

Does matrix resistance influence Red squirrel (*Sciurus vulgaris* L. 1758) distribution in an urban landscape?

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Abstract

In determining isolation effects in fragmented populations, the landscape matrix is not often considered. Usually simple distance measures are used to quantify degree of isolation. We tested the effect of the matrix on the presence of red squirrels in 354 wooded patches in the Brussels Region, by comparing several isolation measures. These were 1) distance to the nearest source patch, 2) the Hanski-measure (a combination of distance to and size of all possible sources), 3) effective distances calculated from different least cost models using the ArcView grid extension 'Cost Distance' (a combination of distance and resistance of the landscape, with different resistances for different landscape types) and 4) some combinations of the Hanski-measure and the effective distances. Size and quality of the target patches were always included in the tests of the predictive power of different isolation measures on squirrel presence/absence. All variables examined (patch size, quality and isolation) significantly influenced squirrel presence. Models using the effective distances gave the best results. Models including the Hanski-measure improved significantly when Euclidean distance was replaced by effective distance, showing that parameterisation of matrix resistance added significant additional explanatory power when modelling squirrel presence.

Introduction

The occurrence of a species in a habitat patch may depend on many different factors, like patch size, patch quality (e.g., food, shelter) and patch isolation (Andr n 1994; Hanski 1994; Harrison and Bruna 1999; Tischendorf and Fahrig 2000; Vos et al. 2001b; Tschamtko et al. 2002; Verbeylen et al. 2003). Patch isolation will be determined by the connectivity of the landscape, i.e., the degree to which the landscape facilitates or impedes movement of organisms among patches (Taylor et al. 1993; Tischendorf and Fahrig 2000). This not only depends on the specific mobility

of the organism (functional connectivity, Tischendorf and Fahrig 2000), but also on characteristics of the landscape (structural connectivity), such as amount of habitat surrounding the patch, distance to other (source) patches, orientation of corridors and barriers, matrix composition, etc. (Ricketts 2001). Previous studies have rarely considered the matrix in determining isolation of habitat patches for a certain species. Often used isolation measures are solely based on distance (e.g., distance to the nearest (occupied) habitat patch and to the nearest source area) or a combination of distance to and size of possible source areas (Whitcomb et al. 1981; Cclada et al. 1994;

Hanski 1994; Matthysen 1999; Moilanen and Nieminen 2002; Verbeylen et al. 2003). In these measures the implicit assumption is made that the matrix environment is homogeneous with respect to animal movement. Sometimes barriers like mountains, roads and rivers (Bélisle and St. Clair 2001; Vos et al. 2001a) or landscape elements that facilitate dispersal like density of corridors or area of habitat surrounding a habitat patch (Harms and Opdam 1989; van Apeldoorn et al. 1994; Berggren et al. 2001; Vos et al. 2001a) are taken into account, but further efforts in including the matrix (e.g., the exact position and orientation of small landscape elements) are rarely taken.

However, matrices are seldom homogeneous. Barriers change the dispersal path and unsuitable habitat influences the dispersal speed and survival during dispersal (Kareiva 1983; Johnson et al. 1992). Due to habitat preferences, animals seldom move randomly (Dunning et al. 1995; Hastings 1996).

Thanks to the new possibilities offered by GIS-systems, landscape complexity can be included in the isolation measure when modelling dispersal (Schippers et al. 1996; Tischendorf 1997; Halpin and Bunn 2000; Ferreras 2001; Graham 2001; Chardon et al. 2003). Unfortunately the studies that do include this landscape complexity usually do not look at more simple isolation measures at the same time. Consequently nothing is known about the extra information these complex measures bring.

The aim of this study was to test if the 'Cost Distance' approach (see further) – using measures of landscape resistance – gives better results than the often used more simple isolation measures, like the Euclidean distance and the Hanski-measure (Hanski 1994). We used the Red squirrel population in the Brussels Capital Region – a forest species in an urban environment – as a case study.

Urban environments present landscape mosaics where habitat remnants are typically small and surrounded by strongly inhospitable forms of land-use. In such a mosaic, traditional and simple connectivity measures such as distance between habitat patches are unlikely to reflect the true functional connectivity. Therefore, these environments present an ideal test-case for integrated connectivity measures that take into account all landscape elements, as well as their orientation. At the same time, these urban landscapes may represent ecological traps for local squirrel populations, so maintaining connections between these habitat remnants and source areas outside the

city may be necessary for their conservation (Sukopp et al. 1990; Pickett et al. 2001).

Material and methods

Study area

Habitat patches

The Brussels Capital Region (4°22'E 50°50'N, 163 km²) encompasses the urban area of Brussels as well as fringes of the more rural landscape surrounding it. It also contains part of the Zoniën Forest (total area: 4783 ha) to the southeast. Studying all patches with possible squirrel habitat within the Brussels Region would have been very time-consuming, since then every garden with trees should have been visited. Therefore we selected all forest patches, parks and private domains of at least 0.1 ha, and also 23 patches between 0.01 and 0.1 ha (since these were already digitised, IBGE-BIM 2001), giving a total of 354 patches (Figure 1), with sizes from 0.01 to 1915 ha (mean \pm s.d. = 7.65 \pm 101.72 ha, median = 0.72 ha). Tree species composition varied greatly between these patches, with most occurring species being common ash *Fraxinus excelsior*, plane *Platanus* sp., sycamore *Acer pseudoplatanus*, common beech *Fagus sylvatica*, Corsican pine *Pinus niffra*, Scots pine *Pinus sylvestris*, common hazel *Corylus avellana*, sweet chestnut *Castanea sativa*, horse chestnut *Aesculus hippocastanum*, hornbeam *Carpinus betulus*, poplar *Populus x canadensis*, willow *Salix* sp., lime *Tilia* sp., Norway spruce *Picea abies*, European larch *Larix decidua*, common oak *Quercus robur*, red oak *Quercus rubra*, silver birch *Betula pendula*, common alder *Alnus glutinosa* and a number of ornamental trees.

Based on GIS-maps the size of each habitat patch was calculated using ArcView (version 3.2, ESRI, California). For forest patches the total area was used. For other patches (parks, gardens, lawns and graveyards) only part of the total area was taken into account, depending on the degree of coverage with trees which was estimated during the field visits.

