The Effect of Small-Size Habitat Disturbances on Population Density and Time to Extinction of the Prairie Vole

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Abstract

We present a study, based on simulations with SERDYCA, a spatially-explicit individual-based model of rodent dynamics, on the relation between population persistence and the presence of numerous isolated disturbances in the habitat. We are specifically interested in the effect of disturbances that do not fragment the environment on population persistence. Our results suggest that the presence of disturbances in the absence of fragmentation can actually increase the average time to extinction of the modeled population. The presence of disturbances decreases population density but can increase the chance for mating in monogamous species and consequently, the ratio of juveniles in the population. It thus provides a better chance for the population to restore itself after a severe period with critically low population density. We call this the "disturbance-forced localization effect".

Keywords: *discrete simulation, fragmentation, habitat, persistence, time to extinction, percolation*

1 Introduction

Human activities disrupt species habitats in various ways. Oil exploration and development cause fragmentation of natural environments through the building of roads and aboveground pipelines which represent barriers to smaller species. Oil development activities often lead to the occurrence of oil or brine spills of various sizes [7] which cause long-term damage to the affected habitat sites. These polluted areas are avoided by some species [7]. This leads to a long-term modification of the habitat geometry that could affect the whole ecosystem by causing extinction of local herbivore populations and subsequently, of their predators.

Clearly, disturbances such as the above always create habitat loss and can lead to habitat fragmentation in some cases. The role of habitat loss and fragmentation on species survival has been the topic of a fast increasing volume of scientific literature, both from the applied ecologist's and modeler's point of view (see [1, 10, 5, 6, 2], among many others). Habitat loss is widely accepted as the leading cause of local population extinctions, [3, 8, 9]. It was ranked as the most serious threat for species diversity in the comprehensive assessment of Wilcove et al. [17]. In a recent modeling study [12] of vole populations we quantified the dependence of the population's average time to extinction (ATE) on habitat area (A) for undisturbed, continuous habitats of varying sizes and found that the ATE versus A curve is strictly increasing. Thus, our theoretical study confirms that decreasing habitat area leads to decreased population persistence.

Habitat fragmentation is defined as the process of subdividing a continuous habitat into smaller, isolated pieces [1]. As a result of this process, animal movements between the fragments are either impossible or impeded and local populations on the fragments become isolated. Habitat fragmentation inevitably causes habitat loss and separating the effects of these two factors on species persistence has been rarely attempted as was pointed out by Simberloff [15]. Even in cases when this was done, results were contradictory. We can conclude that the few studies were not performed and compared in a sufficiently detailed way to understand the cause for the discrepancies. Simberloff pointed to some mechanisms that could lead to effects caused by the mere presence of fragmentation on species persistence. Basically all proposed mechanisms boiled down to effects of the non-habitat sites on the properties of the remaining habitat fragments. Some of these mechanisms can have negative and other can have positive effect on species persistence and these can vary across species.

Our vole study relating ATE to habitat area implied that fragmentation should lead to decreased persistence even when the total habitat area of the fragmented habitat is equal to the area of an unfragmented habitat simply because the ATE on each fragment will be smaller than the ATE on the unfragmented habitat. We must note that our conclusions are based on a restricted model that does not take into account the presence of multiple species. Actually fragmentation could have a beneficial effect on one species by contributing to the extinction of a competing (for resources) species.

During frequent oil exploration drilling, local disturbances such as oil and brine spills can be large in number but small in size. If their frequency is below a certain threshold, they will not cause fragmentation of the habitat but will change its geometry and will cause habitat loss. Spills can be one of many mechanisms that cause such habitat modification. However, we need a term that denotes a relatively small disturbance area within the grass-type habitat, in a way similar to the term "gap" used in forest patch dynamics models [14] but also bearing connection to the long-term damage effect that makes the site of the "spill" unsuitable and therefore avoided by the species under study. Thus, we shall continue to use the term "spill" with this more general meaning. Percentages of "spills" above the threshold would cause more and more frequently

habitat fragmentation and will decrease the ATE. In this study we investigate the effect of various percentages of "spills on the ATE.

We perform our study via simulations with SERDYCA, a spatially-explicit, data-driven individual-based model of rodent dynamics [12], customized for prairie vole (*Microtus Ochrogaster*) populations. SERDYCA is a virtual ecological environment in which we perform *in silico* experiments and observations. To separate the "spill" effect from the habitat area loss effect, we consider series of virtual square landscapes with varying areas but with the same habitat area. As it is with any modeling approach, our conclusions should not be treated as predictions or absolute truth but rather as scientific hypotheses that need further testing *in vivo*. Our simulations establish that increasing the ratio of "spill" disturbance leads to decline in population density but "spill" percentages up to a certain threshold level exert a positive effect on the persistence of prairie vole populations by increasing the average extinction time. We offer an explanation for these results. The problem, the results and the interpretations obtained from them are, to the best of our knowledge, new and unique.

2 Statement of problem

2.1 Definitions

We use a routine representation of a landscape as a collection of square cells [5, 10]. Each cell has the size of the home range of the considered species (in the case of voles it is equal to 30m^2). Each cell is of one of two types: *habitat* or *non-habitat*. The habitat cells are assumed to contain varying amounts (that could be also zero) of vegetation consumed by the modeled species. The collection of habitat cells represents the *habitat*. The number of habitat cells is called the *habitat size*. The non-habitat cells either contain unsuitable vegetation but can be entered by the animals or are completely unsuitable for habitation and are by all means avoided by them. In the first case the non-habitat cells are called *penetrable*, in the second - *impenetrable*. We call the impenetrable non-habitat cells *"spills"* referring to the original motivation of our study. Thus, in this study each "spill" is of the size of a home range. All eight square cells surrounding a cell are considered its neighbors and an animal can move from a cell to each of its penetrable neighbors. Thus, both the "nearest" (sharing an edge) and the "next-to-nearest" neighbors (sharing a corner) of a cell are considered cell neighbors in our model. A *path* is defined as a set of cells, such that each one has a neighbor belonging to the set. A *nearest-neighbor path* is defined as a path such that any two neighboring cells in it are nearest neighbors. Two habitat cells are called *connected habitat cells* if they belong to a path containing only habitat cells. The habitat is *connected* if all habitat cells are connected. If a habitat is not connected, each connected subset of it is called a *fragment*.

