local population density in linearly shaped habitat for two model species representing hedgerow birds. For species with limited movement ability, we predict local high density of individuals in intersections and low population density or absence in linear parts, whereas compact habitat sites were frequently occupied (Figure 3). This can be explained by stochastic, spatially uncorrelated mortality and limited movement of individuals to unoccupied sites in linear habitat. When sites around the intersections (with high values for their relative position c_i ; Figure 2) become unoccupied because of mortality, they can be recolonised from surrounding occupied sites. Sites in linear parts (with low values for their relative position c_i ; Figure 2) may remain unoccupied for a long time as individuals have low probability to reach them. The resulting population distribution is spatially autocorrelated as sites in and around the intersections have high occupation probability, whereas the sites in between have low occupation probability. Such endogenous (or 'inherent') demographic processes are known to be one of the causes for spatial autocorrelation in species distributions (Legendre 1993, De Knecht *et al.* 2010). For species with high movement ability, local differences in density disappear because all unoccupied sites can be (re-)colonised without movement limitations. These predictions are valid for organisms occurring in linear habitat with limited movement relative to the dimensions their habitat, and whose movement is directed by their habitat.

Our findings contribute to the emerging theory on dendritic networks (Campbell Grant *et al.* 2006) because it demonstrates that movement ability of species largely determine their spatial distribution and local population density in networks of habitat when the species show mainly within-network movements and relatively few out-of-network movements