Since for most habitat patches no information was available on the tree species composition, a coarse quality estimate was made during the field visits. Quality was based on the percentage of good trees, i.e., trees bearing seeds edible for squirrels (Wauters et al. 1992) and was divided into eight classes, with class I (0-12.5%) being the lowest (e.g., a birch or

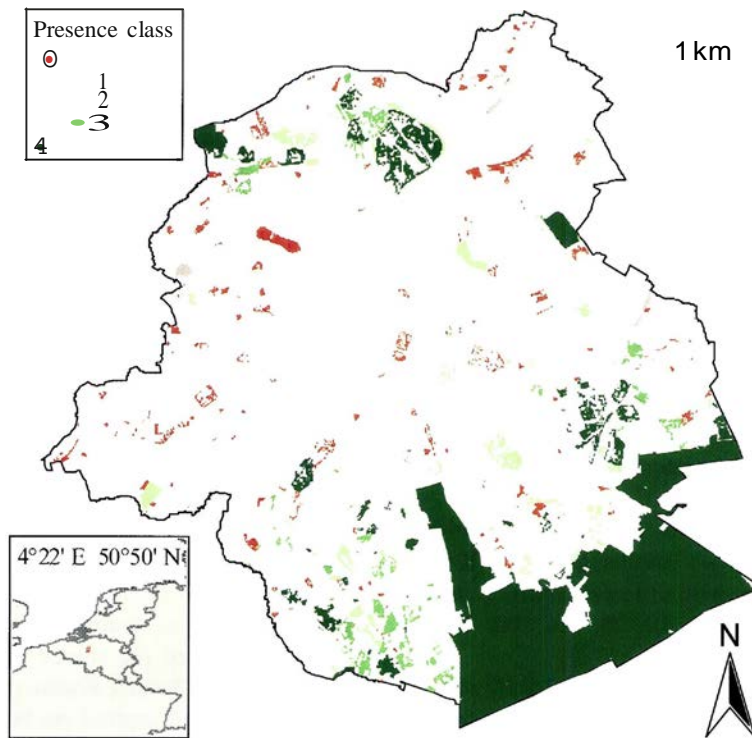


Figure 1. Map of the Brussels Capital Region with presence of squirrels in all studied habitat patches: 0 = never observed, 1 = observed once, 2 = present during part of the year, mostly autumn, 3 ..., present at least part of the year, possibly year round and 4 ..., present year round.

poplar forest) and class 8 (87.5-100%) being the highest (e.g., a pine forest).

Characteristics of the matrix

Different isolation measures were calculated per patch, all expressing the difficulty of reaching the target patch from a source patch.

Cost Distance. Since we can assume with relatively high certainty that a squirrel will for example move more easily and at lower (mortality) risk through a garden or meadow than through a densely built city or across a broad river, isolation of a habitat patch will depend not only on distance from a source patch, but also on the spatial configuration and resistance of different land cover types in the landscape. To quantify isolation based on matrix resistance the 'Cost Distance' extension of Spatial Analyst in ArcView 3.2 was used.

Using 'least cost' modeling (Villalba et al. 1998; Bunn et al. 2000; Ferreras 2001; Chardon et al. 2003), Cost Distance calculates the minimal cost to reach a

given spot in the landscape (grid cell) from a source patch or complex of source patches.

To run Cost Distance, two grid maps are needed: a source layer indicating all source patches, and a resistance/friction layer indicating the resistance value for every cell. In this study cell resistance is based on the land cover type assigned to the cell. The result of a Cost Distance analysis is a cost grid map, with for each grid cell a minimum cost value to reach the cell from a given source patch, a combination of the effects of (Euclidean) distance and landscape resistance. In this article, this cost value will be referred to as the 'effective distance' (see also Michels et al. 2001) between patch and source. Optionally the least cost path (the path resulting in the observed minimal cost value) between source and target cell can be calculated and visualised.

In this study the surrounding landscape outside the Brussels Region was not considered. Most likely this surrounding landscape will have no or almost no effect on the populations inside the study area, since there are no large forest patches in these surroundings.

A complete land cover map was produced using different data sources (see Appendix). Table 1 shows all used land cover types (25). This polygon map was converted to a grid map with a 2 x 2 m cell size to avoid smaller and linear elements from disappearing or becoming fragmented in the grid map.

Since no published data are available on the resistance of different land cover types for squirrels (Vilalba et al. 1998), values were assigned based on our own field knowledge of the species. By varying the resistance values and the number of classes, we tried to find the model that best explained our field data. We used the following resistance sets (see Table 1):

- R1: all landscape elements have a resistance of 1, so only distance is taken into account and the landscape effect is eliminated,
- R2-R10: resistance sets with 2 classes, distinguishing high vegetation types (shrubs, trees, ...) (R = 1) from everything else (with different contrasts in resistance values: R = 2, 5, 10, 25, 50, 100, 1000, 10000, 100000)
- R11-R16: the best resistance set of R2-R10 with a third class added by distinguishing between forest (R = 1) and other high vegetation types (with different contrasts in resistance values: R = 2, 5, 10, 20, 50, 500),
- R17-R21: the best resistance set of R11-R16 with a fourth class added by distinguishing between buildings and canal (R = 1000) and other 'high resistance' types (with different contrasts in resistance values: R = 500, 600, 700, 800, 900),
- R22-R30: the best resistance set of R17-R21 with a fifth class added by distinguishing between types 18-24 (R = 10) and types 13-17 (with different contrasts in resistance values: R = 20, 50, 100, 200, 300, 400, 500, 600, 800),
- R31-R34: the best resistance set of R22-R30 with one, two and five extra classes added, to distinguish more relatively high resistance classes,
- R35-R36: the best resistance set of R31-R34 with two and four classes added, to distinguish more intermediate resistance classes.

Based on the land cover map and these 36 resistance sets, 36 friction layers were produced. All patches of at least 15 ha (Rodríguez and Andrés 1999) with a reasonable quality (at least class 3) were selected as source patches. These were seven forests (Figure 6), in all of which squirrels were present. By Cost Dis-

tance analyses, the combinations of source and friction layers were converted to cost grids ('costR1' to 'costR36').

