A theoretical framework for a three-state spatial population model with applications

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Abstract

The theoretical work of this contribution is motivated by our efforts to understand spatiotemporal dynamics of biological systems whose main features can be roughly captured by three states. The general model is constructed and approximate sub-models are used to help increase (eventually) our understanding of the dynamics of three-state systems. The pair approximation method is used to construct a spatial sub-model with nearest neighbor interaction. The spatially implicit mean-field approximation of the three-state model is also investigated to study the dynamics of the null-model, that is the dynamics of a model without the spatial component. Dynamics of our approximation are compared with a stochastic computer simulation (based on continuous-time Poisson processes) of the full model. The reliability of the pair approximation and the mean field model is discussed. The model is applied to the protection of crops against infestation and the spread of influenza in a closed environment with temporary vaccination.

1 Introduction

Recently there has been interest in spatial mathematical models in biology. Spatial models include some degree of spatial correlation over a population while traditional mathematical models, such as mean-field approximations, ignore these correlations. Including space in a model allows one to include the distance over which interactions in a population take place. Traditional models assume homogeneous mixing, while spatial models allow interactions to take place on various scales, such as interactions between nearest neighbors. Pair approximation models have been applied by Hiebeler [15] to study block disturbances on a locally-dispersing population. Spatial population models have also been applied to the study of the spread of plant disease [1, 9] and forest gap dynamics [16]. There have also been epidemiological spatial models such as a spatial SIS model [14].

Each modeling technique has different advantages. While mean-field approximations neglect spatial correlations they are the simplest mathematically and the equations can be solved analytically for equilibrium points. Pair approximation models include some spatial correlations, and therefore may produce more biologically accurate results, but the equations are more complicated and extensive analysis may not be able to be performed. Stochastic computer models are even more accurate because they do not neglect any spatial correlations, but are only numerical and no analytical results can be obtained from them.

The model presented here uses stochastic computer simulations in continuous time and the pair approximation technique to investigate the dynamics of a three-state model with normal, infested, and protected states. The transitions between the states can be caused by large-scale block protection events, spatially local spread of infestation, or a site losing its protection. This paper also examines several applications of the model including spraying of pesticides to reduce crop infestation by Argentine ants and temporary vaccination to

protect against the influenza virus. The general framework for the model proposed here is applicable to situations where something contagious is spread among neighbors and sites can be temporarily protected. The effectiveness of various spraying and vaccination techniques is also examined.

In Section 2, an introduction to pair approximation is presented. In Section 3, the details of the model for both the pair approximation equation and computer simulation are discussed. In Section 4, the mean field approximation of the model is studied. In Sections 5 and 6 applications of the general model are shown. In Section 7, results from all three models are shown and in Section 8, conclusions from the models discussed.

2 Introduction to Pair Approximation

Pair approximation is a modeling technique which allows local spatial correlations to be included in a mathematical population model. Pair approximation models are approximations because they assume that the only spatial correlations which exist are ones between nearest neighbors. Often spatial correlations develop over distances greater than local distances between nearest neighbors, which makes pair approximation models most accurate when larger scale correlations are less prevalent.

Pair approximation models contain a set of differential equations which describe configurations of 2×1 blocks (pairs) of sites. Sites of 2×1 blocks (pairs) are considered due to their simplicity compared to larger blocks of pairs of sites. Larger blocks, called local structure approximations, tend to be far less tractible [11].

Pair approximation models are more accurate than the traditional spatially implicit approach where the equations only describe single sites when models involve local spatial interactions. Examples of spatially explicit models are infestation spreading amongst neighboring plants, influenza spreading amongst neighboring sites in closed environments,

the spread of rumors, or even the spread of fear and panic. Other methods such as mean field approximation will not give as accurate results because they fail to account for spatial characteristics.

In pair approximation models the system is described with state variables which are probabilities of pairs of sites being in certain states. For example, $P[ab]$ is the probability that the first site is in state a and the second site is in state b. Pair approximation models assume spatial symmetry, so in a model where local neighbors are considered to be the four nearest neighbors (i. e. N, S, E, W neighbors) the probabilities $P[ab]$, $P[ba]$, $P[\begin{smallmatrix} a \\ b \end{smallmatrix}]$, and $P[\begin{smallmatrix} b \\ a \end{smallmatrix}]$ would be the same. A marginal single-site probability is found by summing over all the possible ways the first site could be in that state and the second can be in any other state. For instance in a two-state model with states a and b, $P[a] = P[aa] + P[ab]$.

The conditional probability that a randomly chosen neighbor of a site in state b is in state a is given by

$$Q[a|b] = Q_{a|b} = \frac{P[ab]}{P[a]}. \tag{1}$$

Because pair approximation only involves correlations between neighboring sites, the conditional probability that in three adjacent sites the last one will be in state c given the first two are in state a and b is actually the same as the conditional probability discussed previously, $Q_{c|b}$ [13]. That is,

$$P[**c|ab*] = P[**c|*b*] = \frac{P[*bc]}{P[*b*]} = \frac{P[bc]}{P[b]} = Q_{c|b}. \tag{2}$$

3 The Model

3.1 General Model

This three-state spatial model has the states N, S, and I. A site in the normal state is represented by N, S a site in the sprayed or protected state, and I a site in the infested state. These states were chosen to model the effect of protection by pesticide to mitigate crop damage caused by insect infestation. The model discussed will be general and can be applied to any situation involving protection to mitigate damage spread locally in a population.

Several events can cause transitions between the states. Sites on a landscape which are normal (N) can be infested by their local neighbor. Infested sites attempt to infest their neighbors at rate ϕ. Sites which are sprayed (S) can have the protection wear off in this case the sites become individually normal again. This transition occurs at rate μ. The other event that can occur is that sites of any state may be protected in a block. The protection block event causes any state (N, S, or I) to transition to state S. A site in state S remains protected in state S if it is affected by the protection block event. Not all states in the block are successfully protected, and c is the proportion of sites within the protection block that successfully transition to state S. The dimensions of the protection blocks are $b_1 \times b_2$. The rate of protection blocks occuring, the rate that blocks of sites transition to state S, is $\frac{\sigma}{c(b_1 \times b_2)}$. The per-site spray rate, the rate that single sites transition to state S, is the same regardless of the block size or concentration and is σ. These rates and parameters are summarized in Table 1.

3.2 Pair Approximation Model

To construct the pair approximation equations, the possible configurations of pairs of sites and transitions between them were first examined. There are three states so there are nine

Table 1: Summary of parameters

N	normal site
I	infested site
S	sprayed site
ϕ	rate of sites becoming infested
μ	rate of protection wearing off
σ	rate of sites becoming protected
b_1 and b_2	length and width of protection block
c	probability within a block that a site will be protected

possible pairs of states. The nine probabilities of two neighbors being in certain states are $P[NN]$, $P[NS]$, $P[II]$, $P[IN]$, $P[IS]$, $P[SS]$, $P[SI]$, $P[SN]$, and $P[NI]$. Due to symmetry, $P[NI] = P[IN]$, $P[IS] = P[SI]$, and $P[SN] = P[NS]$. $P[NN]$ can be written as $1 - 2P[NI] - 2P[NS] - 2P[SI] - P[II] - P[SS]$ because all probabilities must add up to 1. The state variables for the model are then $P[SI]$, $P[NI]$,$P[NS]$, $P[II]$, and $P[SS]$. The other pair probabilities can be written in terms of these state variables.

In order to obtain the diagram used to create the pair approximation equations as shown in Figure 1 one must check each of the state variables one at a time. The idea is to examine which states go in and out of a given state provided the transitions are allowed and also given that only one event can occur at a time. In order to get the system of five differential equations, one must take the probability of each state (e.g $P[NI]$, $P[II]$, and $P[NS]$) going into the state variable (e.g $P[SI]$), then multiply the probability with its respective transitioning rate into the target state. Then, we need to subtract the product of the probability of the current state (e.g $P[SI]$) and the sum of the rates transitioning out of the state. The rate $r_{A\to B}$ denotes the rate of transition from state A to state B. The rate $r_{*a\to Sa}$ denotes the rate of transition from a pair where one site is in state $*$ and the other is in state a to a pair where one site is in state S and the other is in state a, here $* \in \{N, I, S\}$ and $a \in \{N, I\}$

