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Investigation Of Spatial Ecologies

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Abstract

Cyclic interactions between species exists within nature, among marine sessile organisms and different strains of bacteria. But the development of these systems are not understood well. This paper attempts to shed some light on these types of systems, including why these some particular systems are stable over long time periods, and others quickly collapse with species becoming extinct. The mathematical model is investigated, as well as various computer simulations that give stable invasion sets. From these results some patterns emerge, including an interesting result that given certain conditions, biological evolution of one species can cause the extinction of another species, without net gain by the newly evolved species.

Acknowledgements

I would like to thank my supervisor Marcus Frean for reading multiple drafts of this report, and listening to the varying story of what the simulations were showing.

I would also like to thank Chris Grigson for the help with solutions to simultaneous equations, which formed the bulk of the Mean Field work.

Lastly I would like to thank my family for 4 years of support while I have been attending university.

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1 Introduction

Biology is full of examples of cyclic interactions between species, where all the species are invading each other (and being invaded in turn), but no one species gains the upper hand and completely takes over the environment. There are concrete examples where species compete for space in a cyclic manner and which, over time, are asymptotically stable. But by the principle of competitive exclusion, at equilibrium, the number of competing species which can coexist is no greater than the number of limiting resources (Hardin [8]). If equilibrium is reached then only one species will survive, so there must be some factors within these biological systems that remove the threat of equilibrium. Usually these systems have complex networks of competitive interactions, so it is hard to see how and why these interactions exist.

There has been much work recently discussing specific systems, mostly with only 2 or 3 species. But there has been little consideration for the factors which give rise to these systems in the first place, and what makes these systems biologically plausible, when other systems (say with 4 or more species) are not seen often. These systems of species interactions are explored here. I consider competition between multiple species, specifically what are the factors that make a system dynamically stable. Although I use the term *species* here, the same analysis applies to any group of differing replicators with similar interactions.

In this paper I will explore what sort of interactions exist within these systems, and why they act to prohibit equilibrium. I look at systems with infinite space limitations, showing that these can give no firm conclusions about the structure. Then I introduce size limitations, and show that if spatial structure is included I can get asymptotically stable systems. Finally I discuss these systems, and attempt to describe what make these systems stable over time.

1.1 Previous Work

There is a large amount of previous work on this subject, including biological examples of these types of systems, described in several papers. Mating strategies of side-blotched lizards are described in Sinervo and Lively [18], which showed the classic Rock-Paper-Scissors (three species) cycle [1]. Other examples include overgrowths by marine sessile organisms (Burrows and Hawkins [1]) and competition between mutant strains of yeast (Paquin and Adams [15]). Cycles involving several species are described in Szabo and Czaran papers ([19] and [20]) .

Two species systems have been shown to be unstable, with one species becoming extinct (see Weissing [22]), provided the two species differ only in their competitive ability. If one species has a natural growth element we have predator-prey system's described in numerous sources (see Hastings [10] or Hofbauer and Sigmund [11] for example).

Cyclic competitive systems with three species have been shown to be dynamically stable in Gilpin [7], Durrett and Levin [5], Frean and Abraham [6] and Weissing [22]. These

[1] See section 1.2 for a description of this system

papers discuss the three species system in depth, both including and excluding spatial size limitations.

Other aspects of this system have been explored in some depth. The affect of evolution (of the invasion rates between species) has been explored in Frean and Abraham [6] as well as Lehman and Tilman ([14]), showing that diversity is maintained through counterintuitive "survival of the weakest". Durrett and Levin [4] have discussed the tradeoff between dispersal range and competitive ability within cyclic competition systems. And Huisman and Weissing [12] have described the fractal boundaries within multispecies competition for multiple resources (including, but not exclusively, spatial competition), concluding that the outcome is completely unpredictable from the initial conditions.

Johnson [13] show the fundamental importance of spatial structure in maintaining cyclic competition systems, when space size limitations are included. This was discussed for systems involving multiple (≤ 30) species.