We also created some extra cost grids in order to evaluate specific effects. First we created a grid map where buildings and canal were regarded as absolute barriers (best resistance set with R = 10000 for buildings and canal, cost grid 'cost-barrier'). Second, to evaluate the effect of the contribution of the extra digitalisations, two extra maps were produced. In one map, the tree lines were omitted (best resistance set, cost grid 'costR26-trees'). In a second map all extra digitalisation was dropped by using an existing polygon map (map 'Begroening - eilanden', IBGE-BIM 2001) indicating the percentage of green (i.e., covered with any type of vegetation, including grass, herbs, trees) in each polygon. Resistance values were calculated as: $(1 - \text{proportion green}) * (\text{maximum resistance value of the best model})$ (cost grid 'cost-green'). Third, to evaluate the effect of the source grid, we reduced the source from seven patches to only the large Zoniën Forest (the only forest larger than 100 ha) and applied the best resistance set (cost grid 'costR26-zonien').

Since in the Hanski-measure (see below) distances to and sizes of all sources are included and the effective distance takes only the 'most reachable' source into account, we calculated a comparable measure by calculating the effective distances to each source patch separately (for the best model) and summing them.

Because the aim of our analysis was to separate effects of Euclidean distance from source patches and landscape resistance, we recalculated the effective distances obtained in each analysis, as the residuals from a regression of these values against the effective distances obtained with resistance set R1, i.e., with a uniform landscape resistance (= Euclidean distance from the nearest source patch, see above). These residuals are an integrated measure of the landscape resistance along the least cost path, independent of Euclidean distance. This approach is valid since the relative and not the absolute values of the different landscape elements are important to construct the different landscape models (Adriaensen et al. 2003).

'Hanski-measure' (Hanski 1994). We used the Hanski-measure to calculate a weighed index of the distance from habitat patches to the different source

patches, as follows:

$$\text{Connectivity } S_i = \sum_j P_j \exp(-a d_{ij}) A_j$$

$P_i = 1$ for the 7 source patches and 0 for all other patches

d_{ij} = Euclidean distance (km) between patch i and j

A_i = size (ha) of source patch i

a = a constant for the rate of mortality of migrants over distance d_{ij}

The model was tested for $a = 0.5, 1, 2, 3, 4$ and 5 ($a = 0$ would implicate no distance effect and $a = 5$ means that less than 1% of the squirrels disperse further than 1000 m). To make Hanski and Cost Distance models more comparable, the effective distances obtained with resistance set R1 were used instead of the 'real' Euclidean distances. Because A_i is supposed to reflect the source population sizes, we multiplied patch size by the estimated proportion of 'good' trees. This proportion is a good indication for squirrel density (Verbeylen et al. 2003).

We also tested a combination of the Hanski-measure and effective distance. We replaced the ' d_{ij} ' in the formula by the effective distances of model 27 (the best Cost Distance model) to the seven sources. Another modification was made by replacing the Euclidean distance d_{ij} in the formula by the length of the 'least cost path' (again for model 27). To find out the importance of including size and quality of the source patches in the Hanski-measures with Euclidean distances, least cost path distances and effective distances, we also calculated these measures for the best models leaving out size and quality.

To make models comparable, we standardised by dividing Euclidean distances, least cost path distances and effective distances in the Hanski-measure by their mean value.

Squirrel survey

All habitat patches were visited at least once during ten days in April and three days in May 2001. Pres-

ence of squirrels was checked by looking for food remains and squirrel nests (Tittensor 1970; Wauters and Dhondt 1988; Wauters and Dhondt 1990). The presence or absence of these signs and how recent they are (fresh and/or old) give information on the duration of squirrel presence. When these data did not give conclusive evidence for squirrel presence or to decide whether squirrels were present all year or only

part of the year, supplementary information was gathered by questioning owners, park and forest wardens and visitors and some people provided information in response to an article in the press.

Based on these data an estimate was made of the duration of squirrel presence in a habitat patch during the last 2-3 years. Habitat patches were assigned to classes 0 (never observed), 1 (observed once), 2 (present during part of the year, mostly autumn), 3 (present at least part of the year, possibly year round) and 4 (present year round) (Figure 1). For some analyses we lumped all patches where squirrels were observed at least once (i.e., classes 1-4).

Statistical analysis

Effects of patch size (log transformed), patch quality, distance and landscape resistance (or various Hanski - measures) on the presence of squirrels (5 classes) were tested with a logistic model for ordinal response data (proc logistic, SAS 6.12, SAS 1989). The 67 habitat patches in class 3 were not used in this analysis, since it was not known whether or not these habitat patches were occupied permanently. A similar analysis was done using only two classes, i.e., patches with and without squirrel observations. In this case class 3 patches were included.

These models were first tested with patch size and quality only, then distance and finally landscape resistance (i.e., residual effective distance) were added. For each model adjusted R-square (Nagelkerke 1991) and AIC values (Akaike 1974) were calculated. The best model has the lowest AIC value. Models that differed in AIC by 2 or less are considered to be equally good approximations of the data.

Results

In all tested models all factors explained a significant part of the variation in squirrel presence (see Table 2). The model with only patch size and quality (model 1) explained 29-38% of the variation. Squirrels were more permanently present in larger and higher quality habitat patches (Figure 2). Only for patches of at least 5 ha there was a high chance of temporary or permanent occupation. Adding distance (model 2) explained an extra 9-12% of the variation. Patches were longer occupied when located closer to a source patch (Figure 3).