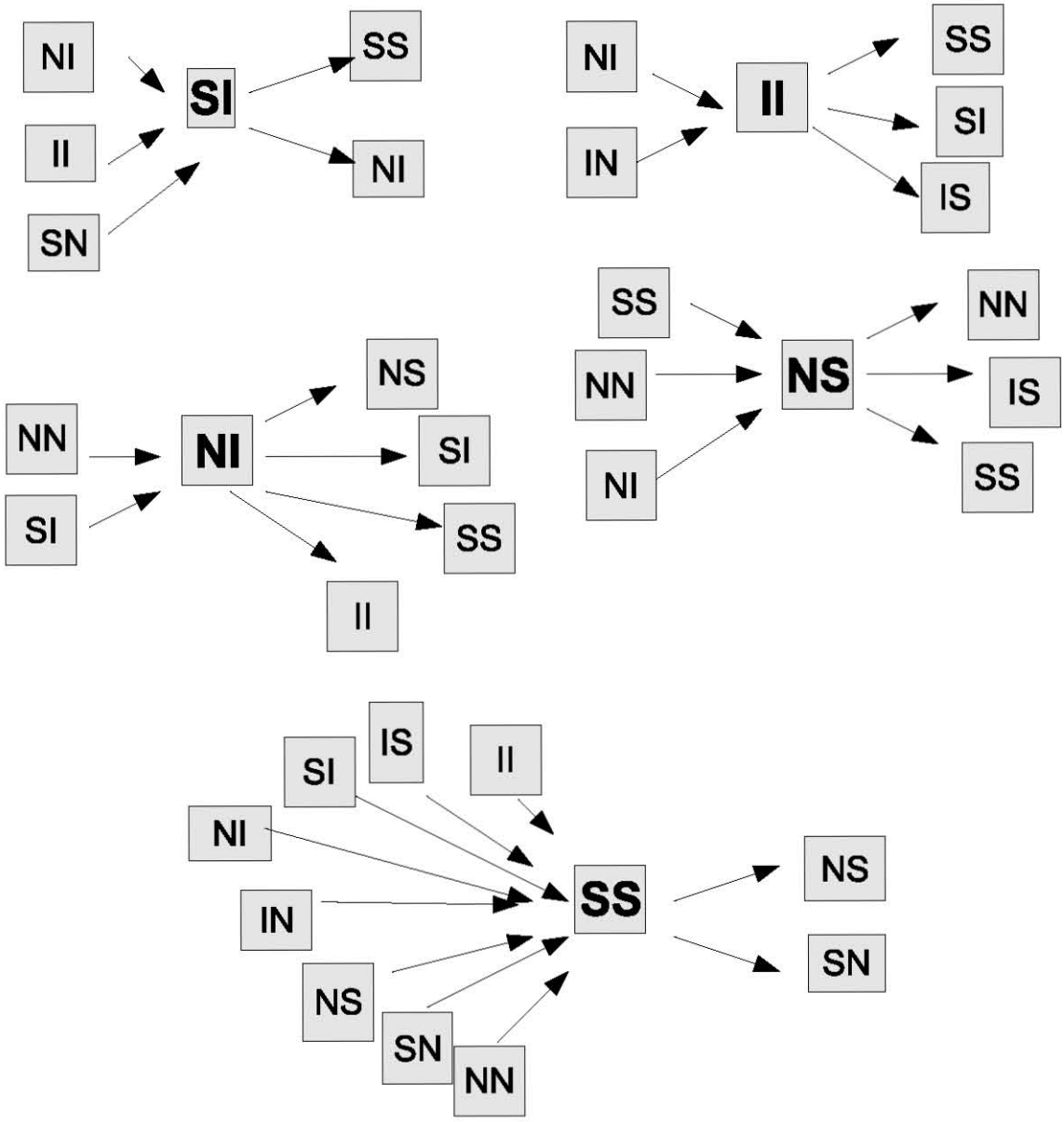

Figure 1: The possible transitions into and out of each state variable.

The system of five differential equations with all possible transitions are given by:

$$\frac{dP[SI]}{dt} = P[NI]r_{*a\to Sa} + P[II]r_{*a\to Sa} + P[NS]r_{N\to I} \tag{3}$$
$$- P[SI](r_{*a\to Sa} + r_{**\to SS} + r_{S\to N}),$$
$$\frac{dP[NI]}{dt} = P[NN]r_{N\to I} + P[SI]r_{S\to N} - P[NI](r_{*a\to Sa} + r_{*a\to Sa} + r_{**\to SS} + r_{N\to I}), \tag{4}$$
$$\frac{dP[II]}{dt} = 2P[NI]r_{N\to I} - P[II](r_{**\to SS} + 2r_{*a\to Sa}), \tag{5}$$
$$\frac{dP[NS]}{dt} = P[SS]r_{S\to N} + P[NN]r_{*a\to Sa} + P[NI]r_{*a\to Sa} \tag{6}$$
$$- P[NS](r_{S\to N} + r_{N\to I} + r_{*a\to Sa} + r_{**\to SS}),$$
$$\frac{dP[SS]}{dt} = 2P[SI](r_{*a\to Sa} + r_{**\to SS}) + 2P[NI]r_{**\to SS} + 2P[NS](r_{*a\to Sa} + r_{**\to SS}) \tag{7}$$
$$+ P[NN]r_{**\to SS} + P[II]r_{**\to SS} - 2P[SS]r_{S\to N}.$$

In this paper, $Q_{I|N}$ is used to describe the conditional probability that one's neighbor is infested given that he is normal. In order to find this conditional probability one must divide $P[NI]$ by $P[N]$, therefore

$$Q_{I|N} = \frac{P[NI]}{P[N]} = \frac{P[NI]}{1 - P[NI] - 2P[SI] - P[II] - P[SS] - P[NS]}. \tag{8}$$

The probability that a particular neighbor of a sprayed site is also sprayed is given by β, where

$$\beta = c\left(1 - \frac{1}{2}\left(\frac{1}{b_1} + \frac{1}{b_2}\right)\right). \tag{9}$$

This is the probability that the first site is not on the edge of the block (implying that its neighbor is also contained within the block), and that the neighbor is also successfully affected by the spraying.

With substitutions made for the rates:

$$\frac{dP[SI]}{dt} = P[NI]\sigma(1-\beta) + P[II]\sigma(1-\beta) + P[NS]\frac{3}{4}\phi Q_{I|N} - P[SI](\sigma+\mu), \tag{10}$$

$$\frac{dP[NI]}{dt} = P[NN]\frac{3}{4}\phi Q_{I|N} + P[SI]\mu - P[NI]\left(2\sigma(1-\beta) + \sigma\beta + \frac{1}{4}\phi + \frac{3}{4}\phi Q_{I|N}\right), \tag{11}$$

$$\frac{dP[II]}{dt} = 2P[NI]\left(\frac{1}{4}\phi + \frac{3}{4}\phi Q_{I|N}\right) - P[II]\Big(\sigma\beta + 2\sigma(1-\beta)\Big) \tag{12}$$

$$\frac{dP[NS]}{dt} = P[SS]\mu + P[NN]\sigma(1-\beta) + P[NI]\sigma(1-\beta) - P[NS]\left(\mu + \frac{3}{4}\phi Q_{I|N} + \sigma\right), \tag{13}$$

$$\frac{dP[SS]}{dt} = 2P[SI]\sigma + 2P[NI]\sigma\beta + 2P[NS]\sigma + P[NN]\sigma\beta + P[II]\sigma\beta - 2P[SS]\mu. \tag{14}$$

In Equation 10, $\frac{3}{4}$ arises from $\frac{3}{4}\phi Q_{I|N}$ because we know that one adjacent neighbor is protected, therefore 3 out of 4 neighbors remaining can infest the target site. Also, in Equation 11, the $\frac{1}{4}\phi$ term arises because the normal site may become infested by its neighbor within the block which is known to be already infested. Note that the system of five differential equations above is not in terms of the state variables since the substitution for $P[NN]$ and $Q_{I|N}$ is not done. Pair approximation is very useful when we are dealing with spatial models. Although computer simulations generate more accurate results, one would prefer to use pair approximation because results are generated much more quickly.

3.3 Computer Simulation

Computer simulations were designed by imlementing continuous-time Poisson processes. Continuous-time Poisson processes have independent times between events. To simulate such a process, the time of the next event is calculated by adding the time of the previous event to an exponentially distributed random number with parameter one over the sum of the rates of the possible events, where L is the lattice size, and the time of the next event

is given by:

$$t_i = t_{i-1} + \text{rand}\left[\exp\left(\frac{1}{\phi P[I] + \mu P[S] + \frac{L^2\sigma}{c(b_1 \times b_2)}}\right)\right]. \tag{15}$$

All of the computer simulations were carried out on a lattice size of 200, meaning the dimensions of the landscape is 200×200. A "step" in the model is defined to be L^2 events. This means that on average, each site is updated once every step. The boundaries in the simulation are wraparound, meaning that the landscape is shaped like a torus. The simulation stops after the proportions $P[N]$, $P[S]$, and $P[I]$ have equilibrated. A proportion was determined to be equilibrated when a linear regression was fit over the values for that proportion over the last 100 simulation steps and the slope of the regression line was less than 0.001. The simulation was run five times and the average values of $P[N]$, $P[S]$, and $P[I]$ over the five runs were used for data collection.

The pseudocode for the computer simulation is as follows:

```
Place initial sprayed, infested, and normal sites on lattice according to
     the initial proportions specified

While the simulation is not equilibrated
     Calculate the probability of an infestation event
     Calculate the probability of a spray (protection) event
     Calculate the probability of a spray wearoff event
     Calculate the time of the next event
     Get next event based on probabilities of the events

     If infestation event
          Choose infested site
```

```
        Attempt to infest the infected site's neighbor
    If wear off event
        Choose sprayed site
        Change sprayed site to normal
    If spray event
        Choose a target site
        Make a b1 x b2 or b2 x b1 sized block around the target
            site where each site within the block has
            probability c of being protected
    Check if simulation equilibrated by doing regression
        Stop if equilibrated
```

A screenshot of a running computer simulation is shown in Figure 2.