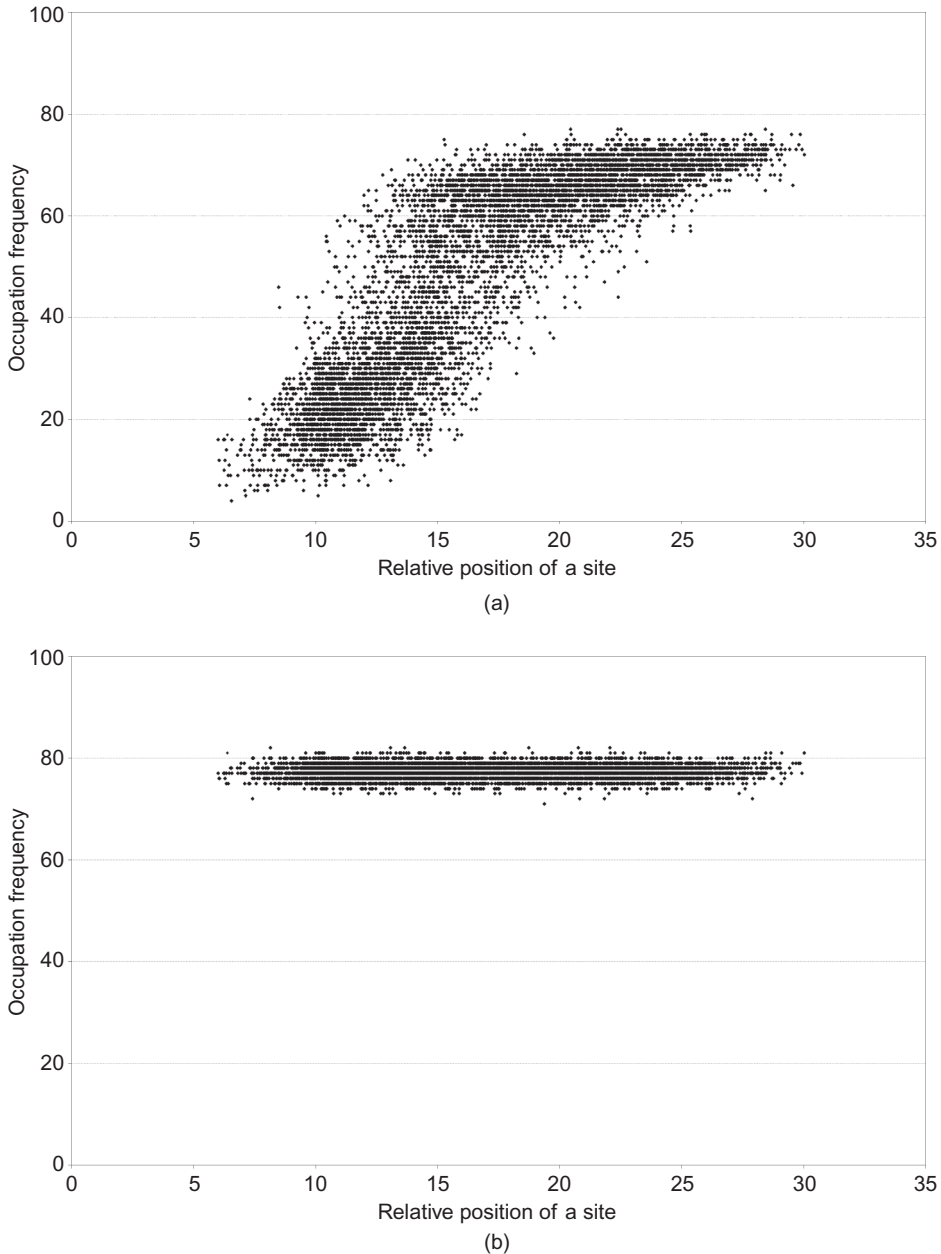


Figure 2. Relationships between the frequency that sites are occupied by our model species with (a) low and (b) high movement ability and the relative position of these sites in the habitat (c_i). The relative position of each site i was approximated as the reciprocal of the shortest effective distances d_{ij} to all other sites j . Low values of c_i imply that site i is at the periphery of the habitat, that is, long distances to other sites, whereas high values represent sites that are in intersections and in the centre of compact habitat. For parameter values, see Figure 1.

(i.e. movement through the habitat) versus relatively many out-of-network movements (i.e. movement through the non-habitat). We did not include issues such as spatial and temporal differences in the quality of habitat, differences between individuals and their movement ability, but we advocate that our simple approach is useful as it provides testable hypotheses.

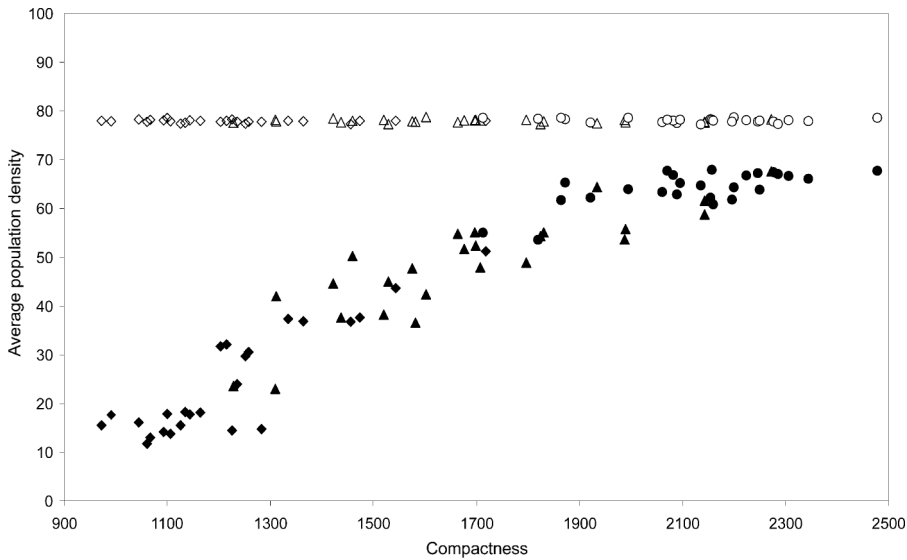


Figure 3. Relationships between average population density in habitat (for the last 50 time steps) and the habitat compactness C . Open symbols are for the model species with high movement ability and closed symbols for the model species with low movement ability. Different symbols represent different probability distributions to generate the model landscapes: (\diamond) 0.98-0.01-0.01, (Δ) 0.8-0.1-0.1 and (\circ) 0.33-0.33-0.33. The first set was generated based on the probability of 0.98 that each next grid cell was located adjacent to the previous one in the same direction as the previous one, and on the probabilities of 0.01 that it was located at either the left-hand side or the right-hand side of the previous one. The second set was generated with the probability of 0.8 for assigning each next grid cell in the forward direction, and the probability of 0.1 for each of the sideward directions. The third set was generated with an equal probability of 0.33 for assigning the next grid cell in the forward or each of the sideward directions. For parameter values, see Figure 1.

