



# Modelling the negative effects of landscape fragmentation on habitat selection



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## ARTICLE INFO

### Article history:

Received 28 December 2014

Received in revised form 6 August 2015

Accepted 28 August 2015

Available online 5 September 2015

### Keywords:

Animal movement

Spatially-structured population

Grid-based model

Habitat fragmentation

Source-sink dynamics

## ABSTRACT

Landscape fragmentation constrains movement of animals between habitat patches. Fragmentation may, therefore, limit the possibilities to explore and select the best habitat patches, and some animals may have to cope with low-quality patches due to these movement constraints. If so, these individuals experience lower fitness than individuals in high-quality habitat. I explored this negative effect of fragmentation on habitat selection in a modelling study. Model landscapes were generated containing different amounts of habitat with differences in the degree of connectivity. In these landscapes, the behaviour of two model species was simulated with different dispersal ranges. I found that habitat selection of the species with limited dispersal range increasingly deviates from optimal selection when fragmentation increases. This effect of fragmentation on habitat selection largely limits the spatial distribution of species with limited dispersal range because constrained habitat selection is expected to result in lower mean reproductive output when more individuals occur in low-quality habitat. In addition to the often suggested causes for extinction in small, isolated patches, i.e. increased sensitivity to environmental and demographic stochasticity, constrained habitat selection may lead to an increase in extinction probability of populations when a large fraction of the individuals occur in low-quality habitat.

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## 1. Introduction

Landscape fragmentation is known to constrain movement of animals between habitat patches and can result in high extinction probabilities of local populations in small, isolated patches (e.g. Hanski, 1994; Prugh et al., 2008; Van Langevelde, 2000). Metapopulation theory can explain these widely observed patterns, identifying the factors affecting the spatial and temporal dynamics of populations in fragmented landscapes (Hanski, 1998, 1999). Although habitat quality determines local population densities, its role in metapopulation dynamics is highly debated (Armstrong, 2005). Several studies have assessed the role of habitat quality in metapopulation dynamics. Some have not found an additive effect of quality next to patch area and isolation (Moilanen and Hanski, 1998), others have found that habitat quality and patch isolation are both important determinants of local extinction and recolonization (Franken and Hik, 2004; Jacquiéry et al., 2008; Thomas et al., 2001), and some studies have shown that habitat quality explains the most variance in occupancy and turnover in habitat patches (Fleishman et al., 2002; Krauss et al., 2005).

In cases where habitat quality of patches has been found to determine metapopulation dynamics, habitat quality is positively related to occupancy, local densities and colonisation and negatively with extinction (Franken and Hik, 2004; Thomas et al., 2001). In one study, an interaction between local habitat quality and connectivity was found to increase the colonisation rate, and the authors interpret this interaction as the ability of the immigrants to target high-quality patches (Jacquiéry et al., 2008). This ability to target high-quality patches has also been found in an experiment (Baguette et al., 2011).

Habitat selection expresses how well an organism is able to find habitat where its fitness is maximised. Habitat selection is, however, not free of costs (Rosenzweig, 1981). Optimal foraging theory predicts that the gains that an individual achieves by selecting one patch over another must compensate for the time and energy spent travelling to the selected patch (Hengeveld et al., 2009). When movement has high costs and habitat selection is consequently constrained, the positive relation between habitat quality and population density may break down (Gilroy and Sutherland, 2007). Indeed, when fragmentation limits movement, some animals may have to cope with low-quality patches when they are not able to explore all unoccupied habitat due to these movement constraints. If so, these individuals may experience lower fitness than individuals in the best habitat patches.

In this paper, I will explore the negative effect of fragmentation on habitat selection in a modelling study. The questions addressed in this paper are: does habitat selection differ between landscapes that differ

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in degree of fragmentation, and if so, what are the effects at a population level? To address these questions, I used a spatially explicit, stochastic model to simulate the occupancy of breeding sites by a certain species in patchy landscapes. In the simulations, the amount and spatial configuration of habitat were varied.

## 2. Methods

### 2.1. Model structure

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://pcraster.geo.uu.nl/>, see also Van Langevelde and Grashof-Bokdam, 2011). The model landscapes for the simulations were rasters of 125 × 125 grid cells. In each landscape, the grid cells contained either breeding or non-breeding habitat. The amount of breeding habitat ( $B$  in % of the total amount of grid cells, 2%, 5%, 10% and 20%) varied between the model landscapes. Half of the breeding habitat was high-quality ( $O$  in number of grid cells) and the other half was low-quality ( $M$  in number of grid cells).