We keep the number A_h of habitat cells fixed and choose increasing numbers A_n of "spill" cells distributed randomly among habitat cells, so that $A_h + A_n$ is an exact square. Each such square is called a *landscape of size* $A_h + A_n$. There are many landscapes with the same size having different spatial distributions of habitat and "spill" cells, called *landscape patterns*. We denote each of the various landscape patterns as D_α, where α varies between 1 and the maximum number of possible different patterns, $N(A_h, A_n)$.

The simulation model is initialized by creating an initial animal distribution of model animals distributed over the landscape at the initial time 0. Initially, each spatial cell contains a certain, randomly generated number (that could be zero) of animals with randomly generated characteristics (age, size, etc.). Further, for the same animal distribution, a certain quantity of landscape patterns is created in a random manner.

For each given pattern D_α and initial animal distribution $P(0)$, we perform a simulation for a fixed time T_{max} and denote by $T[A_h, A_n, D_\alpha, P(0)]$ the time for which the population with the given initial distribution dies out (the total number of individuals becomes 0). It is implicitly assumed that $T < T_{max}$ but if the population persists up to time T_{max}, then we set $T[A_h, A_n, D_\alpha, P(0)] = T_{max}$.

We define the average time of extinction of the population depending on the landscape size $A_h + A_n$ and the given initial animal distribution as

$$ATE(A_h + A_n) = \frac{\sum T[A_h, A_n, D_\alpha, P(0)]}{N(A_h, A_n)} \tag{2.1}$$

where the sum is taken over all possible spatial patterns.

Further, if $P_\beta(0), \beta = 1, ..., M(A_h, A_n)$ are all possible initial spatial animal distributions for a landscape of size $A_h + A_n$, we define the *average time to extinction associated with landscape size* $A_h + A_n$ as

$$A\hat{T}E(A_h + A_n) = \frac{\sum T[A_h, A_n, D_\alpha, P_\beta(0)]}{N(A_h, A_n).M(A_h, A_n)} \tag{2.2}$$

where the sum is taken over all possible spatial patterns and all possible animal distributions.

Finding the exact value of $A\hat{T}E$ is theoretically possible, because all the possible initial animal and "spill" distributions are finite. In practice however, it is impossible in reasonable time to perform even a comparable number of simulations covering the variety of initializations because their number is enormous. For example, for a fixed animal distribution, the number of possible "spill" distributions is $\frac{(A_h+A_n)!}{A_h!A_n!}$. This number has to be multiplied by the number of possible animal distributions which is at least 2^{A_h}. Even for small landscapes this number can be huge. Keeping in mind that the larger the landscape, the longer the time for a single simulation (with SERDYCA for landscapes with 100^2 cells the calculation time is 1 min/simulation but for a landscape with 250^2 cells it is 13 minutes/simulation), in practice, we can perform only a relatively small amount of simulations in reasonable time and calculate average times which represent approximations to the ATE and $A\hat{T}E$.

2.2 Effect of "spill" disturbances on the ATE

Results from simulations with SERDYCA on homogeneous landscapes, i.e. ones with no spills ($A_n = 0, \alpha = 1$), reported in [12], showed that the population persistence, measured by the $A\hat{T}E(A_h)$, is positively correlated with the habitat size A_h. For a large amount of simulations with different homogeneous habitat areas and various values of predation levels, the $A\hat{T}E$ was a strictly increasing function of area.

When landscapes with "spills" are considered, two separate effects may occur. First, the presence of "spills" may fragment the landscape. If the experimentally found positive correlation between habitat size and $A\hat{T}E$ is universally true, any formation of fragments between which the individuals from a given species do not migrate, would lead to the reduction of the $A\hat{T}E$ of this species because the considered population is subdivided into local subpopulations with smaller habitat sizes and each of them has a shorter $A\hat{T}E$.

Second, it is possible that "spills" are distributed among the habitat cells so that the habitat remains connected. This is the case of interest in this study. It is unclear whether the very presence of "spills" has an effect on the persistence. If the size of the habitat is the only factor affecting the ATE of any population then for all connected habitats with fixed A_h, the relations $ATE(A_h) = ATE(A_h + A_n)$ and $A\hat{T}E(A_h) = A\hat{T}E(A_h + A_n)$ should hold true for all A_n. If the presence of "spills" has some effect on persistence, then these relations will not hold for some of the unfragmented habitats.

The probability that the first or second case will or will not occur is higher when the ratio $\rho = \frac{A_n}{A_n+A_h}$ is, respectively, relatively large or small. When $\rho \approx 0$, the non-habitat cells are too few to fragment the habitat, when $\rho \approx 1$ the habitat cells are scattered among the non-habitat ones in most of the cases and the habitat is highly fragmented. To illustrate, Figure 1 represents three landscapes of 50^2 habitat square cells each and an increasing number of non-habitat cells representing, respectively, 14%, 52% and 70% of the total landscape. While the first habitat is connected, the second has a small amount of small isolated fragments, but most of the remaining habitat is connected, and the third consists only of numerous small isolated fragments. For some intermediate "critical" value ρ_c of ρ the probability of occurrence of more than one fragment of habitat becomes relatively high. Thus for $\rho > \rho_c$ we would expect that the ATE will drop compared to the ATE in non-fragmented habitat of equal size.