Table 2. Significance level of the effect of the tested factors (patch size (log transformed), patch quality, distance, landscape resistance and isolation (Hanski-measure and modified Hanski-measures)) on the presence (2 and 5 classes) of squirrels in the studied habitat patches, and explained variation (R^2) and AIC value of the different models. P values are for the factor(s) added to the model in comparison with the previous model. The best models in each group are given in italics.

model	2 classes		5 classes		p	AIC
	p	AIC	p	AIC		
Size + Quality only	0.376	<0.0001	370.57	0.293	<0.0001	457.64
2 1 + Distance (costR1)	0.496	<0.0001	326.31	0.378	<0.0001	431.16
3 2 + Resistance (costR2) (2 classes: 2-1)	0.538	0.0002	310.58	0.424	0.0003	416.92
4 2 + Resistance (costR3) (2 classes: 5-1)	0.537	0.0002	310.93	0.422	0.0005	417.38
5 2 + Resistance (costR4) (2 classes: 10-1)	0.538	0.0002	310.36	0.425	0.0003	416.36
6 2 + Resistance (costR5) (2 classes: 25-1)	0.538	0.0002	310.41	0.423	0.0004	416.97
7 2 + Resistance (costR6) (2 classes: 50-1)	0.539	0.0002	309.89	0.423	0.0005	417.12
8 2 + Resistance (costR7) (2 classes: 100-1)	0.542	0.0001	308.85	0.424	0.0004	416.58
9 2 + Resistance (costR8) (2 classes: 1000-1)	0.544	0.0001	307.56	0.426	0.0004	415.94
10 2 + Resistance (costR9) (2 classes: 10000-1)	0.545	0.0001	307.51	0.426	0.0004	415.96
11 2 + Resistance (costR10) (2 classes: 100000-1)	0.545	0.0001	307.51	0.426	0.0004	415.96
12 2 + Resistance (costR11) (3 classes: 1000-2-1)	0.545	<0.0001	307.46	0.426	0.0003	415.85
13 2 + Resistance (costR12) (3 classes: 1000-5-1)	0.545	<0.0001	307.33	0.427	0.0003	415.74
14 2 + Resistance (costR13) (3 classes: 1000-10-1)	0.546	<0.0001	307.07	0.428	0.0003	415.43
15 2 + Resistance (costR14) (3 classes: 1000-20-1)	0.545	<0.0001	307.29	0.428	0.0002	415.26
16 2 + Resistance (costR15) (3 classes: 1000-50-1)	0.541	<0.0001	308.99	0.426	0.0002	416.13
17 2 + Resistance (costR16) (3 classes: 1000-500-1)	0.530	0.0002	313.74	0.419	0.0001	418.47
18 2 + Resistance (costR17) (4 classes: 1000-500-10-1)	0.545	<0.0001	307.34	0.427	0.0002	415.48
19 2 + Resistance (costR18) (4 classes: 1000-600-10-1)	0.546	<0.0001	307.08	0.428	0.0002	415.35
20 2 + Resistance (costR19) (4 classes: 1000-700-10-1)	0.546	<0.0001	306.94	0.428	0.0002	415.28
21 2 + Resistance (costR20) (4 classes: 1000-800-10-1)	0.546	<0.0001	306.93	0.428	0.0002	415.29
22 2 + Resistance (costR21) (4 classes: 1000-900-10-1)	0.546	<0.0001	306.98	0.428	0.0003	415.35
23 2 + Resistance (costR22) (5 classes: 1000-800-20-10-1)	0.548	<0.0001	306.08	0.430	0.0002	414.61
24 2 + Resistance (costR23) (5 classes: 1000-800-50-10-1)	0.551	<0.0001	304.64	0.433	0.0001	413.42
25 2 + Resistance (costR24) (5 classes: 1000-800-100-10-1)	0.553	<0.0001	303.77	0.435	<0.0001	412.60
26 2 + Resistance (costR25) (5 classes: 1000-800-200-10-1)	0.555	<0.0001	303.06	0.437	<0.0001	411.89
27 2 + Resistance (costR26) (5 classes: 1000-800-300-10-1)	0.555	<0.0001	302.79	0.438	<0.0001	411.46
28 2 + Resistance (costR27) (5 classes: 1000-800-400-10-1)	0.555	<0.0001	302.90	0.438	<0.0001	411.37
29 2 + Resistance (costR28) (5 classes: 1000-800-500-10-1)	0.554	<0.0001	303.13	0.438	<0.0001	411.41
30 2 + Resistance (costR29) (5 classes: 1000-800-600-10-1)	0.554	<0.0001	303.23	0.438	<0.0001	411.43
31 2 + Resistance (costR30) (5 classes: 1000-800-800-10-1)	0.554	<0.0001	303.43	0.438	<0.0001	411.54
32 2 + Resistance (costR31) (6 classes: 1000-800-700-300-10-1)	0.555	<0.0001	302.75	0.438	<0.0001	411.43
33 2 + Resistance (costR32) (6 classes: 1000-900-800-300-10-1)	0.555	<0.0001	302.95	0.438	<0.0001	411.66
34 2 + Resistance (costR33) (7 classes: 1000-900-800-700-300-10-1)	0.555	<0.0001	302.75	0.438	<0.0001	411.43
35 2 + Resistance (costR34) (10 classes: 1000-950-900-850-800-750-700-300-10-1)	0.555	<0.0001	302.94	0.438	<0.0001	411.59
36 2 + Resistance (costR35) (8 classes: 1000-800-700-300-200-15-10-1)	0.556	<0.0001	302.44	0.439	<0.0001	411.18
37 2 + Resistance (costR36) (10 classes: 1000-800-700-300-250-200-15-10-5-1)	0.557	<0.0001	302.14	0.439	<0.0001	411.00
38 2 + Resistance (cost-barrier)	0.555	<0.0001	302.88	0.438	<0.0001	411.70
39 2 + Resistance (costR26-trees) (without tree lines)	0.546	0.0001	306.80	0.428	0.0005	415.45
40 2 + Resistance (cost-green) ((1 - proportion green)*1000)	0.523	0.0014	316.66	0.413	0.0111	420.99
41 2 + Resistance (costR26-zonien) (one source patch)	0.553	<0.0001	303.86	0.434	<0.0001	412.92
42 1 + Hanski-measure ($\alpha = 0.5$, $d =$ Euclidian distance)	0.485	<0.0001	330.77	0.386	<0.0001	428.56
43 1 + Hanski-measure ($\alpha = 1$, $d =$ Euclidian distance)	0.490	<0.0001	328.52	0.388	<0.0001	427.67
44 1 + Hanski-measure ($\alpha = 2$, $d =$ Euclidian distance)	0.493	<0.0001	327.25	0.387	<0.0001	428.30
45 1 + Hanski-measure ($\alpha = 3$, $d =$ Euclidian distance)	0.489	<0.0001	329.10	0.379	<0.0001	430.98
46 1 + Hanski-measure ($\alpha = 4$, $d =$ Euclidian distance)	0.481	<0.0001	332.38	0.369	<0.0001	434.35
47 1 + Hanski-measure ($\alpha = 5$, $d =$ Euclidian distance)	0.472	<0.0001	335.93	0.360	<0.0001	437.59