Multiple species systems have also been explored, within two Szabo and Czaran papers ([19] and [20]). These papers cover cyclic competition systems with different strains of bacteria. Through a complex interaction of toxins (which kill unprotected bacteria strains), antitoxins (which protect a strain, but at the cost of production), and quicker growth rates (for 'natural' strains not producing either toxins or antitoxins), cycles containing 6 or 9 different bacteria strains are shown to exist. The first paper covers 4 systems containing 6 different strains, and the second paper covers a system with 9 strains, both finding these to be dynamically stable.

1.2 Motivation

It is worth looking at the Rock-Paper-Scissors (three species) model in detail, as this forms a basis for this work. Most of this discussion comes from Frean and Abraham [6]. Here there are three species, r (rock), p (paper) and s (scissors), which occur in proportions d_r, d_p and d_s (where $d_r + d_p + d_s = 1$). An individual of species r can invade an s with probability P_r, an s invades a p with probability P_s,an p invades a r with probability P_p, and all other invasion probabilities are zero. With N available sites, in the limit of large N (i.e. as $N \to \infty$), the rate of change of population density are given by the mean field equations:

$$\frac{\delta d_r}{\delta t} = d_r(d_s P_r - d_p P_p)$$

$$\frac{\delta d_s}{\delta t} = d_s(d_p P_s - d_r P_r)$$

$$\frac{\delta d_p}{\delta t} = d_p(d_r P_p - d_s P_s)$$

The population densities form closed orbits around the non-trivial fixed point of the mean field equations, obtained by setting the rates of change to zero. If R is the population density of species r at the fixed point, it follows that:

$$R = \alpha P_s, S = \alpha P_p, P = \alpha P_r$$

where:

$\alpha = (P_r + P_s + P_p)^{-1}$

This shows that the populations are not controlled by their own invasion rates, but by the invasion rates of the species that they invade. This means that the most aggressive species will never have the highest fixed-point population.

When the population is finite (i.e. $N \not\to \infty$), but the dispersal (or interaction) range is infinite, then random fluctuations tend to force the populations to overshoot these orbits. This will eventually lead to one species becoming extinct.

This paper also considered what happens when the limit of N is smaller (i.e. not ∞), and the interactions between species are local - i.e. one individual at a site can only affect the sites in the neighbourhood around them, for some well defined neighbourhood (the Moore neighbourhood is used here, which are the eight sites directly adjacent to the site chosen). While a species may become locally extinct, distantly separated sub-populations will not affect each other, and on a large N (sites), global extinction's are unlikely. It is shown that the mean field point is an attractor within the system, quickly forcing the densities of the species to fall into some predictable oscillation pattern.

The thrust of my paper is an attempt to generalise this analysis of the system, and to discover if the same results apply. I also attempt to discuss why this system arises naturally in biological systems, and what forces act to reduce a complex system of many interacting species to this relatively simple system of interactions.

2 Mean Field Model

The first step in analysing these systems is to consider the domain with the least amount of restrictions. Consider a model which has a square lattice of N sites. Each site is occupied by 1 (of M) species, which have a density of d_i (where $\sum_{j=1}^{M} d_j = 1$). This system has no imposed structure to the mixing of the species, allowing unlimited interaction distance, and no limit on the size, or number of sites (consider the model as the limit $N \to \infty$).

2.1 Generalised Model

The number of encounters between different species occur with probabilities depending on the densities of each species, so the rate of change of the population densities are given by the Mean Field equation (Takeuchi [21]). For species i:

$$\frac{\delta d_i}{\delta t} = d_i(r_i + \sum_{j=1}^{M} d_j(p_{ij} - p_{ji}))$$

where:

r_i is the intrinsic growth rate

p_{ij} is the invasion rate from species i to species j, p_{ji} is the reverse invasion rate.

These equations describe the amount of change seen in each time-step for each species. There are two elements to this equation. The first is $d_i r_i$, which gives the amount of change as the current density of the species multiplied by the natural growth of the species. The second element of this equation states that the rate of change is describing the amount of change resulting from invasions of other species. If species i invades species j, then the amount of change of species i will be a positive amount related to the density of these two species, i.e. $d_i d_j *$net-invasion-rate. Otherwise if species j invades species i then this net-invasion-rate will be negative and thus the amount of change will be decreased respectively.

As there are no empty sites on our lattice the intrinsic growth rate is zero ($r_i = 0$). The only way species densities change are through invasions from another species.