The value ρ_c can be expected to be close to the site percolation threshold [16] for square lattices (≈ 0.592746, [16]). This is the value for which an infinite nearest neighbor path appears in an infinite lattice. For a "large" finite square lattice and $\rho > \rho_c$ the probability of a nearest neighbor path connecting two of the square's boundaries is closer to 1. Closest-neighbor paths connecting two boundaries would split the square in at least two fragments as is easy to see, unless the path coincides with a boundary, which is a case of probability close to zero.

In this paper our objective is to study the relation between $ATE(A_h + A_n)$ and $ATE(A_h)$ for given A_h and initial animal distribution and for increasing values of A_n. While insights from percolation theory lead us to expect that $ATE(A_h + A_n)$ would drop below A_h if ρ is above 0.6, we do not have an initial hypothesis for the behavior of this relation for ρ below the threshold.

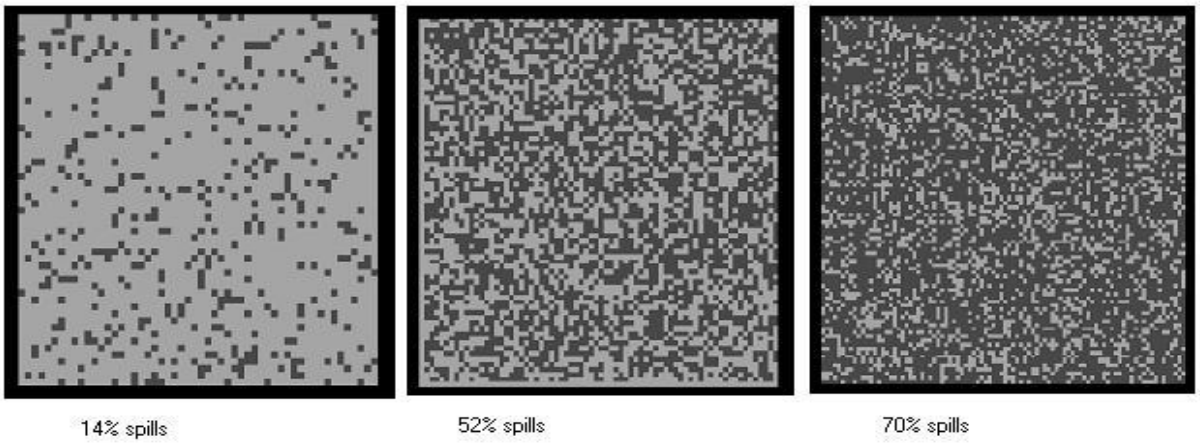

Figure 1: Landscapes of 50^2 habitat cells (grey) each and an increasing number of non-habitat and impenetrable cells (dark gray) representing, respectively, 14%, 52% and 70% of the total landscape. The black boundary consists of penetrable non-habitat cells.

2.3 Ecological complexity issues

Most of the modeling studies of fragmentation and habitat loss have been done with simple abstract models that take into consideration a small amount of spatially dependent factors (for a review see [4]). We find such an approach rather restrictive.

The dependence of the persistence of a species on the geometry of the space it occupies is based on the action of numerous space-related factors. For example, persistence is strongly dependent on the availability of food (vegetation) which is usually distributed unevenly in space. When food resource is low, animals move from location to location in search of forage. These movements are determined by the geometry of the available space and by the bioenergetic status of the animal. The animal's bioenergetic status determines how long it will survive while searching for food in an environment with a specific pattern determined by the specific distribution of habitat and non-habitat areas. On the other hand the bioenergetic status depends on the energy the animal spends and on whether the animal's metabolic needs have been met, both of which depend on the specific pattern of the landscape. Similarly, the mating and offspring production process depend on the availability and geometry of the habitat. The life span of each individual thus depends on the characteristics of the space it occupies through a variety of factors. The persistence of the population is an emerging property of the livelihoods of the individual animals.

Expressed in mathematical form, if μ is a measure of population persistence and if persistence depends on factors $\Phi_1, ..., \Phi_k$, each of which depend on some spatial characteristic σ (like, for example, the percentage of "spills" on the landscape), then the dependence of μ on σ is conditioned by the dependencies of $\Phi_i, i = 1, ..., k$.

$$\mu(\sigma) = \mu(\Phi_1(\sigma), ..., \Phi_k(\sigma))$$

Some of the factors in this equation might be especially sensitive to spatial patterns. Omitting to consider such factors will produce incorrect estimates.

Thus, a true assessment of the dependence of population persistence on spatial characteristics requires to consider the complexity of interwoven factors that act upon the population and depend on spatial patterns (to the extent of our knowledge of these). For example, such factors include, but are not limited to, vegetation availability, metabolic requirements of the species, mating mechanism, predation, movement patterns, etc. Such an effort requires a spatially-explicit approach. Persistence should be quantified in a suitable manner allowing comparison between various cases. One way to quantify persistence is by measuring the time to extinction of the model population. Continuous models are not suitable for this purpose because they do not produce finite times of extinction. Thus, a discrete complex spatially-explicit individual-based model is best suited for studying the persistence of a population.

With these considerations in mind, we studied the effect of habitat heterogeneity created by various

quantities of randomly distributed "spills" in landscapes of constant habitat sizes on population persistence by performing simulations with SERDYCA, described shortly below.