The model simulates the occupancy of breeding sites by pairs. The model species represent animals that have territories and the juveniles disperse looking for unoccupied habitat (many birds and mammals). Each grid cell with habitat in the model landscapes represents a site that can be occupied by the model species. During simulations, I assumed that the number, size and habitat quality of the sites remained constant. I differentiated between cells that were 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 of the population density that can reproduce during the next year. Each simulation started with 25% randomly-selected occupied sites with pairs. I did not find an effect of different starting values on the outcomes. Each time step (one year) starts with all sites occupied by a pair,  $N_t$ . 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 in the next time step.

During the breeding season, each pair has a probability  $P_r$  that  $J$  juveniles are produced. Both  $P_r$  and  $J$  depend on habitat quality, but are independent of density. After reproduction, the juveniles move away from their natal site and search for unoccupied sites. Individuals that do not find an unoccupied site are not explicitly further followed. The model landscapes were considered as closed systems, no immigration occurred. When they occupy a territory, adults and juveniles have an independent survival probability,  $P_a$  and  $P_j$ , which depends on habitat quality and the character of the winter (normal or severe). During winter (especially severe winters), low-quality habitat is assumed to provide low food availability to ensure survival. Due to these differences, high-quality habitat acts as a source and low-quality habitat as a sink.

After winter, the remaining population with size  $N_{t+1}$  can reproduce during the next year. The population size at the beginning of the next year will be:

$$N_{t+1} = P_a N_t + P_j P_r J N_t \quad (1)$$

Parameters in the model can be divided into determinants of the spatial pattern of the model landscapes and of the demographics and movement of the model species (Table 1).

### 2.2. Connectivity of the model landscapes

For variation in habitat geometry, I distinguished two spatial scales at which the habitat was either clumped or randomly arranged

**Table 1**

Parameters and values used for the simulation study.

Spatial pattern of the model landscapes		
Landscape size	125 × 125 cells	
Fraction breeding habitat $B$	Varied (2, 5, 10 or 20%)	
Fraction high-quality habitat	0.5	
Demographics of the model species		
Probability of a severe winter	0.2	
	High-quality $O$	Low-quality $M$
Reproduction probability $P_r$	0.6	0.3
Size of offspring $J$	3	2
Survival probability of adults $P_a$		
In normal winters	0.8	0.6
In severe winters	0.7	0.45
Survival probability of juveniles $P_j$		
In normal winters	0.6	0.4
In severe winters	0.3	0.2
Movement of the model species		
Landscape resistance for movement		
Breeding habitat	1	
Non-breeding habitat	2	
	Model species 1	Model species 2
Dispersal range of juveniles $R_d$	15 cells	50 cells
Resettlement range of adults $R_s$	3 cells	15 cells

(Fig. 1). The algorithm to generate the model landscapes is explained in Appendix A. To quantify the connectivity of each model landscape, I 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, 2002; Van Langevelde, 2000):

