

The Dynamics of a Spatial Cyclic Competition System

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August 3, 2009

Abstract

We analyze the long term behavior of a system involved in cyclic competition similar to the rock-paper-scissors game. Previous studies have used cellular automata simulations to model the stochastic interactions and mean field equations to approximate this stochastic model. However, mean field approximation does not properly account for spatial correlations, leading to loss of spatial significance. We use pair approximations to model the local interactions with a system of differential equations. We then investigate the outcome of various initial conditions of the pair approximation model using numerical integration. Three categories of initial conditions are found that lead to three distinct behaviors: one species is present, all three species oscillate around the fixed point resulting in a heteroclinic cycle, or convergence to an interior fixed point. We also explore the relative importance of initial conditions and lattice size on fixation probabilities for each species. We finally discuss the implications of these results in a biological context.

1 Introduction

Identification of processes that maintain biodiversity is a central goal of theoretical ecology [1, 12]. Empirical observations suggest that systems of more than two species often interact in traditional acyclic hierarchies of dominance. Species higher up on the dominance-chain displace those that are below them which could lead to a decrease in biodiversity [2]. This, however, is not the case with cyclic hierarchies. The simplest type of cyclic dominance hierarchy is characterized by the game rock-paper-scissors, RPS, [8, 4]. In this game, rock beats scissors, scissors beats paper, and paper beats rock. Here there is no completely dominant species and the possibility for stable coexistence arises. However, the removal of one species leads to a linear dominance chain, and the loss of biodiversity. It is therefore important to investigate the behavior of the system around the equilibria where diversity is maintained. A common example of an RPS system in nature is the three mating strategies in populations of male Side-blotched Lizards (*Uta stansburiana*: [11]). Furthermore, three strains of *Escherichia coli* display RPS dynamics where colicin, a bacteriocide toxic to other strains of *E. coli* is produced. Although we use the terms RPS throughout, our analyses can be applied to any biological systems with cyclic competition interactions of three species.

Stochastic and deterministic methods have been used to examine cyclic competition between three or more species [4]. Spatial lattice models that incorporate these stochastic interactions as a Poisson process can be found in [4, 6]. The advantage of using the lattice model is that it captures some of the randomness in nature and it is relatively easy to construct [8]. However, it is difficult to analyze since simulations with the same input will often have different results due to the stochastic nature of the system. Therefore, approximating the stochastic model with a deterministic model is helpful as a way of measuring the behavior of the system. Mean field equations, MF, were used in previous studies to approximate the lattice model with a set of differential equations describing the change of the rock, paper and scissors densities over time [3, 10, 4]. However, the MF describes a homogeneous system without spatial correlations, leading to loss of spatial significance, which may be a key driver in the dynamics of the system [10]. Lattice models and MF equations have been previously used to describe various biological systems that exhibit cyclic competition [8, 4].

Here, we incorporate the use of pair approximations, PA, to model local interactions. These approximations take into account some of the structure of the spatial viability via a system of differential equations [9, 5]. The results of the mean field and pair approximation will be compared based on their ability to capture the dynamics of the lattice model. Finally, we will thoroughly investigate the outcomes of various initial conditions of the PA model and the lattice model in an effort to demonstrate the behavior of the system.

2 Lattice Model

We begin by constructing a simulation for the dynamics of the RPS system on a lattice. In constructing our lattice, we utilized a method similar to that of previous studies [5]. This stochastic cellular automata occurs on an $n \times n$ square matrix with each site populated

by either a rock, paper, or scissors. Each individual site has the ability to attempt to replace a neighboring site with rate ϕ_i for rock, paper, and scissors respectively. However, a replacement is only successful if the spreading site beats the site being replaced. For example, rock replaces scissors, but fails to replace paper or another rock. For the purposes of our investigation, we define $\phi := \phi_R = \phi_S = \phi_P$. In order for each site to have four neighbors, the edges are wrapped-around, identifying our lattice as a torus.

We set the initial conditions for the system by assigning the proportions of each state on the $n \times n$ lattice. These proportions are then used to randomly fill each site in the lattice with rock, paper, or scissors. Once the initial lattice is created, a series of replacement events occur. Each event begins with the selection of a species that is attempting to spread. Since the replacement rates have been assumed equal, the probability for each species to be selected is the proportion of that species on the lattice. Next, a site containing the spreading species is chosen from a list of all sites that species occupies. This site then chooses at random one of its von Neumann neighbors (North, East, South, or West) with equal probability. If the replacement is successful, meaning that the spreading site beats the replaced site (i.e. rock invading scissor), then the replaced site's state will become the state of the spreading site. Otherwise the lattice does not change. The simulation continues for a specified number of events or until fixation is reached, meaning one species occupies the entire lattice.

Previous work has shown that when a lattice model is constructed using different replacement rates and three species, the species with the smallest replacement rate will tend to occupy the largest number of sites on average, a phenomenon coined "survival of the weakest" [4]. However, behavior similar to survival of the weakest can also occur when invasion rates are identical. A specific case that we consider in detail is when the initial proportion of one species is much greater than the other two. To investigate this we initialize a lattice with: $P[R] = 0.9$, $P[P] = 0.05$, and $P[S] = 0.05$. We then record where the system is after 100 epochs. An epoch is defined as a number of events equal to the number of sites in the lattice. It corresponds to the number of events required for the expected number of invasion attempts for each site to be 1.

After 100 epochs, the system will be in one of four states. Three correspond to fixation of one of the species and the last corresponds to a mixture of species at the end time. This final type will be termed mixture. The simulation is repeated for 1000 trials for each square lattice size, which is varied from 5×5 to 75×75 for the same initial conditions as earlier.

Figure 1 shows that as lattice size increases the probability that fixation is reached in the first 100 epochs decreases with the given initial conditions. For very large lattice sizes, mixture occurs almost every time. It is not clear what this lack of quick fixation means about the system. It is therefore necessary to estimate the probabilities of fixation for each species for a system that has not reached fixation in the first 100 epochs. Using 10,000 trials on lattice sizes between 10×10 and 20×20 , we found that each species fixated with about an equal probability if the system had not fixated in under 100 epochs.