To simplify the analysis of this equation, I combine the term $p_{ij} - p_{ji}$ into one single term, a_{ij}, which is the net invasion rate from species i to species j. It follows trivially that $a_{ij} = -a_{ji}$.

Since this is a set of related simultaneous equations, they can more concisely be described in vector form:

$$\text{i.e. } \vec{d'} = \vec{d}(\mathbf{A} \cdot \vec{d})$$

$$\begin{pmatrix} d'_1 \\ d'_2 \\ \vdots \\ d'_M \end{pmatrix} = \begin{pmatrix} d_1 \\ d_2 \\ \vdots \\ d_M \end{pmatrix} \left[\begin{pmatrix} a_{11} & a_{12} & \dots & a_{1M} \\ a_{21} & a_{22} & \dots & a_{1M} \\ \vdots & \vdots & \ddots & \vdots \\ a_{M1} & a_{M2} & \dots & a_{MM} \end{pmatrix} \begin{pmatrix} d_1 \\ d_2 \\ \vdots \\ d_M \end{pmatrix} \right]$$

where:

The array $\mathbf{A}$ is the net invasion rate $a_{ij} = p_{ij} - p_{ji}$ (i.e. $\mathbf{A} = \mathbf{P} - \mathbf{P}^T$)

Now this will be stable only when the change in the densities of each species is zero (i.e. $\vec{d'} = 0$), and thus when:

$$\vec{d}(\mathbf{A} \cdot \vec{d}) = \vec{0}$$

Since trivial solutions are useless (it just says that all the species die out over time), it is required that all species have stable, positive populations (i.e. $\forall i : d_i \neq 0$) [2], so:

$$\mathbf{A} \cdot \vec{d} = \vec{0}$$

$$\begin{pmatrix} a_{11} & a_{12} & \dots & a_{1M} \\ a_{21} & a_{22} & \dots & a_{1M} \\ \vdots & \vdots & \ddots & \vdots \\ a_{M1} & a_{M2} & \dots & a_{MM} \end{pmatrix} \begin{pmatrix} d_1 \\ d_2 \\ \vdots \\ d_M \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}$$

[2] This assumption will be investigated later, see section 2.3

This expands out to a set of linear equations to solve:

$$d_1 a_{11} + d_2 a_{12} + \ldots + d_M a_{1M} = 0$$

$$d_1 a_{21} + d_2 a_{22} + \ldots + d_M a_{2M} = 0$$

$$\vdots$$

$$d_1 a_{M1} + d_2 a_{M2} + \ldots + d_M a_{MM} = 0$$

Finally we also include the density restriction equation, which simply forces the sum of the densities to be 1:

$$d_1 + d_2 + \ldots + d_M = 1$$

Now if $\mathbf{A}$has an inverse (i.e. the determinant of $\mathbf{A}$ is non-zero), then:

$$\vec{d} = \vec{0} \cdot \mathbf{A}^{-1}$$

$$\text{therefore: } \vec{d} = \vec{0}$$

which is the trivial solution. So there are only nontrivial solutions when the matrix $\mathbf{A}$ has no inverse.

The solution to these equations are the stable point where the 'change of density' of each species are 0, and all of the densities are greater than 0. This is the Mean Field solution.

2.2 Rock-Paper-Scissors Example

It is worth at this point to run through an example, to aid understanding and to check the correctness of these results. Consider the Rock-Paper-Scissors example that was given in the introduction. Rock invaded Scissors with probability P_r, Scissors invaded Paper with probability P_s, Paper invaded Rock with probability P_p, and all other invasion probabilities are zero. Thus the following $\mathbf{A}$ matrix arises:

$$\mathbf{A} = \begin{pmatrix} 0 & -P_p & P_r \\ P_p & 0 & -P_s \\ -P_r & P_s & 0 \end{pmatrix}$$

