Spatial Autocorrelation, Dispersal and the Maintenance of Source-Sink Populations

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December 12, 1997

Abstract

Populations may be regulated by both local density-dependent factors and spatial variation in habitat quality. I explore the influence of spatial autocorrelation in habitat quality on the survival of model populations. Dispersal is modeled as Markov transitions between patches. A finite rate of population increase was assigned to each patch. Total habitat area and mean dispersal distance had strong effects on overall population persistence. The effect of spatial autocorrelation was relatively weak, but interacted with dispersal distance. The results suggest that landscape pattern can play an important role in population survival, but its importance depends crucially on dispersal behavior.

1 Introduction

It is often assumed that population growth is limited by an upper bound or carrying capacity of the environment, below which a population increases and above which the population decreases (Murdoch 1994). Pulliam (1988) recognized that population growth may be regulated by an alternative mechanism: dispersal among habitats of varying quality. Pulliam referred to those areas where birth rates exceed death rates as demographic "source" populations and those areas where death rates exceed birth rates as "sinks." Coupled together via dispersal, population sources and sinks present a number of interesting scenarios. For example, sink populations may persist despite high mortality rates because of immigration from nearby source habitats (Pulliam 1988). Furthermore, source-sink population structure can lead to situations in which the majority of individuals in a population are poorly adapted to the habitats in which they occur (Dias 1996).

There are a number of factors that can influence the survival source-sink populations and these relate both to the extent and spatial arrangement of source and sink habitats, and the life-history traits of the species of concern. Primary, of course, are the demographic parameters of a given species: All things equal, a species with high rate of reproduction and low mortality has a lower risk of extinction than a species with high mortality and low reproduction.

However, persistence can also be influenced by behavioral attributes such as whether a species typically disperses long distances to find new habitat areas versus a species that remains close to home. Species that disperse long distance may be more successful in finding unoccupied territories or, in the case of plants, a forest gap. On the other hand, a species that disperses short distances may avoid becoming lost or ending up in a large area of inhospitable habitat. Another attribute of dispersal is directed versus passive dispersal. Directed dispersal occurs when an organism actively searches for high quality habitats, whereas with passive dispersal, propagules land in a random pattern some distance from where they started. A classic example of passive dispersal is the "seed shadow" surrounding trees whose seeds are dispersed primarily by wind and gravity.

1.1 Spatial autocorrelation

The outcome of dispersal events depends not only on dispersal behavior, but on the spatial arrangement of source and sink habitats. In landscapes where source habitats often occur in close proximity to sink habitats, source and sink habitats will be strongly coupled, even for organisms that disperse relatively short distances. The proximity of source and sink habitat can be quantified in terms of a "two-point" autocorrelation function. Consider pairs of points chosen from the landscape at random, but constrained to be distance k apart. The (sample) autocovariance function is

$$g_k = \sum_{x=k+1}^{n} (y_x - \bar{y})(y_{x-k} - \bar{y})/n \qquad (1)$$

where y_x is a point located at x and $\bar{y}$ is the mean value of y across the landscape (Diggle 1990). For a 2 dimensional landscape, x should of course be a vector pair of coordinates, but I will use the simpler 1 dimensional notation above. The autocorrelation function is then

$$r_k = g_k/g_0 \qquad (2)$$

where g_0 is the variance of the y's. A large autocorrelation at a particular scale (distance) in a landscape says that moving that distance will result in only a small change in habitat quality. On the other hand, a small autocorrelation means that the habitat quality changes rapidly. Generally, as the degree of spatial autocorrelation increases, landscapes become less fragmented, having fewer, but larger patches. Because spatial correlation implies larger patches, individuals dispersing away from source habitats in a correlated landscape will tend to encounter higher quality habitats and be less likely to disperse into a demographic sink.