Table 2. Continued.

model	2 classes			5 classes		
	R ²	p	AIC	R ²	p	AIC
48 + Hanski-measure (ex = 0.5, d = least cost path distance)	0.508	<0.0001	321.28	0.408	<0.0001	420.77
49 + Hanski-measure (ex = 1, d = least cost path distance)	0.516	<0.0001	317.92	0.414	<0.0001	418.53
50 + Hanski-measure (a = 2, d = least cost path distance)	0.523	<0.0001	315.03	0.417	<0.0001	417.4R
51 + Hanski-measure (a = 3, d = least cost path distance)	0.521	<0.0001	315.80	0.411	<0.0001	419.49
52 + Hanski-measure (ex = 4, d = least cost path distance)	0.515	<0.0001	318.34	0.402	<0.0001	422.81
53 + Hanski-measure (a = 5, d = least cost path distance)	0.507	<0.0001	321.48	0.392	<0.0001	426.36
54 + Hanski-measure (ad; = effective distance)	0.534	<0.0001	309.91	0.428	<0.0001	413.15
55 Model 44 without size and quality of source patches	0.481	<0.0001	332.37	0.368	<0.0001	434.84
56 Model 50 without size and quality of source patches	0.534	<0.0001	310.00	0.387	<0.0001	428.14
57 Model 54 without size and quality of source patches	0.607	<0.0001	276.7R	0.482	<0.0001	392.35
58 + sum(effective distances to each source patch) (costR26)	0.562	<0.0001	297.77	0.444	<0.0001	407.07

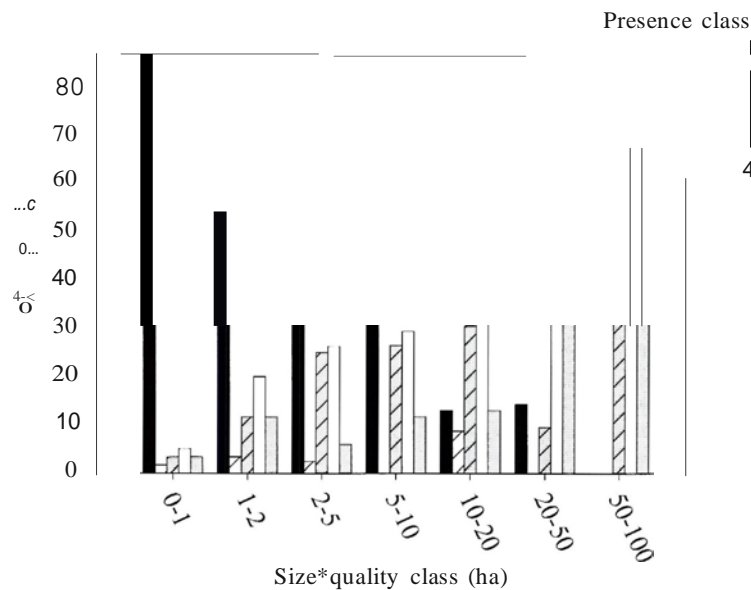


Figure 2. Relation between squirrel presence and patch size*patch quality class. For the definition of the presence classes, see Figure 1.

Adding landscape resistance (models 3-37) explained another 4-6% of the variation for all models. Patches with a lower landscape resistance value to a source patch were occupied longer (Figure 4, Figure 5, values are for model 27). Squirrel presence was rarely observed in patches that were poorly connected to the nearest source patch (positive residuals, higher than average resistance).

Out of the 2-class models (model 3-11), the best one (model 9) had a large difference between the resistance classes with high vegetation (R = 1) and low or no vegetation (R = 1000). Increasing this already very high resistance (to R = 10000 or 100000) did not

further improve the model. By increasing the number of classes and varying the resistance values, we were able to explain significantly more variation. We always continued with the best model for the 2 presence classes (bold in Table 2), which sometimes differed (non-significantly) from the best model for 5 presence classes. The overall best model (model 27, Figure 6) was one of the 5-class models, with the highest resistance for buildings and the canal (R = 1000), a high resistance for the other land cover types with low or no vegetation (R = 800) and also a relatively high resistance for part of the high vegeta-

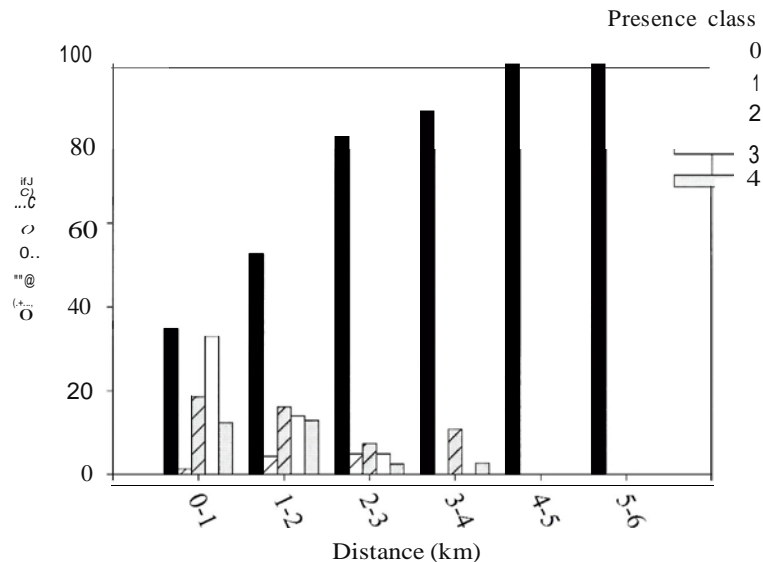


Figure 3. Relation between squirrel presence and distance to the nearest source. For the definition of the presence classes, see Figure 1.

tion types ($R=300$). Adding more classes further improved the model, but not significantly.

