Stochastic Skellam Model
R.A. Kraenkel and D.J. Pamplona da Silva
Instituto de Física Teórica - UNESP, R. Pamplona 145, 01405-900 São Paulo, Brazil

Abstract
We consider a spatially explicit model for a single species on a habitat consisting of alternating favorable and adverse patches whose sizes are distributed randomly. For the one-dimensional case we define a stochastic analogue of the classical critical patch size. We address the issue of viability of a population and we show that the minimum fraction of the length of favorable segments to the total length is always smaller in the stochastic case than in a periodic arrangement. In this sense, spatial stochasticity favors viability of a population.

Key words: population dynamics, Fisher-Kolmogorov equation, fragmentation

1. Introduction

The way that the spatial structure of a habitat influences the dynamics of a certain population or biological community is a central point to theoretical ecology[1, 2]. Issues like the viability of a population [3], coexistence of competing species[4, 5], invasibility [6, 7], and proneness to local extinctions[8, 9, 10] are influenced by spatial heterogeneities. Habitat fragmentation - an instance of spatial heterogeneity of a habitat – is at the core of the concerns of conservation and landscape ecology, and has being perceived as a threat to biodiversity [11].

To mathematically model the effects of spatial heterogeneities one searches for simple formulations that can encompass a particular class of phenomena[12, 13]. In the simplest cases one can single out a population that perceives the remaining biotic and abiotic factors as the habitat over which its dynamical changes take place. The natural spatial variations of these factors will impact the population yielding regions which are harsher and others which are more favorable for the population in focus.
Central to the understanding of spatial effects in population biology is the fact that populations dwelling in limited portions of space have their size depleted with respect to a situation with unlimited space, [9, 14, 15, 16]. This depletion comes to a point where a critical area (or length) is reached, below which the population density goes to zero, representing a local extinction. This is a consequence of the diffusive rates dominating over growth rates. This phenomenon is well-established at the laboratory scale, [17]. At an ecological scale, observational results indicate a correlation between area and population depletion, [8, 18] and can lead to concrete recommendations concerning restoration and management of, e.g., tropical forests [19].

The mathematical description of the situation depicted above can be multifold. Spatial variability is most frequently treated either in the metapopulation sense [20] or else as spatial dependence of coefficients in reaction-diffusion equations approach, [12].

We will be interested here in the effects arising from a particular kind of fragmented habitat. For sake of simplicity, we will consider a single species that inhabits a one-dimensional habitat that is composed of two kinds of segments: a first one, whose conditions for the growing of the population are good and a second one where they are not. Segments alternate between adverse and favorable. Adverse segments will be characterized by a negative intrinsic growth rate and favorable segments by a positive one. This is a kind of minimal model to illustrate patchiness in natural habitats. In particular, the intrinsic growth takes on only two possible values. A similar system has been explored in [21, 22, 23] for periodically alternating adverse and favorable regions. It has also been extended to continuously varying reproductive rates, [24]

A further element of spatial variability will be introduced by allowing segments to be of different sizes. Specifically, we will consider that adverse segments are all of the same size, but the size of the favorable ones is possibly variable. Our interest lies in the study of how this kind of variability affects the population, namely, we want to know when a population will be viable or not, depending on parameters describing variability. In other words, we pose the question: given an initially small population, characterized by its density, will it grow in time until saturation comes in, or will its density tend to zero for large times?

Next, to make the problem precise, we have to state the laws governing the sizes of the favorable segments. We will do so by considering them
to follow a stochastic distribution of sizes. This brings into play another important factor of natural habitats. Indeed, stochasticity is a widespread element of patchy environments and occurs naturally in many situations. Patch size stochasticity is relevant to fragmented regions, either in process of habitat loss or in regeneration. Moreover, stochasticity in the form of temporal changes of environmental conditions has been shown experimentally to enhance long-term persistence in chains of connected sink habitats, [25]. It is thus a natural question also to explore the effects of spatial stochasticity.