The fractal dimension (Mandelbrot 1982) D of a landscape is directly related to the autocorrelation function. In fact, saying that a landscape is fractal, requires the autocorrelation function to take a particular form. Let the mean value of the landscape $\bar{y} = 0$, then

$$v_k = g_o(1 - r_k) \qquad (3)$$

where v_k is the variance of point a distance k apart (Diggle 1990). In the geostatistics literature, v_k is known as the "variogram" (Cressie 1993). For a fractal landscape with dimension D, then

$$v_k \propto k^{2H} \qquad (4)$$

where $H = 3-D$ (because, in this case we have 2 spatial dimensions and 1 dimensions for habitat quality). The symbol H is known as the "Hurst exponent." Thus, the autocorrelation function can be related directly to the fractal dimension by

$$r_k \propto 1 - \frac{k^{2H}}{g_0} \qquad (5)$$

where, again, $D = 3 - H$.

The important thing to keep in mind is that the four factors mentioned, local population growth rate, dispersal range, active versus passive dispersal, and landscape structure all interact because they affect the density of individuals that reside in population sinks versus population sources, and thus the overall viability of the metapopulation. In this paper, I evaluate the impact of these four factors on population viability in a spatially-explicit model of source-sink dynamics. The results are presented in the form of an "impact table," a devise for communicating the effects of landscape alteration on population viability. For readers interested in the mathematical details of the source-sink model, a more detailed analysis is presented in Appendices A and B.

2 Models and methods

2.1 Population processes

Models are often constructed because we gain insight from building and analyzing the model, even if the model is not an exact replica of nature. I begin with the simplest of metapopulation models, the so-called "BIDE" model in which

$$\text{Local Population Growth} = B + I - D - E \qquad (6)$$

where B is the local birth rate, D is the death rate, I is the immigration rate, and E is the emigration rate. Thus, a demographic sink (source) is patch in which $B < D$ ($B > D$). An interesting property of the model is that a demographic source can decline to extinction if $E - I > B - D$, i.e., excess emigration overcomes local population growth. (In Pulliam's [1988] original model, sources could never go extinct, because emigration only occurred after the source population reached its carrying capacity.)

The BIDE model can be extended to a network of habitat patches each with its own rates of birth, death, immigration, and emigration. In the current paper, I will only consider a situation in which each patch is assigned to one of two habitats, a source habitat ($B > D$) and a sink habitat ($D > B$). The rates of immigration to and emigration from each patch depends on the spatial arrangement of the source and sink patches across the landscape as described below.

The problem then is to determine the population growth rate of the entire network of patches. It is easy to show (see Appendix A) that the long-term growth rate of the metapopulation only depends on the local growth rates in source and sink patches and the fraction of population occurring in each patch. Letting λ be the finite rate of metapopulation growth,

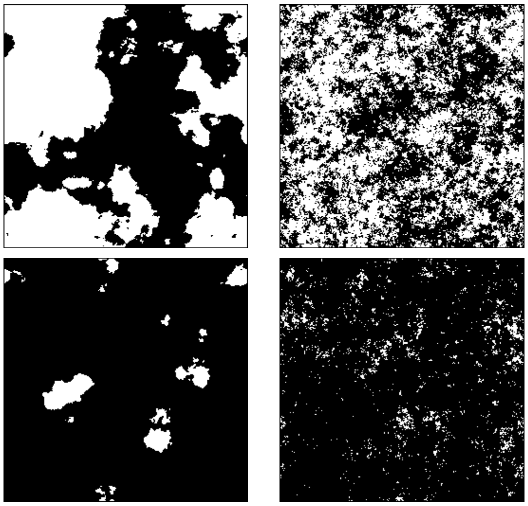

Figure 1: Fragmented landscapes with 50% (top panels) and 5% (bottom panels) remaining habitat. Remaining habitat is either grouped into several large patches (left side) or many small patches (right side).

then

$$\lambda = \sum_{i}^{M} \alpha_i v_i \tag{7}$$

where M is the number of patches, α_i is the finite rate of increase ($= B_i - D_i$) in patch i and v_i is the fraction of the entire metapopulation that resides in patch i at any given moment. For the purposes of this paper, note that if λ is greater than 1, the metapopulation is considered viable; if λ is less than one, the metapopulation will go extinct.

In all modeling scenarios, the finite growth rate of source patches was equal 1.2 (20% increase per year). Sink patches had a growth rate equal 0.2.