Our findings agree with increased population densities of species at intersections (Forman and Godron 1986, Forman 1995, Riffell and Gutzwiller 1996, Deckers *et al.* 2005) and bird species in particular (Gutzwiller and Anderson 1987, Lack 1988, Némethová and Tirinda 2005, Lindenmayer *et al.* 2007). They also agree with higher species diversity found in intersections, which has been found not only for hedgerow birds (Lack 1988, Oostenbrink *et al.* 1994, Némethová and Tirinda 2005, Lindenmayer *et al.* 2007), but also for plants (Riffell and Gutzwiller 1996), small mammals (Gelling *et al.* 2007) and insects. For example, Dover (1996) found a higher number of butterfly species at intersections of field boundaries.

In our model landscapes, habitat quality in linear elements and intersections was similar. Hence, the often suggested explanation of higher habitat quality or a higher structural diversity in intersections (Forman and Godron 1986, Gutzwiller and Anderson 1987, Lack 1988, Forman 1995) cannot be applied to explain our results (see also, Lindenmayer *et al.* 2007). The movement of animals living in linear habitat, in our case hedgerow birds, is limited in open areas and largely restricted to linear elements leading to 'funnelling' of movements (Lindenmayer *et al.* 2007) in our modelling exercise because of the lower costs of movement in habitat than in non-habitat. Our results provide therefore an alternative explanation for the local concentrations in intersections, that is, the geometry of habitat limits (re-)colonisation possibilities. These findings contribute to a better understanding of differences in population density found in linear elements. When comparing different

regions to test our predictions, it might be difficult to separate this intersection effect from the effect of higher hedgerow density (Hinsley and Bellamy 2000, Whittingham *et al.* 2005, 2009) as higher hedgerow density could result in an increase in number of intersections. It would be interesting to test whether such interaction effect results in increased local density of hedgerow birds in regions with high hedgerow density compared to intersections in regions with low hedgerow density.

It has been suggested that the preservation of linear habitat may be important in maintaining metapopulations in agricultural landscapes (Baudry *et al.* 2000, Grashof-Bokdam and Van Langevelde 2005, Gelling *et al.* 2007). Metapopulation theory predicts that as available habitat decreases, the spatial arrangement of the remaining habitat becomes increasingly important (Hanski 1999), and linear elements could serve as movement corridors between remaining habitat patches (Soule and Terbough 1999). We found that structurally connected linear habitat does not necessarily imply that organisms can reach each site within that habitat with equal probability. It has indeed been shown that metapopulation dynamics can be found in structurally connected habitat (With *et al.* 1999), which resulted in the proposition that landscape connectivity requires a functional or process-oriented definition of landscape structure (e.g. Bêlisle 2005). In our study, 'patchy' distributions were found in linear habitat with local differences in occupation frequency (including local absence) instead of one large contiguous population.

For application, model species and landscapes should be validated using field observations. Although it is a theoretical study in which we applied model bird species (ignoring behavioural details of finding mates, defending territories, etc.), it may contribute to the understanding of biodiversity in agricultural landscapes (Baudry *et al.* 2000, Grashof-Bokdam and Van Langevelde 2005). Testing the predictions would also require including differences in habitat quality next to habitat geometry. Our findings support the importance of intersections of linear habitat for biodiversity in these landscapes, as these may serve as refuges from which individuals can (re-)colonise unoccupied habitat. Our results imply that land management should design such intersections at regular distances to increase connectivity (see also Lindenmayer *et al.* 2007). On the contrary, some birds might need some spacing between trees (Whittingham and Evans 2004). In addition to testing the generated hypotheses in real landscapes, we advocate that the dynamics of population and communities in linear habitat deserve further theoretical study on design and management of such linear networks.