Examining fixations after 150 and 200 epochs, we found similar results with fixation proportions for each species being about equal. We then conjecture that this behavior will

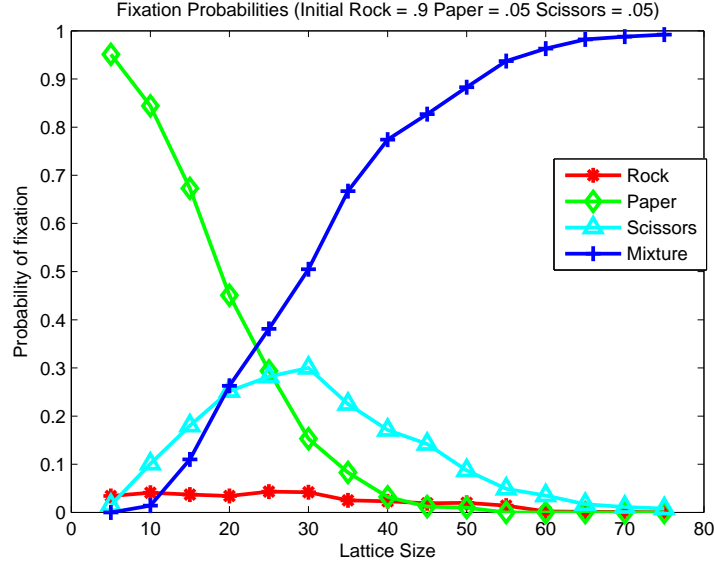


Figure 1: The probabilities of fixation or mixture for initial proportions of .9 rock, .05 scissors, and .05 paper.

Lattice Size	Rock	Paper	Scissors
10	59	52	46
11	83	71	72
13	162	188	191
14	256	238	200
15	364	345	361
16	384	416	403
17	494	529	490
18	648	610	606
19	769	726	733
20	869	819	824

Figure 2: The results of fixations after 100 epochs for 10000 trials on square lattices of size 10×10 and 20×20 . Notice that the fixations for rock, paper, and scissors are about the same.

extend to larger lattices. Unfortunately it is difficult to test since the time to fixation increases greatly with an increase in lattice as shown on the left in Figure 3. If the 100 epoch observation is extended to larger lattices, a third of the oscillations could be assigned to each species from the earlier graph to yield a better idea of the probabilities of fixation for each species as shown on the right in Figure 3. Note that the prey of the dominant species actually has the highest probability of victory for square lattice sizes from 30×30 to 60×60 ,

which is similar to “survival of the weakest” with equal replacement rates. As the lattice size increases, the probabilities of fixation for each species become about equal.

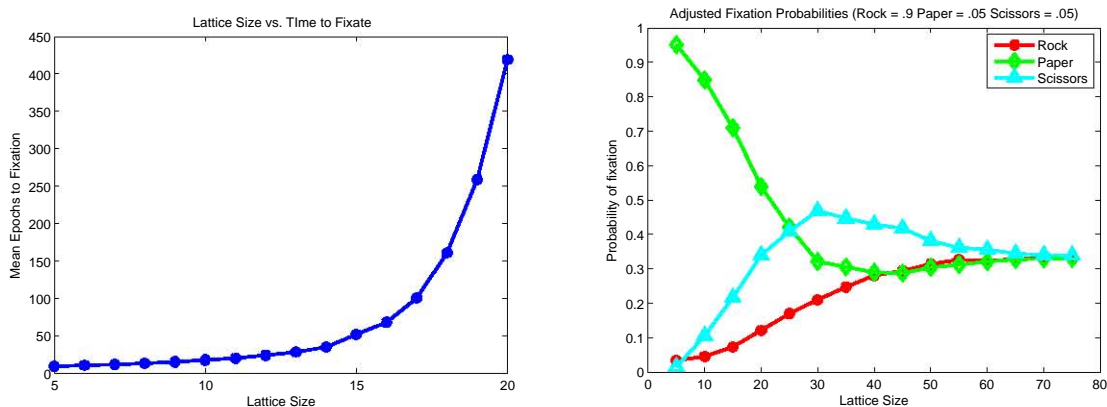


Figure 3: The left graph shows the mean time to fixation against lattice size. The right graph shows the probabilities of fixation for each species assuming that fixation after 100 epochs is distributed uniformly.

The previous methods can be used for other initial conditions as shown in Figure 4. The other initial conditions we looked at produced similar behavior as lattice size increased. Initial conditions that have a large proportion of one species will fixate in the first 100 epochs more often. However, as the lattice size increases early fixation occurs less frequently and eventually a size for the lattice is reached where fixation almost never occurs in the first 100 epochs. We may now use our earlier observation that fixations after 100 epochs are uniformly distributed between the possible species. Thus, for large lattices, the probability of fixation will be equal for all the species assuming that uniform fixation after 100 epochs holds for the larger lattice sizes and all 3 species are represented in the initial conditions. It is important to note that the simulations were run are for a limited number of initial conditions. Although we conjecture that this result holds for a broader range, our trials were not exhaustive.

