

What size is a biologically relevant landscape?

Heather Bird Jackson · Lenore Fahrig

Received: 20 October 2011 / Accepted: 7 May 2012 / Published online: 6 June 2012
© Springer Science+Business Media B.V. 2012

Abstract The spatial extent at which landscape structure best predicts population response, called the scale of effect, varies across species. An ability to predict the scale of effect of a landscape using species traits would make landscape study design more efficient and would enable landscape managers to plan at the appropriate scale. We used an individual based simulation model to predict how species traits influence the scale of effect. Specifically, we tested the effects of dispersal distance, reproductive rate, and informed movement behavior on the radius at which percent habitat cover best predicts population abundance in a focal area. Scale of effect for species with random movement behavior was compared to scale of effect for species with three (cumulative) levels of information use during dispersal: habitat based settlement, conspecific density based settlement, and gap-avoidance during movement. Consistent with a common belief among researchers, dispersal distance had a strong, positive influence on scale of effect. A general guideline for empiricists is to expect the radius of a landscape to be 4–9 times the median dispersal

distance or 0.3–0.5 times the maximum dispersal distance of a species. Informed dispersal led to greater increases in population size than did increased reproductive rate. Similarly, informed dispersal led to more strongly decreased scales of effect than did reproductive rate. Most notably, gap-avoidance resulted in scales that were 0.2–0.5 times those of non-avoidant species. This is the first study to generate testable hypotheses concerning the mechanisms underlying the scale at which populations respond to the landscape.

Keywords Landscape context · Spatial scale · Habitat fragmentation · Focal patch · Buffer · Informed dispersal · Habitat selection · Edge-mediated dispersal · Boundary behavior

Introduction

Landscape structure (habitat amount and fragmentation) has important effects on populations and communities (Laurance et al. 2002; Fahrig 2003), but the scale at which landscape structure should be measured is not always clear. A common solution to this problem is to measure landscape structure within multiple buffers surrounding a focal patch (Brennan et al. 2002). Called the scale of effect, the appropriate scale is the one at which the ecological response (e.g. abundance) in the focal area is best predicted by the landscape structure (e.g. habitat amount). This method ensures that landscape is measured at a scale

Electronic supplementary material The online version of this article (doi:10.1007/s10980-012-9757-9) contains supplementary material, which is available to authorized users.

H. B. Jackson (✉) · L. Fahrig
Geomatics and Landscape Ecology Laboratory,
Department of Biology, Carleton University, 1125
Colonel Drive, Ottawa, ON K1S 5B6, Canada
e-mail: heather.b.jackson@gmail.com

appropriate to the species of interest and has the benefit of maximizing the probability of finding a relationship with landscape structure, if one exists. The disadvantage of this method is that the scale of effect is discovered after sampling, when it is too late to use that information to design the study. Empiricists must therefore sample focal areas far apart to ensure that landscapes of unknown size are non-overlapping and independent. If empiricists could accurately predict the scale of effect beforehand, they could increase the number of landscapes sampled and reduce the time and resources spent travelling among focal areas. Landscape managers, who may not have the opportunity to empirically derive the scale of effect before crucial decisions are made, may benefit even more than empiricists from an ability to accurately predict the scale of effect.

The scale of effect varies across species (e.g. Holland et al. 2005a), but which species traits influence the scale of effect is unknown. Increased body size has been associated with increased scale of effect for seven long-horned beetles (Holland et al. 2005a) and four parasitoid flies (Roland and Taylor 1997), but was not associated with scale of effect for 56 North American songbird species (Tittler 2008). Mobility, a correlate of body size (Bowman et al. 2002; Bowman 2003), is generally thought to be an important cause for increased scale of effect (Holling 1992; Carr and Fahrig 2001; Ricketts et al. 2001; Horner-Devine et al. 2003; Ritchie 2010). This belief is supported by the fact that other scales of land use that are important to species, such as home range in mammals (Bowman et al. 2002) and territory size in birds (Bowman 2003), are positively related to both dispersal distance and body size. But the fact that body size is not always positively related to scale of effect suggests that other factors besides mobility affect this relationship.

Reproductive rate, which is negatively correlated with body size (Fagan et al. 2010), may explain some of the variation in the relationship between body size and scale of effect. Theory suggests that reproductive rate can strongly mediate the relationship between populations and the landscape by allowing populations to persist with less habitat (Fahrig 2001). Indeed, reproductive rate is associated with a lower minimum habitat requirement for birds (Vance et al. 2003) and wood-boring beetles (Holland et al. 2005b). Untested is whether an ability to persist with less habitat translates into a reduced scale of effect.

Informed (i.e. non-random) movement behavior (Clobert et al. 2009) may also influence the scale of effect. Whereas many seeds and aquatic larvae disperse passively, animals often respond to cues to determine where to settle (e.g. in high quality habitat or where fewer conspecific competitors are present, Bowler and Benton 2005). Information use can affect not only settlement, but also movement (movement is sometimes referred to as inter-patch movement, Bowler and Benton 2005, or displacement, Baguette and Van Dyck 2007). For example, many species are unlikely to enter unsuitable habitat (matrix), but instead change direction in order to continue movement within suitable habitat (e.g. Ries and Debinski 2001; Schultz and Crone 2001; Jackson et al. 2009).

The influence of movement behavior on the scale of effect will most likely result from its influence on the probability of long-distance dispersal. With an impact disproportionate to their numbers, rare long-distance dispersers influence other large scale spatial properties of populations and species such as the rate of range expansion (Kot et al. 1996), the spatial patterns of gene flow (Nichols and Hewitt 1994), and speciation (Guo and Ge 2005). If instead of settling randomly like a seed, an animal settles in the first available habitat, then we expect the distribution of dispersal distances to be strongly right-skewed (i.e., a “fat-tailed” dispersal kernel, Turchin 1998), with most individuals settling close to their natal area but some travelling long distances to find available habitat. If individuals avoid high-densities of conspecifics during settlement, then they are expected to move farther from their natal habitat on average than if they select habitat without considering conspecific density. This density-dependent settlement pattern is expected to result in a smaller difference between maximum and average dispersal distances (a “thin-tailed” dispersal kernel) than habitat settlement alone (Hawkes 2009) and may reduce the scale of effect. Gap-avoidance may simply make dispersal distances so context dependent that a scale of effect measured across multiple landscapes is hard to identify.