The model with buildings and the canal as strong barriers (model 38) was not different from the best model (model 27). As expected, the model with tree lines (model 27) performed better than the model without tree lines (model 39) and the model based on the existing map with percentages of green (model 40) was much worse than the model with assigned resistances (model 27). Finally, the model considering only the largest forest as source patch (model 41) performed less well than the model with seven source patches (model 27), but this difference was not significant.

Among the Hanski-models (models 42-53), those with $a=2$ performed best. When the Hanski-measure with Euclidean distances was used instead of distance and landscape resistance, less of the variation was explained. In comparison with the model with only distance (model 2), the model with the best Hanski-measure explained an equal amount of variation for 2 presence classes (model 44) and more variation for 5 presence classes (model 43). Replacing the Euclidean distances in the Hanski-measure with the distances of the least cost path for model 27 (model 48-53) gave better results, but not as good as the best model based on the effective distances only (model 27). Replacing the 'adi.i' in the Hanski-measure by the effective distances of model 27 (model 54) yielded even lower

AIC values, but still higher than for the best model based on the effective distances only (model 27).

Leaving out size and quality of the source patches in the Hanski-models explained less variation for the Hanski-measure with Euclidean distances (model 55) and for the Hanski-measure with least cost path distances (model 56) in the case of 5 presence classes. The Hanski-measure with least cost path distances (model 56) did perform better without size and quality in the case of 2 presence classes. Finally, the Hanski-measure with effective distances (model 57) performed even much better without size and quality, and yielded the best model of all, explaining almost 61% of the variation.

By replacing the Hanski-measure by the sum of the effective distances to each source patch (model 58), more variation was explained than by model 27, but model 57 still remained best.

Figure 6 shows as an example the Cost Distance output values for model 27 (best model when landscape resistance is included), together with the least cost paths, resulting from the Cost Path analysis.

Discussion

Model comparison

Studies that use least cost modelling when looking at isolation are rather rare (for examples see Walker and

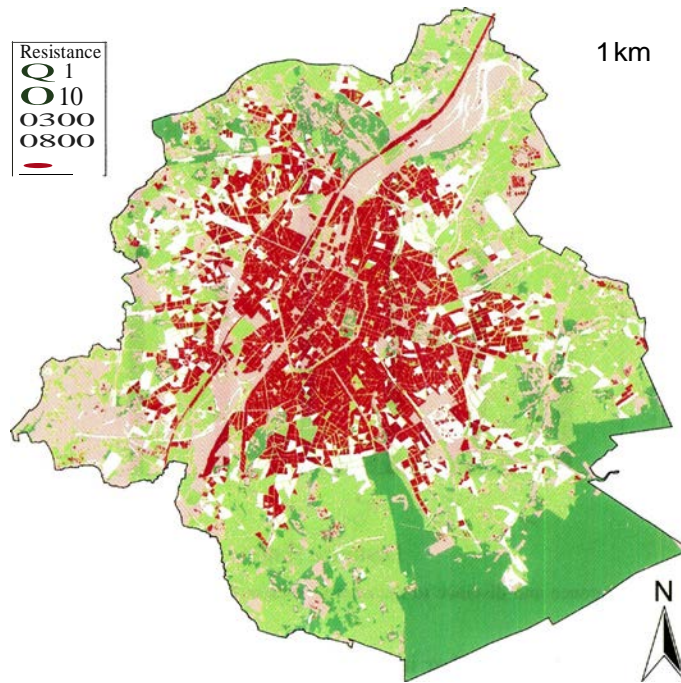


Figure 4. Friction layer for the best resistance set (set 26).

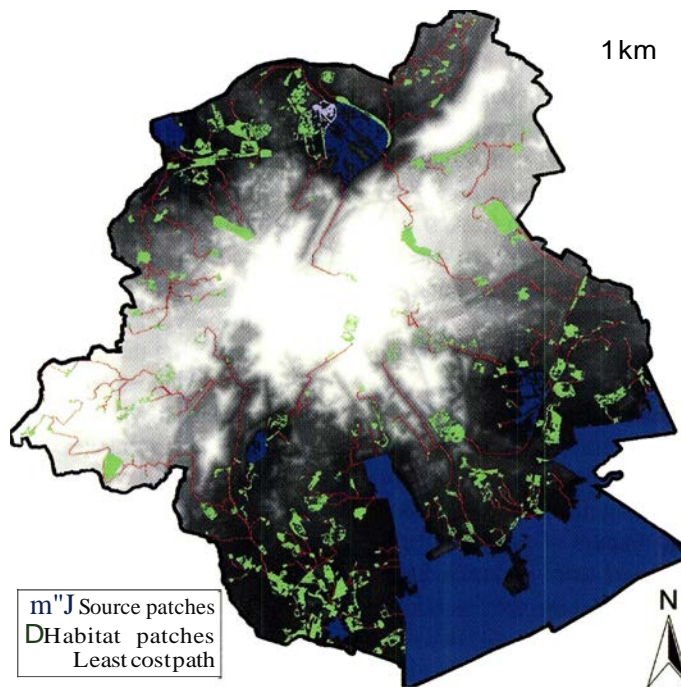


Figure 6. Cost grid map for model 27, ranging from black (low cost = high connectivity) to white (high cost = low connectivity). The least cost path between all habitat patches and the 'easiest to reach' source patch is given.

Craighead 1997; Bunn et al. 2000; Ferreras 2001; Graham 2001; Michels et al. 2001; Chardon et al.