4 Mean-field Approximation

Mean-field approximations are different from pair approximations since mean-field approximations do not involve space. The mean-field approximation reduces to an N, S, I model that does not involve pairs of states. Some of the variables which we used in pair approximation b_1, b_2, and concentration c, do not appear in mean field approximations because these variables only apply to the spatial component of the model. Concentration is related to space because it tells the quantity per unit area, and area is a spatial characteristic. Quantities b_1 and b_2 involve space because they describe the width and length of the given blocks. Mean-field approximations allow for basic analysis due to the fact that we can compute the equilibrium points and perform a stability analysis on them. However, in pair approximation a computer may need to be used to solve numerically for the equilibrium solutions and a general, analytical answer can not always be found. In the

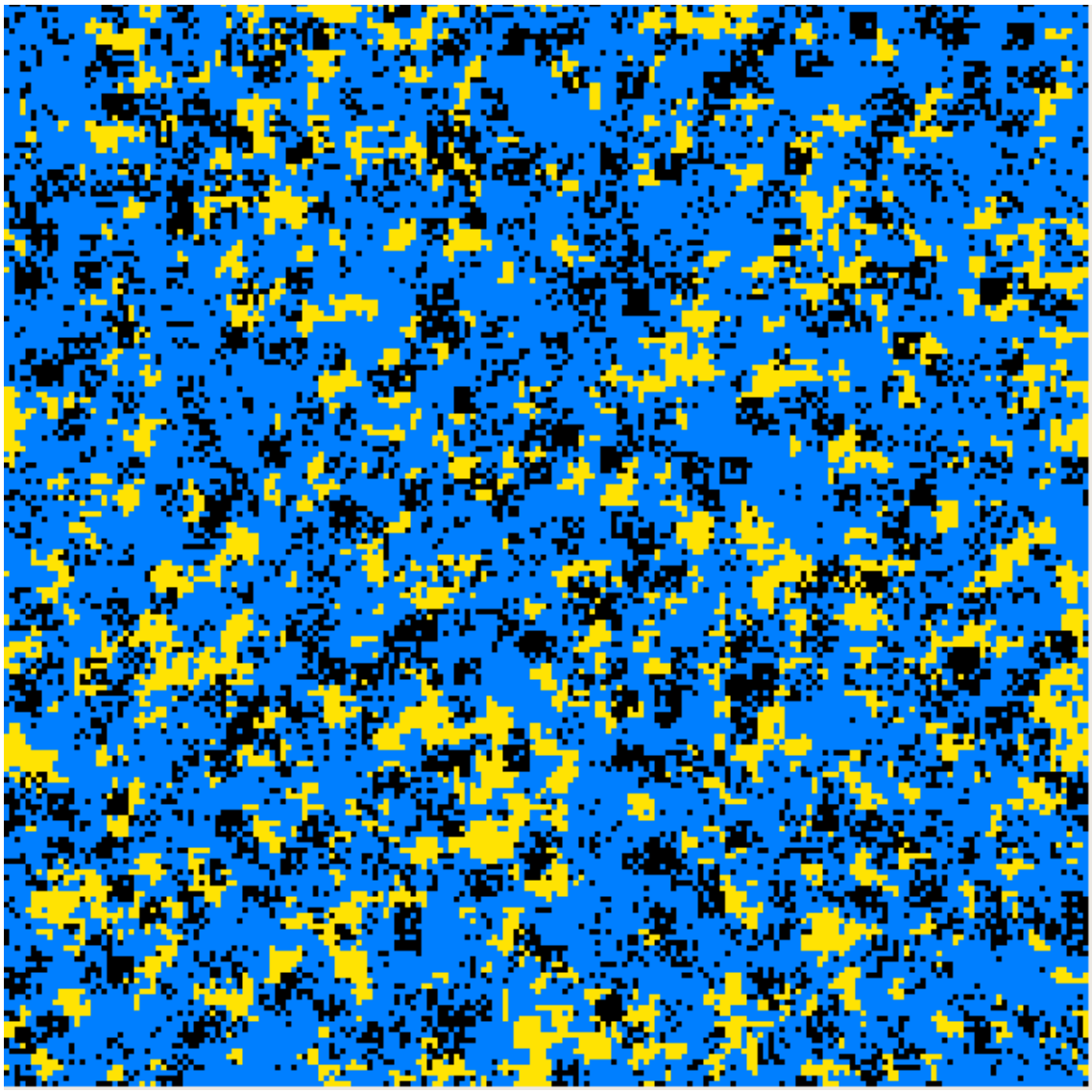

Figure 2: A screenshot of a running computer simulation where $\mu = 4$, $\phi = 3$, $\sigma = 1$, $c = 0.8$, $b_1 = b_2 = 5$, and $P[N] = 0.73$, $P[S] = 0.19$, $P[I] = 0.06$ at equilibration. Normal sites are dark gray, sprayed sites are black, and infested sites are light gray.

mean-field approximation, N, S, and I represent the proportion of normal, sprayed, and infested sites respectively, $N + S + I = 1$. So $\frac{dN}{dt} + \frac{dI}{dt} + \frac{dS}{dt} = 0$ and S can be written in terms of N and I where $S = 1 - N - I$.

The mean-field approximation for this system is:

$$\frac{dN}{dt} = S \cdot r_{S \to N} + I \cdot r_{I \to N} - N \cdot (r_{N \to I} + r_{N \to S}), \tag{16}$$

$$\frac{dI}{dt} = N \cdot r_{N \to I} + S \cdot r_{S \to I} - I \cdot r_{I \to S} - I \cdot r_{I \to N}. \tag{17}$$

The rate going from sprayed (S) to normal (N) in (16) is the rate of protection wearing off, μ. The rate going from infested (I) to N in (16) and (17) is the rate that an infested plant will become normal. This rate is equal to zero because an infested plant can become normal only through being sprayed first. The rate that sites turn from N to I in (16) and (17) is the rate of sites becoming infested, represented by ϕ. The rate that sites turn from S to I in (17) is the rate that plants become infested from a sprayed site. This rate will be equal to zero because one cannot go directly from the sprayed state to the infested state without first going through the normal state. The rate that sites turn from I to S in (17) is the rate of infested sites becoming sprayed or protected. The equations for (16) and (17) are obtained by figuring out all of the states that can become normal or infested and all the states that normal or infested can change to within one event. Equations (16) and (17) then become:

$$\frac{dN}{dt} = S\mu - N(\phi I + \sigma), \tag{18}$$

$$\frac{dI}{dt} = NI\phi - I\sigma. \tag{19}$$

In equations (18) and (19), $N\phi$ is multiplied by I because normal sites can only become

infested by a neighboring infested site.

The equilibrium points for (18) and (19) are:

$$(N_1,\ I_1) = \left(\frac{\mu}{\mu+\sigma},\ 0\right), \tag{20}$$

$$(N_2,\ I_2) = \left(\frac{\sigma}{\phi},\ \frac{\mu}{\mu+\sigma} - \frac{\sigma}{\phi}\right). \tag{21}$$

To find the stability of (N_1, I_1), the eigenvalues of the Jacobian matrix of equations (18) and (19) are obtained. The eigenvalues are:

$$\lambda_1 = -(\mu+\phi) \text{ and} \tag{22}$$

$$\lambda_2 = \frac{\mu\phi}{\mu+\phi} - \sigma. \tag{23}$$

An equilibrium point is locally asymptotically stable when the real part of the eigenvalues is negative. The real part of (22) is always negative because the parameters for the equations are always positive. The real part of (23) is negative when $\frac{\mu\phi}{(\mu+\sigma)\sigma} < 1$. So the infestation-free equilibrium point, (N_1, I_1), is stable when

$$R_0 = \frac{\mu\phi}{(\mu+\sigma)\sigma} < 1. \tag{24}$$

R_0 is known as the basic reproductive number. It gives the average number of new infestations produced by a typical infested site in a collection of normal sites [10, 2]. The same expression for R_0 can be obtained using the next generation operator method [18].

In this case, R_0 is given by the proportion of N sites which can be infested, $\frac{\mu}{\mu+\sigma}$, times the average time before spraying, $\frac{1}{\sigma}$, times the rate at which sites become infested, ϕ.

Theorem 1. *If $R_0 < 1$ then the infestation-free equilibrium (N_1, I_1) is locally asymptotically stable. If $R_0 > 1$ then the infestation-free equilibrium is unstable [3].*

If the infestation-free equilibrium point is unstable then the endemic equilibrium (N_2, I_2) is born and is locally asymptotically stable.

5 Applications

5.1 Crop Protection

One application of a three state model with normal, infested, and protected states is the protection of agricultural crops such as citrus groves and vineyards from damage due to Argentine ants. The Argentine ant lives in warm, moist climates such as California and the southeastern United States and is an invasive species originally from Argentina. Argentine ants are usually associated with outbreaks of mealybugs and aphids which cause damage to agricultural crops.

The Argentine ant collects honeydew which is secreted by the aphids as its principal food source. In return the Argentine ant protects the aphids and mealybugs from natural predators and parasites. It is the aphids and mealybugs, not the Argentine ant, that actually attack the plant. In order to help the agricultural economy by reducing crop damage by the aphids and mealybugs it is highly desirable to protect crops from the Argentine ant. The most common agricultural practice is to spray barrier pesticide on the crops which repel the Argentine ant. Eliminating or sharply reducing the population of Argentine ants will greatly lower the population of aphids and mealybugs which will lower the amount of crop damage [7].

In a mathematical model, the damage to the crops caused by the presence of the Argentine ant can be studied by considering the possible states of the crop only without directly considering the ants, aphids, or mealybugs. The state of an individual plant could be normal (no ant infestation or protection from pesticide), sprayed (protected by pesticide), or infested (with ants). The events that can cause a change of state are spraying

of pesticide, the protection from the pesticide wearing off, and the spread of the infestation.