Having introduced an element of stochasticity in the description of the habitat, we are compelled to give answers in a probabilistic sense. This means that instead of stating that a given population is viable or not, we should state the viability probability in terms of the parameters characterizing the stochastic distribution of patches in our habitat.

The procedure we will adopt here is to consider the spatio-temporal evolution of the population as described by the Fisher-Kolmogorov-Petrovskii-Piskunov equation (FKPP) with spatially varying intrinsic growth rate (as outlined above) obeying a stochastic distribution. However, as our interest is viability analysis of an initially small population, we effectively do not need to consider the nonlinear intra-specific competition term, so that in fact we are studying a stochastic Skellam model. We will numerically solve the equation for a given realization of the stochastic series, repeat the process 20 times keeping track at each realization of the outcome (viable or not) and defining a viability probability as the ratio of viable outcomes in the total. Next, we take different values of the parameters characterizing the statistical distribution of the lengths of the favorable regions and study the dependence of the viability probability on these parameters. We complete the study by a comparison with the periodic case. It will ultimately turn out that covering a region will segments of favorable regions whose lengths are stochastically distributed is more effective than doing it periodically.

2. Mathematical Model

As previously discussed, our model is mathematically described by the FKPP equation, which, in a convenient non-dimensional form, reads

$$u_t = u_{xx} + a(x)u - u^2,$$

where $u(x, t)$ is the population density and subscripts denote partial differentiation. In the right-hand side of Eq. (1) we have a diffusive term (second
derivative in $x$), a saturation term $(-u^2)$ and a growth parameter $a(x)$. The parameter $a(x)$ is space dependent and will be used to describe the effects of patchiness on the population. It intercalates between positive and negative values, corresponding to favorable and adverse patches respectively.

In order to give a clear meaning to our results we will compare them with the case where the distribution of patches is periodic instead of stochastic. Therefore we will study two cases: periodic and stochastic.

2.1. Periodic case

In this case, favorable patches have length $L$ and adverse ones have length $s$. Both $L$ and $s$ are fixed. The reproductive factor is given by:

$$a(x) = \begin{cases} a_0 & \text{if the patch is favorable} \\ -a_0 & \text{if the patch is adverse} \end{cases}$$

(2)

Fig. (1a) illustrates this case. Using periodic boundary conditions we may solve Eq. (1) in just a cell, see Fig. (1b).

![Figure 1: $a(x)$ describing a profile of infinite patches with same size: Periodic case.](image)

2.2. Stochastic case

The reproductive rate $a(x)$ is still given by Eq. (2) but now the distribution of the size of the favorable regions is not constant anymore. The size of each favorable patch will be random and will obey a probability distribution. There is obviously some arbitrariness in the choice of a definite
distribution, but one would expect the exact form of such a distribution not to be of central importance to the results. Here we will use a lognormal distribution given by:

\[
f(y|\mu, \sigma) = \frac{1}{y\sigma \sqrt{2\pi}} e^{-\frac{(\ln y - \ln \mu)^2}{2\sigma^2}},
\]

where \(\mu\) is the median and \(\sigma\) the standard deviation. In Fig.(2) one generic random profile is depicted.

**Figure 2:** One generic realization of \(a(x)\) describing patches with different sizes in the stochastic case

3. Numerical Results

3.1. Periodic Case

The results for the periodic case, where there is no variation in the length of the favorable regions (and neither in the unfavorable ones), will be compared with the ones obtained in the next section, so to put into evidence the effects due to stochastic variability of the length of the favorable regions.

To integrate Eq.(1), it is necessary to choose a set of values for the parameters of the problem. We take \(a_0 = 1\) and \(s = 0.8\), without loss generality because a change of these values does not introduce any qualitative changes in the description of our model.
We next integrate the model with various values of $L$. For each case, we give a small initial condition, which will evolve in time. If it grows, we say that the population under inspection is viable, if it goes to zero, we say that the population is not viable. We numerically establish a critical value, $L_p^*$ (the subscript denoting “periodic”) such that if $L < L_p^*$ the population is not viable, being viable otherwise.