Informed movement behavior may also influence scale of effect by improving dispersal success. Greater success at finding breeding habitat would lead to an increased population growth rate. Gap-avoidance, for example, was found to be the most important factor increasing population density when compared with the effects of increased numbers of patches and reduced distances between patches in a simulation model

(Tischendorf et al. 2005). If increased population growth rate decreases the scale over which habitat influences a population, then informed movement behavior may decrease scale of effect.

We used an individual-based simulation model to develop quantitative predictions concerning the relationship between species traits (dispersal distance, reproductive rate, and movement behavior) and the scale of effect of habitat amount on abundance. We tested movement behavior that incorporated increasingly more information: (1) random settlement (RS, in which individuals settle after a randomly selected number of steps); (2) habitat-settlement (HS, settlement in the first territory, i.e. habitat cell, that is encountered); (3) density-dependent habitat settlement (DHS, settlement in the first territory, i.e. habitat cell, encountered that is unoccupied by conspecifics); and (4) density-dependent habitat settlement with gap-avoidance (DHSG). We expected the scale of effect to be most strongly associated with average dispersal distance, but that this relationship would be modified by reproductive rate and movement behavior.

Methods

Overview

We developed a simulation model (“TraitScape”) that simulates dynamics of hypothetical species in

hypothetical landscapes. For a given species type (characterized by a fully factorial set of species parameters, Table 1), we conducted multiple simulation runs, each in a different landscape. We then analyzed the set of runs to determine the scale of effect of landscape structure on population abundance for that species type. To make our results as useful as possible for field researchers, we constructed the simulations such that the output data were the same as what would be collected by field ecologists conducting a “focal patch” landscape-scale study (Brennan et al. 2002), i.e., where the response variable (e.g. population abundance) is measured at the centers of multiple sites and the predictors are landscape structure variables (e.g. habitat amount) measured in the landscapes surrounding the focal sites. By conducting multiple sets of simulations, with different values for the parameters that determine species type, we tested the predictions (see “Introduction” section) that dispersal distance, reproductive rate, and movement behavior should influence the scale of effect of the landscape, and we quantified their effects. In addition, we used information concerning secondary outcomes (e.g. population size, shape of dispersal kernel, variation among runs in average dispersal distances) collected from each treatment combination to explore the mechanisms linking dispersal distance, reproductive rate, and movement behavior to scale of effect.

Table 1 Input parameter values that were experimentally varied

Parameter	Experimental treatments	Description
Movement step size (34 levels) ^a	$\alpha = 0.1\text{--}2.0$ by increments of 0.1, 2–15 by increments of 1	Step size \sim Exponential(α)
Reproductive rate (R_0)	$R_0 = 1.5, 2.5, 3.5, 4.5$	Number of offspring \sim Poisson(F), where $F = \frac{R_0}{1 + \frac{(R_0-1)N_a}{k}}$, K is carrying capacity of a cell (held constant at 2), and N_a is current number of adults in a cell
Movement behavior (MOVE) in order of increasing use of information	RS	Individuals settle when energy reserves are depleted, regardless of cell type
	HS	Individuals settle in the first habitat cell encountered or when energy reserves are depleted, whichever comes first
	DHS	Same as HS, but individuals do not settle in cells occupied by other individuals unless energy has been depleted
	DHSG	Same as DHS, but individuals avoid stepping into matrix

^a Median dispersal distance (d_{50}) and maximum dispersal distance (d_{\max} , see Table 3), not step size, are used in analyses of experimental outcomes, because dispersal distance is the trait most often measured empirically

Model description

TraitScape is an individual-based spatially-explicit model developed using NetLogo (Wilensky 1999). Freely available online (ccl.northwestern.edu/netlogo), TraitScape provides abundance in the focal area and landscape characteristics as output; the scale of effect must be calculated by the user.

In TraitScape, individuals represent generic mobile animals and are defined by four state variables: original position (x_0, y_0), current position (x, y), age (0 or 1), and energy level (lifetime number of movement steps possible). Original position and energy are determined at birth, current position is

updated after each movement step, and age is updated once a year.

Simulations are run in a 127×127 grid with reflective boundaries (Table 2; Fig. 1). This grid size is large enough to allow ten potential scales of effect (concentric radii from 9 to 63 cells), but small enough to keep the global population at a computationally manageable size (generally $<20,000$ individuals). The odd number of cells (127×127) is an artifact of the midpoint displacement algorithm (Saupe 1988) which is used to generate naturalistic random landscapes (see “Submodels” section). Grid cell size does not represent an absolute spatial unit (e.g. meters); instead, the size of grid cells is only meaningful with respect to the step size

Table 2 Input parameters which were held constant for all simulation runs

Parameter	Value
Landscape size	16,129 cells (127×127)
Length of run	The first of the following: 5000 years when global extinction occurs when population size varies by less than 10 % between decades for 10 consecutive decades
Spatial autocorrelation of habitat (H)	0.5
Amount of habitat	Drawn before landscape setup from Uniform(5, 95 %)
Size of focal area	149 cells (radius = 7)
Initial number of individuals	1,612 (one per 10 cells)
Energy level per individual (potential number of steps taken during lifetime)	Drawn at birth from Exponential(9)
Yearly adult mortality	100 % after reproductive season
Movement direction	First move: $\theta_{t=1} \sim \text{Uniform}(0, 2\pi)$ for first move Subsequent moves: $\theta_t \sim \theta_{t-1} + 2 * \arctan\left(\frac{1-\rho}{1+\rho} \pi[\text{Uniform}(-0.5, 0.5)]\right)$, where $\rho = 0.9$