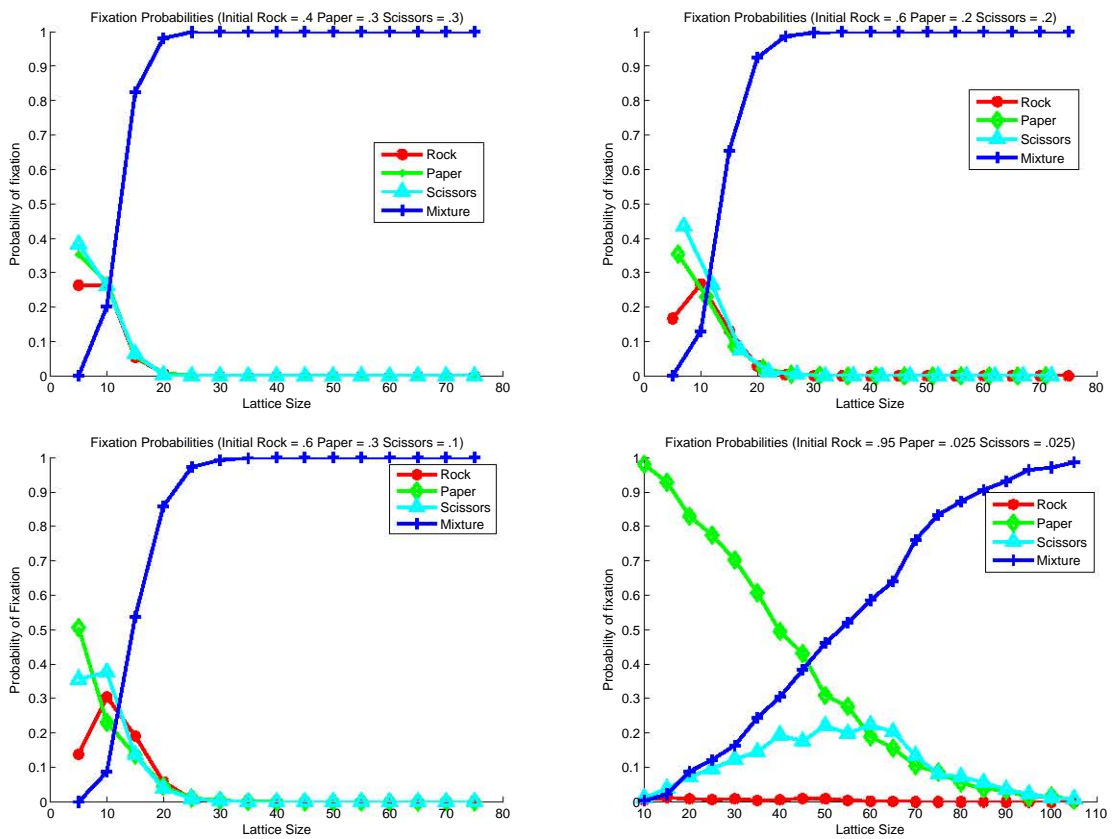


Figure 4: The probability of fixation or mixture after the first 100 epochs for various initial proportions.

3 Mean Field

The mean field approximation represents a straight forward approach of approximating the stochastic model with a set of differential equations that describe the change of the three state densities over time [3, 10]. The assumption of this model is that the state of all adjacent sites on the lattice are independent. Three state variables, $P[R]$, $P[P]$, and $P[S]$, describe the proportion of the lattice in a particular state (i.e. $P[R]$ is the proportion of the lattice in state R). They also correspond to the probability that a randomly chosen site on the lattice is a rock, paper or scissors respectively. The change in the proportion of the lattice in state i over time is given by the following equation:

$$\frac{dP[i]}{dt} = \sum_{j \neq i} (P[j]r_{j \rightarrow i}) - P[i] \sum_{j \neq i} (r_{i \rightarrow j}). \quad (1)$$

In Eq [1] the positive term includes $P[j]$, the probability of a site being in a state other than i , and $r_{j \rightarrow i}$, rate at which it j is replaced by state i . The negative term includes $P[i]$, the probability of a site being in state i , and $r_{i \rightarrow j}$, the transition rate from i to j [6].

Using Eq [1], the differential equations for $P[R]$ is:

$$\frac{dP[R]}{dt} = P[S]\phi Q_{R|S} - P[R]\phi Q_{P|R}. \quad (2)$$

The conditional probability $Q_{i|j}$ represents the probability that a randomly chosen site in state j has neighbor in state i . Since we are assuming sites are independent in the lattice, then $Q_{i|j}$ is equivalent to $P[i]$ (i.e. $Q_{P|R} = P[P]$). We may then derive the following equations:

$$\frac{dP[P]}{dt} = P[R]\phi P[P] - P[P]\phi P[S] \quad (3)$$

$$\frac{dP[R]}{dt} = P[S]\phi P[R] - P[R]\phi P[P], \quad (4)$$

Since, $P[R] + P[P] + P[S] = 1$ the sum of the differential equations for the change in the three states' proportions must be 0. Therefore, the differential equation for $P[S]$ can be expressed in terms of $\frac{dP[P]}{dt}$ and $\frac{dP[R]}{dt}$:

$$\frac{dP[S]}{dt} = -\frac{dP[P]}{dt} - \frac{dP[R]}{dt}. \quad (5)$$

The mean field equations have been previously studied and shown to yield four fixed points [10]. Three are trivial, with only one species present: $(P[R], P[P], P[S]) = (1, 0, 0)$, $(0, 1, 0)$, or $(0, 0, 1)$. These are saddle points since the equilibrium is stable along one edge, and unstable along the other edge. The last fixed point is a non-trivial, $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$, where all three species coexist; this is a center.

4 Pair Approximation

The use of the mean field assumption to approximate the behavior of a lattice model ignores any local spatial interactions on the lattice which may be key to the dynamics of the process. Therefore it is important to include an approximation that can capture some of the local spatial behavior on the lattice. Pair approximation accomplishes this goal [6, 7]. This requires the inclusion of terms for all of the probabilities of adjacent pairs of sites being in a particular configuration: $P[RR]$, $P[RP]$, $P[RS]$, $P[PR]$, $P[PP]$, $P[PS]$, $P[SR]$, $P[SP]$, and $P[SS]$. By assuming rotational symmetry, which means that $P[ij] = P[ji]$ for all i and j , we are able to trim the number of state variables to six. The probabilities for each pair change at rates according to the proportion of the state in the lattice times the rate that a transition occurs:

$$\frac{dP[ab]}{dt} = \sum_{i,j \in \{R,P,S\}} (P[ij]r_{ij \rightarrow ab}) - \sum_{i,j \in \{R,P,S\}} (P[ab]r_{ab \rightarrow ij}), \quad (6)$$

where $r_{ij \rightarrow ab}$ is the rate of transition from ij to ab . Using the pair approximation assumption which reads that the state of a site is independent of a second site conditioned on their shared neighbor we get that