3 Short overview of SERDYCA

3.1 Model description

A detailed description of SERDYCA (Spatially-Explicit Rodent DYnamics Computation and Analysis) is provided in [12]. SERDYCA models the availability of the vegetation the rodent forages on and the growth and decline of the rodent population over a given landscape, represented as a collection of square cells. Spatial cells can be of the following types: a) habitat cells, having the type of vegetation the modeled species consumes, b) penetrable non-habitat cells, having vegetation the modeled species would not consume and c) impenetrable, avoided by the modeled species.

The rate of change of the amount of vegetation in each cell is calculated as the sum of two quantities: the rate determined by climatic factors and the rate of grazing determined by the metabolic needs of the animals present in the cell. The first was calculated in advance by using temperature and precipitation data and the package CENTURY 4, [13] and is used as caloric equivalent input, while the second one is obtained by calculating the caloric equivalent of the metabolic needs of the animals per day and is subtracted from the first.

The metabolic need of each animal is calculated as a power function of its weight which depends on the status (pregnant, lactating, other) of the animal. The weight of each animal is calculated using a rule that takes into consideration whether its metabolic need can be met by the vegetation available in the cell and also takes into consideration the animal's age and the maximum possible weight of the species. In the case of insufficient amount of vegetation in the cell, animals lose weight and leave the cell in search of a new one.

An animal can have the status of a resident or a floater. Floaters change their cells each day until they become residents. A resident becomes a floater if it has to leave the cell because of lack of forage or when it reaches adulthood. A male floater becomes a resident if he finds a cell with no male residents but having a female resident and having enough vegetation to meet its need. A female floater becomes a resident if it finds a cell with no female residents that meets its needs. Adult (over the maturation age) male and female residents produce offspring. Pregnancies last an amount of time called the generation time and can occur only in the months February-November. Births produce offspring equal to the litter size and the offspring is 50% male and 50% female.

Death occurs if an animal has been starving for a certain maximum amount of days or if it has lost too much weight, if it has become a victim of predation or when it reaches the maximum age for the species.

Predation is density-dependent: a certain percentage of animals is removed from the population each day. The percentage is proportional to the current density of animals and the constant of proportionality is different for adult and juvenile animals, currently being twice larger for juveniles.

The manner in which floaters choose a new cell is, what we call, "conditionally random". Floaters prioritize the quality of cells giving highest preference to neighbor habitat cells with no residents and availability of forage, second preference to neighbor habitat cells with no residents, even if forage is insufficient, third preference to penetrable neighbor non-habitat cells and last preference to cells having residents. Floaters move in a randomly chosen neighbor cell of the highest available preference.

Thus, if a floater is located in a cell that has a neighboring non-habitat penetrable cell and if all other neighboring habitat cells have residents, the floater will move into the non-habitat cell. In the cases when the non-habitat penetrable cell is on the boundary of the modeled region the animal leaves the region forever. This mechanism accounts for dispersion due to population pressure and territorial competition. If the boundary of the region has several layers of penetrable non-habitat cells, the floater might wander on the boundary with the possibility of returning to the habitat by finding an empty habitat cell or might disperse out of the region.

The model uses discrete time steps of one day. At time 0 it starts with a random spatial distribution of animals of randomly generated age, weight and gender.

The model uses metabolic and other data for the prairie vole obtained from a vast literature study and is based on published observations on the life histories of prairie voles. It was implemented in C++ with a Python graphic user interface (GUI). The GUI is a new feature of the model. The GUI is a convenient tool to define landscapes with "spills" or structures creating fragmentation. Given the coordinates of a

certain region on the landscape and the desired number of "spills", the GUI sets the configuration of the simulation so that the given amount of "spills" is distributed in the predefined region in a random manner for each simulation experiment. The GUI also has a landscape editor that allows the modification of an already loaded landscape, for example making it fragmented, redefining the vegetation types of cells, etc. The editing can be done graphically by drawing on the screen curves, rectangles and circles.

Most of the parameters used in SERDYCA for the prairie vole simulations are relatively well established values. The coefficients modeling the density dependent predation are the only completely hypothetical parameters. The prairie vole maximum population density decreased with increasing the predation coefficients while the ATE first increased, reaching a maximum and then decreased when predation increased. We established values for the predation coefficients by assuming that the adult predation coefficient is twice larger than the juvenile coefficient and then calibrating the model by fitting a value for the adult coefficient for which the maximum density was in the experimentally reported bounds for tallgrass prairie. Interestingly, the calibrated predation was such that it resulted in ATE close to the maximal. We named this predation level "optimal predation". The model predicts correctly prairie vole population fluctuations, both the annual locations of minima and maxima and the periodicity of the multiannual fluctuations, [11]. These results give a reasonable validation to the model.

4 Description of the simulations

The vegetation daily growth rates of tallgrass vegetation used in SERDYCA were calculated from a file containing a simulation data set for the daily dry mass quantities per m^2 for a 30 year period. The latter are obtained by using weather data for the years 1960-1990 from the Tulsa, Oklahoma airport weather station and a Konza Prairie vegetation parameter set used to initialize the model of grassland dynamics CENTURY 4 [13]. The plot of the vegetation density can be seen in a previously published paper [12].

The simulations are carried out for time $T_{max} = 30$ years (limited by the scale of the vegetation data set). Since the prairie vole life span is less than half a year, this period represents 60 generations.

Boundary conditions.

The landscape is a square region whose boundary consists of 4 layers of penetrable non-habitat cells. The landscapes represented on Figure 1 are of this type. This structure was used to ensure that animals that are at the boundary of the habitat do not disappear forever if forced to leave by population pressure. Animals might wander on the boundary and possibly find an empty cell to enter the region again. However, if this does not happen for a certain amount of time (the starvation limit) the animal perishes. The rationale for choosing the number 4 is as follows. The maximum time of full starvation of a vole is taken to be 4 days after which period the animal dies. This value was estimated from literary sources [12]. If a vole is forced to enter the boundary layers, it will either return back to a habitat cell in the course of 4 days or will die. Therefore, the need for defining boundary conditions on the outermost boundary layer disappears as animals who reach it would die anyway.

