# Mean Time to Extinction of Source-Sink Metapopulation for Different Spatial Considerations

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#### Abstract

In a stochastic spatial source-sink process, we model the spread of a single species through a patchy landscape (i.e. one that arises as a result of increasing urban sprawl). This landscape contains discrete patches, known as sink and source patches, that are associated with low and high habitat quality respectively.

First, we generate different spatial relations of sink and source patches and place an initial population randomly throughout the grid of patches. We then simulate several discrete generations in which the species is exposed to different probabilities of reproduction and death, and we observe the mean time to extinction of the species with different combinations of patch distributions. Finally, we . show that the size of source patch groupings has an effect on the mean time to extinction.

# **1 Introduction**

This paper addresses several issues regarding source-sink metapopulation models. Hanski and ... Gilpin (1997) define a source-sink metapopulation as, "a metapopulation in which there are

patches in which the population growth rate at low density and in the absence of immigration is negative (sinks) and patches in which the growth rate at low density is positive (sources)" (11). In our study we consider a particular source-sink metapopulation model based on specific grid configurations. First, we select a given landscape of discrete patches. These patches are categorized as having high or low habitat quality. The model then shows how a particular species will behave in this landscape throughout a given number of generations. In this landscape, we establish propagation and extinction rules that control the species dynamics. The next step is to estimate some relevant parameters (probabilities of extinction and propagation) necessary to calculate mean time to extinction. From this, we are able to calculate the optimal patch arrangement at a specific ratio of source and sink patches.

First, in the beginning of Section 2, we present a series of helpful definitions, followed by the deterministic S-I-S model, which considers two types of susceptibles (source and sink patches). Our model is based on the one developed by Marquet & Velasco-Hernandez (1996) with two major differences: we do not include degradation, and we do assume a constant number of patches. Section 2 continues by introducing the stochastic S-I-S model. This model describes a birth-death process and the Chapman-Kolmogorov equations. In section 3 we present a pseudocode for our computer simulation. Then; we present statistical analyses on our data in Section 4. Finally, in section 5, we draw appropriate conclusions based onthe statistical and stochastical results.

## **2 Sink - Source Metapopulation Model**

In 1969 Richard Levins first introduced the term "metapopulation" in his article "Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control." The word suggests a population of populations, in which the colonization and extinction of local populations are analogous to births and deaths of individuals in a local population. The original metapopulation concept includes several assumptions, each of which simplifies the modeling process. First, Levins' concept assumes that the space is discrete. Second, it assumes that it is possible to distinguish between habitat patches. Finally, Levins' concept assumes that patches can accommodate panmictic (locally breeding) populations. These assumptions allow us to distinguish patch type easily and to assign specific qualities to the patches. In turn, this allows us to study the dynamics of the population in each landscape type that we wish to study.

In order to understand Levins' model, some definitions are useful. A "source patch" refers to a defined area where the population growth rate at low density and in the absence of immigration is positive. That is, a species can propagate better than it can in a sink patch, an area where propagation is lower and extinction probabilities are high. On the other hand, a "sink patch" is a place where propagules are produced less often than in a source patch. It is formally defined as an area where the population growth rate at low density and in the absence of immigration is negative. A sink patch is usually separated from other patches by unsuitable habitat. The spatial arrangement of these patches, wherein the species are free to migrate, is referred to as the "metapopulation structure." (It is implied that at any given time, each of these patches, whether source or sink, may be occupied or empty.)

Combining the above terms, we have a natural definition for a source-sink metapopulation. The term "Levins' metapopulation" refers to such a metapopulation structure in which local dynamics occur at a much faster rate than metapopulation dynamics. It is also used in a broader sense to denote systems in which all local populations, even if they may differ in size, have a significant risk of extinction.

All of these concepts are incorporated into our model, which is a spatially explicit metapopulation model. Our model considers a particular species in a defined landscape. To define this landscape, we use a grid that is divided into smaller, equal parts called "patches." We categorize these patches according to habitat quality. Habitat quality refers to reproduction and survival probabilities; thus, high quality favors propagation, while a low quality can drive a population to extinction. We refer to high quality patches as "source patches" and low quality patches as "sink patches." Since our main objective is to find the mean time to extinction in different landscapes, we create six different grid types. Each grid has the same percent of sink and source patches, but the distribution of these patches changes for each landscape. We randomly assign n organisms of a particular species to n patches on the grid. When there is an organism assigned to a patch, the patch is "occupied" and immediately reaches its carrying capacity. After each generation, the organisms in all of the occupied patches have three options: they can die; they can live without producing any offspring; or they can produce offspring that propagate to one of four adjacent patches. Thus, for each of the six grids or landscapes, we can watch how the population changes throughout time.