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

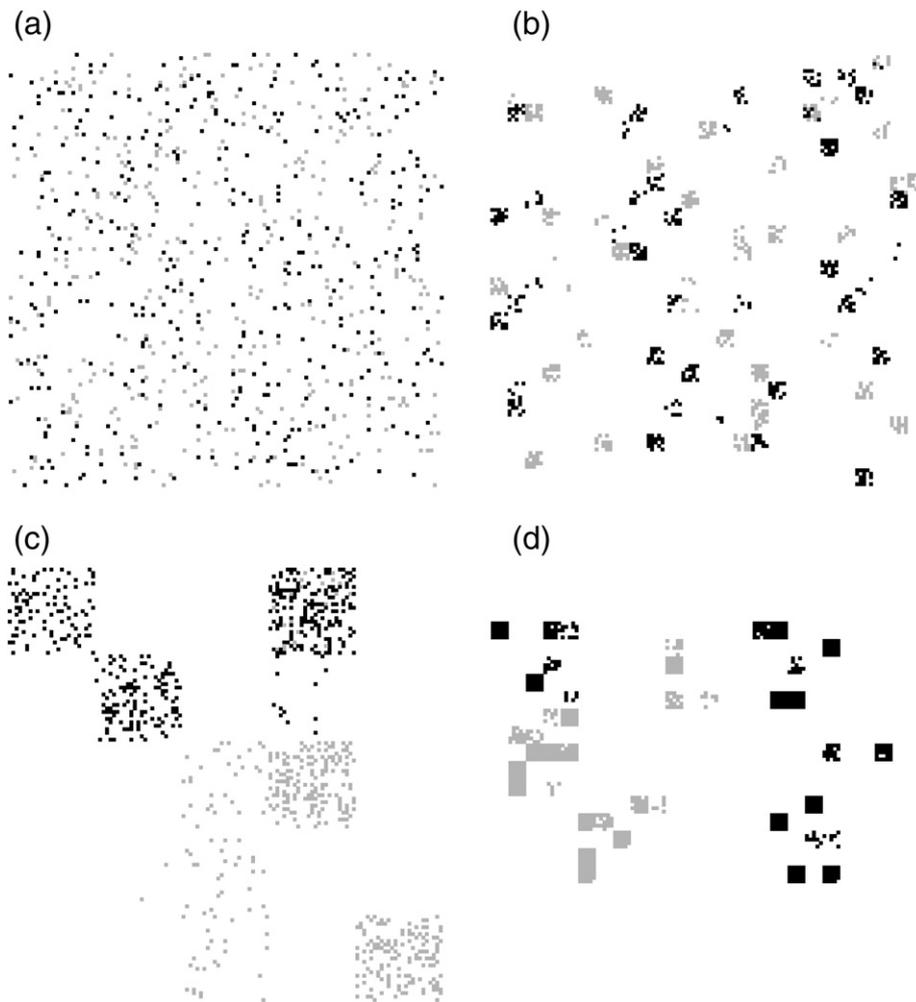
where  $n$  is the total number of breeding sites within the landscape. The calculation of the distance  $d_{ij}$  was weighed using values for the resistance for movement (see below). Low values of  $c_i$  imply that site  $i$  has a low connectivity to all other sites, i.e. it has a long distance to other sites. The connectivity of landscape  $k$  was then calculated by summing the values for the relative position of all sites and corrected for the amount of breeding habitat as:

$$C_k = \frac{\sum_{i=1}^n c_i}{O_k + M_k} \quad (2)$$

Low values of  $C_k$  indicate highly fragmented habitat.  $C_k$  can be used for comparison between the landscapes that differ in amount of habitat (Van Langevelde and Grashof-Bokdam, 2011; Van Langevelde et al., 1998).

### 2.3. Movement of the model species

After reproduction, the juveniles and the unpaired individuals search for unoccupied sites within a certain radius, i.e. the maximum movement distance  $D$ . This distance is defined as the maximum number of grid cells an individual can move from its natal site. I assumed 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  $P_m = 0.1^{d_{ij}/D}$ . 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. The probability that an unoccupied site within this radius will be selected depends on the distance to this site and the costs of



**Fig. 1.** Examples of model landscapes with varying degree of patchiness of the habitat: high-quality habitat is black, low-quality habitat is grey. The amount of breeding habitat  $B = 5\%$ . The clustering of the breeding habitat is conducted at two spatial scales (see Appendix A): (a) is generated with  $l = 1$  at the region level and  $l = 1$  at the subregion level, (b) with  $l = 4$  at the region level and  $l = 1$  at the subregion level, (c) with  $l = 4$  at the region level and  $l = 4$  at the subregion level, and (d) with  $l = 1$  at the region level and  $l = 2$  at the subregion level.

movement (Hanski, 1999). Therefore, the effective distance from the natal site to unoccupied sites was calculated to conform with Adriaensen et al. (2003). This effective distance is a measure of the distance modified by the costs to move based on the landscape to be crossed, as well as behavioural aspects of the organism. I assumed that there are no costs for moving through breeding habitat, while the matrix has high costs for movement. These high costs also account for mortality (e.g. due to predation) during movement across the matrix.

The distances to unoccupied sites indirectly determined the search direction because the colonisation probability  $P_m$  was multiplied by 1 for high-quality habitat and by 0.5 for low-quality habitat. This represents individuals' search behaviour: they may search for another site when they initially reach a low-quality site. When two juveniles choose the same site, the one with the highest colonisation probability will occupy it. Two individuals in the same grid cell are assumed to form a breeding pair, where differences in sex are neglected for reasons of simplicity.