2.2 Landscape model

In order to evaluate the effect of landscape pattern on population processes it is necessary to define a model describing spatial pattern. Here, I use a model based on fractal geometry (Mandelbrot 1982) that incorporates both habitat density and habitat fragmentation. The technical details of the model can be found in Appendix A. The model has two parameters: the first p controls the total amount of source habitat on the landscape; the second H controls the number of patches among which the source habitat is distributed. The two parameters can be varied independently so that it is possible to emulate a wide variety of landscape scenarios (Fig. 1). Simulated landscape can be strongly autocorrelated ($H \approx 1.0$) or uncorrelated ($H \approx 0.0$) and the density of source habitat p may be varied continuously between 0.0 and 1.0.

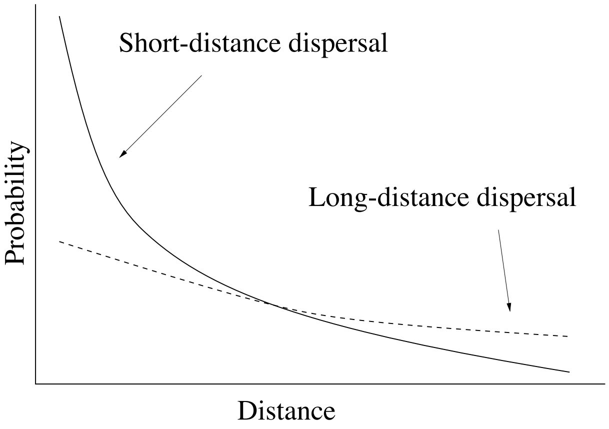

Figure 2: Dispersal curves for short- and long- distance dispersal.

An important property of the landscape models is that, within the constraints imposed by the tuning parameters, the landscapes are random with respect to the spatial arrangement of patches. Thus, each successive landscape is *statistically independent* from the previous landscape. If I had chosen some *ad hoc*, non-random algorithm, it would be impossible to know whether the results were biased by an undescribed and uncontrolled aspect of the spatial model.

In all simulations presented here, landscapes were 32×32 arrays of habitat patches. Each habitat patch was designated either as a source patch or a sink patch according to the fractal landscape model. Periodic boundary conditions were used such that in individual leaving one edge of the landscape would appear on the opposite edge.

2.3 Dispersal model

Most organisms exhibit a leptokurtic dispersal pattern, i.e., most individuals disperse a short distance, whereas a few disperse very long distances (Neubert et al. 1995). The shape of the dispersal curve, particularly in the long-distance tail, is extremely important in determining the rate of spread of an organism (Kot et al. 1996). Most data suggest either a power-law or negative exponential function. Dispersal models based on Fickian diffusion (i.e., a random walk) generally underestimate the frequency of long-distance dispersal events, often with profound consequences on model predictions (Kot et al. 1996). A more fruitful approach is to model the dispersal curve directly.

Table 1: Summary of model parameters

Parameter	Treatments
Source Habitat Density	Medium Density (50% source habitat) Low Density (5% source habitat)
Landscape Autocorrelation	Autocorrelated (Source habitat in several large patches) Uncorrelated (Source habitat in many small patches)
Dispersal distance	Short distance (mean distance equal one patch width) Long distance (mean distance equal landscape width)
Dispersal behavior	Passive (random direction) Active (dispersal biased towards source habitats)

I modeled dispersal using a negative exponential dispersal function. The dispersal function determines the probability that an individual will disperse a given distance across the landscape (Fig. 2). Two scenarios were examined: short-distance dispersal corresponded to a mean dispersal distance equal the width of a single habitat patch or 1/32 the width of the entire landscape; for long-distance dispersal, the mean dispersal distance was 32 patch-widths or the entire width of the landscape.

A second aspect of the dispersal models was active versus passive dispersal. In passive dispersal, individual disperse in a completely random direction, independent of any landscape features. Passive dispersal models systems such as seed dispersal in plants (assuming wind and other factors do not bias the dispersal direction). In active dispersal, individuals bias their dispersal such that they land in source patches more often then sink patches. The extent of the bias towards or away from a given patch was proportional to its "quality," defined here as the local population growth rate. Active dispersal emulates a situation in which an organism searches for high quality habitat.