### **2.1 Susceptible-Infected-Susceptible (S-I-S) Model**

It is interesting to note that the deterministic model of this particular case is the S-I-S model for the spread of disease, in which there are two types of "susceptibles" – unoccupied source and sink patches- and in which the "infection" that spreads is the species itself. This model (deterministic) is a helpful tool for the complete understanding of the source - sink metapopulation dynamics.

These are the equations that model this dynamic:

$$
\frac{dP_1}{dt} = \epsilon_1 P_{11} - b \frac{P_1}{P} (\sigma P_{21} + P_{11}) \tag{1}
$$

$$
\frac{dP_{11}}{dt} = -\epsilon_1 P_{11} + b\frac{P_1}{P}(\sigma P_{21} + P_{11})
$$
\n(2)

$$
\frac{dP_2}{dt} = \epsilon_2 P_{21} - b\frac{P_2}{P}(\sigma P_{21} + P_{11})
$$
\n(3)

$$
\frac{dP_{21}}{dt} = -\epsilon_2 P_{21} + b\frac{P_2}{P}(\sigma P_{21} + P_{11})
$$
\n(4)

where

 $P_1 =$  Number of unoccupied source patches.

 $P_2$  = Number of unoccupied sink patches.

 $P_{11}$  = Number of occupied source patches.

 $P_{21}$  = Number of occupied sink patches.

 $\epsilon =$  Extinction rate = patch production rate.

 $\sigma =$  Depression in the propagule production rate imposed on the organism by sink patches.

 $b =$  Number of offspring per unit time.

This model takes into consideration the number of occupied source and sink patches from direct contact or colonization of a particular species at time *t.* The rate at which source patches become unoccupied or susceptible is denoted by  $\frac{dP_1}{dt}$ . The occupied or infected rate of a source patch is denoted as  $\frac{dP_{11}}{dt}$ . Likewise, the rates at which sink patches become unoccupied and occupied are denoted by  $\frac{dP_2}{dt}$  and  $\frac{dP_{21}}{dt}$  respectively. In these equations, s represents a factor in the environment that inhibits the reproduction of a species in a sink patch. From this we know that the probability for extinction in a sink patch is always higher than the probability of extinction in a source patch. Written mathematically, if a source patch has a probability of extinction,  $\phi$ , then a sink patch is a defined area that has a probability of extinction  $\phi + \delta$ ,  $\delta > 0$ .

We are assuming  $P = P_1 + P_{11} + P_2 + P_{21}$  to be a constant. That is, the total number of patches, whether they are occupied or not, remains the same.

Then we have:

$$
\frac{dP}{dt} = \frac{dP_1}{dt} + \frac{dP_{11}}{dt} + \frac{dP_2}{dt} + \frac{dP_{21}}{dt}
$$
\n(5)  
\n= 0. (6)

So  $\frac{dP}{dt} = 0$ , which implies  $P = \text{constant}$ .

This model is based on the one developed by Marquet & Velasco-Hernandez (1996). Our model does not consider degradation; source patches will never degrade into sink patches. Both source and sink patches remain as such through time.

#### **2.2 Stochastic Model**

**In** the stochastic model, we generalize Levins' classical model by introducing spatial considerations . The S-I-S model follows Levins' assumptions that space is discrete; it is possible to distinguish between habitat patches; and patches can accommodate panmictic (locally breeding) populations. Our spatial model treats space as well-defined, discrete sink or source patches; the probabilities associated with extinction and propagation allows us to differentiate between sink and source patches; and finally we assume that the species under study can reproduce within the patch. The main purpose of our project is to study the stochastic version of the S-I-S model presented above. We first show what the birth - death process looks like. To do so, we define the following variables:

 $\mu_1 =$  Rate at which source patches are becoming unoccupied.