2003). To our knowledge this is the first study that compares the predictive power of different model

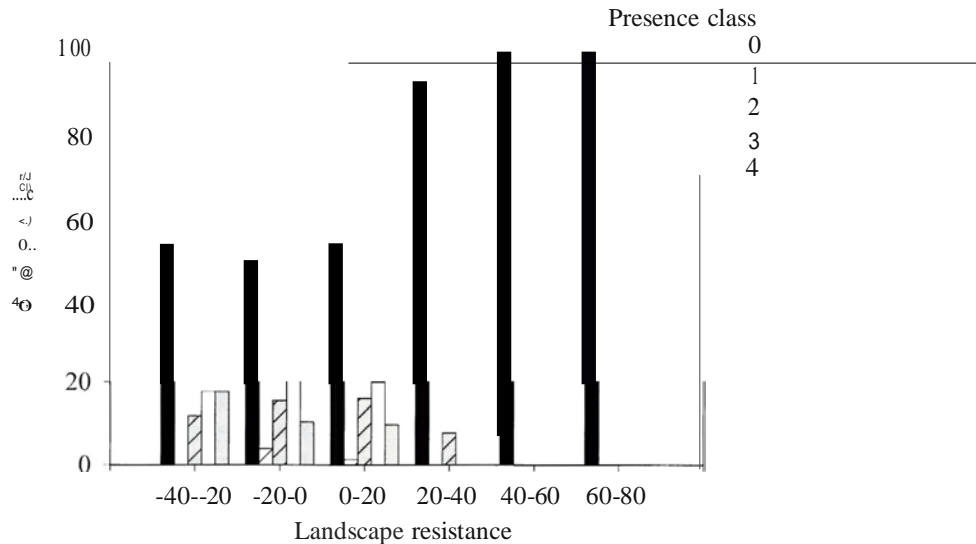


Figure 5. Relation between squirrel presence and landscape resistance class (for model 27). For the definition of the presence classes, see Figure 1.

types and the sensitivity of least cost models to variation in resistance values and landscape scenarios. We compared different isolation measures (Cost Distance, Euclidean distance, the widely used Hanski-measure (Hanski 1994)) and showed that including the matrix into the analyses yielded better models to predict presence/absence of squirrels in an urban environment (see also Ricketts 2001).

The Cost Distance analysis only includes the source patch to which the effective distance is shortest and is independent of source population size. The Hanski-measure on the other hand, combines the distances to and sizes of all possible source patches. Nevertheless, the effective distances gave a better result than the Hanski-measure. But combining both measures by calculating and summing the effective distances to each source patch separately improved the model even more, so taking all source patches into account is still best. Including least cost path distance and effective distance improved the Hanski-measure and leaving out size and quality of the source patches led to the best model of all. So population sizes in source patches do not seem to have a major effect in this study, especially not after matrix effects were included.

The different landscape types were ordered in terms of increasing resistance for moving squirrels, based on best professional judgement: literature on dispersal distance and dispersal behaviour (Wauters et al. 1994; Bak and Lagendijk 1995) and our own

long-term experience with the species. The most appropriate number of resistance classes to be included in the landscape model and the best resistance values were found by varying these factors and looking for an optimum. In this study we started off with 2 different resistance classes (high vegetation – low or no vegetation) and gradually increased the landscape complexity to 10 classes. Although we do not have any empirical evidence on the correctness of the resistance values nor of the resistance classes (see also Walker and Craighead 1997; Ferreras 2001), the results of this study do show sensitivity to variation in these resistance values and allowed us to deduct a 'most likely' resistance set.

The more resistance classes were used in the Cost Distance model, the better the results were, but the best model (with 10 classes) did not differ significantly from a more simple model with 5 classes. So a relatively coarse division in resistance classes seems to be sufficient in this case. This may not always be the case. So when maps are composed, sufficient and relevant details should be included. The available maps may not always allow the distinction between certain landscape elements that might be important for a certain study species and extra digitalisation may be required.

In our study including tree lines did improve the model significantly. The map with the percentages of green though did not give very good results, which was to be expected since 'green' includes landscape