2.4 Modeling scenarios

The combination of the landscape and dispersal models resulted in four model parameters: source habitat density, habitat autocorrelation, mean dispersal distance, and active versus passive dispersal behavior. I evaluated the impact of each of these parameters on metapopulation viability using a full factorial experimental design. For each of the parameters, two values were chosen (see Table 1). All factorial combinations of the parameter values resulted in 16 different scenarios. Ten replicate landscapes were evaluated for each scenario.

3 Results and discussion

Results of the analysis are presented in the form of impact tables (Tables 2 and 3). Each column of the impact table lists a landscape attribute (the columns correspond to the landscapes shown in Fig. 1). The rows are species attributes, here, dispersal distance. Two tables are shown, one for passive dispersal and one for active dispersal. The entries in the table are qualitative assessments of the impact of landscape alteration. Imagine we begin with a landscape completely filled with source habitat and then remove 50% of the landscape leaving behind many small source habitat patches. The relative impacts under this scenario are given in column two of the tables.

Several general patterns emerged from the analysis. As expected, population viability declined as the amount of source habitat was reduced. Landscape configuration also affected viability: when the source habitat was clumped into larger patches (increased autocorrelation), the metapopulation growth rate was higher. Somewhat surprisingly, long distance dispersal resulted in lower population viability. There was no mortality penalty for long distance dispersal, rather, individuals that disperse long distances away from source habitat more often end up in sink habitats, thus lowering the overall growth rate of the metapopulation. Generally, as one would expect, passive dispersal resulted in lower viability for much the same reason as long distance dispersal: more individuals landed in the sink.

The relative magnitude of effects from different parameters and parameter interactions is given in Table 4. The parameter that had the greatest affect on population viability was source habitat density, followed by dispersal distance, and passive versus active dispersal. These were followed by several interaction effects. Decreasing source habitat density inflated the effect of long distance dispersal on viability. In short, when there was little habitat available on the landscape, individuals were better off staying

Table 2: Impact table for passive dispersal

	50% Habitat Remaining, Several Large Patches	50% Habitat Remaining, Many Small Patches	5% Habitat Remaining, Several Large Patches	5% Habitat Remaining, Many Small Patches
Short Distance Dispersal	Low	Moderate	Moderate	High
Long Distance Dispersal	Moderate	Moderate	Very High	Very High

close to home. There was a three way interaction between search strategy, habitat density, and dispersal distance, indicating that both dispersal behavior and habitat density need to be considered in viability studies.

The influence of spatial autocorrelation on viability was the sixth largest effect, followed by an interaction between autocorrelation and dispersal distance. The interaction between the Hurst exponent and dispersal distance occurred because more correlated landscapes favor short distance dispersal. It is interesting that the impact of spatial autocorrelation occurred so low in the ranking, below all other single parameters and several interactions. It is possible that the importance of landscape configuration was underestimated in the current source-sink model. The model does not consider the possibility of high intensity environmental disturbances that can cause local extinctions, i.e., classical metapopulation dynamics (Levins 1969, Hanski and Gilpin 1991). In the presence of local extinction and colonization, the importance of long distance dispersal may be much greater than represented here.

3.1 Management implications

Given that the total area of source habitat is the most important factor affecting population viability, should we care about landscape geometry? It depends somewhat on the situation. Clearly, one needs to consider the life-history traits, such as mean dispersal distance and dispersal mode, of the species of concern before making a blanket statement regarding the importance of landscape configuration. These results do suggest that in situations where we are able to preserve large areas of high quality, source habitats, we should do so.

It is important, however, to realize that virtually all habitat management decisions involve tradeoffs between competing and sometimes conflicting goals. In an ideal world, we would set aside all habitats as reserves. However, in reality, we must pick and choose. If we are constrained, owing to budgetary, social, or political factors, in the amount of habitat we can preserve, landscape configuration can be an important consideration in maximizing the effectiveness of conservation efforts. For example, given a target of preserving 50% of the available habitat for a species, the analysis presented here suggests that the species will have greater viability if the habitat is clumped into several large patches.

The interesting problems arise, of course, when there are tradeoffs to be made between total area and landscape connectivity. Should one maximize habitat area at the expense of connectivity? There is no simple answer, because both area and connectivity are important. The answer will generally depend on how a species uses the landscape. However, even simple analysis of landscape pattern can be useful in prioritizing conservation decisions, and in general, landscape connectivity can be enhances with little or no loss in the total habitat area preserved.