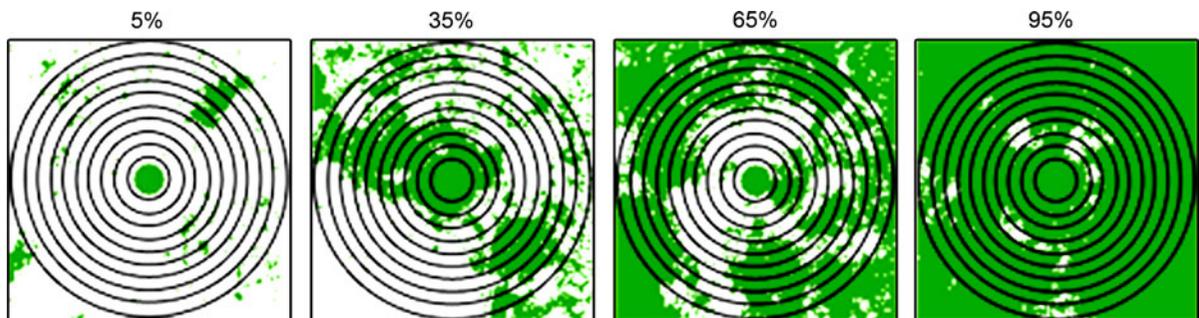


Fig. 1 Examples of randomly generated landscapes used in TraitScape. Percentages indicate the global habitat amount. Green grid cells correspond to habitat, and white grid cells are matrix. A

focal area (seven cell radius) at the center of each landscape is 100 % habitat. Concentric circles indicate the radii at which percent cover of habitat was measured. (Color figure online)

of individuals which can vary with user input. Grid cells are the finest grain at which habitat type is categorized. Density-dependence in reproduction and settlement (when applicable) is modeled within grid cells.

Grid cells are classified as either suitable habitat (hereafter “habitat”) or unsuitable habitat (hereafter “matrix”). To simplify our model, we did not explicitly model mortality during movement, whether in matrix or habitat. All adults die at the end of reproduction. Therefore, if an individual settles in the matrix it dies without reproducing. Individuals with informed movement behavior (Table 1) are responsive to cell type during settlement and/or movement, and are consequently less likely to settle in matrix.

The model proceeds in time steps, which we call “years” and which are equivalent to generations. In order to allow populations to stabilize, each run lasts up to 5,000 years. Most runs are much shorter because a run is ended when the global population size reaches a steady state (i.e. if population size varies by less than 10 % from decade to decade for at least 10 decades) or when the global population goes extinct.

TraitScape simulates the yearly processes of adult death, juvenile movement (which ends in maturation), and adult reproduction, in that order (Fig. 2). Each process is completed before the next process begins. Within each process, each individual fully completes its action (e.g. movement) before the next randomly selected individual initiates action. Within years, time is not explicitly represented; instead each process continues until completion and then the next process immediately begins.

Submodels

Setup An individual simulation run begins by setting up a random landscape using the midpoint displacement algorithm (Saupe 1988; Figs. 1 and 2). This algorithm produces realistic-looking landscapes and allows independent control of the amount of habitat and the configuration of habitat (for examples see Saupe 1988; With and King 1999). The algorithm creates fractal landscapes which can vary in the amount of spatial autocorrelation according to the parameter H . The main difference among landscapes in our runs is the amount of habitat, not the configuration of habitat. H is held constant at 0.5 (moderate spatial autocorrelation, Table 2), but the amount of habitat is randomly selected at the

beginning of each run from a uniform distribution between 5 and 95 %.

Once a random landscape is generated, a focal area is added to its center. The focal area is the sampling area within which population abundance is sampled. To keep local conditions constant among runs, the focal area is always 100 % habitat. Its radius is seven cells (Table 2; Fig. 1).

At the beginning of a simulation run, individuals are placed randomly in the landscape; runs begin with 1,612 individuals (one for every 10 grid cells, Table 2). Random distribution of individuals without regard for habitat ensures that the initial density of individuals in breeding habitat is independent of the amount of habitat in the landscape (Fahrig 2001). All starting individuals are juveniles. After initial setup, the model runs on a yearly time step with three main submodels: adult death, juvenile movement, and adult reproduction.

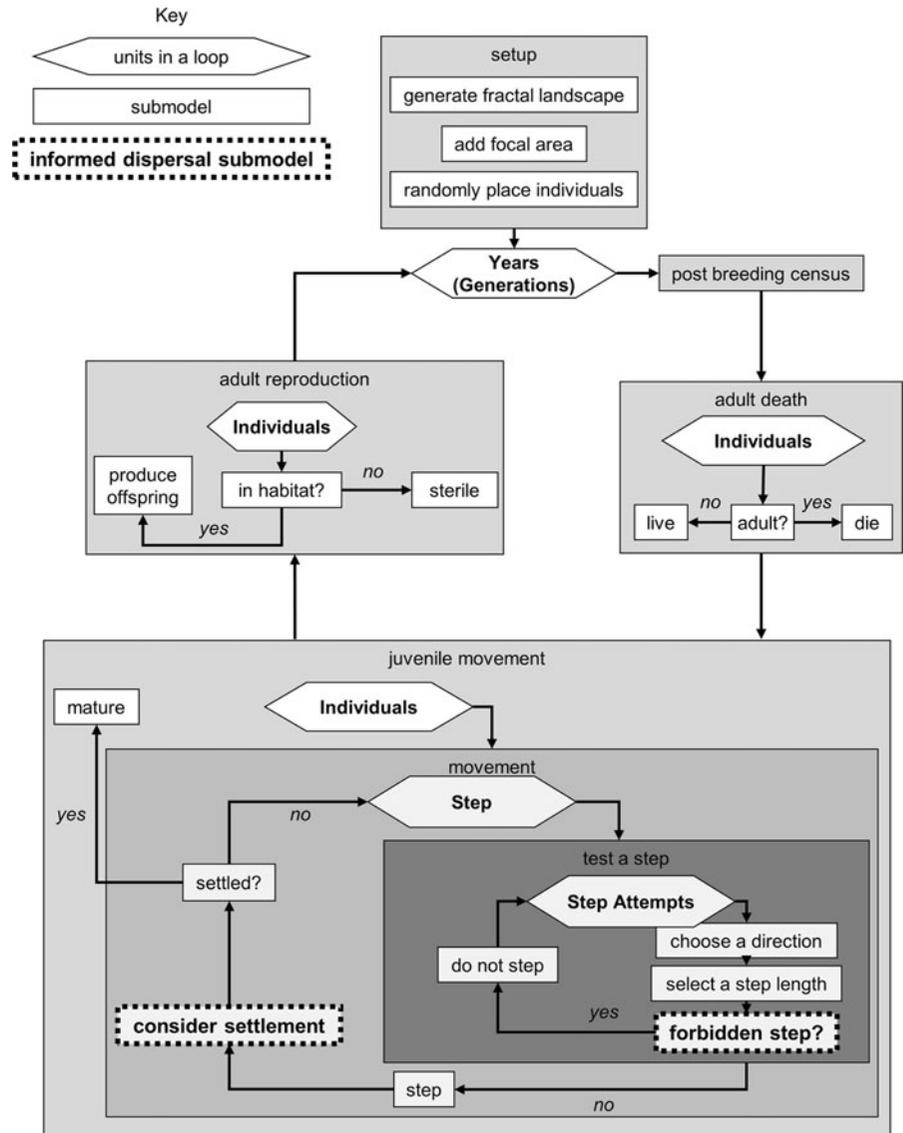
Adult death

At the beginning of each year, all adults die (Table 2).