Initial conditions.

The simulations are initialized by generating random initial animal and "spill" distributions. Initially the landscape inside the boundary consists of $K = A_h + A_n$ habitat cells. The boundary then consists of $(\sqrt{K} + 8)^2 - K$ cells. The habitat cells inside the boundary are initially populated with a random number (between 0 and 2) of floaters with randomly generated initial age, weight and gender in each cell. All randomly generated animals are "floaters". A_n of these cells are randomly chosen, redefined as impenetrable ("spills") and their vegetation quantity is set to zero. Various landscapes are produced following this procedure, keeping A_h constant and varying A_n so that K is an exact square. The animals present at the polluted cells, being floaters in an unsuitable environment, will leave these cells at the first iteration time according to the rules of conditionally random choice of a new cell (see above).

The vegetation simulation data starts in January 1960 and has peaks in the summers of each year as well as minima in December or January of each year. The model assumes that the growth rates of vegetation are the same in all habitat cells; it is the different rates of grazing that produce different vegetation densities. At the initial time of the simulation all cells have the same initial vegetation density.

Persistence bottlenecks.

Some of the vegetation minima, although positive, are very close to zero. Such amounts of vegetation in each cell can support very low numbers of animals and in these months most of the animals die of starvation. The time periods following these minima serve as bottlenecks for the persistence of the population.

Depending on the distribution of "spills", the same population (starting with the same initial spatial animal distribution) persists (i.e. the total population number is not 0) for different amounts of time. The average of these times over all possible "spill" distributions is the ATE (formula (2.1)).

Simulations.

We carried out 200 simulations for landscapes of 100^2, 75^2 and 50^2 habitat cells and various amounts of "spills", while using the same initial spatial population distribution for each landscape. For each set of 200 simulations we calculated the average time to extinction and the density of the total population per hectare as well as of the densities of the adults, juveniles, floaters and settled animals. Table 1 summarizes the types of landscapes simulated.

Table 1: Types of landscapes with constant habitat size for which simulations were carried out.

Habitat size (number of habitat cells)	Percentage of "spills" from the total landscape size
50^2	0, 14 ,28, 35, 44, 52, 58, 63, 70
75^2	14, 24, 34, 41, 54, 62, 72
100^2	5, 10, 13, 18, 24, 28, 33, 38, 44, 50, 55, 60, 64, 67

All experiments were done for the "optimal" predation coefficients from [12] calibrating the model for tallgrass prairie population densities.

5 Results and interpretation

Keeping the same initial animal distribution over a landscape and performing simulations with different arrangements of equal amounts of "spills" yields a wide variety of times to extinction across the simulations. However, calculating the ATE shows definite trends.

Figure 2 summarizes the simulation results on the effect of "spill" disturbances on the ATE. Keeping in mind that all simulations were done for the same initial spatial animal distribution, let TE_0 be the time to extinction in the case with no "spills" for the fixed initial animal distribution. The "spills" do not have any substantial *negative* effect on the ATE until they become at least 50% of the total area for all the three considered habitat sizes. For "spill" percentages higher than 60% the ATE drops significantly. The sharp reduction of the ATE at these values is most probably due to the fragmentation of the habitat into a growing number of small fragments because as expected (in Section 2.2), the threshold number of $\approx$ 60% is very close to the site percolation number for square lattices. For "spill" percentages lower than the percolation threshold the habitat should be connected in most of the cases and therefore, no decrease of the ATE due to fragmentation should be expected. We could assume that whatever the observed effect of "spill" percentages below 50% on the ATE is, it should be due to the presence of "spills" and not to fragmentation as this one would rarely occur.

The observed effect is, surprisingly, positive. The ATE is slightly higher than TE_0 for the 75^2 habitat size and is substantially larger than TE_0 for the largest 100^2 habitat size. The ATE is larger than TE_0 for high "spill" percentages (30-50%) for the smallest habitat but slightly lower than this value for "spill" ratios less than 30%. Thus, the larger the habitat, the stronger the positive effect of "spill" disturbances.

Taking into account only the ATE is not sufficiently informative. If L is the number of simulations (out of all performed) for which $\mathrm{TE} \geq \mathrm{TE}_0$, let us denote these TE by $\mathrm{TE}_i^{>}, i = 1, ..., L$. If M is the number of simulations for which $\mathrm{TE} < \mathrm{TE}_0$, let us denote these TE with $\mathrm{TE}_i^{<}, i = 1, ..., M$. Then, the ATE approximation calculated from these simulations can be written as

$$\mathrm{ATE} = \frac{\sum_i \mathrm{TE}_i^{>}}{L} \frac{L}{L+M} + \frac{\sum_j \mathrm{TE}_j^{<}}{M} \frac{M}{L+M}.$$