$$Q_{i|j} = \frac{P[ij]}{P[j]}. \quad (7)$$

With these equations we calculate the rates of change for each proportion. We use $P[RR]$ as an example. The pair SR and RS can become RR which can in turn become RP and PR . The transition rates for all other combinations are zero. For the rate $r_{RS \rightarrow RR}$, knowing that the R in the pair may replace the S , there is a $\frac{1}{4}$ probability that the R spreads towards the S rather than in the direction of one of the three other neighbors and a rate ϕ at which invasion occurs. There is also the possibility for one of the other neighbors of S to be an R and replace the S . There are 3 other neighbors which could be a rock each with probability $Q_{R|S}$ and replace S with rate $\frac{\phi}{4}$. The equation for the conversion of RS to RR is therefore:

$$r_{RS \rightarrow RR} = \frac{3}{4}\phi Q_{R|S} + \frac{\phi}{4}. \quad (8)$$

Since $SR = RS$, we double the RS term to yield a total change of $2P[RS] \left(\frac{3}{4}\phi Q_{R|S} + \frac{\phi}{4} \right)$. The probability of a transition that reduces RR can be calculated in a similar fashion. The total equation for change in RR is therefore:

$$\frac{dP[RR]}{dt} = 2P[RS] \left(\frac{3}{4}\phi Q_{R|S} + \frac{\phi}{4} \right) - 2P[RR] \frac{3}{4}\phi Q_{P|R}, \quad (9)$$

Using this method we can also calculate the change in proportion for the pair RP . The pairs RR and SR can become RP which can in turn become RR and RS . We may, as earlier, construct the rates of these four transitions and use them to form the equation

$$\frac{dP[RP]}{dt} = \frac{3}{4}P[RR]\phi Q_{P|R} + \frac{3}{4}P[PS]\phi Q_{R|S} - P[RP] \left(\frac{3}{4}\phi Q_{P|R} + \frac{\phi}{4} + \frac{3}{4}\phi Q_{S|P} \right). \quad (10)$$

The remaining four equations are formed in the same manner:

$$\frac{dP[RS]}{dt} = \frac{3}{4}P[RP]\phi Q_{S|P} + \frac{3}{4}P[SS]\phi Q_{R|S} - P[RS] \left(\frac{3}{4}\phi Q_{R|S} + \frac{\phi}{4} + \frac{3}{4}\phi Q_{P|R} \right), \quad (11)$$

$$\frac{dP[PP]}{dt} = 2P[RP] \left(\frac{3}{4}\phi Q_{P|R} + \frac{\phi}{4} \right) - 2P[PP] \frac{3}{4}\phi Q_{S|P}, \quad (12)$$

$$\frac{dP[PS]}{dt} = \frac{3}{4}P[RS]\phi Q_{P|R} + \frac{3}{4}P[PP]\phi Q_{S|P} - P[PS] \left(\frac{3}{4}\phi Q_{S|P} + \frac{\phi}{4} + \frac{3}{4}\phi Q_{R|S} \right), \quad (13)$$

$$\frac{dP[SS]}{dt} = 2P[PS] \left(\frac{3}{4}\phi Q_{S|P} + \frac{\phi}{4} \right) - 2P[SS] \frac{3}{4}\phi Q_{R|S}. \quad (14)$$

In an attempt to analyze the fixed points of the pair approximation equations, we used marginalization, $P[i] = \sum_{j \in \{R,P,S\}} P[ij]$, to construct the differential equations for $P[R]$, $P[P]$, and $P[S]$:

$$\frac{dP[R]}{dt} = \phi(P[RS] - P[RP]), \quad (15)$$

$$\frac{dP[P]}{dt} = \phi(P[RP] - P[PS]), \quad (16)$$

$$\frac{dP[S]}{dt} = \phi(P[PS] - P[RS]). \quad (17)$$

For non-zero ϕ , the solution to these equations equaling zero is $x = P[RP] = P[RS] = P[PS]$, creating a set of fixed points for Equations (15)-(17). However, this does not guarantee that Equations (9)-(14) are zero. Substituting x back into Equations (9)-(14) yields fixed points occurring when either $x = 0$ or $P[RR] = P[PP] = P[SS] = \frac{5x}{2}$.

We first consider the fixed points that occur when $x = 0$. Assume there are at least two species on the lattice. There must be two neighboring sites that are not in the same state. This is a contradiction, since $x = 0$. Therefore, the lattice must be covered by one species, giving us three fixed points, either $P[RR] = 1$, $P[PP] = 1$, or $P[SS] = 1$, which describe when the lattice is completely covered with rock, paper, or scissors, respectively.

When graphing $P[R]$ vs $P[P]$ vs $P[S]$, a triangular simplex arises as shown in Fig. 5. This is an invariant plane due to $P[R] + P[P] + P[S] = 1$, on which all solutions to the PA system exist. The three fixed points representing one species on the lattice, are the corners of this triangle and each edge of this triangle is a heteroclinic orbit. The only initial conditions that go to these fixed points are ones that are located on the heteroclinic orbits, in which there are only two species present. This behavior is shown in Fig. 6, where $P[RR]$ starts close to 1 and steadily decreases to 0, $P[RP]$ increases as the lattice becomes roughly half rock and paper, and $P[PP]$ starts close to 0 but steadily increases to 1. This is because there are only two species present causing the dominance to be linear instead of cyclic.

We now consider the fixed points that occur when $P[RR] = P[PP] = P[SS] = \frac{5x}{2}$. The sum of the probabilities of all possible states must equal one, $\sum_{i,j \in \{R,P,S\}} P[ij] = 1$. Using

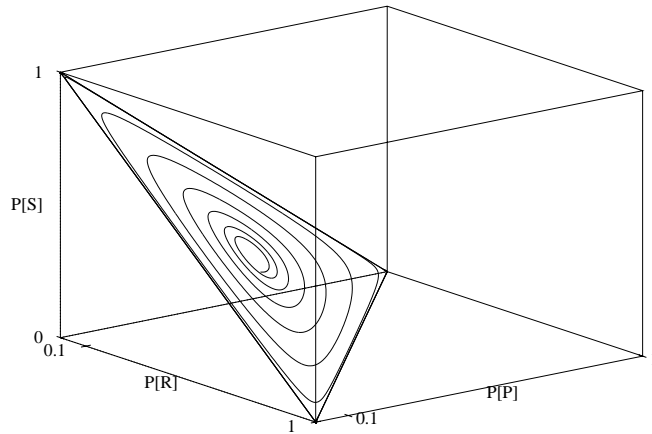


Figure 5: A graph of $P[R]$ vs. $P[P]$ vs. $P[S]$ showing the invariant plane. This particular trajectory started near the middle and is spiraling outwards into a heteroclinic cycle.