Juvenile movement Movement is modeled one individual at a time. Each individual takes successive steps until settlement occurs. Before each step, an exploratory loop cycles through possible steps until an acceptable step (i.e. one in which no forbidden steps are made) is randomly drawn (Fig. 2). A step outside of the grid is always forbidden. With DHSG, a step into the matrix is always forbidden.

Like many animals (Kareiva and Shigesada 1983), model individuals move according to a correlated random walk. In a correlated random walk subsequent movement directions are correlated such that highly correlated movement paths are nearly straight (Turchin 1998). In the model, the initial direction of movement for each individual is selected randomly from between 0 and 2π radians. Thereafter, the direction of a step is drawn from a wrapped Cauchy distribution with a mean direction equal to the previous direction (Table 2, Fletcher 2006). The concentration around the mean direction is determined by ρ , where $\rho = 0$ results in a random walk and $\rho = 1$ results in a perfectly straight line. For our simulations, we fixed ρ at 0.90 (nearly straight) which is close to the optimal linearity for finding new habitat (Zollner and Lima 1999; Fletcher 2006; Barton et al. 2009, Table 2).

Fig. 2 Flow chart of TraitScape. Informed movement behavior is an option in the “consider settlement” and “forbidden step?” submodels. In the “consider settlement” submodel, individuals decide whether to settle by considering their energy level (all movement behaviors), the quality of the cell (HS, DHS, DHSG), and the presence of conspecifics (DHS, DHSG). In the “forbidden step?” submodel, individuals consider whether they are still in the model grid (all movement behaviors) and whether they have stepped into matrix (DHSG only). If a step takes an individual outside the model grid or causes an individual to step into matrix (DHSG only) that step is rejected and a new step is considered



Each step length is drawn from a negative exponential distribution with a mean determined by the experimental treatment (range = 0.1–15.0 cells, Table 1). We manipulated average dispersal distances by altering step length rather than number of steps because theory suggests that body size is associated with space use (e.g. home range size) via its influence on step size or sampling scale (Jetz et al. 2004; Ritchie 2010).

After a step is taken, an individual considers settlement (the end of dispersal). The choice to settle depends on (a) the number of steps already taken and, for most treatments, (b) the conditions in the cell. The

maximum number of steps possible for each individual is assigned at birth, and an individual must settle once the maximum number of steps has been reached even if it is in matrix. The number of steps is drawn from a negative-exponential distribution with a mean of nine for all runs in our simulations. With RS, the only reason an individual settles is that it has reached the maximum number of steps assigned at birth, but in other treatments, conditions in the cell can cause movement to stop earlier. With HS, individuals stop at the first habitat cell they encounter. With DHS and DHSG, individuals stop at the first habitat cell they encounter that is not occupied by another individual.

Once an individual has settled, its status is changed from juvenile to adult and it no longer has the opportunity to move.

Both step size and number of steps are drawn from negative exponential distributions to produce negative-exponentially distributed dispersal distances (straight-line distance between origin and settlement). A negative-exponential distribution is a common method used to model “fat-tailed” dispersal, or more long-distance dispersal than expected under a Gaussian distribution (e.g. Kot et al. 1996; Chapman et al. 2007). Fat-tailed dispersal is exhibited by many species in nature (Okubo 1980; Turchin 1998).

Reproduction If settled in habitat, an adult has the opportunity to reproduce, with the number of offspring governed by logistic growth (see also Barton et al. 2009). The number of offspring per individual is drawn from a Poisson distribution (the distribution commonly used for simulating stochastic fecundity, Akçakaya 1991) with a mean determined by reproductive rate, the carrying capacity for a cell ($k = 2$ in our runs), and the density of individuals within a cell (Table 1).

Simulation experiments

In designing our simulation experiments our goal was to develop theory that could be used to provide guidance to empiricists and managers with a rough estimate of the scale of effect of the landscape on a given species or species group. The scale of effect, or the radius at which the relationship between abundance in the focal area and percent habitat cover in the surrounding landscape is strongest, emerged from analysis of outputs from Traitscape.

We manipulated (1) step size (in order to influence dispersal distance), (2) reproductive rate, and (3) movement behavior in a full-factorial experimental design (Table 1). Step sizes were selected to ensure that they spanned the full range of possibilities from an average dispersal distance of a few cells to an average distance equal to the width of the grid. One hundred and fifty runs were conducted for each of the 544 treatment combinations. This provided enough replicates to ensure that a sufficient number of samples were present after removing those in which extinction occurred.

Model analysis

Output

Analyses were conducted on data summarized for each hypothetical species (i.e. each treatment combination), rather than on raw output of each run (or landscape). The following raw data were collected from the last generation of each run (Table 3): the amount of habitat (A_s) in each of 10 concentric buffers around the focal area, median dispersal distance (d_{50}), maximum dispersal distance (d_{\max}), population size in the focal area (N), and size of the dispersal kernel tail ($((d_{\max} - d_{50})d_{50}^{-1})$). A dispersal kernel is the full distribution of dispersal distances in a population. Measuring the tail (the right side of the dispersal kernel) indicates how much farther some individuals move relative to the average disperser. For each set of runs from the same treatment combination (i.e. with the same step size, reproductive rate, and movement behavior, Table 1), raw output from each run was summarized into primary and secondary outcomes (Table 3). Primary outcomes included scale of effect (S^* , see below) and the median of both median (\bar{d}_{50}) and maximum (\bar{d}_{\max}) dispersal distances. Secondary outcomes included median population size (\bar{N}), median size of dispersal tails ($\overline{((d_{\max} - d_{50})d_{50}^{-1})}$), and variation in median dispersal distances ($CV_{d_{50}}$).