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- $\mu_2$  = Rate at which sink patches are becoming unoccupied.
- $\lambda_1$  = Rate at which source patches are becoming occupied.
- $\lambda_2$  = Rate at which sink patches are becoming occupied.
- $V =$  Empty Source Patches.
- $W =$  Empty Sink Patches.
- *x* = Occupied Source Patches.
- *Y* = Occupied Sink Patches.

The first step in a stochastic birth-death process is to calculate the rates of 'birth' and 'death.' **In** our case birth is the rate of occupation or colonization. Because we have two types of patches, we have two birth rates and two death rates. The birth and death rates for a source and sink patch can be written as the following:



To find the probabilities associated with the above rates, we divide the specified rate by the sum of the rates,  $SR = X(\lambda_1 V + \mu_1)$ .



Also, we are considering discrete time: Therefore, time is not exponentially distributed, but we can still make time considerations if we update every unit of time as follows:

- $T = Time$ (discrete)
- $R_1 = \lambda_1 XV$
- $R_2 = \mu_1 X$
- $R_3 = \lambda_2 YW$
- $R_4 = \mu_2 Y$

For discrete time we have:



In order to give our model a complete theoretical background, we have to study the Chapman - Kolmogorov equations. For a particular patch at a unit of time, any of the following five events can happen: a source patch can be occupied (a); a sink patch can be occupied (b); nothing can happen (c); a source patch can be unoccupied (d); and finally, a sink patch can be unoccupied (e). In general, equation (refchk) represents the probabilities of five possible events.

Chapman - Kolmogorov equation:  $P\{n_1(T+h) = X, n_2(T) = Y\}$ 

$$
= P\{n_1(T+h) = X + 1, n_2(T+h) = Y\} \cdot P\{\text{Type 1 colonized in time } (t, t+h)\} + P\{n_1(T+h) = X, n_2(T+h) = Y + 1\} \cdot P\{\text{Type 2 colonized in time } (t, t+h)\} + P\{n_1(T+h) = X, n_2(T+h) = Y\} \cdot P\{\text{No colonization occurs in time } (t, t+h)\} + P\{n_1(T+h) = X - 1, n_2(T+h) = Y\} \cdot P\{\text{Type 1 uncolonized in time } (t, t+h)\} + P\{n_1(T+h) = X, n_2(T+h) = Y - 1\} \cdot P\{\text{Type 1 uncolonized in time } (t, t+h)\} = P\{n_1(T+h) = X + 1, n_2(T+h) = Y\} \cdot (\lambda_1 XVh) + P\{n_1(T+h) = X, n_2(T+h) = Y + 1\} \cdot (\mu_1Xh) + P\{n_1(T+h) = X, n_2(T+h) = Y\} \cdot (1 - (\lambda_1 XVh \cdot \mu_1Xh)) + P\{n_1(T+h) = X - 1, n_2(T+h) = Y\} \cdot (\lambda_2 YW) + P\{n_1(T+h) = X, n_2(T+h) = Y - 1\} \cdot (\mu_2Y)
$$
 (7)

and

 $N_1$  = Number of patches of type 1. (Source).

 $N_2$  = Number of patches of type 2. (Sink).

 $N =$ Total number of patches.

 $n_1(t) =$  Number of occupied patches of type 1.

 $n_2(t)$  = Number of occupied patches of type 2.

 $X =$  Population in a source patch.

 $Y =$  Population in a sink patch.

 $h = An$  integer value that updates time.

# **3** Computer Simulation

We transfer the stochastic model to a computer simulation that takes spatial considerations into account. We generate different spatial relations of sink and source patches and place an initial population in random patches in the grid of source-sink patches. We then simulate several discrete generations in which the species is exposed to different probabilities of reproduction and death, and we observe the mean time to extinction of the species with different combinations of land configuration.

### **3.1 Assumptions**

We assume (to simplify the model) that once populated, the patch reaches its carrying capacity, and that once a pair of the species is settled into a grid patch, it will remain there until death. Our model allows the newborn species, however, to move about the grid in a limited fashion in each generation. The newborns, assumed to move in reproducing pairs, can settle into a location one grid patch away from their birthplace and can move there only if this patch is currently unpopulated. The newborns will randomly choose from the available neighboring patches; in other words, they will have no knowledge of the quality of the land upon which they will settle. If there are no available patches, we assume that the newborns fail to move to a neighboring patch and die. We also assume that source patches do not degrade into sink patches and that sink patches do not improve to become source patches.