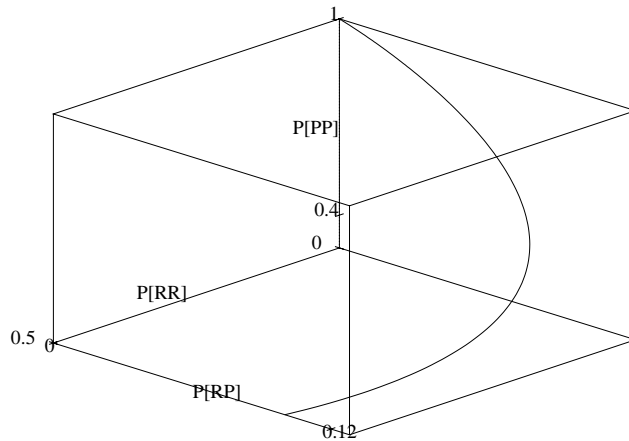


Figure 6: This is a graph depicting the situation in which there was only rock and paper present on the lattice and shows that paper completely dominates.

the x from earlier, this can be rewritten as $6x + \frac{3(5x)}{2} = 1$. Solving this for x , we get that $x = \frac{2}{27}$. Therefore, the point with $P[RP] = P[RS] = P[PS] = 2/27$ and $P[RR] = P[PP] = P[SS] = 5/27$ is the internal fixed point of our system, where all three species coexist with equal proportions and interactions. When shown on Fig. 5, this is the point $(\frac{1}{3}, \frac{1}{3}, \frac{1}{3})$, which is in the middle of the triangle.

To analyze the stability of the internal fixed point, we compute the Jacobian of our system and evaluate it at the fixed point. Solving for the eigenvalues yields $-\frac{1}{2}$, 0 , $\frac{-3 \pm \sqrt{-7 \pm 16i\sqrt{3}}}{12}$.

These six eigenvalues can be written approximately as -0.5 , 0 , $-0.523755 \pm 0.351501i$, $0.0237548 \pm 0.351501i$. Since there is an eigenvalue with positive real part, this fixed point is unstable but, because there's a zero eigenvalue, other methods must be utilized to describe the behavior around it more fully.

We find a basin of attraction for the internal fixed point by making the substitutions, $x = P[RP] = P[RS] = P[PS]$ and $y = P[RR] = P[PP] = P[SS]$, into Equations (9)-(14). The resulting two equations were:

$$\begin{aligned}\frac{dx}{dt} &= \frac{3x^2}{4(2x+y)} + \frac{3xy}{4(2x+y)} - x \left(\frac{1}{4} + \frac{3x}{2(2x+y)} \right), \\ \frac{dy}{dt} &= -\frac{3}{2(2x+y)} + 2x \left(\frac{1}{4} + \frac{3x}{4(2x+y)} \right).\end{aligned}$$

Using $6x + 3y = 1$, we eliminated one equation. Leaving us with $\frac{dx}{dt} = -\frac{27x^2}{4} + \frac{x}{2}$. Taking the derivative of this new equation and evaluating at our fixed point, $x = \frac{2}{27}$, we get an eigenvalue of $-\frac{1}{2}$. Since this eigenvalue is negative, points starting on the line $6x + 3y = 1$ will converge to the fixed point. One example of this convergence to the fixed point is shown in Fig. 13 and Fig. 14, the initial condition used to generate those graphs was $P[RR] = P[PP] = P[SS] = \frac{2}{15}$ and $P[RP] = P[RS] = P[PS] = \frac{1}{10}$ which lies on the line of attraction.

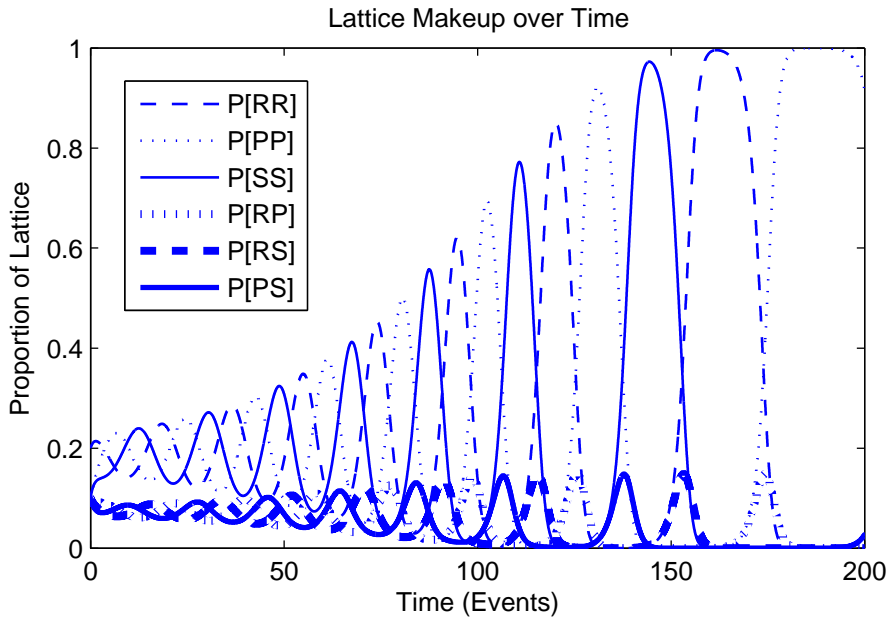


Figure 7: A graph of all six state variables of the PA system over time.

In order to attempt to capture all of the types of behavior, we numerically integrated a wide range of initial conditions and discovered only three behaviors. The first of the

three behaviors is that if the initial condition only represents two species, then one species dominates completely. The second is a subset of initial conditions that converges to the internal fixed point. The final behavior is oscillation becoming a heteroclinic cycle.