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References

- Adriaansen, F., *et al.*, 2003. The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, 64, 233–247.
- Baudry, J., Bunce, R.G.H., and Burel, F., 2000. Hedgerows: an international perspective on their origin, function and management. *Journal of Environmental Management*, 60, 7–22.
- Bêlisle, M., 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology*, 86, 1988–1995.
- Bêlisle, M., Desrochers, A., and Fortin, M.-J., 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology*, 82, 1893–1904.

- Brown, D.R. and Long, J.A., 2007. What is a winter floater? Causes, consequences, and implications for habitat selection. *Condor*, 109, 548–565.
- Campbell Grant, E., Lowe, W.H., and Fagan, W.F., 2006. Living in the branches: population dynamics and ecological processes in dendritic networks. *Ecology Letters*, 10, 165–175.
- De Knegt, H.J., et al., 2010. Spatial autocorrelation and the scaling of species-environment relationships. *Ecology*, 91: 2455–2465.
- Debinski, D.M. and Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology*, 14, 342–355.
- Deckers, B., et al., 2005. Effects of landscape structure on the invasive spread of black cherry *Prunus serotina* in an agricultural landscape in Flanders, Belgium. *Ecography*, 28, 99–109.
- Dover, J.W., 1996. Factors affecting the distribution of butterflies on arable farmland. *Journal of Applied Ecology*, 33, 723–734.
- Fagan, W.F., 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, 83, 3243–3249.
- Fitzgibbon, C.D., 1997. Small mammals in farm woodlands: the effects of habitat, isolation and surrounding land-use patterns. *Journal of Applied Ecology*, 34, 530–539.
- Forman, R.T.T., 1995. *Landscape mosaics*. Cambridge, UK: Cambridge University Press.
- Forman, R.T.T. and Alexander, L.E., 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics*, 29, 207–231.
- Forman, R.T.T. and Godron, M., 1986. *Landscape ecology*. New York: Wiley and Sons.
- Gelling, M., Macdonald, D.W., and Mathews, F., 2007. Are hedgerows the route to increased farmland small mammal density? Use of hedgerows in British pastoral habitats. *Landscape Ecology*, 22, 1019–1032.
- Gillings, S., et al., 2005. Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proceedings of the Royal Society B*, 272, 733–739.
- Grashof-Bokdam, C.J. and Van Langevelde, F., 2005. Green veining: landscape determinants of biodiversity in European agricultural landscapes. *Landscape Ecology*, 20, 417–439.
- Green, R.E., Osborne, P.E., and Sears, E.J., 1994. The distribution of passerine birds in hedgerows during the breeding-season in relation to characteristics of the hedgerow and adjacent farmland. *Journal of Applied Ecology*, 31, 677–692.
- Gutzwiller, K.J. and Anderson, S.H., 1987. Multiscale associations between cavity-nesting birds and features by Wyoming streamside woodlands. *Condor*, 89, 534–548.
- Haddad, N.M., et al., 2003. Corridor use by diverse taxa. *Ecology*, 84, 609–615.
- Hanski, I., 1999. *Metapopulation ecology*. Oxford: Oxford University Press.
- Hinsley, S.A. and Bellamy, P.E., 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: a review. *Journal of Environmental Management*, 60, 33–49.
- Joyce, K.A., Holland, J.M., and Doncaster, C.P., 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. *Bulletin of Entomological Research*, 89, 523–531.
- Kleijn D., et al., 2001. Agri-environmental schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, 413, 723–725.
- Kleijn, D. and Van Langevelde, F., 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, 7, 201–214.
- Koizumi, I. and Maekawa, K., 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. *Freshwater Biology*, 49, 973–981.
- Lack, P.C., 1988. Hedge intersections and breeding bird distribution in farmland. *Bird Study*, 35, 133–136.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659–1673.
- Lindenmayer, D.B., et al., 2007. Farmland bird responses to intersecting replanted areas. *Landscape Ecology*, 22, 1555–1562.
- McGarigal, K. and Marks, B.J., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA For. Serv. Gen. Tech. Rep. PNW-351.
- Michel, N., et al., 2007. Role of habitat and landscape in structuring small mammal assemblages in hedgerow networks of contrasted farming landscapes in Brittany, France. *Landscape Ecology*, 22, 1241–1253.
- Morris, A.J., et al., 2001. Foraging habitat selection by yellowhammers (*Emberiza citronella*) nesting in agriculturally contrasting regions in low England. *Biological Conservation*, 101, 197–210.