5.2 Influenza

Influenza is a respiratory infection which produces symptoms such as fever, sore throat, muscle pains, severe headache, cough, along with general feelings of weakness and fatigue. Influenza rapidly spreads from person to person and is spread by droplets from the nose or throat of an infected person to another nearby person [8]. If influenza spreads in a closed environment such as a classroom in an elementary school, bunk beds in boarding school, or office space then it can be spread locally unlike in a global environment which will allow the flu to jump to a distant neightbor because infected people could travel far distances. The influenza vaccine provides immunity against a virus strain or "closely" related virus strains contained in the vaccine. With influenza the pair approximation states become susceptible, infected, and vaccinated/recovered. The possible transitions between the states include a person becoming infected with influenza, a person recovering, people being vaccinated, and people becoming susceptible to another strain of influenza.

A person who is susceptible is neither sick nor vaccinated or recovered. A susceptible person can become infected by a neighboring person who is infected. People would also be able to become vaccinated from any state, but they may transition out of the vaccinated/recovered class by becoming susceptible to other strains of influenza. If a person is infected they may recover and move to the vaccinated/recovered class meaning that they will not immediately be susceptible to the same strain of influenza. In this model the effect of cross-immunity is not taken into account.

6 Three-state Model for Influenza

6.1 Pair Approximation Model

The influenza model is very similar to the original pair approximation model. In the influenza model, S represents the susceptible state, N in the original model, the infested state I becomes the infected state I, and the sprayed state S becomes the vaccinated/recovered state V in the influenza model.

There is also one additional rate not found in the original model, ρ. It is the rate of individuals recovering from influenza, the rate of transition from state I to state V. Vaccinations (protection events) still occur in blocks which can cause transitions from any state (S, I) to state V. In the influenza model, β has the same meaning as in the original model. The difference is that the β here is equal to the old β times the probability that a site that became vaccinated was vaccinated as part of a block and did not recover individually, that is

$$\beta = c\left(1 - \frac{1}{2}\left(\frac{1}{b_1} + \frac{1}{b_2}\right)\right)\left(\frac{\sigma}{\sigma + \rho}\right). \tag{25}$$

All other parameters and rates have the same meaning and describe the same transitions as in the original model.

The differential equations which describe the pair approximation model for influenza

are:

$$\frac{dP[VI]}{dt} = P[SI]\sigma(1-\beta) + P[II]\left(\sigma(1-\beta)+\rho\right) + P[SV]\frac{3}{4}\phi Q_{I|S} - P[VI](\sigma+\mu) \quad (26)$$

$$\frac{dP[SI]}{dt} = P[SS]\frac{3}{4}\phi Q_{I|S} + P[VI]\mu - P[SI]\left(2\sigma(1-\beta) + \sigma\beta + \frac{1}{4}\phi + \frac{3}{4}\phi Q_{I|S} + \rho\right) \quad (27)$$

$$\frac{dP[II]}{dt} = 2P[SI]\left(\frac{\phi}{4} + \frac{3}{4}\phi Q_{I|S}\right) - P[II]\left(\sigma\beta + 2\sigma(1-\beta) + \rho\right) \quad (28)$$

$$\frac{dP[SV]}{dt} = P[VV]\mu + P[SS]\sigma(1-\beta) + P[SI](\sigma(1-\beta)+\rho) - P[SV]\left(\mu + \frac{3}{4}\phi Q_{I|S} + \sigma\right) \quad (29)$$

$$\frac{dP[VV]}{dt} = 2P[VI](\sigma+\rho) + 2P[SI]\sigma\beta + 2P[SV]\sigma + P[SS]\sigma\beta + P[II]\sigma\beta - 2P[VV]\mu \quad (30)$$

6.2 Mean-field Approximation

The mean-field approximation of the influenza model is very similar to the mean-field approximation of the original model presented in equations (18) and (19). Replacing N, S, and I with S, I, and V and adding in the rate ρ for individual transitions from state I to state N the mean-field approximations become:

$$\frac{dS}{dt} = V\mu - S(\phi I + \sigma), \quad (31)$$

$$\frac{dI}{dt} = SI\phi - I(\sigma+\rho). \quad (32)$$

As before, $V = 1 - S - I$. These equations are exactly the same as the mean-field equations (18 and 19), except that equation (32) contains an $I(\sigma+\rho)$ rather than an $I\sigma$. This is because a site that is infected can become vaccinated/recovered by either being vaccinated as part of a block at rate σ or recover individually at rate ρ.

The equilibrium solutions for (31) and (32) are as follows:

$$(S_1, I_1) = \left(\frac{\mu}{\mu+\sigma},\ 0\right), \tag{33}$$

$$(S_2, I_2) = \left(\frac{\sigma+\rho}{\phi},\ \frac{1}{\sigma+\rho+\mu}\left[1 - \frac{\sigma+\rho}{\phi} - \frac{\sigma(\sigma+\rho)}{\phi}\right]\right). \tag{34}$$

To find the stability of (S_1, I_1), the eigenvalues of the Jacobian matrix of equations (31) and (32) are obtained. The eigenvalues are:

$$\lambda_1 = -(\mu+\phi) \text{ and} \tag{35}$$

$$\lambda_2 = \frac{\mu\phi}{\mu+\phi} - (\sigma+\rho). \tag{36}$$

An equilibrium point is locally asymptotically stable when the real parts of the eigenvalues are negative. The real part of (35) is always negative because the parameters for the equations are always positive. The real part of (36) is negative when $\frac{\phi\mu}{(\mu+\phi)(\sigma+\rho)} < 1$. So the infection-free equilibrium point, (S_1, I_1), is stable when

$$R_0 = \frac{\phi\mu}{(\mu+\sigma)(\sigma+\rho)} < 1. \tag{37}$$

In this case R_0 is given by the proportion of susceptible individuals which can be infected, $\frac{\mu}{\mu+\sigma}$, times the average time before vaccination or recovery, $\frac{1}{\sigma+\rho}$, times the rate at which individuals become infected, ϕ. The same result for the condition of stability for (S_1, I_1) can be obtained using the next generation operator method.

Theorem 2. *If $R_0 < 1$ then the infection-free equilibrium (S_1, I_1) is locally asymptotically stable. If $R_0 > 1$ then the infection-free equilibrium is unstable.*

If the infection-free equilibrium point is unstable then the endemic equilibrium (S_2, I_2) is

born and is locally asymptotically stable.

6.3 Parameters

Estimated values for the individual recovery rate ρ and infection rate ϕ from the 2002-2003 influenza season in the US were used [6]. These values are $\rho = 1.224$ and $\phi = 9.99$. The parameter c was taken to be the proportion of individuals who receive the flu vaccine. The CDC estimates the percentage of individuals who receive a flu vaccine for various categories including at-risk adults, in this case, the elderly, and children, and these percentages vary widely depending on the category [5]. A concentration of $c = 0.80$ was chosen, meaning that 80% of the population received the vaccine. The vaccination rate, was taken to be the rate at which blocks of the population are vaccinated.

An influenza vaccine doesn't wear off over time, but instead in a multiple strain model of influenza like the one considered here the vaccine only protects against a particular strain of influenza. Influenza vaccines are only effective against antigenically similar strains of the virus, and in influenza seasons where antigenically different strains of the virus are prevalent, an influenza vaccine can have a low efficacy rate [17, 4]. The rate of transition from state V to state S, μ, was related to the vaccine efficacy rate. A lower μ qualitatively corresponds to a higher vaccine efficacy rate, and a higher μ corresponds to a lower vaccine efficacy rate. For instance, in an influenza season with several antigenically different strains of the virus and a vaccine which only protects against one strain, μ would be relatively high.

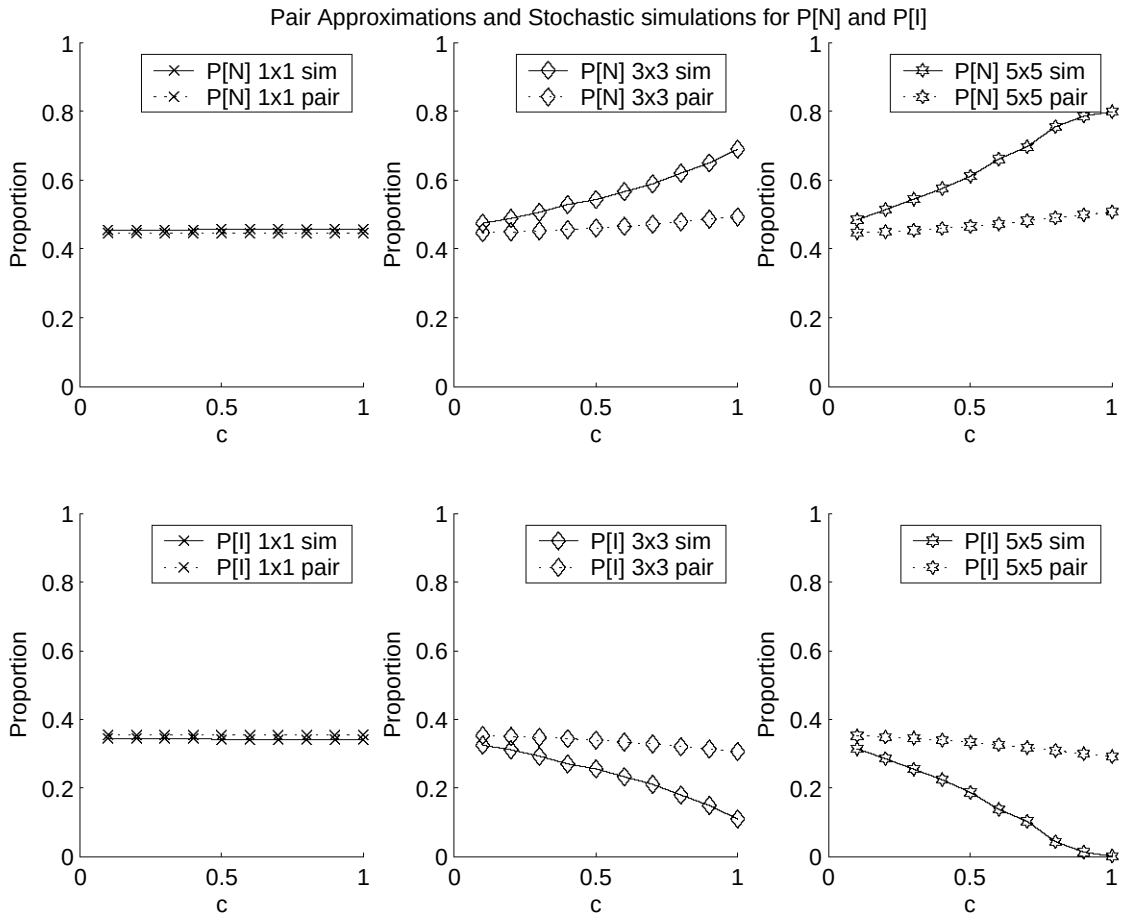

Figure 3: Original model: Varying concentration and block size for pair approximation and computer simulations. $\mu = 4$, $\phi = 3$, $\sigma = 1$.