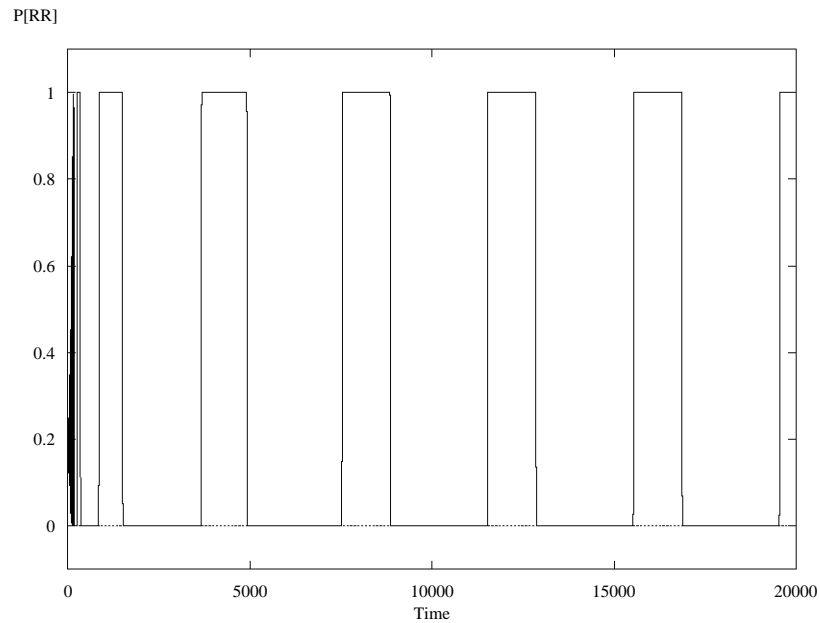


Figure 8: A graph of $P[RR]$ vs. Time showing that the oscillations continue over time.

As a representative of this type of initial condition, we use $P[RR] = 0.2$ and $P[RP] = P[RS] = P[PP] = P[PS] = P[SS] = 0.1$. Numerically integrating yields curves as shown in Fig. 7. The three curves that oscillate on the bottom are the graphs of $P[RP]$, $P[RS]$, and $P[PS]$, while the three curves that oscillate with increasing amplitude and period are of $P[RR]$, $P[PP]$, and $P[SS]$. The figure depicts that there is a spike of a heterogeneous pair during the transition from dominance of one homogeneous pair to the dominance of another homogeneous pair. This continues as time approaches infinity, as shown in Fig. 8, due to there being a heteroclinic cycle. Each state variable spends more time near its value at the trivial equilibria, as time increases. This can also be seen in Figs. 9, 10, 11, 12.

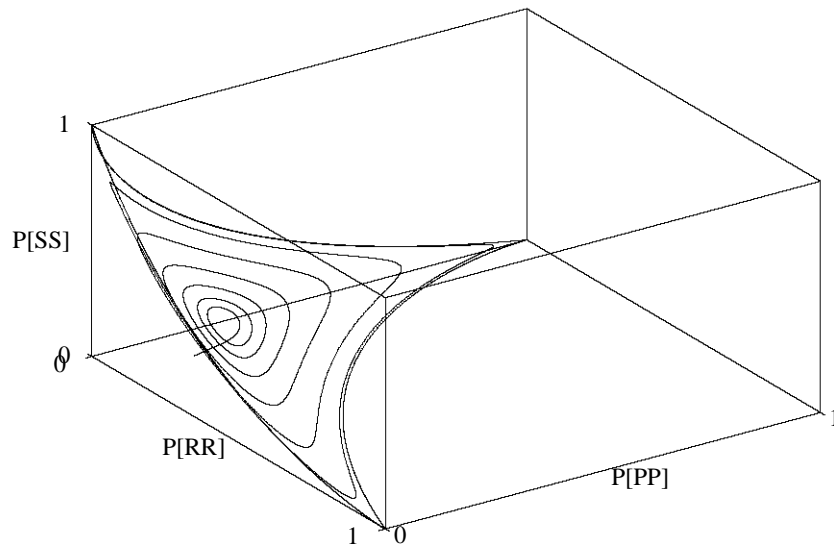


Figure 9: A graph of $P[RR]$ vs $P[PP]$ vs $P[SS]$ that shows a trajectory starting below the curved plane, coming up to it, and then spiraling out into a heteroclinic cycle.

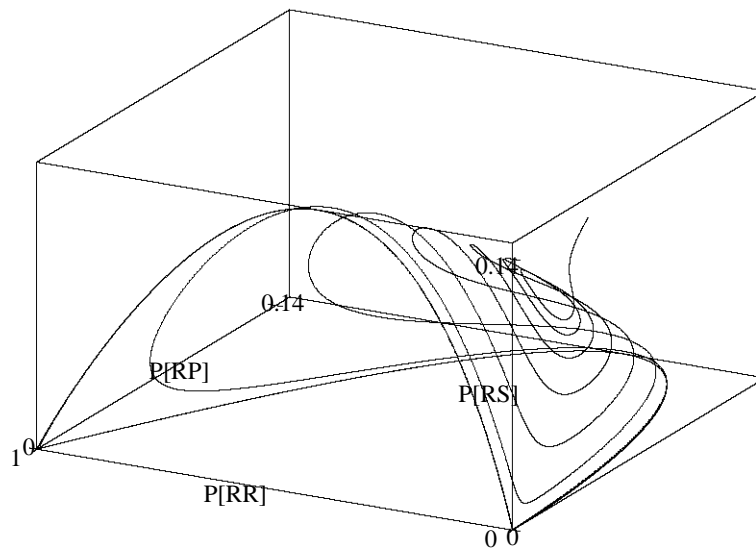


Figure 10: A graph of $P[RR]$ vs $P[RP]$ vs $P[RS]$ that shows a trajectory starting above the curved plane, coming down to it, and the spiraling out into a heteroclinic cycle.