### **3.2 Simulation Details**

We wish to clearly distinguish the difference between source and sink patches in our model in accordance with the given definitions. **In** order to make the probability of propagation in the source patch substantially larger than in the sink, we somewhat arbitrarily assign the probability of propagation in a sink patch to be .3 lower than that in a source patch. Likewise, we make the probability for local extinction in the sink patch to be .2 greater than that in a source patch. Then, for different combinations of these birth/death probabilities, we do the following:

**In** order to achieve a balance between reasonable resolution of landscape configurations (ranging from a large, single clump of source patches to completely randomly located patches) and computer capabilities, we choose a 50x50 grid. We also wish to model a situation of potential risk to the species, and therefore, we choose a "low" percentage of source patches

to total Jand area; in this case we choose 32%, making a convenient 800 source patches to be placed in the grid. We assign to the grid in random fashion a somewhat arbitrary initial population of 75 pairs, with the choice of number arising from an effort to choose an initial population that is close neither to initial extinction nor initial saturation. To avoid the problem of boundary values, we stipulate that the edges of our 50x50 grid wrap around to the other side, so that the area we analyze is not a plane but a planar representation of a torus. We thus present the following grid types, each with 32% source and 68% sink patches distributed throughout the 50x50 grid:

Grid 1: A single clump of 800 source patches arranged in an approximately  $28 \times 28$  grid. This will model the existence of a reservoir in an otherwise species-unfriendly environment. (The square configuration is chosen throughout, when possible, for its simplicity in programming and in visualization.)

Grid 2: A structured configuration of 2 smaller  $20 \times 20$  clumps of source patches. This models smaller reservoirs interspersed throughout the land.

Grid 3: Three  $10 \times 15$  source patches with the remaining 350 source patches distributed randomly, all within half of the area of the landscape (the other half again being entirely sink patches). This was the first of two configurations that were added midway through research. We noted a remarkable difference in performance between the completely clumped arrangements and the completely random arrangements of source patches in Grids 1 through 4. Here is where we start to bridge the gap between strictly clumped and strictly random source patches. Note: the change in clump proportion arose from a desire to eliminate uniformity of the distance between source clumps, a difficult task with 4 grids of substantial size in a  $50 \times 50$  grid. An analog is the above development of half of a landscape with more reservoir-type considerations involved in the remaining half.

Grid 4: Four  $10 \times 10$  source patches modelled with the remaining 400 patches generated randomly throughout the grid. This is the second of the two configurations that we added midway through research. **In** this way we continue to reduce the clump size and increase the randomness of both the source patch and source clump location.

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 $\label{eq:2} \frac{1}{2} \sum_{i=1}^n \frac{1}{2} \sum_{j=1}^n \frac{1}{$ 

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Grid 5: A random dispersal of source patches throughout the grid. This models the behavior of the species with random removal of source land (example: clearcutting the environment of the spotted owl).

 $\label{eq:2.1} \mathcal{F}^{\mathcal{A}}_{\mathcal{A}}=\frac{1}{2}\left(\frac{1}{2}\sum_{i=1}^{n} \frac{1}{2} \mathcal{F}_{\mathcal{A}}^{(i)}\right)^{2} \mathcal{F}_{\mathcal{A}}^{(i)}$ 

the property of the country of the same that the company

 $\mathcal{L}^{\text{max}}$ 

 $\label{eq:2} \mathcal{L}_{\text{max}} = \frac{1}{2} \sum_{i=1}^{N} \frac{1}{2} \sum_{i=1}$ 

Grid 6: A random dispersal of source patches throughout one half of the grid. This models the behavior of the species with random removal of source land occurring less often, but with a large area of source land, as in the development of a natural environment coupled with consumption of nearby natural resources. Here we can also observe any effect on effectively increasing the density of the random patches without increasing the percentage of source land.

We run the simulation 15 times each for 100 generations or until species extinction, whichever comes first. The program returns to us the final time recorded for each simulation on each land type, along with the mean, standard deviation, and variance of the final times for each landscape type.