7 Results

7.1 Crop Protection Model

The equilibrium solutions for pair approximation were numerically found using MATLAB. The source code can be found in Appendix A. The stochastic simulation code for MATLAB can be found in Appendix B. There is an alternative source code for the stochastic computer simulation written in C which runs much more quickly.

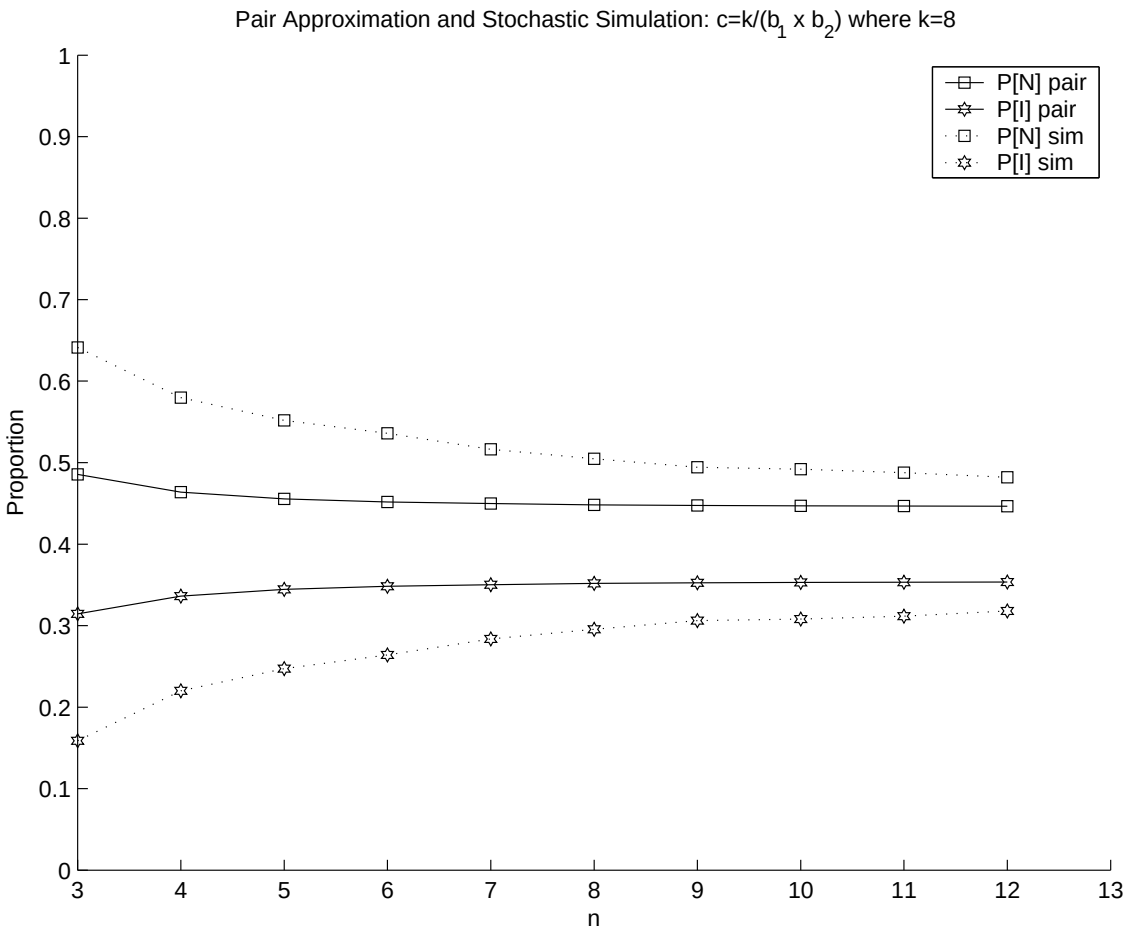

Figure 4: Original model: Varying concentration as a function of block size where $k = 8$ and $c = \frac{k}{b_1 \times b_2}$. $\mu = 4$, $\phi = 3$, $\sigma = 1$, square $n \times n$ blocks were used.

Figure 3 shows that as the concentration c increases, the proportions of N increase a lot faster in the computer simulation than the proportions of N for the pair approximation. The same is true for I, for simulation it decreases very fast compared to the proportion of I for the pair approximation. This shows that as concentration increases the pair approximation can not predict what's happening with proportions of N, I.

Figure 4 shows how k number of sites are affected regardless of block size:

$$k = c * (b_1 \times b_2) = 8 \tag{38}$$

$$c = \frac{k}{b_1 \times b_2} \tag{39}$$

while keeping k constant and allowing c and $b_1 \times b_2$ to change. The figure shows that at small block size the porportions of N is higher and as the block size are larger that proportions of N levels off for the stochastic simulations. For the pair approximation the leveling off occurs at small block size and stays the same as the block size is increasing.

Figure 5 shows proportions of $P[N]$, $P[S]$, and $P[I]$ for the pair approximation, stochastic simulation, and the mean-field approximation. This graph shows that the mean-field approximation does not accurately reflect the qualitative dynamics of the system. Recalling that mean-field does not take into account the spatial characteristic of our model, therefore we can see from the pair approximation that spatial correlation is very strong for our model.

One can also see that the pair approximation does not reflect what the stochastic simulation is showing as the spraying block sizes are increasing. Pair approximation was considered because it is a very fast and easy way to approximate the solution to our model at small block sizes. It is easy since MATLAB can numerically solve the system of differential equations to approximate the solution.

For the stochastic simulation Figure 6 shows that as μ increases then the proportion of $P[I]$ also increases. The proportion of $P[I]$ for the pair approximation differs from the computer simulation because the pair approximation values for $P[I]$ starts decreasing at some value of μ, may be due to the overestimation of P[I] for smaller μ. From this figure, the pair approximation can approximate the solution very well for this model around $\mu = 6$. Pair approximation is faster than computer simulation, although it does not

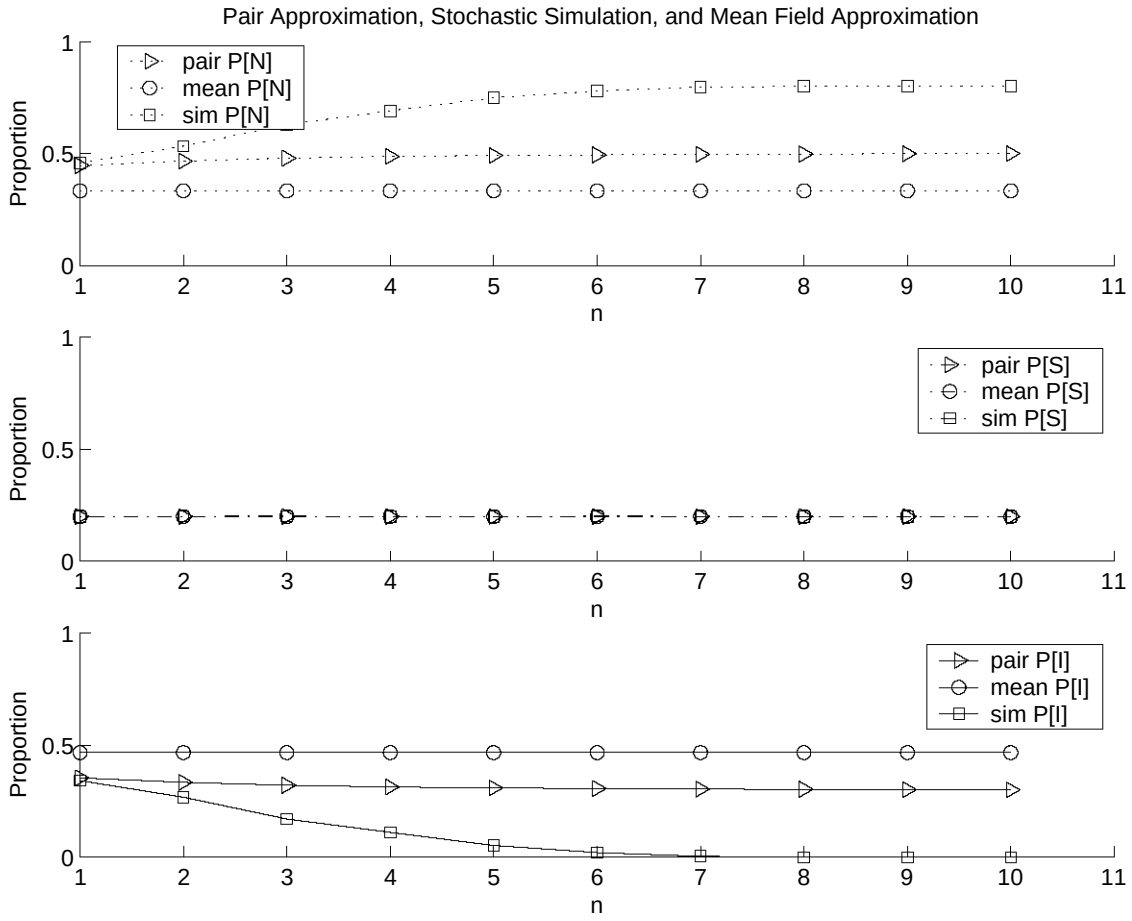

Figure 5: Original model: Comparison of pair approximation, mean field approximation, and computer simulations varying block size. $c = 0.8$, $\mu = 4$, $\phi = 3$, $\sigma = 1$, square $n \times n$ spray blocks.