Only juveniles and unpaired individuals disperse over relatively long distances after leaving their natal site. In the simulations, I separately applied model species with low and high movement ability relative to the size of the model landscapes ( $D = 15$  and 50 cells, respectively). Once settled, adults are less likely to leave their territory. Those that leave for an unoccupied site of higher quality, if it becomes available, move over short distances only ( $D = 3$  and 15 cells, respectively). This opportunistic shift to neighbouring sites takes place before the winter by adult pairs of all ages.

#### 2.4. Simulations and analysis

Due to the stochastic character of the model, I conducted 10 simulations for each model landscape. Each simulation ran for 100 time steps. Model species 1 was simulated in the model landscapes with  $B = 2, 5, 10$  and 20%. Simulations with model species 2 were conducted in the model landscapes with  $B = 2$  and 5%. For each simulation, I calculated the mean fraction of occupied breeding habitat, using the population sizes from time step 51 until 100. Also, the mean fraction of occupied low- and high-quality habitat ( $Sm_k$  and  $So_k$  for landscape  $k$ , respectively) was calculated to quantify habitat selection. I calculated the mean values of these response variables over the 10 runs per landscape.

The simulated fractions of occupied low- and high-quality habitat were compared with the expected fractions based on the optimal distribution of the animals. To calculate the expected fractions, the sites with high-quality habitat are assumed to be occupied first. The remaining pairs are then expected to occupy the low-quality sites. Due to environmental and demographic stochasticity, the mean occupation probability of a high-quality site by adults is 0.78 [obtained by  $(4 \times 0.8 + 0.7) / 5$ , see Table 1]. The expected mean fraction of occupied sites with high-quality habitat  $Eo_k$  and with low-quality habitat  $Em_k$  in landscape  $k$  were calculated as

$$Eo_k = \frac{N_k}{O_k} \wedge Eo_k = 0 \quad \text{if} \quad N_k \leq 0.78 \times O_k \quad (3a)$$

$$Eo_k = 0.78 \wedge Em_k = \frac{N_k - O_k}{M_k} \quad \text{if } N_k > 0.78 \times O_k \quad (3b)$$

in which  $N_k$  is the mean population size (calculated for time step 51–100) and  $O_k$  and  $M_k$  are the numbers of high- and low-quality sites, respectively.

Finally, I also calculated these fractions based on a random selection  $Ro_k$  and  $Rm_k$ , where there is no preference for either high-quality or low-quality habitat:  $Ro_k = Rm_k = 0.5 N_k / (O_k + M_k)$ . In a graph, the space for habitat selection is bounded by three lines (Fig. 2a): (1) optimal selection according to Eq. (3a), (2) optimal selection according to Eq. (3b), and (3) random selection  $Ro_k = Rm_k$ . The simulated selection, the optimal selection and the random selection can be plotted in the graph using the fractions of occupied high-quality sites and the fractions of occupied low-quality sites as coordinates (see Fig. 2b for an example).

### 3. Results

As expected, the fraction of occupied habitat ( $Eo_k + Em_k$ ) decreases with decreasing connectivity especially for the highly fragmented landscapes ( $B = 2\%$ ) and the model species with limited dispersal ranges (Fig. 3a). This effect is absent for the landscapes that are not fragmented ( $B = 10\%$  and  $20\%$ ), especially for the model species with large dispersal ranges. In these landscapes, the fraction of occupied habitat is higher than in the highly fragmented landscapes.

The simulated, expected and random fractions of occupied low- and high-quality habitat are plotted in the space given by Fig. 2a to illustrate the habitat selection by the two model species (Fig. 4). The habitat selection of model species 1 in the highly fragmented landscapes ( $B = 2\%$  and  $5\%$ ) largely deviates from the expected optimal selection, whereas model species 1 in the landscapes with more habitat ( $B = 10\%$  and  $20\%$ ) select their habitat close to the optimal selection. This is especially true for model species 2, whose simulated habitat selection agrees with the optimal selection.

The constrained habitat selection of model species 1 in the highly fragmented landscapes ( $B = 2\%$  and  $5\%$ ) illustrates that individuals are also occupying low-quality habitat whereas high-quality habitat is unoccupied. If so, then the reproductive output is expected to be lower in these highly fragmented landscapes where habitat selection deviates from optimal, as relatively more low-quality habitat is occupied than in the landscapes with a high amount of habitat. I calculated the reproductive output as:  $Eo_k P_r J + Em_k P_r J$  (the values of  $P_r J$  for high-quality and low-quality, respectively), which is the average number of juveniles per pair. The reproductive output is lowest in the highly

fragmented habitat with  $B = 2\%$ , followed by the landscapes with  $B = 5\%$ , both for model species 1. In contrast, the landscapes with  $B = 10\%$  and  $20\%$  for model species 1 and with  $B = 2\%$  and  $5\%$  for model species 2 have the highest reproductive output and are the same. This difference in reproductive output reflects the constrained habitat selection by model species 1 with limited dispersal ranges due to the low connectivity in the highly fragmented landscapes.