- Némethová, D. and Tirinda, A., 2005. The influence of intersections and dead-ends of line-corridors networks on the breeding bird distribution. *Folia Zoologica*, 54, 123–134.
- Oostenbrink, W., Schotman, A., and Reijnen, R., 1994. Broedvogels in lijnvormige begroeiing. Een voorspellingsmodel voor effecten van landinrichting. *Landschap*, 11, 3–15.
- Paradis, E., et al., 1988. Patterns of natal and breeding dispersal in birds. *Journal of Animal Ecology*, 67, 518–536.
- Petit, S. and Burel, F., 1998. Effects of landscape dynamics on the metapopulation of a ground beetle (Coleoptera, Carabidae) in a hedgerow network. *Agriculture, Ecosystems and Environment*, 69, 243–252.
- Riffell, S.K. and Gutzwiller, K.J., 1996. Plant-species richness in corridor intersections: is intersection shape influential? *Landscape Ecology*, 11, 157–168.
- Rutila, J., Latja, R., and Koskela, K., 2002. The Common Cuckoo *Cuculus canorus* and its cavity nesting host, the Redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *Journal of Avian Biology*, 33, 414–419.
- Slagsvold, T., 1989. On the evolution of clutch size and nest size in passerine birds. *Oecologia*, 79, 300–305.
- Soule, M.E. and Terborgh, J., 1999. *Continental conservation: scientific foundations of regional reserve networks*. Washington, DC: Island Press.
- Tilman, D. and Kareiva, P., 1997. *Spatial ecology*. Princeton: Princeton University Press.
- VanderMeer, J. and Carvajal, R., 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist*, 158, 211–220.
- Van Dorp, D., Schippers, P., and Van Groenendael, J.M., 1997. Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automaton model. *Landscape Ecology*, 12, 39–50.
- Van Langevelde, F., 2000. Scale of habitat connectivity and colonization in fragmented nuthatch populations. *Ecography*, 23, 614–622.
- Van Langevelde, F., Van der Knaap, W.G.M., and Claassen, G.D.H., 1998. Comparing connectivity in landscape networks. *Environment and Planning B*, 25, 849–863.
- Wehling, S. and Diekmann, M., 2008. Factors influencing the spatial distribution of forest plant species in hedgerows of North-western Germany. *Biodiversity and Conservation*, 17, 2799–2813.
- Weibull, A.C., Bengtsson, J., and Nohlgren, E., 2000. Diversity of butterflies in the agricultural landscape: the role of farming system and landscape heterogeneity. *Ecography*, 23, 743–750.
- Weidinger, K., 2001. Laying dates and clutch size of open-nesting passerines in the Czech Republic: a comparison of systematically and incidentally collected data. *Bird Study*, 48, 38–47.
- Whittingham, M.J. and Evans, K.L., 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis*, 146, 210–220.
- Whittingham, M.J., et al., 2005. Habitat selection by yellowhammers *Emberiza cintrinella* on lowland farmland at two spatial scales: implications for conservation management. *Journal of Applied Ecology*, 42, 270–280.
- Whittingham, M.J., et al., 2009. Habitat associations of British breeding farmland birds. *Bird Study*, 56, 43–52.
- With, K.A., Cadaret, S.J., and Davis, C., 1999. Movement responses to patch structure in experimental fractal landscapes. *Ecology*, 80, 1340–1353.