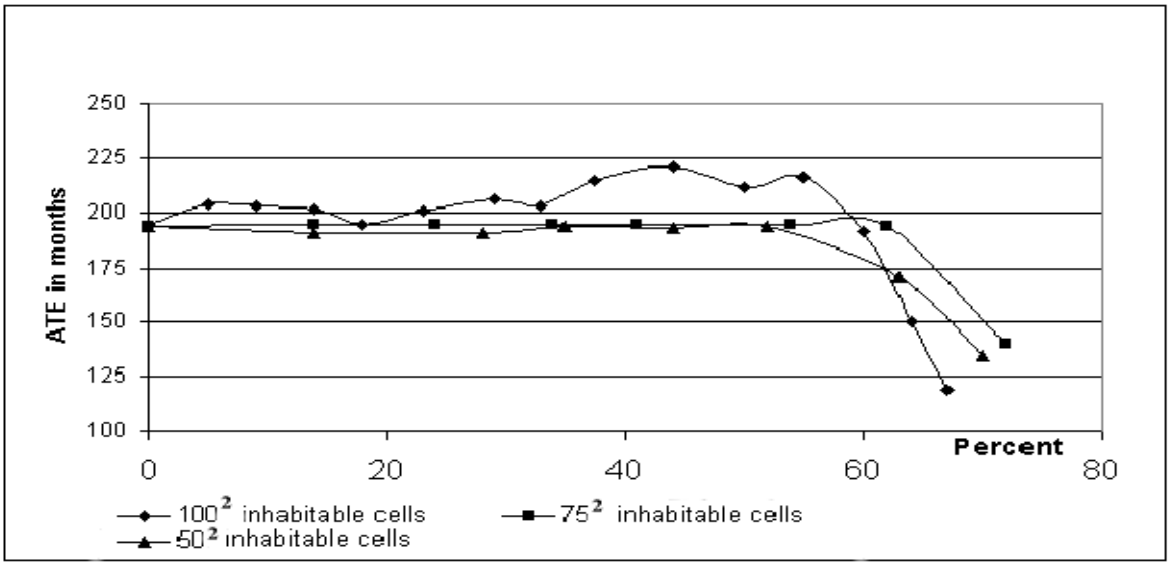

Figure 2: The dependence of the ATE on various percentages of "spills" in landscapes with the same amount of habitat. See text.

Thus, the ATE is determined by the ratios $\frac{L}{L+M}$ and $\frac{M}{L+M}$ as well as by the means $ATE^{>} = \frac{\sum_i \mathrm{TE}_i^{>}}{L}$ and $ATE^{<} = \frac{\sum_i \mathrm{TE}_i^{<}}{M}$. So, the ATE might be slightly lower than the TE_0 (as it is for the 50^2 habitat, Figure 2) but still for a certain amount of simulations $\mathrm{TE} \geq \mathrm{TE}_0$.

Figure 3 represents the percentage of simulations (out of the performed 200) for each "spill" level for which the TE was larger than the TE_0 for the landscapes with 100^2 and 50^2 habitat cells. It shows that for up to 60% "spills" a certain part of the simulations demostrate higher population persistence than in the case without "spills". This part is higher in the larger landscape. An interesting tendency is the existence of an interval of "spill" percentages higher than 30% for which the cases with TE higher than TE_0 increases.

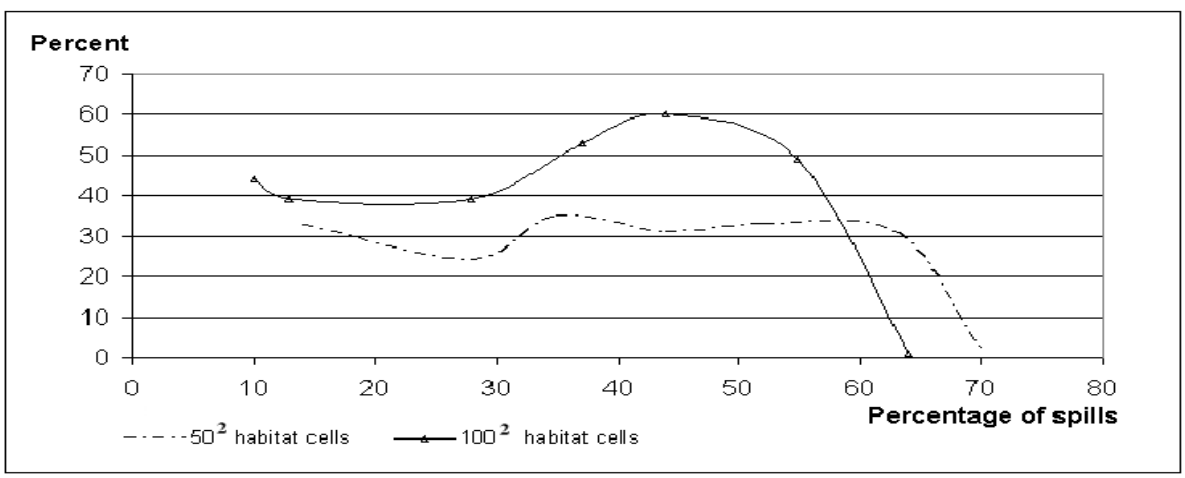

Figure 3: Percentage of simulations on landscapes with "spills" for which the TE was higher than TE_0.

Trying to explain these observations, we study the effect of "spills" on population density. The population density measured as the total density divided by the area (in hectares) is a quantity that turns out to be affected by the percentage of "spill" disturbances. Specifically, the maximum and minimum densities seem to be determined by the percentage of "spill" disturbances and not affected by the specific spatial arrangements of the "spills".

It is somewhat surprising that although the two-dimensional time series of the spatial population density patterns are different between simulations with different spatial arrangements of "spills", the one-dimensional time series of the total population densities have similar patterns and the maximum and minimum densities are in the same range for a fixed percentage of "spills". This is demonstrated on Figure 4 for 50^2 habitat cells and 14% "spills" but occurs in all simulations we performed. The different density curves correspond to different "spill" distributions. The spatial distributions of the animals for the same time moments are completely different across the cases (we do not present illustrations for lack of space) but the density time series have a very similar shape. The maximum and minimum densities occur at the same times and have close values.