- Ferreras P. 2001. Landscape structure and asymmetrical inter-patch connectivity in a metapopulation of the endangered Iberian lynx. *Biological Conservation* 100: 125-136.
- Gonzales E.K. 2000. Distinguishing between modes of dispersal by introduced eastern grey squirrels (*Sciurus carolinensis*). Master's Thesis, University of Guelph, Guelph, Canada. <http://www.uoguelph.ca/zoology/research/squirrel/thesisrev.pdf>
- Graham C.I. 2001. Factors influencing movement patterns of Keel-billed Toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology* 15(6): 1789-1798.
- Halpin P.N. and Bunn A.G. 2000. Using GIS to compute a least-cost distance matrix: a comparison of terrestrial and marine ecological applications. Proceedings of the Twentieth Annual ESRI User Conference, June 2000. <http://www.esri.com/library/userconf/proc00/proc00/professional/papers/PAP890/p890.htm>
- Hanski I. 1994. A practical model of metapopulation dynamics. *Journal of Animal Ecology* 63: 151-162.
- Harms W.B. and Opdam P. 1989. Woods as habitat patches for birds: application in landscape planning in the Netherlands. In: Zonneveld I.S. and Forman R.T.T. (eds), *Changing landscapes: an ecological perspective*, pp. 73-97. Springer-Verlag, New York, New York, USA.
- Harrison S. and Bruna E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225-232.
- Hastings A. 1996. Models of spatial spread: a synthesis. *Biological Conservation* 78(1-2): 143-148.
- IBGE-BIM 2001. Maps 'Omtrek BHG' and 'Begroening - eilanden': URBIS 104, maps 'Gebieden', 'Zones ngi', 'Gebieden en vijvers' and 'Kanaal': Gegevensbank Groen Netwerk, 1998. Maps of the Brussels Institute for Environmental Management, DEV-AGR, Brussels, Belgium.
- Johnson A.R., Wiens J.A., Miine B.T. and Crist T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecology* 7: 63-75.
- Kareiva P.M. 1983. Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia* 57: 322-327.
- Matthysen E. 1999. Nuthatches (*Sitta europaea*: Aves) in forest fragments: demography of a patchy population. *Oecologia* 119: 501-509.
- Michels E., Cottenie K., Neys L., De Gelas K., Coppin P. and De Meester L. 2001. Geographical and genetic distances among woplankton populations in a set of interconnected ponds: a plea for using GIS modelling of the effective geographical distance. *Molecular Ecology* 10: 1929-1938.
- Moilanen A. and Nieminen M. 2002. Simple connectivity measures in spatial ecology. *Ecology* 83: 1131-1145.
- Nagelkerke N.J.D. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78: 691-692.
- NGI 1994. Topografische kaart van België, kaartbladen Wemmel 31/2 Noord, Anderlecht 31/2 Zuid, Brussel 31/3 Noord, Brussel 31/3 Zuid, Zaventem 31/4 Noord, Sint-Pieters-Woluwe 31/4 Zuid, Sint-Pieters-Leeuw 31/6 Noord, Ukkel 31/7 Noord, Linkebeek 3117 Zuid, Tervuren 31/8 Noord (schaal 1:10000). Nationaal Geografisch Instituut, Belgium.
- Pickett S.T.A., Cadenasso M.L., Grove J.M., Nilon C.H., Pouyat R.Y., Zipperer W.C. and Costanza R. 2001. Urban ecological systems: linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Ann. Rev. Ecol. Syst.* 32: 127-157.
- ESRI European User Conference, Copenhagen, Norway. ESRI, Redlands, California, USA. <http://www.esri.com/library/userconf/proc97/proc97/to150/pap116/p116.htm>
- Wauters L.A. and Dhondt A.A. 1988. The use of red squirrel (*Sciurus vulgaris*) dreys to estimate population density. *Journal of Zoology* 217: 179-187.
- Quinby P., Trombulak S., Lee T., Lane J., Henry M., Long R. and MacKay P. 1999. Opportunities for wildlife habitat connectivity between Algonquin Park, Ontario and the Adirondack Park, New York. Report prepared for The Greater Laurentian Wildlands Project, Burlington, Vermont. Ancien! Forest Exploration & Research, Toronto. <http://www.ancientforest.org/a2a.html>
- Ricketts T.H. 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158: 87-99.
- Rodriguez A. and Andr n H. 1999. A comparison of Eurasian red squirrel distribution in different fragmented landscapes. *Journal of Applied Ecology* 36: 649-662.
- SAS 1989. SAS/STAT User's Guide, version 6, 4th edn., Vol. 1 and 2. SAS Institute, Cary, North Carolina, USA.
- Schippers P., Verboom J., Knaapen J.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.
- Singleton P.J. and Lehmkuhl J.F. 2000. I-90 Snoqualmie Pass. Wildlife Habitat Linkage Assessment. Final Report. Wenatchee Forestry Sciences Lab, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Wenatchee, Washington, USA. http://www.wsdot.wa.gov/PPSC/Research/Testl_90/I-90May_2000.htm
- Sukopp H., Hejny S. and Kowarik I. 1990. Urban Ecology. Plants and plant communities in urban environments. SPB Academic Publishing bv, Den Haag, The Netherlands.
- Taylor P.D., Fahrig L., Henein K. and Merriam G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68: 571-573.
- Tischendorf L. 1997. Modelling individual movements in heterogeneous landscapes: potentials of a new approach. *Ecological Modelling* 103: 33-42.
- Tischendorf L. and Fahrig L. 2000. On the use and measurement of landscape connectivity. *Oikos* 90: 7-19.
- Tittensor A.M. 1970. Red squirrel dreys. Notes from the Mammal Society No. 21: 528-533.
- Tscharntke T., Steffan-Dewenter I., Kruess A. and Thies C. 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecological Research* 17: 229-239.
- van Apeldoorn R.C., Celada C. and Nicuwhuizen W. 1994. Distribution and dynamics of the red squirrel (*Sciurus vulgaris* L.) in a landscape with fragmented habitat. *Landscape Ecology* 9: 227-235.
- Verbeylen G., De Bruyn L. and Matthysen E. 2003. Patch occupancy, population density and dynamics in a fragmented red squirrel *Sciurus vulgaris* population. *Ecography* 26: 118-128.
- Yillalba S., Gulinck H., Verbeylen G. and Matthysen E. 1998. Relationship between patch connectivity and the occurrence of the European red squirrel, *Sciurus vulgaris*, in forest fragments within heterogeneous landscapes. In: Dover J.W. and Bunce R.G.H. (eds), *Key Concepts in Landscape Ecology*, pp. 205-220. JALE, Preston, UK.
- Vos C.C., Antonisse-De Jong A.G., Goedhart P.W. and Smulders M.J.M. 2001a. Genetic similarity as a measure for connectivity between fragmented populations of the moor frog (*Rana arvalis*). *Heredity* 86: 598-608.
- Vos C.C., Verboom J., Opdam P.F.M. and Ter Braak C.J.F. 2001b. Towards ecologically scaled landscape indices. *American Naturalist* 157: 24-41.
- Walker R. and Craighead L. 1997. Analyzing wildlife movement corridors in Montana using GIS. In: Proceedings of the 1997 of Zoology 214: 179-187.
- Wauters L. and Dhondt A.A. 1990. Nest-use by red squirrels (*Sciurus vulgaris* Linnaeus, 1758). *Mammalia* 54: 377-389.
- Wauters L., Swinnen C. and Dhondt A.A. 1992. Activity budget and foraging behaviour of red squirrels (*Sciurus vulgaris*) in coniferous and deciduous habitats. *Journal of Zoology* 227: 71-86.

Wauters L., Casale P. and Dhondt A.A. 1994. Space use and dispersal of red squirrels in fragmented habitats. *Oikos* 69: 140-146.

Wauters L.A., Currado I., Mazzoglio P.J. and Gurnell J. 1997. Replacement of red squirrels by introduced grey squirrels in Italy:

evidence from a distribution survey. In: Gurnell J. and Lurz P. (eds), *The Conservation of Red Squirrels, *Sciurus vulgaris* L.*, pp. 79-88. People's Trust for Endangered Species, London, UK.

Whitcomb R.F., Robbins C.S., Lynch J.F., Whitcomb B.L., Klimkiewicz M.K. and Bystrak D. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: Burgess R.L. and Sharpe O.M. (eds), *Forest island dynamics in managed landscapes*, pp. 125-206. Springer-Verlag, Berlin, Germany.

Xu J. and Lathrop R.G.J. 1995. Improving simulation accuracy or spread phenomena in a raster-based Geographic Information System. *International Journal of Geographical Information Systems* 9: 153-168.

Zarnnit A.E. 1999. *A Proposal for Identifying Wildlife Corridors Using Geographic Information Systems*. University of Waterloo, Department of Geography, Waterloo, Ontario, Canada.