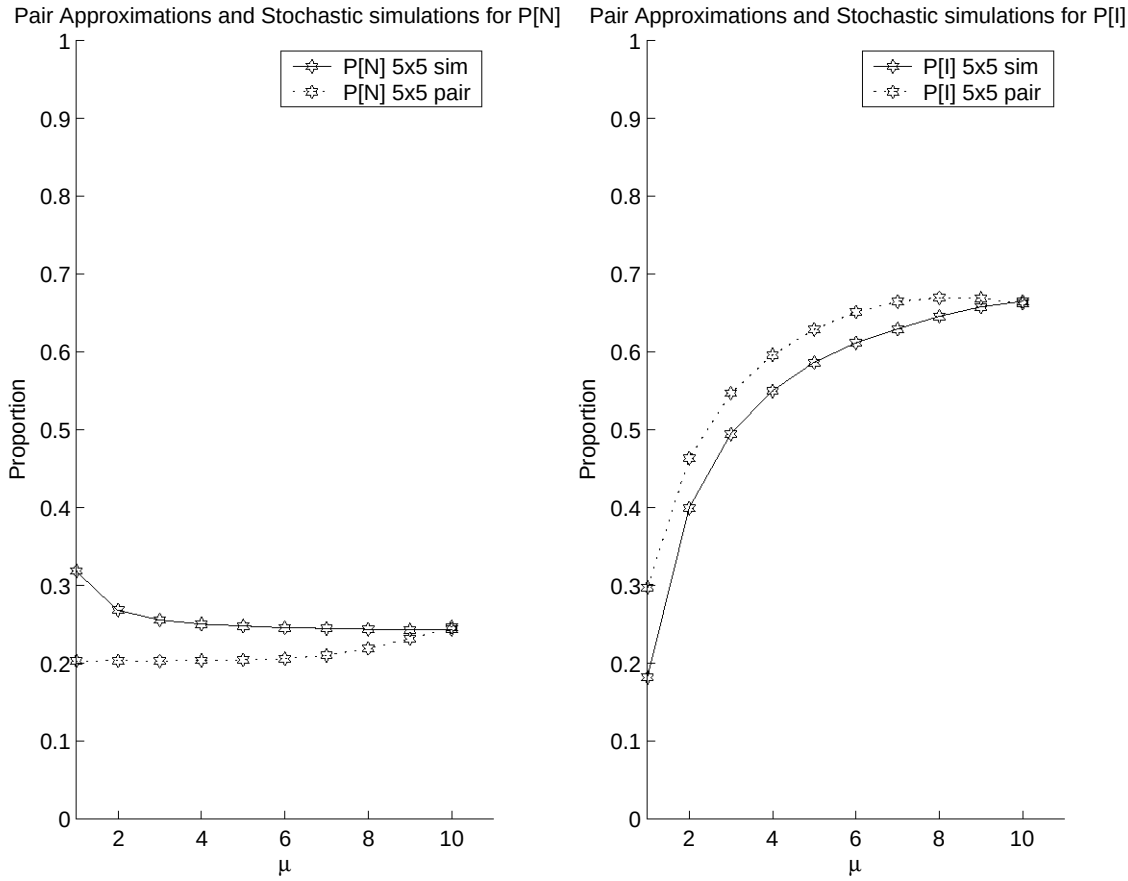

Figure 6: Original model: Comparison of pair approximation and computer simulations varying μ.

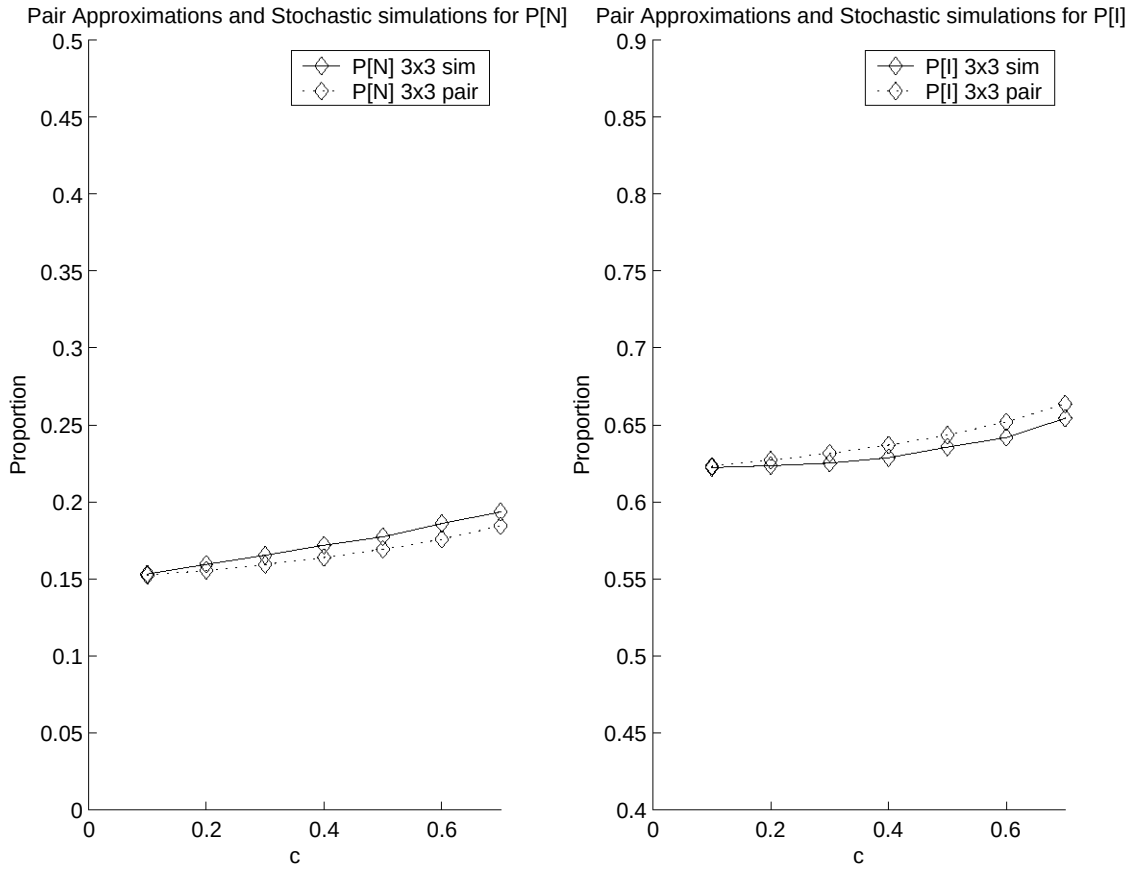

Figure 7: Original model: Comparison of pair approximation and computer simulations varying c with $\mu(c) = \frac{r}{log(c)-log(x^*)}$ where $r = 10$, $x^* = 0.05$.

always accurately approximate the computer simulation results.

The rate μ in Figure 7 was chosen to be an inverse logarithmic decaying function of c to mimic how pesticide effectiveness decreases over time. Pesticide loses its effectiveness gradually over a period of time, so to capture this once the pesticide level decreased below the threshold x^* the pesticide was said to be ineffective. The dependence of μ on an inverse logarithmic decaying function says that if the pesticide is sprayed at a higher concentration, it will take longer for the pesticide to lose its effectiveness.