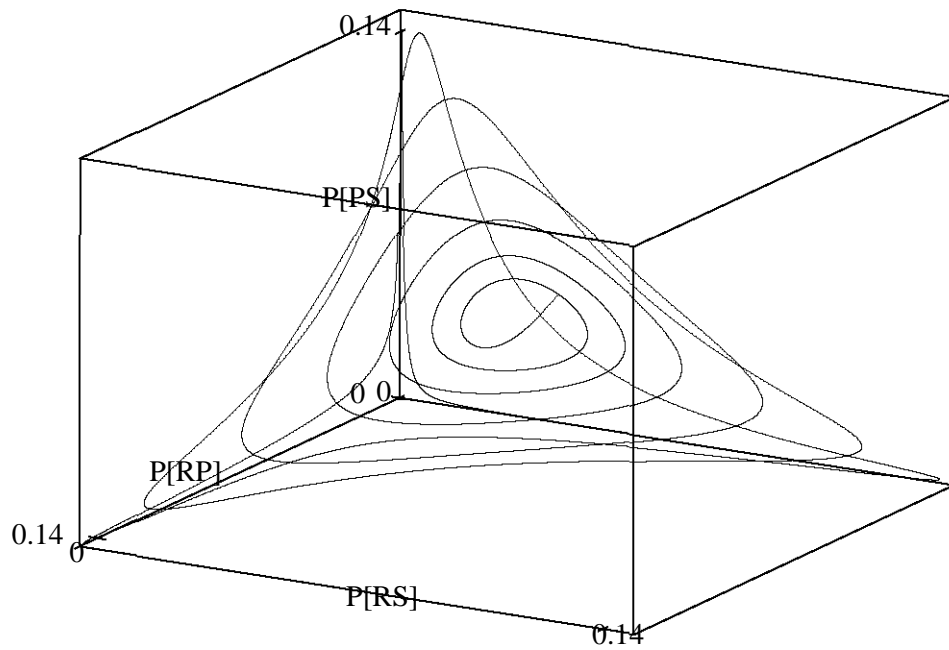


Figure 11: A graph of $P[RP]$ vs $P[RS]$ vs $P[PS]$ that shows a trajectory starting away from the origin and spiraling inwards to a heteroclinic cycle.

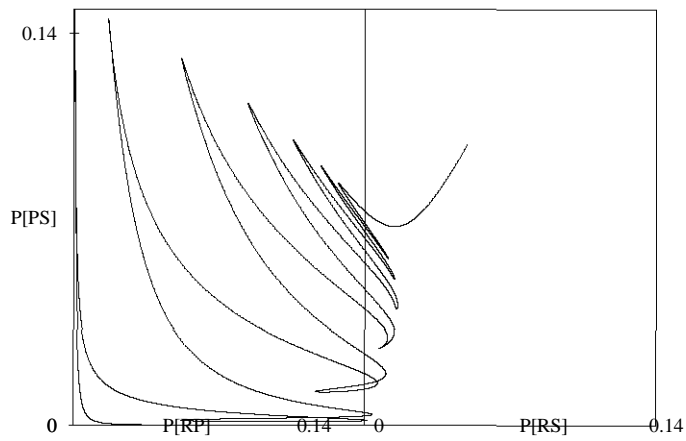


Figure 12: A 2d view $P[RP]$ vs $P[RS]$ vs $P[PS]$ which better shows that the trajectory started away from the origin and then oscillated towards the axis into the heteroclinic cycle.

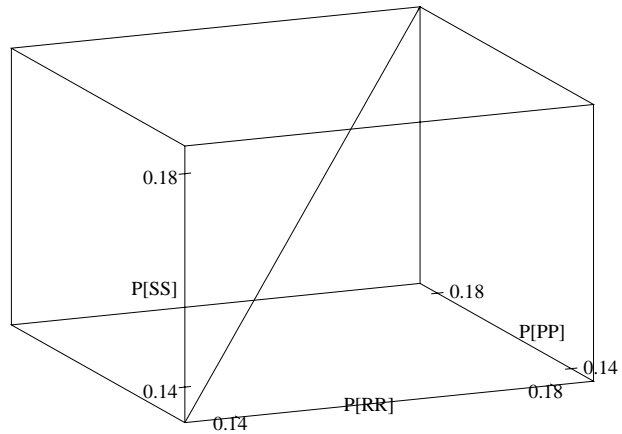


Figure 13: A graph of $P[RR]$ vs. $P[PP]$ vs. $P[SS]$ shows a trajectory in which all three variables start near 0.14 and converge at the same rate, hence the linear graph, and they all converge to $5/27$ or 0.185.

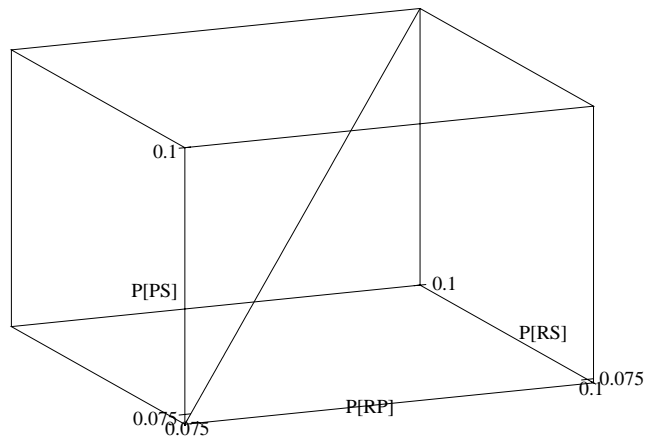


Figure 14: A graph of $P[RP]$ vs. $P[RS]$ vs. $P[PS]$ shows a trajectory in which all three variables start at 0.1 and converge at the same rate, hence the linear graph, and they all converge to $2/27$ or 0.075.

5 Discussion and Conclusion

Now that we have shown the behavior of the mean field and pair approximation equations, we can compare their abilities to capture the qualitative behavior of the lattice model. To do this, we run the lattice model, recording the values of each pair (RR, RP, etc.) periodically. We then run the same initial conditions through the pair approximation and mean field equations and compare the trajectories.