Calculating scale of effect

We evaluated scale of effect using the approach commonly taken by empiricists (Figure S1, Brennan et al. 2002), i.e., by selecting the landscape radius at which habitat cover best predicted abundance in the focal area. This was done for each treatment combination (defined by step size, reproductive rate, and movement behavior, Table 1). Ten linear regression models were created for each treatment combination—one for each of the 10 landscape radii (9–63 cells). The landscape radius resulting in the regression with the lowest AIC value was taken as the scale of effect (Figure S1, Table 3). Note that the scale of effect was the same if R^2 was used as the selection criterion (data not shown). The response variable in each regression was the abundance in the focal area during the last year (N) and the predictor variable was habitat amount (A_s). To ensure that the relationship

Table 3 Model output was collected during the final generation of each run (A). These run-level data were then summarized for each treatment combination (B, i.e. each “species” or each unique combination of step size, reproductive rate, and movement behavior)

Parameter	Description
(A) Output for each run	
N	Number of adults in the focal area
A_s	Habitat amount (proportion of cells which are habitat) within a circle of radius S cells. $S = 9, 15, 21, \dots, 63$.
d_{50}, d_{\max}	Median and maximum dispersal distances of all adults
$(d_{\max} - d_{50})d_{50}^{-1}$	Size of the dispersal kernel tail, standardized by median dispersal distance.
(B) Summary statistics for each treatment combination	
S^*	Scale of effect which is calculated using the regression of abundance, N , on habitat amount, A_s , for each spatial scale, S (Figure S1). S^* is the spatial scale (radius) where the AIC of the regression of N on A_s is minimized.
$\bar{d}_{50}, \bar{d}_{\max}$	Median of median (d_{50}) and maximum (d_{\max}) dispersal distances
\bar{N}	Median number of adults in the focal area (N)
$(d_{\max} - d_{50})d_{50}^{-1}$	Median size of the dispersal kernel tail ($(d_{\max} - d_{50})d_{50}^{-1}$)
$CV_{d_{50}}$	Coefficient of variation in median dispersal distance (d_{50}), calculated by subtracting the 2.5th percentile from the 97.5th percentile of all d_{50} and dividing by \bar{d}_{50}

was linear, only runs with $N > 0$ were used in regression analyses. In addition, we excluded from analysis any treatment combinations for which the maximum dispersal distance (\bar{d}_{\max}) was greater than the width of the grid (127 cells) or the median dispersal distance (\bar{d}_{50}) was less than one cell. Finally, we deleted treatments for which scale was unimportant when using habitat amount to predict abundance. We considered scale of effect unimportant when the difference in AIC between the “best” scale and the “worst” scale was less than 7 (Burnham and Anderson 2002).

Relationship between scale of effect and species traits

We used multiple linear regressions to summarize the relationships between scale of effect and experimental treatments (dispersal distance, reproductive rate, movement behavior). The analysis was performed twice, once with median dispersal distance used to summarize dispersal distance and once with maximum dispersal distance. All two-way interactions were included in the models. Because of the large sample sizes available in simulation models, small differences can yield statistically significant but not necessarily biologically meaningful results (Zollner and Lima 1999). Thus, instead of focusing on p -values and F -statistics, we provide the percent sum of squares

(%SS) of predictors to indicate the percent of the variation explained by independent variables (Fletcher 2006).

That increased dispersal distance will increase the area over which individuals (and populations) interact with the landscape is an intuitive concept, but reproductive rate and movement behavior were expected to influence scale of effect indirectly through their influences on secondary outcomes such as population size, size of the dispersal kernel tail, and variation in dispersal distances. To understand these indirect effects we therefore examined the relationships between experimental treatments and these secondary outcomes, and the relationships between secondary outcomes and scale of effect, using multiple linear regression models (Supplementary Material).

Results

As expected, dispersal distance was the strongest predictor of scale of effect, whether median dispersal distance (%SS = 46.8 %, Table 4) or maximum dispersal distance (%SS = 51.9 %, Table S1) was considered. Movement behavior was the next most important predictor and reproductive rate was the least important (Tables 4 and S1).

Scale of effect strongly increased with dispersal distance (Fig. 3). To report the relationship between scale of effect and dispersal distance in terms that are most useful to practitioners, we express the relationship as a ratio. We found this ratio by dividing the expected scale of effect (i.e. the regression lines in Fig. 3) by the dispersal distance (median or maximum, see Figure S2). In most cases (i.e. for medium to large dispersal distances $\bar{d}_{50} \geq 5$ cells or $\bar{d}_{\max} \geq 50$ cells) and when species were not gap avoidant), the scale of effect ranged from 3.94 to 8.72 times the median dispersal distance and 0.28–0.54 times the maximum dispersal distance (Figs. 3 and S2, Table S2). For species with short dispersal distances ($\bar{d}_{50} < 5$ cells or $\bar{d}_{\max} < 50$ cells), the ratio of scale of effect to median and maximum dispersal distances was often higher than for those with longer dispersal distances ($S^* \bar{d}_{50}^{-1} = 4.50 - 18.49$; $S^* \bar{d}_{\max}^{-1} = 0.12 - 0.74$).

Given the same dispersal distance and reproductive rate, RS, HS, and DHS resulted in similar scales of effect, but DHSG dramatically reduced the scale of effect to between 0.19 and 0.47 times the scale found for other movement behaviors (Figs. 3 and S2, Table S2). Furthermore, DHSG often resulted in no discernible scale of effect; 73 % of treatments with DHSG resulted in $\Delta AIC \leq 7$ between best and worse scales (Fig. 4).

The influence of HS on scale of effect was complicated because the outcome depended on whether median or maximum dispersal distances were

considered (Figs. 3 and S2, Table S2). Species using HS had the largest scales of effect when median dispersal distances were considered; Scales with HS were 1.07–1.47 times greater than the treatment with the next greatest scales of effect, RS. Scales of effect were generally smaller but overlapped with RS (HS was 0.18–1.02 times RS) and DHS (HS was 0.25–1.29 times DHS) when maximum dispersal distances were considered.