These values change when the percentage of "spills" changes. The maximum population densities decrease with increasing percentage of "spills". To illustrate, we present a plot of the density on the 50^2 homogeneous landscape, Figure 5. The maximum density in the homogeneous landscape case is between 7.5 and 9 per ha, while in the case with 14% "spills" it is between 6 and 7.5. When the "spill" percentage increases further up to 70%, the maximum density falls to 2 per ha. This monotonicity tendency was observed in all other simulations.

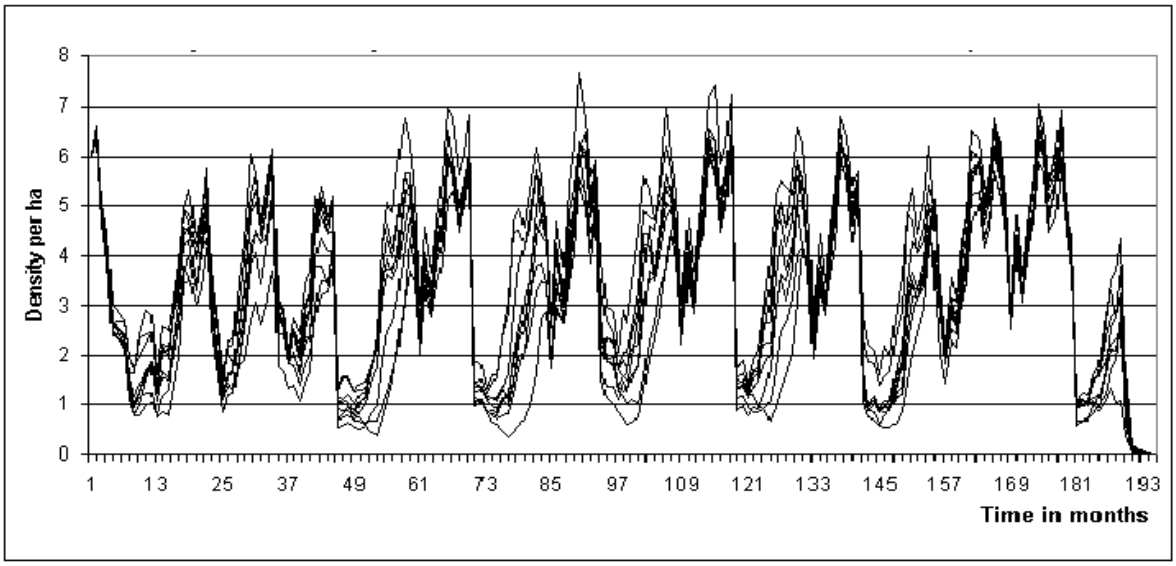

Figure 4: Total population density for a set of simulations on 50^2 habitat cells with 14% "spills"

Why does the density decrease when the percentage of "spills" increases? Why does the ATE increase, although the density decreases? We give the following explanation, which we call the "disturbance-forced localization effect".

After a period of low vegetation density, only scattered groups or single animals survive. These become sources for gradually growing in size and expanding in space isolated local populations. As floaters search for unoccupied space, local populations spread. The floaters in cells having neighbor "spill" cells have less choice of a cell to move to than in the case where all neighboring cells are habitat cells. The restrictions of movement lead to a slower speed of spatial spread of the population. Consequently, local populations occupy smaller spaces and establish high densities at the focal locations. When the next period of scarce vegetation occurs, masses of animals perish at the overpopulated and overgrazed locations. This contributes to lower total population densities.

The simulated juvenile densities become zero in the end of January each year because of the assumed lack of pregnancies in December and January. (The last born animals in the end of December each year reach maturity in the end of January while the first newborns arrive in the end of February.) Extremely low population numbers in the winter's end are characteristic not just for voles, but for many species. The relative success in producing offspring in the end of the severe period is a crucial factor for population persistence. Environmental conditions that contribute to this success should lead to a longer TE. The presence of disturbances acts in this direction. Because of the restricted spatial localization of the populations

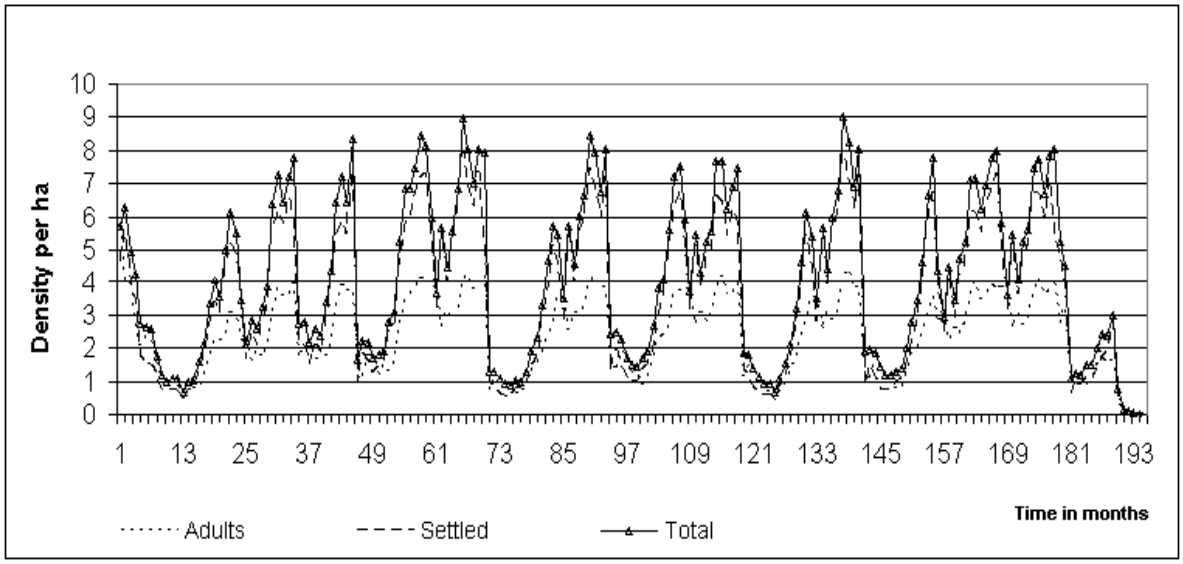

Figure 5: Total, adult and settled population density for a set of simulations on 50^2 habitat cells with 0% "spills"