### 4. Discussion

In this paper, I explored the effect of landscape fragmentation on the selection of habitat sites for two model species, representing animals that have territories and disperse as juveniles looking for their own territory. For species with limited movement ability in highly fragmented habitat, constrained habitat selection is predicted, whereas habitat selection is optimal for species that have large dispersal ranges (Fig. 4). It is well known that fragmentation results in lower population sizes (Prugh et al., 2008) and may lead to unoccupied patches with high-quality habitat (Hanski, 1999). However, the effect of fragmentation on habitat selection also means that low-quality sites are more frequently occupied than expected. This constrained habitat selection can be explained by limited movement of individuals to explore and move to unoccupied high-quality sites that are located beyond their dispersal range. Constrained habitat selection has negative consequences for reproduction, as relatively more low-quality habitat is occupied (Fig. 5). This effect of fragmentation on habitat selection largely limits the spatial distribution of species with limited dispersal range because constrained habitat selection leads to lower reproduction when more individuals occur in suboptimal habitat. Besides other effects of habitat fragmentation, such as increased sensitivity to environmental and demographic stochasticity (Hanski, 1999), constrained habitat selection may explain the high extinction probability of populations when a greater fraction of the individuals occur in low-quality habitat.

The simulation model was designed with a minimum number of parameters that needed specification. Although this single-species model is not based on the life history of one species, its structure is suited to simulate the occupancy of sites by species that are sedentary all the year round, habitat specific and have density-dependent dispersal. Moreover, I considered only two types of breeding habitat. This modeling approach, aimed at illustrating that fragmentation can have negative effects on habitat selection that has been considered before. The role of habitat quality in metapopulation dynamics is much debated (Armstrong, 2005; Franken and Hik, 2004; Jacquiéry et al., 2008; Krauss et al., 2005). The main question in this debate is whether landscape configuration or differences in habitat quality explain occupancy