The remaining differences among groups were relatively minor (Figs. 3 and S2, Table S2). DHS led to scales that were barely smaller than scales found for RS (i.e. DHS was 0.79–0.97 times RS when controlling for median dispersal distances). Increased reproductive rate led to slightly decreased scales of effect; Species with $R_0 = 4.5$ had scales that were 0.63–0.90 times those of species with $R_0 = 1.5$ when controlling for median dispersal distances.

Movement behavior explained the most variation in secondary outcomes (Table S3). Informed movement behavior caused strong increases in population size ($RS < HS < DHS < DHSG$), nonlinear variation in the size of the dispersal kernel tail ($RS \leq DHSG < DHS \ll HS$), and increased variation in dispersal distances ($RS < HS = DHS \ll DHSG$, Figure S3). Reproductive rate had relatively little impact on secondary outcomes; its largest association was a slight positive influence on population size (Figure S3).

The secondary outcome with the strongest association with scale of effect was population size (Figure S4). Population size had a strong negative association with scale of effect. The size of the dispersal tail had a positive association with scale of effect when median dispersal distance was included in the model, but a slightly negative association with scale of effect when maximum dispersal distance was included in the model. Variation in dispersal distances was weakly to moderately negatively related to scale of effect (Figure S4).

Discussion

Our results support the common belief among researchers that the scale of effect is primarily a function of species mobility (Holling 1992; Carr and Fahrig 2001; Ricketts et al. 2001; Horner-Devine et al. 2003). Importantly, we quantified this relationship, allowing practitioners to estimate the scale of effect in

Table 4 Results of multiple linear regression of scale of effect (S^*) on median dispersal distance (\bar{d}_{50}), reproductive rate (R_0) and movement behavior (MOVE)

Predictors ^a	Direction of effect	df	%SS
\bar{d}_{50}	+	1	46.8
R_0	–	3	4.1
MOVE	Relative to RS: HS+, DHS–, DHSG–	3	39.0
\bar{d}_{50} : R_0		3	0.5
\bar{d}_{50} : MOVE		3	4.4
R_0 : MOVE		9	0.5
R^2 (%)			94.2

%SS can be interpreted as the amount of variation explained by each predictor. These outcomes are similar for a model using \bar{d}_{\max} instead of \bar{d}_{50} (Table S1)

^a Predictors are described in Table 1

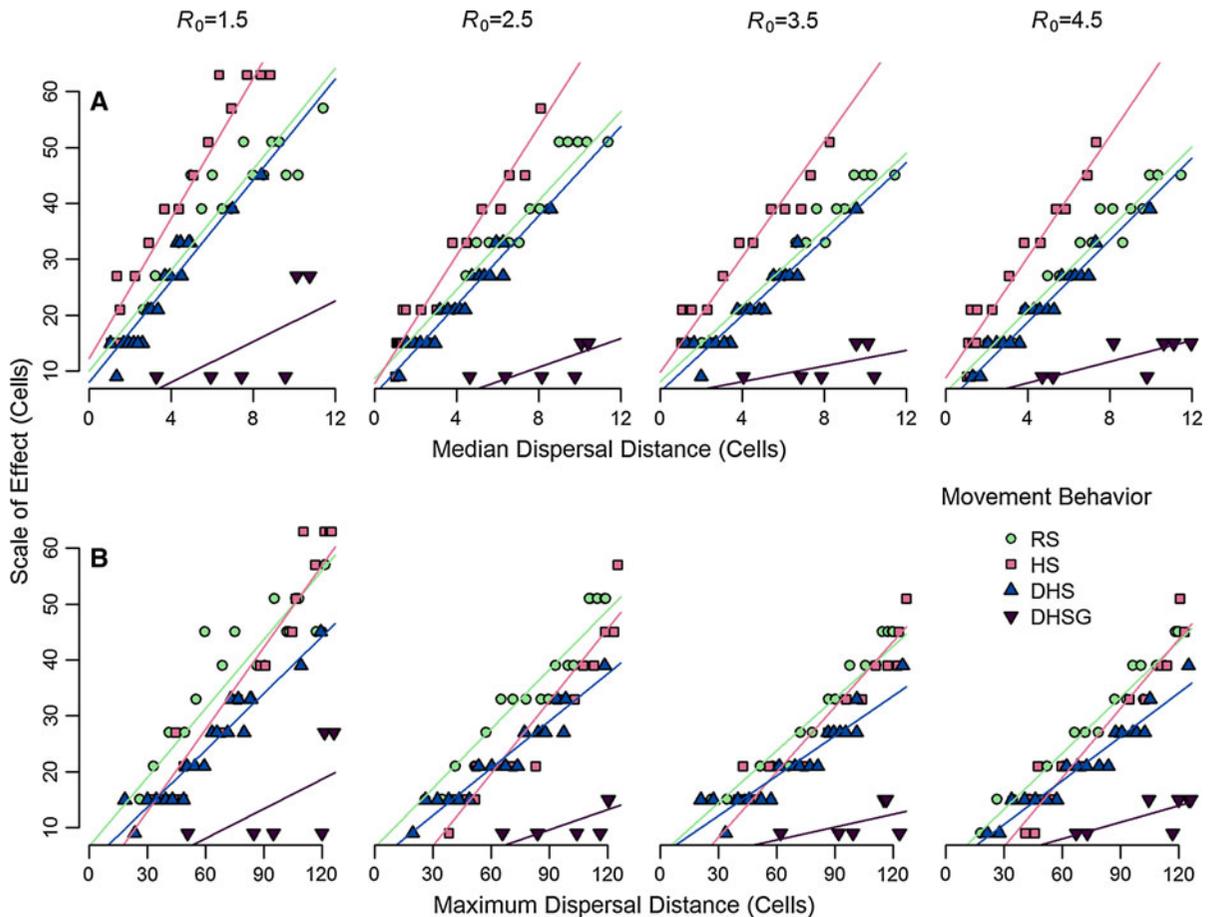


Fig. 3 Relationship between scale of effect (S^* , landscape radius) and movement behavior, reproductive rate (R_0), and **A** median dispersal distance (\bar{d}_{50}) or **B** maximum dispersal distance (\bar{d}_{max}). Movement behaviors (*RS* random settlement, *HS* habitat settlement, *DHS* density-dependent habitat

settlement, *DHSG* density-dependent habitat settlement with gap-avoidance; see definitions in Table 1) are distinguished by color and point shape. Plots depict results with increasing reproductive rate (R_0) from left to right. (Color figure online)

advance of a study: in most cases landscapes should be measured at a radius that is 4–9 times the median dispersal distance or 30–50 % the maximum dispersal distance of the species of interest. This is the first study to generate quantitative predictions concerning the scale at which species respond to landscape structure.