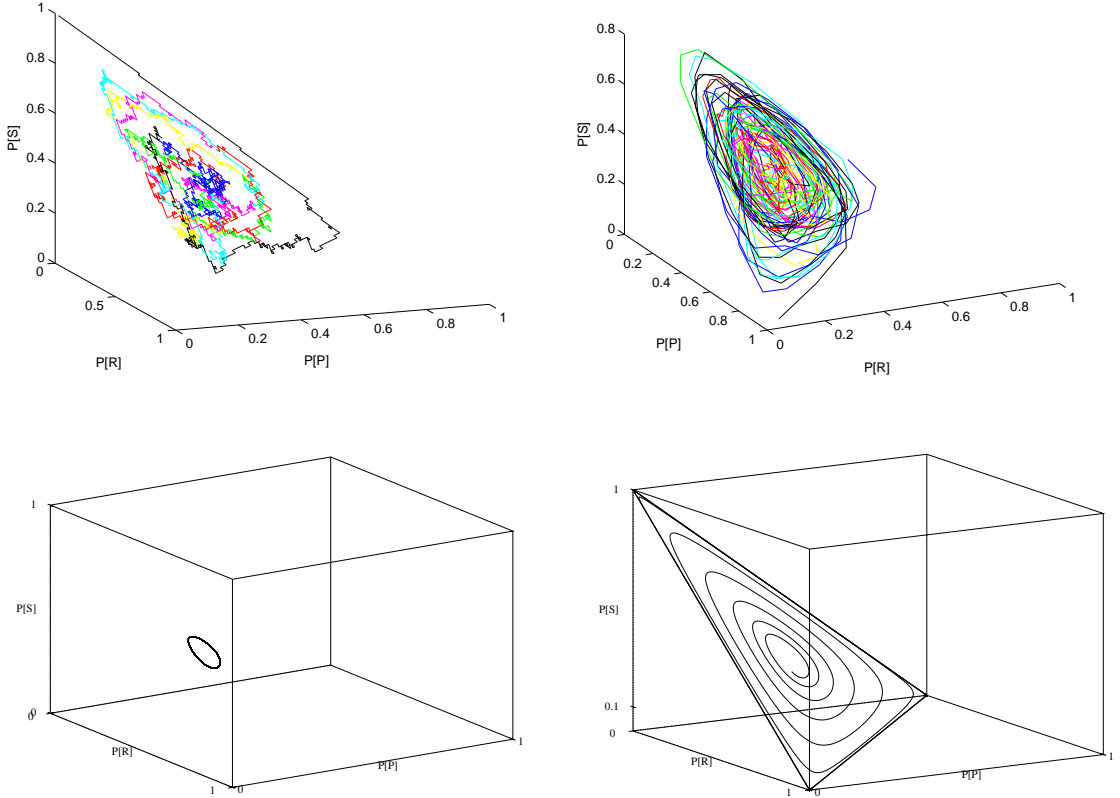


Figure 15: The top left graph shows one simulation on a 10×10 lattice. The top right graph shows one simulation on a 20×20 lattice. The bottom left and right show a numerical integration on the mean field and pair approximation equations respectively using the initial conditions from the 10×10 simulation.

Figure 15 shows that the mean field approximation fails to capture any change in amplitude of the oscillations that occur in the lattice model. For smaller lattice sizes the lattice model behaves closely to the pair approximation with oscillations increasing in amplitude until fixation is reached. However, for larger lattices the oscillations seem to vacillate between large and small amplitudes, not closely resembling either of the models. It is clear that neither the pair approximation nor the mean field do an adequate job of capturing the behavior of the system.

With the lattice model, we have shown that a form of survival of the weakest, where the species with the smallest initial population size is most likely to fixate, can occur for intermediate lattice sizes based on initial conditions even if the invasion rate for each of the three species is the same. We have also shown that by increasing the lattice size, the effect of initial conditions is greatly reduced, although initial conditions that are strongly dominated by one species require larger lattice sizes for fixation to be evenly distributed. Lastly, based on our data, increasing the lattice size increases the mean time in epochs to fixation. In nature, the size of the lattice is likely to be very large. This means that initial population levels will be unlikely to effect fixation and diversity may be maintained for a long period of time.

With the pair approximation model we utilized an alternative assumption to the mean field in order to better capture the behavior of the lattice. We discovered three sets of initial conditions that lead to separate results. The first was starting with two or fewer species leading to quick fixation of one species. The second was starting along a line where the proportion of matching pairs ($P[RR]$, ...) were all equal and the proportion of cross pairs ($P[RP]$, $P[RS]$, ...) were all equal. This leads to an internal fixed point which would not be viable in the lattice model, since its stochastic nature would lead to a perturbation off the stable line. Lastly, all other initial conditions lead to a heteroclinic cycle. Again, since the lattice model is stochastic, it is not able to stay in the heteroclinic cycle and eventually hits a heteroclinic orbit which leads to the fixation of one species.

6 Biological Significance

Pair approximation is successful at approximating the behavior of small habitats; however, due to the increase in oscillation amplitude, coexistence of the three species cannot be maintained for long periods of time. However, pair approximation does not seem to capture the behavior in large habitats. Using the lattice model we showed that by increasing the size of the lattice leads to longer times to fixation. Thus large habitats are likely to maintain diversity. Additionally, when starting with a system that includes each of the three species, we showed that increasing the lattice size decreases the effect of the population proportions on the likelihood of fixation for each species. However, when one of the species in the system is more predominant, a larger habitat is necessary for equal fixation probabilities. In nature, the habitat size is likely to be very large. Consequently, initial population densities will be unlikely to affect fixation and diversity may be maintained for a long period of time. When three species are present and there are no disturbances to the system, species diversity is likely maintained.

7 Future Work

Some of our results from the lattice model were based on extrapolating the behavior after 100 epochs based on the smaller lattice sizes. Unfortunately extrapolation does not always

work and the verification of these results on larger lattices is computationally difficult since the time to fixation increases exponentially with the lattice size. Further study on the larger lattice sizes may be done to validate our assumption. Additionally, the heteroclinic cycle occurs because we set all of the invasion rates equal. If we allow the replacement rates to be different, we may find the hopf bifurcation necessary to have a true limit cycle. Lastly, our system was for 3 states even though cyclical hierarchy can be extended to larger systems.

8 Acknowledgements

This project have been partially supported by grants from the National Science Foundation (NSF - Grant DMPS-0838704), the National Security Agency (NSA - Grant H98230-09-1-0104), the Alfred T. Sloan Foundation and the Office of the Provost of Arizona State University. We would also like to thank Drs. Faina Berezovskaya and Fabio Sanchez for their help and support with this project.

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