A Mathematical models

A.1 Fractal landscapes

Landscapes were modeled as segmented fractional-Brownian surfaces (sfBs) (Keitt and Johnson 1995). SfBs were constructed by first creating a fraction-Brownian surface and then slicing the surface at a particular elevation. All points above the slice were assigned to one class and those below another class (see Fig. 1). Binary sfBs were indexed by two parameters, p which determined the area assigned to one of the classes, and H which set the fractal dimension of the surface (Mandelbrot 1982, Feder 1988, Peitgen and Saupe 1988).

A fractional-Brownian surface is most easily defined in terms of its Fourier transform (Hastings and Sugihara 1993). For fractal patterns, the power-spectrum (square of the Fourier coefficients) scales

Table 3: Impact table for active dispersal

	50% Habitat Remaining, Several Large Patches	50% Habitat Remaining, Many Small Patches	5% Habitat Remaining, Several Large Patches	5% Habitat Remaining, Many Small Patches
Short Distance Dispersal	Low	Low	Low	Moderate
Long Distance Dispersal	Low	Low	High	High

as a power-law of the frequency:

$$S(f) = kf^{\beta} \tag{8}$$

where $S(f)$ is the power at frequency f, k is a normalization constant, and β is a scaling exponent related to the fractal dimension of the surface. For a 2-dimensional surface $\beta = 2H + 1$, where H is known as the "Hurst exponent" (Mandelbrot 1982). The Hurst exponent also determines the fractal dimension $D = 3 - H$.

Fractional-Brownian surfaces are easily created by generating random Fourier coefficients whose variance decays as a power-law function of frequency. An inverse Fourier transform is then applied to produce the fractal landscape.

A.2 Stochastic landscape networks

A stochastic landscape network describes the probability of an individual dispersing from one habitat patch to any other habitat patch in a landscape. The network can be formalized in terms of a matrix T whose elements t_{ij} are transition probabilities from patch i to patch j. We require that each row of T sum to one, because (ignoring for the moment reproduction and mortality) the sum of all individuals leaving a patch must equal the sum of individuals entering other patches. The matrix T thus defines a Markov chain.

For the simple lattices used here, filling the elements of T was simply a matter of computing the distance between two patches and then modeling the probability of dispersal as a function of distance. Here, dispersal was modeled by a negative exponential

$$p(d) = \theta e^{-\theta d} \tag{9}$$

where $p(d)$ is the probability of dispersing a distance d and θ is the dispersal coefficient. The mean dispersal distance was equal $1/\theta$. For the artificial landscapes used here, I simply assigned $t_{ij} = p(d_{ij})/\sum_j p(d_{ij})$ where d_{ij} is the distance between patch i and patch j. This approximation was justified by the fact that each of the 32 × 32 cells on the landscape were considered an individual patch. Thus, all patches were the same size and had a compact shape. In cases where patches are defined with different sizes and sinuous or oblong shapes, corrections to t_{ij} need to be made to account for the irregular patch geometries.

One further modification needs to be made to T in order to incorporate active dispersal. As defined above, T models passive dispersal; the patch transition probabilities only depend on the distance between patches. However, if organisms search for high quality habitats, transitions to better habitat patches should be higher than to poor habitats. I introduce the parameter σ to represent the degree to which dispersal is biased towards high quality habitats. I then define

$$t_{ij} = \frac{(1 - \sigma + \sigma\alpha_j)p(d_{ij})}{(1-\sigma)\sum_j p(d_{ij}) + \sigma \sum_j \alpha_j p(d_{ij})} \tag{10}$$

where α_j is the growth rate in patch j. This function simply biases the transition probabilities towards patches with higher growth rates. When $\sigma = 0$, then $t_{ij} = p(d_{ij})/\sum_j p(d_{ij})$ as before. When $\sigma = 1$, t_{ij} is biased in proportion to the quality of patch j. The degree of bias in t_{ij} is a linear function of σ.