To analyze our results, we observe the decreasing performance of the species with the increase of local extinction probabilities with plots of the mean time to extinction of the 15 simulations for given constant propagation probabilities. We then run an analysis of variance to verify the existence of a difference in time to extinction for these 6 grid types, outlined below.

### **4 Data. Analysis Background**

To find out if there is a significant difference in the time to extinction for different spatial considerations, we perform an analysis of variance test (ANOVA). Single factor balanced ANOVA deals with experiments in which there are r treatments with n observations per treatment. Each treatment has a probability distribution of responses. The usual ANOVA model makes three assumptions: that each of the *r* treatment probability distributions is normal and has the same variance; that each observation within a particular treatment is independent of all other observations within that treatment; and that each of the *r* treatment samples is selected independently of one another (Neter, Wasserman, and Kutner, 1990). The objectives of single factor ANOVA include, among other things, comparing the equality of treatment means, and if the means are not equal, examining how they differ. In this paper, we compare treatment means by calculating the F-statistic.

The F-statistic compares the variation between treatments to the variation within treatments. The measure of disparity among the *r* treatment means is measured by the mean square for treatments, denoted by MSTr. The measure of variation within the n observations of the jth treatment,  $j = 1, 2, \ldots, r$  is called the mean square error, denoted by MSE. The F-statistic is the ratio of the MSTr to MSE. If the F-statistic is greater than 1, there is more variation among the *r* treatments than within treatments. When the F-statistic is greater than

1, under certain specifications, one can conclude that the treatment means differ from one another. These specifications include the amount of confidence that is desired **in** the result (called the a level), the number of treatments, and the number of observations per treatment.

The MSTr is found by calculating the treatments sum of squares (SSTr) and dividing by the total number of treatments minus one. The error sum of squares (SSE) is found by subtracting SSTr from the total sum of squares (SSTo). SSE is divided by the total number of observations minus the number of treatments to get the MSE. Devore and Peck (1993) provide computing formulas for SSTr, SSTo) and SSE, from which MSTr, MSE and thus the F statistic are easily calculated.

$$
SSTr = \frac{t_1^2 + t_2^2 + t_3^2 + \dots + t_R^2}{n} - \frac{t^2}{m}
$$
  
\n
$$
SSTo = \sum_{\text{all } m \text{ obs.}} Y_2 - \frac{t^2}{m}
$$
  
\n
$$
SSE = SSTo - SSTr
$$
  
\n
$$
MStr = \frac{SSTr}{r - 1}
$$
  
\n
$$
MSE = \frac{MSTr}{m - r}
$$
  
\n
$$
F = \frac{MSTr}{MSE}
$$

where

 $t_i$  = the sum of the n observations in treatment j,

 $j = 1, 2, \ldots, r$ 

 $t =$  the grand sum of all m observations,

 $n =$  the sample size for each of the r treatments,

 $m = n \cdot r =$  the total number of observations for all treatments,

 $y =$ one of the m total observations.

The single factor balanced ANOVA model can be expressed as:

$$
y_{ij} = m_j + e_{ij}
$$

where

 $y_{ij}$  is the value of the response to the j<sup>th</sup> treatment at the *i*th observation of this treatment,

 $m_i$  are parameters representing the  $r$  different treatment means,

- $e_{ij}$  are i.i.d.  $N(0, s2)$ ,
	- $i = 1, 2, \ldots, n$ ,
- $j = 1, 2, \ldots, r$ .

Since  $E\{e_{ij}\}=0$ , it follows that  $E\{y_{ij}\}=m_j$ .

That is, the expected value of each observation for a particular treatment is equal to the population mean for that treatment. If the calculated F-value is greater than some critical F-value, then the null hypothesis is rejected, and we can conclude that there is a significant difference between the mean values for each factor or treatment. In this paper we use analysis of variance to compare the times to extinction for different source spatial considerations. If the calculated F-value from this data exceeds a particular F critical value (or the p value is less than .05), we will reject our null hypothesis and conclude that the mean time to extinction is significantly different for the different patch configurations.