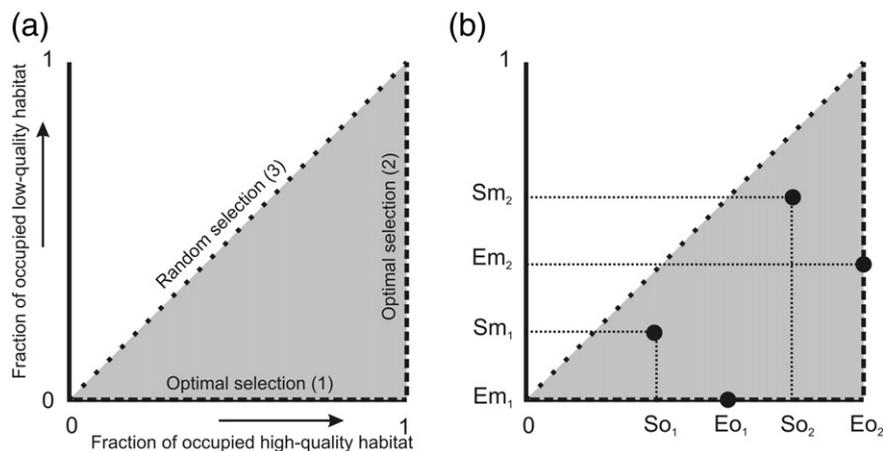
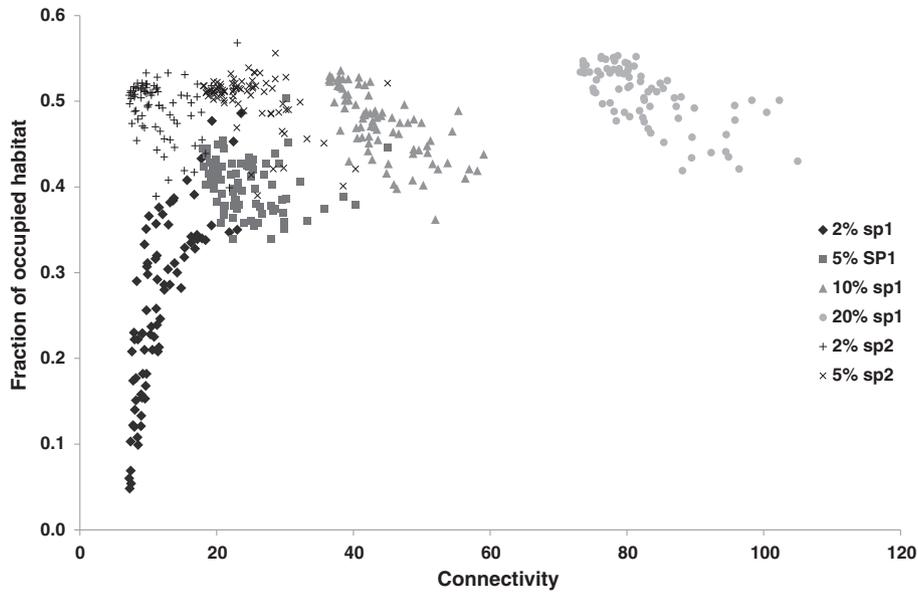
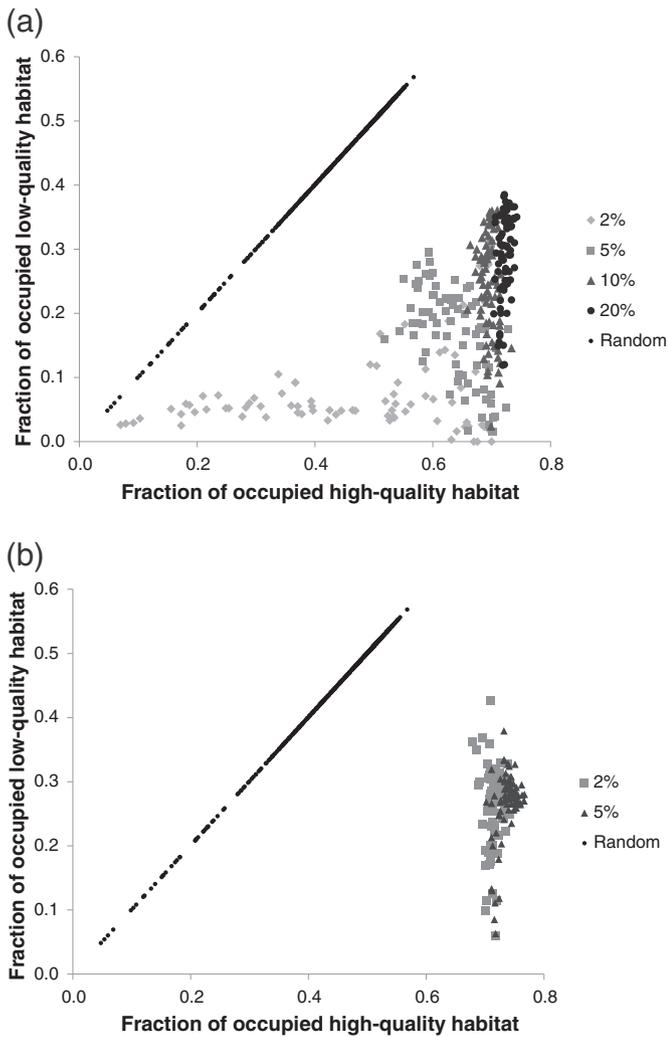


Fig. 2. (a) Space in which habitat selection can be found bounded by optimal selection where the high-quality sites are filled first (1) and then the low-quality sites (2), and by random selection where the fractions of occupied high- and low-quality sites are equal (3). (b) Examples of simulated and expected selection plotted in the graph using the fractions of occupied high-quality sites and the fractions of occupied low-quality sites as coordinates.