Figure 7 shows the results of changing mu as a function of c where

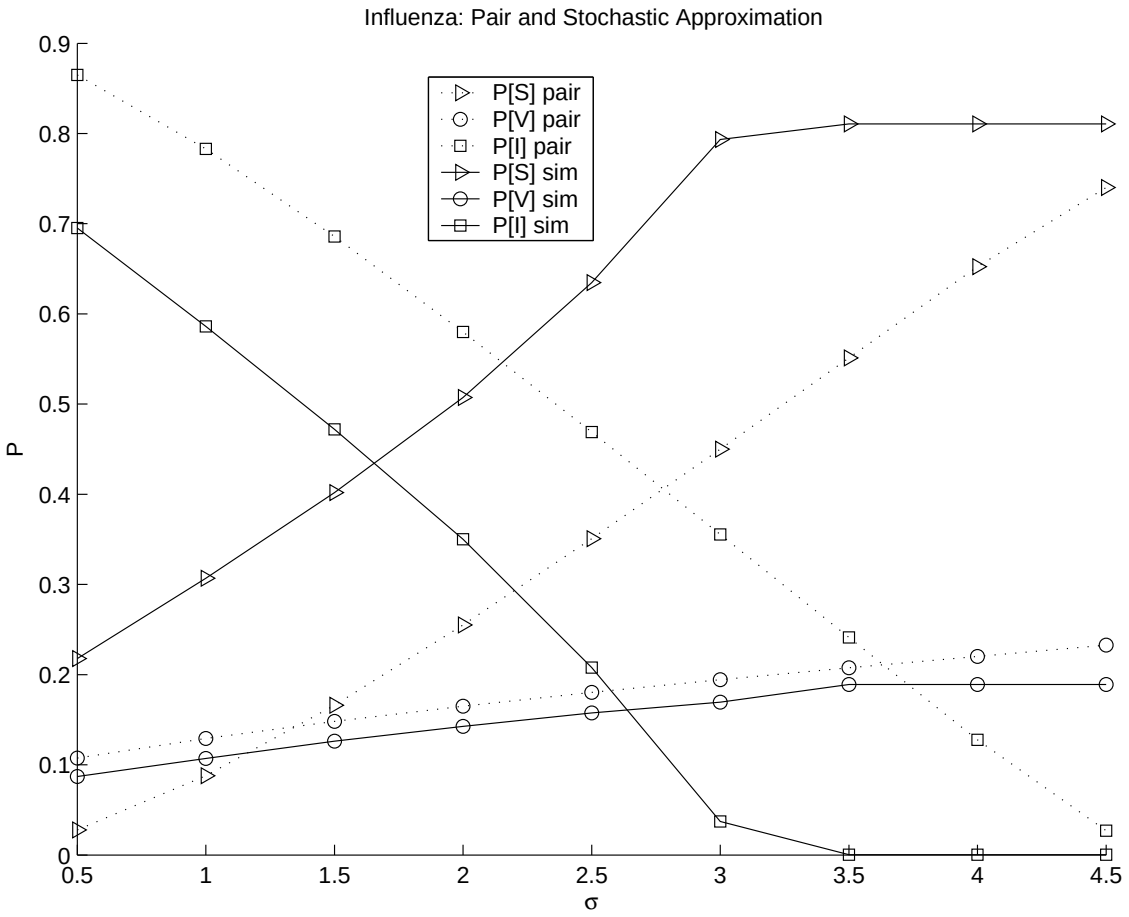

Figure 8: Influenza model: Comparison of pair approximation and computer simulations varying σ. $\phi = 9.99,\ \mu = 15,\ b_1 \times b_2 = 3 \times 3,\ c = 0.8,$ and $\rho = 1.224$

$$\mu(c) = \frac{r}{log(c) - log(x^*)}. \tag{40}$$

Letting μ be a function of c, then one can see that as c is increasing the pair approximation and stochastic simulation agree very closely in their approximation.

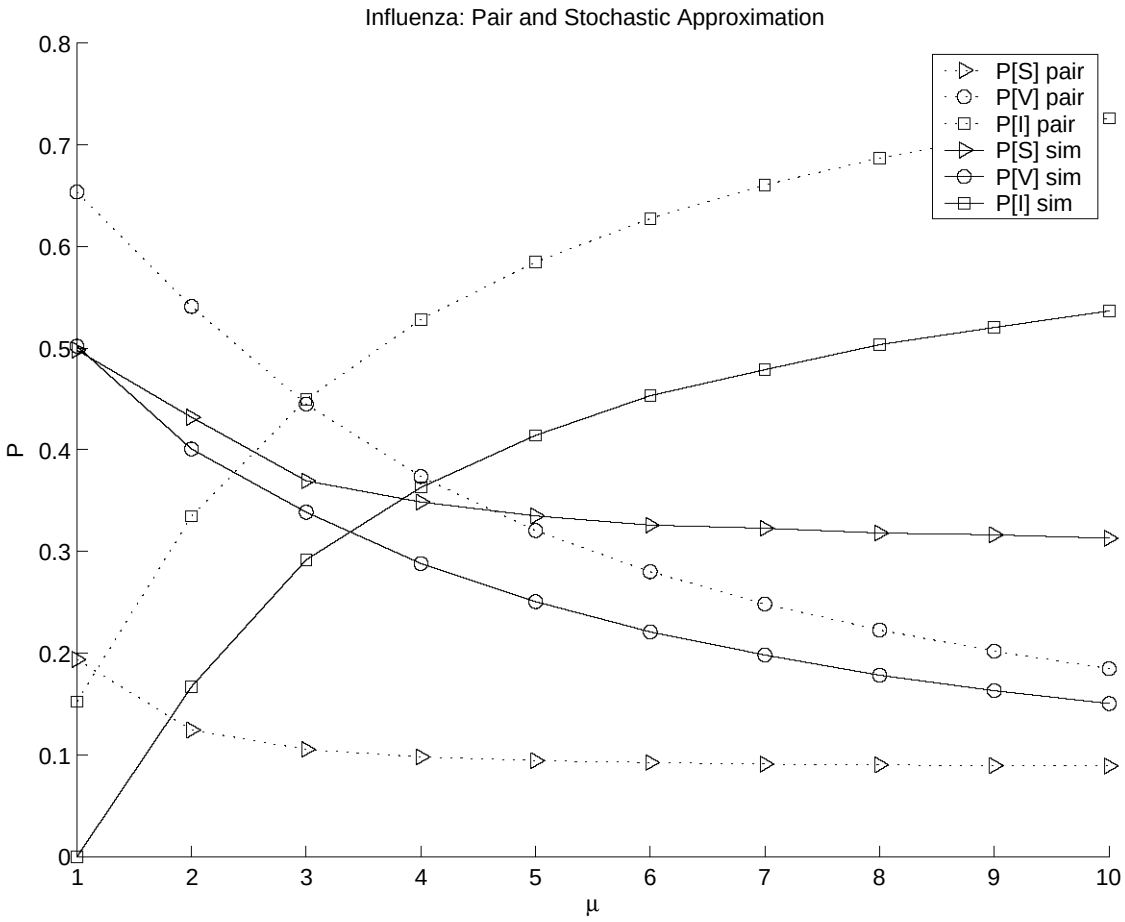

Figure 9: Influenza model: Comparison of pair approximation and computer simulations varying μ. $\phi = 9.99,\ \sigma = 1,\ b_1 \times b_2 = 3 \times 3,\ c = 0.8,$ and $\rho = 1.224$

7.2 Influenza Model

Figure 8 shows that the vaccinated (V) proportion agrees very well for the pair approximation and stochastic simulation. But, for infected (I) there's definitely a gap between the pair and stochastic, but both still follow a general trend of decreasing and reaching zero. Also, notice that pair approximation over estimates the amount I compared to the stochastic simulation.

In Figure 9, the pair approximation does approximate it as accurately as the stochastic

simulation. Varying μ shows that the amount of V agrees for pair and stochastic method. For the amount of I, the pair approximation over estimates compared to the stochastic. It also shows that amount of susceptibles (S) are going to level off for both the pair approximation and stochastic simulation.

8 Discussion

There have been several studies thus far dealing with pair approximations. The model examined in this paper is different because we have three states with only a proportion of sites within a given block are protected. For applications to our three state model, we used Argentine ants infesting crops and influenza spreading among neighbors in a closed environment. It is beneficial to use pair approximation over traditional models, such as mean-field approximation, because mean-field approximation fails to account for spatial characteristics which are of great importance in the model studied in this paper. Although pair approximation is not accurate for large block sizes, it is desirable to use pair approximation because it is much faster to obtain results than in using stochastic simulation. The pair approximation results in this paper would have been improved if more detailed spatial correlations were included beyond the ones stated in this paper, such as larger block (i.e. 2×2 or 4×1) local structure approximations.

Several biological conclusions can be drawn from this model. In the original model applied to crop protection, the most effective technique to control infestation is to spray high concentrations of pesticide over large areas. However, this would be rarely possible due to limitations on resources. If constraints on resources exist, it is more effective to spray in smaller blocks at a high pesticide concentration rather than larger blocks at a lower pesticide concentation even if the same number if sites on average are sprayed. Also, longer-lasting pesticides are most effective. In the influenza model, a higher vaccination

rate leads to a lower proportion of people infected. If there are many antigenically different influenza strains prevalent which the vaccine does not protect against, then the proprotion of infected people increases. An effective influenza vaccine given to many susceptible people is an effective strategy to control influenza.

9 Acknowledgments

We wish to extend our gratitude to Carlos Castillo–Chavez for exposing us to the challenges, rigors and joy of working in an actual research environment.