### **5 Results and Discussion**

As stated previously, the percent of sink-source patches remains fixed while the spread of these patches changes. We found that (when there is no specified stop time) there is a significant difference  $(p = 0.000)$  in the mean time until extinction depending on patch size (for a more detailed explanation, see Appendix, Figure 1). Specifically, the more clumped the patches are, the less likely it is that extinction will occur. All groups in which clumps were assigned greatly outperformed (extinction took a long time) the strictly random patches; Grids 1, 2, 3, and 4 were not faced with extinction before the stop time, 100 generations until the local extinction parameter rose .25. Grids 5 and 6 had nearly identical low times to extinction throughout (see Figure 2). For a source propagation probability of .775, we see some decline in time to extinction for extinction rates of .25 and greater, with Grids 1 and 2 (all clumps, no random patches) having the highest time to extinction (neither performing very distinctly from the other), and grids 3 (clumped and random source patches throughout half of the grid) and 4 (clumped and random throughout the entire matrix) achieving lower, but nearly identical performances (for a more detailed explanation, see Appendix, Figure 2). The results from source propagation probability. 795 are similar; the only difference here is that the minimum

local extinction value to achieve mean times to extinction below the stop time is .35. Finally, we looked at the distribution of the time to extinction. This distribution is skewed to the right (for a more detailed explanation, see Appendix, Figure 3).

### **6 Conclusion**

Our model indicates that for a given percentage of source land area in a landscape, the projected survival of a single species has a direct correlation to the degree to which the source patches are "clumped together." All the grids with specified clumps of source patches (Grids 1,2, 3, and 5 ) greatly outperformed the grid in which source patches are distributed randomly throughout it (Grid 6). Grids 5 and 6, essentially, return the same dramatically lower time to extinction than Grids 1, 2, 3, and 4. In all cases, Grids 1 and 2, each being completely clumped with no random spread of source patches, returned the greatest mean time to extinction (when extinction occurred in all cases before the cutoff time)

These results seem to suggest certain strategies for species preservation efforts. Concerns for the survival of a single species whose good quality habitat is to be limited (for various reasons ) are best addressed by preserving some amount of spatial continuity (referred to throughout as "clumps" or "clumpiness") in the source patches in the landscape.

We were unfortunately unable to resolve better the progression from strictly clumped to strictly random source patches because of time constraints. We anticipate that there is a gradation of declining time to extinction corresponding to declining degree of "clumpiness." Suggested future work might investigate this prediction and might also center around performing some more simulations and with larger cutoff times in order to distinguish better any difference in performance for our cases of maximum survival times (i.e. clumped arrangements of source patches with low local extinction probabilities). We also plan to study the distribution of the time to extinction more thoroughly. Finally we want to find the minimum patch size needed to attain a particular mean time to extinction given particular parameters (minimum viable metapopulation size).

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# **A Appendix**

### **A.I One-Way Analysis of Variance**

We tested to see if the mean time to extinction is the same for each grid type at several different extinction probabilities ( the extinction probability is given at the top of the ANOVA table).





Figure 1: One-Way Analysis of Variance. Low numbered grid types mean large clumps of source patches, whereas small grid numbers mean random or almost randomly assigned sink and source patches.

For every extinction probability that we tested when the data were not affected by a specified stopping time value, we rejected our null hypothesis ( with a p-value equal to 0.0000) and concluded that the grid type has a significant effect on the mean time to extinction. From this we can conclude that the patch size affects the mean time to extinction. More specifically, by looking at this data, we find that there seems to be a defined relationship: the larger the source patches, the more successful the population's survival.

### A.2 Progression of the Time to Extinction as the Probability of Extinction Increases

The plots below show the progression of the mean time to extinction as the probability of extinction increases. The graphs are alos shown in a specific order: the low numbered grids have larger, more clumped source patches. For example, Grid 1 has one large source patch in

its center, and Grid 6 has a random distribution of source patches throughout it. It should be noted that the percent of source patches remains constant in all grids. Also, as the probability of extinction increases, the higher numbered grids go to extinction at approximately the same rate.









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### **Histograms of the Distribution of Time to extinction for different Spatial Consideration**



Figure 7: Source Probability of Propagation = .775. Sink Probability of Propagation = .475. Source Probability of Local Extinction  $= .3$ . Sink Probability of Local Extinction  $= .5$ .

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