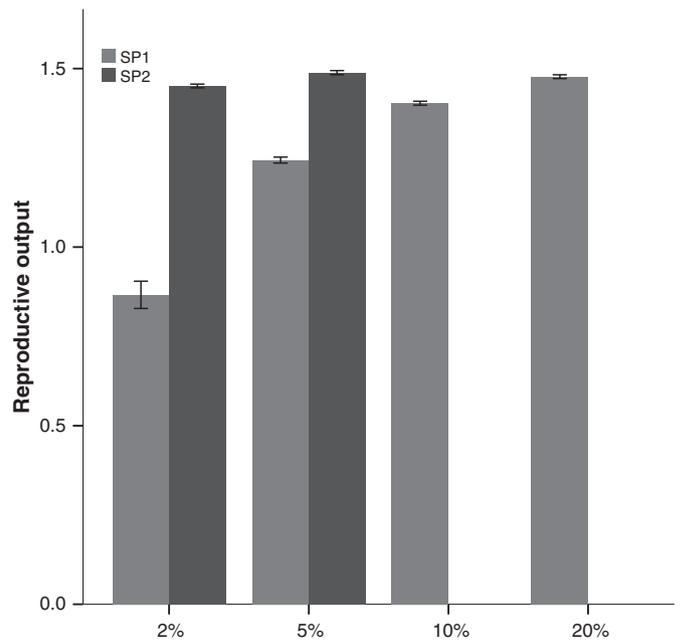
**Fig. 3.** The fraction of occupied habitat in landscapes that differ in amounts of breeding habitat, as a function of the connectivity of each landscape (Eq. (2)) for the two model species (sp1 has a small dispersal range and sp2 a large dispersal range).



**Fig. 4.** Habitat selection by (a) model species 1 and (b) model species 2 in the landscapes with different amount of breeding habitat. The fractions of occupied high- and low-quality sites and the random selection are plotted in the space given by Fig. 2a.

and turnover patterns. This study shows however an additional negative relationship between landscape fragmentation and habitat selection that can explain why a relatively large fraction of low-quality habitat is occupied.

It is considered to be a poor evolutionary strategy to disperse from high-quality habitat where high fitness is expected (sources) to lower-quality habitat with lower fitness (sinks) (Pulliam and Danielson, 1991). Several mechanisms are proposed that generate such source-sink structures in heterogeneous landscapes. One of these mechanisms is based on competition: when dominant individuals occupy source habitat, and population density increases, subordinate individuals will disperse into sink habitats. Also when dispersal is passive and due to factors other than density-dependent interactions,



**Fig. 5.** Differences in the reproductive output between the landscapes that differ in amounts of breeding habitat (see text for explanation). Error bars represent the standard errors.

for example, physical transport processes by wind or water, individuals or propagules can land in sink habitats. The results of this modelling study show that constrained habitat selection can generate source-sink dynamics in fragmented landscapes: individuals are not able to assess the quality of surrounding patches due to the large distances to these patches relative to the distance that individuals can bridge. This distribution affects average reproduction success and survival and maintains a source-sink structure in a metapopulation. Such variation in habitat quality and its influence on occupancy is rarely considered at a metapopulation scale.

#### Appendix A. Algorithm to generate the model landscapes

The model landscapes were divided into 25 square regions, which were each in turn divided into 25 square subregions. Each of these subregions contained 25 grid cells. In the model landscapes, I placed cells with either breeding or non-breeding habitat, based on a stratified assignment procedure. The habitat arrangement in the model landscapes is the product of two random processes. The initial process is a homogeneous Poisson process. The second process iteratively rearranges the initial Poisson distribution by randomly picking up and relocating habitat towards existing clusters of habitat.

First, the available habitat (breeding and non-breeding) was randomly distributed over the regions. Second, an iterative procedure of rearranging the initial random distribution was used to obtain a clumped distribution at the region level. Habitat cells were randomly selected one by one, and assigned to a region based on a probability distribution. This probability distribution was based on the distribution of the habitat amount in each region as result of the first step. Regions that received here a relatively high amount of habitat cells had high probability of receiving more habitat cells in the second step. Each time a habitat cell was picked up and relocated, the distribution of habitat area over the regions changed, and with that, the probability to receive more habitat cells. In the two stages, the high-quality habitat  $O$  was first randomly distributed and iteratively rearranged. Then the low-quality habitat  $M$  followed. The iterative procedure was conducted  $l$  times, for  $l = 1, 2, 3$  and  $4$ . For  $l = 1$ , the initial random distribution was taken. For high values of  $l$ , the procedure resulted in a more clumped pattern.

At the sub-regional level, the same procedure was used. For each  $l$ , the assigned amount of habitat in a region was used as starting point for the distribution of habitat cells over the sub-regions in this region. Exchange of habitat cells between the regions was not permitted. The

iterative procedure was also conducted  $l$  times, for  $l = 1, 2, 3$  and  $4$ . Within a sub-region, the assigned habitat cells were randomly distributed.

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