Given T we can construct the full BIDE metapopulation model and determine its overall growth rate. For a single patch, the BIDE model can be written as

$$n'_j = n_j \sum_i^M t_{ij}\alpha_i \tag{11}$$

where n_j is the local population size in patch j, n'_j is the population size in the following generation, and M is the number of patches in the system. The entire model can be written in matrix form

$$\vec{n}' = AT\vec{n} \tag{12}$$

where A is a matrix whose diagonal elements are the local population growth rates in each patch, and $\vec{n}$ is

Table 4: Most influential parameters and interactions

Rank	Parameter or interaction
1	Source habitat density
2	Dispersal distance
3	Search (passive vs. active)
4	Density × Distance
5	Search × Density × Distance
6	Hurst exponent
7	Hurst × Distance

a vector containing the local population sizes. Thus, the overall growth rate of the metapopulation is the largest eigenvalue λ of the matrix AT.

It is possible to derive λ as a function of the distribution of individuals among patches and the growth rate in each patch as follows. As long as T is positive, there exists an eigenvector $\vec{v}$ associated with λ such that

$$AT\vec{v} = \lambda\vec{v}. \tag{13}$$

We may choose any scaling of $\vec{v}$, so I choose $\sum_i v_i = 1$. Summing across the rows of Eq. 13, we have

$$\sum_j \sum_i t_{ij}\alpha_i v_i = \lambda \sum_j v_j. \tag{14}$$

Noting that $\sum_j v_j = 1$ and that $\sum_i t_{ij} = 1$, and rearranging a bit gives the result in Equation 7.

B Statistical analysis and results

Mean growth rates on which the impact tables were based are shown in Table 5. The precision estimate is one standard error.

The results of an ANOVA on the model output is shown in Table 6. The given p-values are not particularly meaningful, however, the F-value gives a ranking of the effect of each parameter and parameter combinations on population viability.

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Table 5: Mean value of λ for factorial treatments

		$p = 0.50$		$p = 0.05$	
		$H = 1$	$H = 0$	$H = 1$	$H = 0$
$\sigma = 0$	$\theta = 32$	1.0695 ± 0.0351	0.9548 ± 0.0455	0.7261 ± 0.0511	0.5073 ± 0.06097
	$\theta = 1$	0.7064 ± 0.0027	0.7021 ± 0.0016	0.2521 ± 0.0011	0.2507 ± 0.0007
$\sigma = 1$	$\theta = 32$	1.1659 ± 0.0065	1.1322 ± 0.0062	1.0599 ± 0.0247	0.9662 ± 0.0535
	$\theta = 1$	1.0617 ± 0.0020	1.0587 ± 0.0010	0.4694 ± 0.0079	0.4468 ± 0.0046

Table 6: ANOVA results comparing model treatments

	Df	Sum of Sq	Mean Sq	F Value	Pr(F)
Search	1	3.002692	3.002692	3616.080	0.0000000
Density	1	6.291388	6.291388	7576.589	0.0000000
Hurst	1	0.151507	0.151507	182.457	0.0000000
Distance	1	4.335539	4.335539	5221.200	0.0000000
Search × Density	1	0.030375	0.030375	36.580	0.0000000
Search × Hurst	1	0.021660	0.021660	26.084	0.0000010
Density × Hurst	1	0.020432	0.020432	24.605	0.0000020
Search × Distance	1	0.002159	0.002159	2.600	0.1090616
Density × Distance	1	0.685271	0.685271	825.257	0.0000000
Hurst × Distance	1	0.115287	0.115287	138.838	0.0000000
Search × Density × Hurst	1	0.000297	0.000297	0.358	0.5505592
Search × Density × Distance	1	0.417326	0.417326	502.577	0.0000000
Search × Hurst × Distance	1	0.031927	0.031927	38.449	0.0000000
Density × Hurst × Distance	1	0.013578	0.013578	16.352	0.0000854
Search × Density × Hurst × Distance	1	0.002770	0.002770	3.335	0.0698753
Residuals	144	0.119574	0.000830		

Acknowledgments

The support of the Santa Fe Institute is gratefully acknowledged. This paper resulted from an IAI Sponsored workshop: “Habitat Fragmentation and Degradation,” December 9-13, 1996, Marvella, Chile. Discussions with G. Bradshaw, P. Marquet, B. Macready, and E. van Nimwegen were influential in many aspects of this paper.