Our study shows the potential for movement behavior to alter the scale of effect of the landscape. Most notably, scale is not important when a species avoids movement in the matrix. The absence of a clear scale of effect when species were gap-avoidant probably occurred because gap avoidance caused dispersal distances to vary widely as a function of the particular landscape context experienced by individual dispersers. For example, dispersal distances of

gap-avoidant species were more strongly influenced by percent cover than other species (data not shown). There was an identifiable scale of effect for gap-avoidant species with large dispersal distances. This most likely occurred because gaps in habitat were less likely to be “noticed” by individuals, i.e., individual steps were more likely to span gaps in habitat. In other words, increased step size led to a larger “functional grain” or resolution at which individuals responded to spatial heterogeneity (Baguette and Van Dyck 2007).

Our data supported the previously unexplored hypothesis that increased population growth rate can reduce the scale of effect. Surprisingly, this effect was more evident with movement behavior treatments than with reproductive rate treatments. Informed

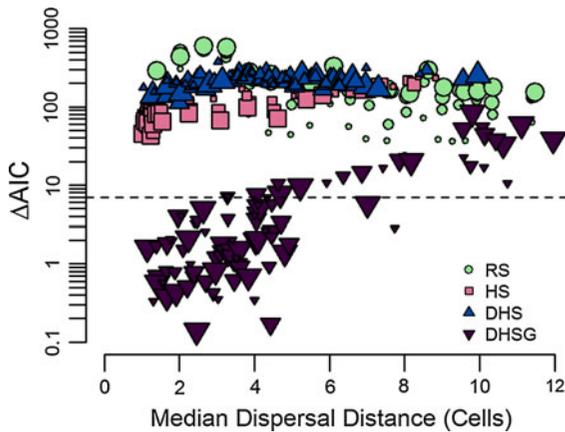


Fig. 4 The influence of median dispersal distance, movement behavior and reproductive rate on the strength of evidence for a scale of effect ($\Delta AIC = AIC_{best} - AIC_{worst}$). Treatment combinations with $\Delta AIC \leq 7$ (the dashed line) showed little evidence of a distinct scale of effect when describing the relationship between habitat amount and population abundance. These treatment combinations were eliminated from analysis. Movement behaviors (RS random settlement, HS habitat settlement, DHS density-dependent habitat settlement, DHSG density-dependent habitat settlement with gap-avoidance) are distinguished by color and point shape. Point size indicates reproductive rate (smallest = 1.5, largest = 4.5). (Color figure online)

movement behavior had a much stronger positive influence on population size than did reproductive rate, presumably because of lower dispersal mortality with informed movement. Populations with gap-avoidance, in particular, were consistently near carrying capacity. A similarly positive effect of gap-avoidance on population density was found in a previous model (Tischendorf et al. 2005). In our model, both gap-avoidance and population size were associated with a strongly decreased scale of effect, suggesting that population size (and the underlying population growth rate that leads to high population size) may be a strong negative predictor of scale of effect. Furthermore, the much larger impact of movement behavior relative to reproductive rate on both population size and the scale of effect emphasizes that loss of individuals to unsuccessful dispersal can have major population consequences (e.g. Fahrig 2001). That high population growth rate is negatively associated with scale of effect is a novel prediction and requires empirical support.

Although a simple description of species' mobility (e.g. median or maximum dispersal distance) was

generally a good predictor of scale of effect, more precise predictions of scale of effect depend on the variation in dispersal distances within the population (i.e. the full dispersal kernel). This supports the idea that single descriptors of dispersal may not always be adequate, and that variation in dispersal should be considered (Baguette and Van Dyck 2007; Clobert et al. 2009). In our model, habitat settlement resulted in particularly fat-tailed dispersal, such that the maximum dispersal distance was much longer than the median dispersal distance. As a result, habitat settlement was positively associated with scale of effect when median dispersal distance was held constant, but was slightly negatively associated with scale of effect when maximum dispersal distance was held constant. This means that for a species known to have fat-tailed dispersal, the scale of effect is near the high end of the range of possibilities when median dispersal is considered (~ 9 times the median dispersal distance), but closer to the low end of the range of possibilities for maximum dispersal distance ($\sim 30\%$ the maximum dispersal distance).

The scale of effect of some real species will be affected by multiple species traits simultaneously, as reflected in our simulations. Density-dependent habitat settlement provides a good example. Density-dependent habitat settlement resulted in fat-tailed dispersal kernels relative to RS and also much larger population sizes. These two secondary outcomes may have counteracted each other (fat-tails increased the scale of effect, but large population sizes decreased the scale of effect), leading to our result that scale of effect for density-dependent habitat settlement was similar to the scale of effect for RS given the same dispersal distances.

We caution that the effects of processes which were not included in our model should be considered before important decisions are made. For example, a potentially important influence on scale of effect is landscape structure itself. In our study, we varied habitat amount across nearly the entire possible range (5–95%), but many species are restricted to landscapes with a narrower range of habitat amounts (10–50%, for example). Because species' settlement and movement is often responsive to landscape structure, variation in habitat amount can be expected to alter dispersal distances. Furthermore, habitat amount has a well-documented positive effect on population size (Fahrig 2003). Therefore, habitat

amount itself may be a strong influence on scale of effect. Other variables that might influence the scale of effect include interspecific interactions and habitat quality. Both could influence population growth rate and movement behavior in ways that could alter the scale of effect.