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A Numerical Integration Source Code

```
% lants.m
% numerical integrates the pair approximation equations for a given set of
% parameters
% order of parameters: x1_i x2_i x3_i x4_i x5_i tf phi mu sigma bi b2 c
function lants(d,e,f,g,h,tf,phi,mu,sigma,b1,b2,c)

t0=0; %intial time
tspan=[t0 tf]; %time span
x0=[d;e;f;g;h]; %intial condtions for diff. eqs.

beta=c*(1-0.5*(1/b1 + 1/b2));

[t,x]=ode45(@ants,tspan,x0,[],phi,mu,sigma,b1,b2,c,beta); %solution output



x_1=x(:,1);
x_2=x(:,2);
x_3=x(:,3);
x_4=x(:,4);
x_5=x(:,5);

pn=1-x_4-2.*x_3-x_2-x_1-x_5;
ps=x_1+x_3+x_5;
poi=1-ps-pn;

hold on
plot(t,pn,'b-');
plot(t,ps,'r-');
plot(t,poi,'g-');
xlabel('time');
```

```
ylabel('Probability');
legend('t vs. P[N]', 't vs. P[S]', 't vs. P[I]');
title('Change of Probability over Time');
P_N=pn(tf) %returns P[N], P[S], and P[I] at equilibration
P_S=ps(tf)
P_I=poi(tf)
% end of lants.m

%     ants.m
%     contains pair approximation equations called by lants.m function
function dx=ants(t,x,phi,mu,sigma,b1,b2,c,beta)
dx = zeros(5,1);

%x(1)=P[SS]
%x(2)=P[II]
%x(3)=P[SI]
%x(4)=P[NI]
%x(5)=P[NS]

%%Five Equations%%
dx(1) = 2.*x(3)*sigma + 2.*x(4)*sigma*beta + 2.*x(5)*sigma + x(2)*sigma*beta
    + (1 - 2.*x(4) - 2.*x(5) - 2.*x(3) - x(2) - x(1))*sigma*beta - 2.*x(1)*
    mu ;
dx(2) = 2.*x(4)*((phi/4) + (3/4)*phi*x(4) / (1 - x(4) - 2.*x(3) - x(2) - x
    (1) - x(5))) - x(2)*(sigma*beta + 2*sigma*(1-beta));
dx(3) = x(4)*sigma*(1-beta) - x(3)*(sigma+mu) + x(2)*sigma*(1-beta) + x(5)
    *(3/4)*phi*(x(4) / (1 - x(4) - 2.*x(3) - x(2) - x(1) - x(5)));
dx(4) = (1 - 2.*x(4) - 2.*x(5) - 2.*x(3) - x(2) - x(1))*(3/4)*phi*(x(4) / (1
    - x(4) - 2.*x(3) - x(2) - x(1) - x(5))) + x(3)*mu - x(4)*(2*sigma*(1-
    beta) + sigma*beta + (phi/4) + (3/4)*phi*(x(4)/(1 - x(4) - 2.*x(3) - x(2)
    -x(1) - x(5))));
```

```
dx(5) = x(1)*mu + (1 - 2.*x(4) - 2.*x(5) - 2.*x(3) - x(2) - x(1))*sigma*(1-
    beta) + x(4)*sigma*(1-beta) - x(5)*(mu + sigma + (3/4)*phi*(x(4)/(1 - x
    (4) - 2.*x(3) - x(2) - x(1) - x(5))));
%%Five Equations%%
```

B Computer Simulation Source Code

```
% antsim.m
% order of parameters: phi mu x sigma b1 b2 c inin inis display_every
    graphics (0 =
% graphics)
% 0=normal, 1=sprayed, 2=infested
function [time,poplist]=antsim(phi,mu,x,sigma,b1,b2,c,inin,inis,
    display_every,graphics)

step_size=1000; % for regression to calculate equilbration of simulation
wait_time=x^2;
regr_data1=zeros(1,100);
regr_data2=zeros(1,100);
regr_data3=zeros(1,100);
regr_time=1:1:100;

poplist=zeros(3,1000000); % list with P[N], P[S], and P[I] over time

Lattice=zeros(x,x);

popn=floor(inin*x^2); % initial normal, sprayed, and infested densities
pops=floor(inis*x^2);
popi=x^2-popn-pops;

cpopi=0; % cumulative infested and sprayed
cpops=0;

infested_coor=zeros(x^2,2); % list of infested and sprayed sites
sprayed_coor=zeros(x^2,2);
```

```
while cpopi<popi % place infested sites on lattice and save in infested site
     list
    r=unidrnd(x^2);
    if(Lattice(r)==0)
        cpopi=cpopi+1;
        Lattice(r)=2;
        [i,j]=ind2sub(size(Lattice),r);
        infested_coor(cpopi,1)=j;
        infested_coor(cpopi,2)=i;
    end
end

while cpops<pops % place sprayed sites on lattice and save in sprayed site
    list
    r=unidrnd(x^2);
    if(Lattice(r)==0)
        cpops=cpops+1;
        Lattice(r)=1;
        [i,j]=ind2sub(size(Lattice),r);
        sprayed_coor(cpops,1)=j;
        sprayed_coor(cpops,2)=i;
    end
end

poplist(1,1)=(x^2-cpopi-cpops)/x^2;
poplist(2,1)=cpops/x^2;
poplist(3,1)=cpopi/x^2;

time(1)=0;

neighbor=[0,-1;0,1;-1,0;1,0;]; % n,e,s,w, neighbor shifts
i=0;
```

```
modi=0;
while (1)
    i=i+1;
    if(mod(i,step_size)==0)
        modi = modi + 1;
    end
    infestprob=phi*cpopi/(phi*cpopi+mu*cpops+x^2*sigma/(c*b1*b2)); %
        probability of infestation event
    wearoff = mu*cpops/(phi*cpopi+mu*cpops+x^2*sigma/(c*b1*b2)); %
        probability of protection wearing off event
    time(i+1)=time(i)+exprnd(1/(phi*cpopi+mu*cpops+x^2*sigma/(c*b1*b2))); %
        time of next event
    rnum=rand;
    if (rnum<infestprob) % infestation event
        target=unidrnd(cpopi);
        targetx=infested_coor(target,1);
        targety=infested_coor(target,2);
        if (Lattice(targety,targetx)~=2)
            error('impossible error #infestation event!');
        end
        rneighbor=unidrnd(4);
        rneighborx=targetx+neighbor(rneighbor,1); % Choose a neighbor
        rneighbory=targety+neighbor(rneighbor,2);
        newx=mod(rneighborx-1+x,x)+1; % wraparound boundaries
        newy=mod(rneighbory-1+x,x)+1;
        if (Lattice(newy,newx)==0) % if normal site, infest it
            Lattice(newy,newx)=2;
            cpopi=cpopi+1;
            infested_coor(cpopi,1)=newx;
            infested_coor(cpopi,2)=newy;
        end
    elseif (rnum<(wearoff+infestprob)) % protection wearing off event
```

```
        target=unidrnd(cpops);
        targetx=sprayed_coor(target,1);
        targety=sprayed_coor(target,2);

        if (Lattice(targety,targetx)~=1)
            error('impossible error #wear off event!');
        end

        Lattice(targety,targetx)=0;
        sprayed_coor(target,1)=sprayed_coor(cpops,1);
        sprayed_coor(target,2)=sprayed_coor(cpops,2);
        cpops=cpops-1;



    else % spray event
        target=unidrnd(x^2);
        [targety,targetx]=ind2sub(size(Lattice),target);
        if (rand<0.5)
            newb1=b2;
            newb2=b1;
        else
            newb1=b1;
            newb2=b2;
        end
        for k=1:newb1
            for m=1:newb2
            if (rand<c)
                newx=mod(targetx-1+x+k,x)+1; % wraparound boundaries
                newy=mod(targety-1+x+m,x)+1;
                if (Lattice(newy,newx)==0) % if normal
```

```
                Lattice(newy,newx)=1;
                cpops=cpops+1;
                sprayed_coor(cpops,1)=newx;
                sprayed_coor(cpops,2)=newy;
            elseif (Lattice(newy,newx)==2) % if infested
                Lattice(newy,newx)=1;

                cpops=cpops+1;
                sprayed_coor(cpops,1)=newx;
                sprayed_coor(cpops,2)=newy;

                global target2
                for(ii=1:cpopi)
                    if(infested_coor(ii,1)==newx & infested_coor(ii,2)==
                        newy)
                        target2 = ii;
                    end
                end

                infested_coor(target2,1)=infested_coor(cpopi,1);
                infested_coor(target2,2)=infested_coor(cpopi,2);
                cpopi=cpopi-1;
            end
        end
    end

end

if(graphics==0)
```

```
    colormap([0 0 0;1 0 1;1 1 0]); % black-normal magenta-sprayed yellow-
        infested
end

if((mod(i,display_every)==0) & (graphics == 0))
     image(Lattice+1);drawnow; % draws simulation graphics
end

if(mod(i,step_size)==0)
    poplist(1,modi+1)=(x^2 - cpopi - cpops)/x^2;
    poplist(2,modi+1)=cpops/x^2;
    poplist(3,modi+1)=cpopi/x^2;
end
 if (i > wait_time)
     if (mod(i,step_size)==0)
         regr_data1=circshift(regr_data1,[0 -1]);
         regr_data1(100)=poplist(1,modi+1);
         poly1=polyfit(regr_time,regr_data1,1);

         regr_data2=circshift(regr_data2,[0 -1]);
         regr_data2(100)=poplist(2,modi+1);
         poly2=polyfit(regr_time,regr_data2,1);

         regr_data3=circshift(regr_data3,[0 -1]);
         regr_data3(100)=poplist(3,modi+1);
         poly3=polyfit(regr_time,regr_data3,1);

          if ( (abs(poly1(1)) <= 0.1) & (i >= wait_time + 100*step_size)
              & (abs(poly2(1)) <= 0.1) & (abs(poly3(1)) <= 0.1))
               break; % equilibration
          end
     end
```

```
    end

end

if(graphics == 0)
    image(Lattice + 1); drawnow;
end

figure;
% plot the time series
hold on
grid on

plot(time(1:modi),poplist(1,1:modi),'g-'); % normal sites
plot(time(1:modi),poplist(2,1:modi),'r-'); % sprayed sites
plot(time(1:modi),poplist(3,1:modi),'b-'); % infested sites
legend('t vs. P[N]', 't vs. P[S]', 't vs. P[I]');
P_N=poplist(1,modi) % output P[N], P[S], and P[I]
P_S=poplist(2,modi)
P_I=poplist(3,modi)
```