on landscapes with "spills", floaters should be more successful in becoming residents and mating. In the homogeneous case floaters spread much farther and have lower probability to end up in a cell that has a resident of the opposite gender because the floaters have a priority to move into unoccupied cells. In the case with "spill" disturbances floaters are more often forced to move into occupied cells and thus end up forming pairs and producing offspring. Thus, at the end of severe (low-vegetation, no offspring production) periods, populations in the inhomogeneous environments should produce offspring at a higher per capita rate. This effect should be more visible after periods when the population has fallen to very low densities.

To check this conjecture, we calculated the monthly ratios of the juveniles to the total population in all 200 simulations and then took the averages for each month. We did these calculations for three landscapes with 50^2 habitat cells and a) without "spills"; b) with 14% "spills" and c) with 44% "spills". The results are presented on Figure 6. All the simulated populations on the landscapes with 0% and 14% "spills" persisted no longer than 194 months while some populations on the 44% "spills" landscape persisted for the whole 30 year period. It is visible (Figure 6) that especially after periods of low population density (after months 73, 121, 145, 181: compare with Figures 5 and 4) the percentage of the juveniles from the total population increases fastest from zero for the 44% "spills" landscape, followed by the 14% "spills" landscape. It is notable that in the last year before the populations on the 0% and 14% "spill" landscapes crashed, the populations on the 44% "spills" landscape had a higher average juveniles per capita ratio and survived the bottleneck period. The explanation is that the abundant juveniles formed a sufficient pool of offspring bearing pairs which were able to regenerate the population.

One would also expect that for higher percentage of "spills" for which no habitat fragmentation has occurred the "disturbance-forced localization effect" will be more pronounced and the time to extinction will be longer. For even higher "spill" percentages the probability that the habitat gets fragmented will increase and the cases with TE higher than the one in the homogeneous case will become less and less frequent. This prediction is supported by the hunch-shaped curve on Figure 3.

6 Conclusion

The "disturbance-forced localization effect" is a purely spatial effect. Its possible existence emphasizes the importance of considering space in population dynamics studies. Additionally, the concept of time to extinction would not have been possible to define without our realistic modeling of the intertwining regulatory mechanisms of climate and trophic herbivore-vegetation relationships.

Of course, the present model can be criticized for its bias on territoriality. In our assumptions, territorial-

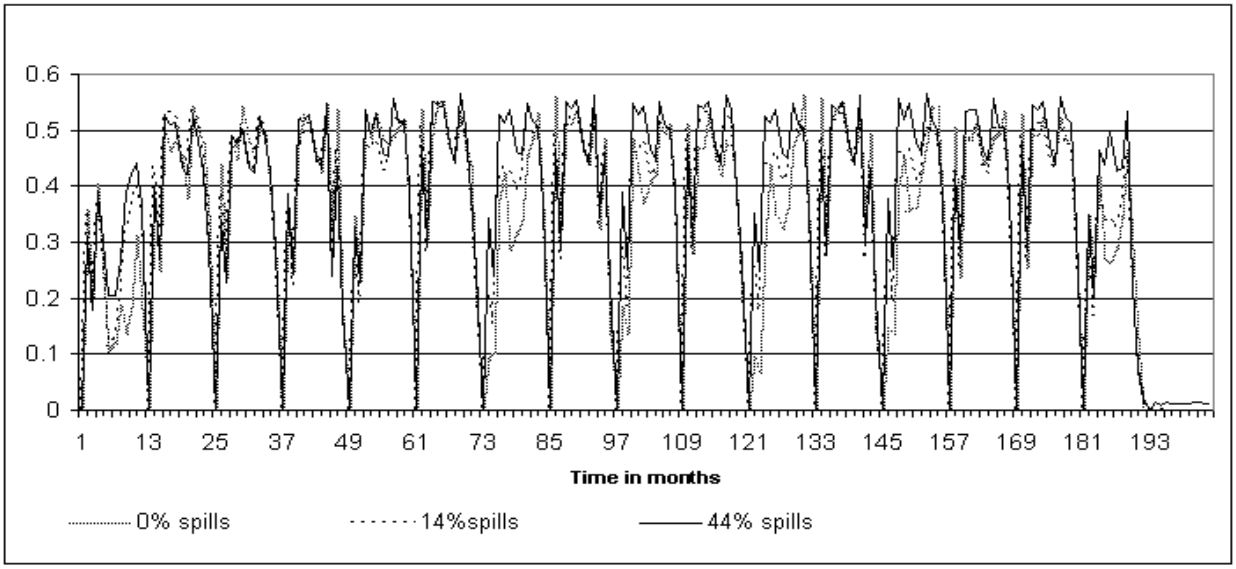

Figure 6: Ratios of the juveniles versus the total population on a landscape with 50^2 habitat cells and three levels of "spill" disturbances.

ity is of higher priority than mating because floaters prefer to occupy empty cells to cells with representatives of the opposite gender. The other alternative would be interesting to explore as well. The model does not account also for a number of possible effects that disturbances could exert. For example, predation could be higher on the boundary between a "spill" and a habitat area because voles could be more easily observed. However, this and other possible effects can be successfully modeled in the frames of the spatially-explicit individual-based paradigm and can be the subject of future studies using slight modifications of SERDYCA.

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