We offer a few suggestions when using our model to guide research design and management policy. First, the predictions from our model are best applied to the scale of effect of habitat amount because other aspects of landscape structure (e.g. habitat fragmentation, landscape heterogeneity) may affect a species most strongly at different scales (Eigenbrod et al. 2008; Smith et al. 2011). Even so, because most studies indicate that habitat amount will usually have a greater effect on populations than other measures of landscape structure (reviewed in Fahrig 2003) our results provide a quantitative estimate of the most important scale of effect of the landscape. Second, the conclusion that scale of effect depends on life history suggests that habitat evaluation at multiple scales will be necessary when assessing habitat for species with disparate dispersal abilities and movement behaviors (e.g. insects and birds). Third, although we considered a small, circular sampling area, the scale of effect should apply to population assessments in large, irregularly shaped regions as well. If, for example, a practitioner needs to evaluate the effect of landscape on a species within an entire park, our model can help determine what portion of the landscape surrounding a park should be included in habitat assessments. We expect land within a buffer as wide as the radius of the scale of effect surrounding a park to influence a species of interest within a park.

Acknowledgments We thank Lutz Tischendorf for his modelling suggestions and for his assistance with NetLogo. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) grants to LF. We thank Nathan Jackson and three anonymous reviewers for their helpful suggestions.

References

- Akçakaya HR (1991) A method for simulating demographic stochasticity. *Ecol Model* 54:133–136
- Baguette M, Van Dyck H (2007) Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecol* 22:1117–1129
- Barton KA, Phillips BL, Morales JM, Travis JMJ (2009) The evolution of an ‘intelligent’ dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118: 309–319
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225
- Bowman J (2003) Is dispersal distance of birds proportional to territory size? *Can J Zool* 81:195–202
- Bowman J, Jaeger JAG, Fahrig L (2002) Dispersal distance of mammals proportional to home range size. *Ecology* 83: 2049–2055
- Brennan JM, Bender DJ, Contreras TA, Fahrig L (2002) Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Liu J, Taylor WW (eds) Integrating landscape ecology into natural resource management. Cambridge University Press, Cambridge
- Burnham KP, Anderson DR (2002) Model selection and inference: a practical information-theoretic approach. Springer, New York
- Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. *Conserv Biol* 15: 1071–1078
- Chapman DS, Dytham C, Oxford GS (2007) Modelling population redistribution in a leaf beetle: an evaluation of alternative dispersal functions. *J Anim Ecol* 76:36–44
- Clobert J, Galliard J-FL, Cote J, Meylan S, Massot M (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* 12:197–209
- Eigenbrod F, Hecnar SJ, Fahrig L (2008) The relative effects of road traffic and forest cover on anuran populations. *Biol Conserv* 141:35–46
- Fagan WF, Lynch HJ, Noon BR (2010) Pitfalls and challenges of estimating population growth rate from empirical data: consequences for allometric scaling relations. *Oikos* 119: 455–464
- Fahrig L (2001) How much habitat is enough? *Biol Conserv* 100:65–74
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515
- Fletcher RJ (2006) Emergent properties of conspecific attraction in fragmented landscapes. *Am Nat* 168:207–219
- Guo YL, Ge S (2005) Molecular phylogeny of *Oryzaeae* (Poaceae) based on DNA sequences from chloroplast, mitochondrial, and nuclear genomes. *Am J Bot* 92:1548–1558
- Hawkes C (2009) Linking movement behaviour, dispersal and population processes: is individual variation a key? *J Anim Ecol* 78:894–906
- Holland JD, Fahrig L, Cappuccino N (2005a) Body size affects the spatial scale of habitat–beetle interactions. *Oikos* 110: 101–108
- Holland JD, Fahrig L, Cappuccino N (2005b) Fecundity determines the extinction threshold in a Canadian assemblage of longhorned beetles (Coleoptera: Cerambycidae). *J Insect Conserv* 9:109–119
- Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol Monogr* 62:447–502
- Horner-Devine MC, Daily GC, Ehrlich PR, Boggs CL (2003) Countryside biogeography of tropical butterflies. *Conserv Biol* 17:168–177

- Jackson HB, Baum K, Robert T, Cronin JT (2009) Habitat-specific and edge-mediated dispersal behavior of a saproxylic insect, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae). *Environ Entomol* 38:1411–1422
- Jetz W, Carbone C, Fulford J, Brown JH (2004) The scaling of animal space use. *Science* 306:266–268
- Kareiva PM, Shigesada N (1983) Analyzing insect movement as a correlated random-walk. *Oecologia* 56:234–238
- Kot M, Lewis MA, van den Driessche P (1996) Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042
- Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, Stouffer PC, Gascon C, Bierregaard RO, Laurance SG, Sampaio E (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv Biol* 16:605–618
- Nichols RA, Hewitt GM (1994) The genetic consequences of long-distance dispersal during colonization. *Heredity* 72:312–317
- Okubo A (1980) *Diffusion and ecological problems: mathematical models*. Springer, New York
- Ricketts TH, Daily GC, Ehrlich PR, Fay JP (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv Biol* 15:378–388
- Ries L, Debinski DM (2001) Butterfly responses to habitat edges in the highly fragmented prairies of central Iowa. *J Anim Ecol* 70:840–852
- Ritchie ME (2010) *Scale, heterogeneity, and the structure and diversity of ecological communities*. Princeton University Press, Princeton
- Roland J, Taylor PD (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386:710–713
- Saupe D (1988) Algorithms for random fractals. In: Peitgen H-O, Saupe D (eds) *The science of fractal images*. Springer, New York, pp 71–113
- Schultz CB, Crone EE (2001) Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892
- Smith AC, Fahrig L, Francis CM (2011) Landscape size affects the relative importance of habitat amount, habitat fragmentation, and matrix quality on forest birds. *Ecography* 34:103–113
- Tischendorf L, Grez A, Zaviero T, Fahrig L (2005) Mechanisms affecting population density in fragmented habitat. *Ecol Soc* 10:13
- Tittler R (2008) *Source–sink dynamics, dispersal, and landscape effects on North American songbirds*. Dissertation, Carleton University, Ottawa
- Turchin P (1998) *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Inc., Sunderland
- Vance MD, Fahrig L, Flather CH (2003) Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. *Ecology* 84:2643–2653
- Wilensky U (1999) Netlogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston
- With KA, King AW (1999) Extinction thresholds for species in fractal landscapes. *Conserv Biol* 13:314–326
- Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030