With these values we obtain a critical size

$$L_p^* = 0.74$$  \hspace{1cm} (4)

3.2. Stochastic Case

For each pair $(\mu, \sigma)$ in Eq.(3) we have a definite probability distribution. We are thus able to generate a realization of the patchy habitat by sampling a sequence of lengths for the variable $L$. We use the same values for $a_0$ and $s$ as in the periodic case.

3.2.1. Preliminary analysis

In a preliminary analysis we scanned the variables $\mu$ and $\sigma$. For a given pair of values, we obtained a realization of the habitat and integrated Eq.(1), again with a small initial condition. We then assigned the value “not viable” if the density $u(x, t)$ goes to zero and “viable” otherwise. Next, we change the values of $\mu$ and $\sigma$ and repeat the process. This is done for 80000 pairs of values $(\mu, \sigma)$, obtaining the plot presented at the Fig.(3), where green points represent “viable”, and red points represent “not viable”.

Associating any green point to a value zero and to red points a value one, we can obtain – for any fixed value of $\sigma$ – the fraction of “non viable” points. This is represented by the dark line in the Fig.(3), which separates viable from non-viable cases.

As is obvious from Fig.(3) that the results obtained in this way give only an indication of general traits, being flawed by fluctuations in the form of red points in the green region, mainly for high $\sigma$. To give a more meaningful result we should average results over several realizations.

3.3. Averaging over many realizations

In order to give a statistically sound result we should repeat the process above a number of times and associate to every point in the $(\mu, \sigma)$-plane a probability of viability. Therefore, instead of “0 = green” and “1 = red” cases, we have in principle a continuous number between 0 and 1. In practice,
Figure 3: $\mu \times \sigma$-space diagram. For each pair $\mu$ and $\sigma$, Eq.(1) was integrated on one realization of the habitat. Green points mean “viable”, red ones mean “not viable”.

average is taken over a limited number of runs. In our case, we have 20 realizations. Thus, for every pair $(\mu, \sigma)$ we generate 20 realizations of the habitat and for each of them we integrate Eq.(1), obtaining the fraction of viable and non-viable cases. The results are plotted in Fig.(4) by using a set of 20 colors. We naturally associate a viability probability to the fraction of viable outcomes corresponding to a given $(\mu, \sigma)$ and denote it by $p_v$. The “non-viability” probability, $p_{nv}$, is just $p_{nv} = 1 - p_v$.

The plot in Fig. (4) clearly shows that we have two regions (green and red) separated by a transition region of small size. This small region becomes larger for higher values of $\sigma$. Consider, for instance, a fixed value of $\sigma$. The viability probability is a function of $\mu$, going from 0 at $\mu = 0$ to 1 asymptotically when $\mu$ becomes large. We define a threshold value in analogy to the procedure in the previous section adding up the non-viability probabilities over $\mu$, that is we define:

$$\mu_0 = \int_0^\infty p_{nv} d\mu .$$

(5)

This threshold value is still a function of $\sigma$. A polynomial interpolation of it is shown on Fig.(4) as a continuous blue line.

For every value of $\sigma$, the viability probability can be interpolated by a hyperbolic tangent as a function of $\mu$. In the simplest form, we write the probability on a viable outcome, $p_v(\mu)$ as

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Figure 4: For each pair \((\mu, \sigma)\), we generate 20 realizations for \(a(x)\) and integrate the FKPP equation. We calculate the fraction of viable outcomes in the total and associate it with viability probability. We used a spectrum of 20 colors to obtain the plot above.

\[
p_v(\mu) = \frac{1}{K+1} (K + \tanh \alpha (\mu - \mu_0))
\]  

(6)

with \(K = \tanh \alpha \mu_0\). \(\mu_0\) was defined above and \(\alpha\) is a parameter related to the steepness of the transition region. Some illustrative examples are given in Fig.(5). In other words, \(1/\alpha\) is the typical width of the transition region. Its dependence on \(\alpha\) is shown in Fig.(6).

4. Analysis and discussion

In the present setting, the parameter \(\mu_0\) is the stochastic analogue of the critical length obtained in the periodic case. It represents the threshold value separating viable from non-viable cases. The value of \(\mu_0\) depends on the standard deviation \(\sigma\) of the distribution, as depicted on Fig(4). The comparison with the periodic case is easily done: the periodic case corresponds to \(\sigma = 0\) and the median and the mean coincide. Therefore we come to the conclusion that \(\mu_0\) is always smaller than the critical length for the periodic case. This is understood in a rather intuitive way: the larger the width of the distribution, more probable is the existence of large fragments which can
make the habitat viable. In this sense, stochasticity enhances viability. The tradeoff is, obviously, that predictions are not deterministic anymore.

Although stochasticity reduces the median of the length of the favorable fragments with respect to a periodic arrangement, we are in the presence of uncertainties. It is thus useful to define a security margin. This is done in analogy to usual statistical analysis. We call $1/\alpha$ the first standard deviation from the probability distribution. It is easy to calculate that approximately $82\%$ of non-viable cases lie between $\mu = 0$ and $\mu = \mu_0 + 1/\alpha$.

4.1. Efficiency analysis

As is patent from the procedure adopted, we have introduced no constraint on the total length covered by the favorable regions. This has been done intentionally so. Let us now compare the estimates of the fraction of the total length covered by favorable patches in the stochastic and in the periodic case at the corresponding critical length $L^*_p$ and $\mu_0$.

For the periodic case, the ratio of the total length of the favorable segments to the total length, $R_p$, is just:

$$R_p = \frac{NL^*_p}{N(L^*_p + s)} = \frac{L^*_p}{L^*_p + s} = 0.48$$ (7)

For the stochastic case, the corresponding ratio can only be estimated, as it depends on the particular realization. For small enough fluctuations, we
can estimate the total length covered by favorable segments by $N < L >$, where $<>$ represents the mean. For a lognormal distribution (3) we have

$< L > = \mu e^{\sigma^2/2}$. Therefore the estimate of the ratio of the length of the favorable regions to the total length at the critical value $\mu_0$ is

$$R_s(\sigma) = \frac{\mu_0 e^{\sigma^2/2}}{(\mu_0 e^{\sigma^2/2} + s)}, \quad (8)$$

which is function of $\sigma$ only.

Some typical values are: $R(0.2) = 0.45$; $R(0.5) = 0.38$; $R(1) = 0.23$. The trait is clear: the fraction of the area covered by favorable regions in the stochastic case is less than in the periodic one.

4.2. Final Comments

The issue addressed in this paper is to compare periodic and stochastic one-dimensional habitats with respect to the viability of a small population to grow on it, eventually coming to a saturation. The model for this is a FKPP equation with space dependent reproductive factor, either periodic or stochastic. We alternated favorable and adverse regions, with adverse ones having a fixed length. Our results indicate that the total patch size of favorable regions necessary for the viability of the population is smaller for a stochastic distribution of favorable patch sizes than for a constant value.
Results presented here were obtained in a one-dimensional habitat and using a lognormal distribution. To perform numerics we had to choose a fixed size for the adverse regions. These issues call for generalization. However, we would like to point out that the general traits obtained here should not be sensible to the size of unfavorable regions or to the precise probability distribution. The issue of extending the results to two-dimensional habitats, [26], represents a more involved challenge, mainly due to time consuming computational implementations.

The above results point out to perspectives of using stochastic patch size distributions in restoration ecology, as long as these patches are distributed in a matrix that is does not completely isolate one from the other. Having different sizes of patches allows some of them to be like sources and others like sinks. Stochasticity of patch sizes distributes putative sinks and sources in a optimized way. Taking such possibility into account could contribute to attempts of optimal design for habitats, [27].

Acknowledgments

The authors thank CNPq (Brazil) and CAPES(Brazil) for partial financial support.

References