Putting this into our vector equation given above, the following set of equations follow:

$$d_r 0 + d_p(-P_p) + d_s P_r = 0$$

$$d_r P_p + d_p 0 + d_s(-P_s) = 0$$

$$d_r(-P_r) + d_p P_s + d_s 0 = 0$$

$$d_r + d_p + d_s = 1$$

rearranging we get:

$$d_s P_r = d_p P_p$$

$$d_r P_p = d_s P_s$$

$$d_p P_s = d_r P_r$$

$$d_r + d_p + d_s = 1$$

Solving the above simultaneous equations the result follows:

$$d_r = \frac{P_s}{P_r + P_p + P_r}$$

$$d_s = \frac{P_p}{P_r + P_p + P_r}$$

$$d_p = \frac{P_r}{P_r + P_p + P_r}$$

Which is exactly the result given above [3]:

$$R = \alpha P_s, S = \alpha P_p, P = \alpha P_r$$

where:

$\alpha = (P_r + P_s + P_p)^{-1}$

2.3 Problems with the Mathematical Model

Within our model above, all the densities are greater than zero ($\forall i : d_i > 0$). It is important here that there exists no notion of negative densities within our conceptual model, because this implies that some species has fewer than 0 individuals within the population. So all negative densities should be regarded as equivalent to 0. But this is not treated correctly within our Mean Field model above, and this causes difficulties.

Initially we have the mean field equation, for some species i, with a zero 'change of density':

$$d_i(\sum_{j=1}^{M} d_j a_{ij}) = 0$$

Assume we have at least one species with negative density (i.e. $\exists k : d_k < 0$). So the above equation will be:

$$d_i(\cdots + d_k a_{ik} + \cdots) = 0$$

where species k will have an impact on the density of species i, with magnitude $|d_k|$, but the reverse direction. That is, if species k invades i this impact will be positive (the reverse of the normal negative impact), and if species i invades k then this impact will be negative. Affecting another species while you have no existence within the world is not a bad feat!

Thus for the mean field equations above, the ($\vec{d}$) solutions to $\mathbf{A} \cdot \vec{d} = \vec{0}$ are no longer the same solutions to $\vec{d}(\mathbf{A} \cdot \vec{d}) = \vec{0}$.

[3] See section 1.2

If we know in advance which particular species will have a final density of < 0, we can reduce the matrix to find solutions. For $d_k \leq 0$, we can simply remove the k^{th} row and column from the **A** matrix, and the k^{th} element in the $\vec{d}$ vector, and solve to find nontrivial solutions. That is, we can consider the system without that species (as if the species does not exist at all).

If we don't know if any species will become extinct (usually the case), we can traverse each possible combination of zero densities. That is, we find the solutions when $\exists i : d_i = 0$, and when $\exists i, \exists j : d_i = 0$ and $d_j = 0$, and on, until we find solutions when only three species have *non-zero* densities (we know that when only one or two species have non-zero densities we get the trivial solution, i.e. only one species will survive). These solutions that have final densities all above 0 are possible solutions to the initial set of species.

This will quickly become intractable for increasing numbers of species , as the number of possible solutions grows exponentially with the number of species.

So in general, for any large number of species this model allows us to work out the stable densities of a group of species if we know that no species should become extinct within the system. This can solve what we think are stable invasion sets within the system, but is unable to determine which species will become extinct if the system is unstable.

3 Simulating Local Interactions

3.1 Finite Domain Size

The analysis of unlimited domains works well when it is known that a stable set of species exists. But if a system of individuals are not stable (that is, over time one species will become extinct) then, in general, we cannot find out which species will survive and their final densities. The above model shown does not help us to discover if a particular system will become stable over time, because it fails to work when one species density drops below 0. The next step, in an effort to uncover which systems persist, is to limit the domain size. That is, we consider simulations where the number of sites (N) are a finite number.

Consider the model given above, with M species distributed over N sites (where $N \not\to \infty$). At each time step, we choose two sites, one as the invader and one as the invadee. The occupant of the first site invades (replaces) the occupant of the second site with a given probability. Not limiting the dispersal range of the interactions between species, the two sites are chosen at random from the entire grid of sites.

It was shown in Weissing [22] that without any spatial structure there is no attractor to the Mean Field points given in the above calculation, and that over time random fluctuations will eventually drive one species to extinction. This was shown to be true for the three species model in Frean and Abraham [6]. This is exactly what I expect to see in simulations, as without any attractor point random fluctuations will eventually drive one species to extinction.

Thus no stable systems should be obtained, and we expect one species to eventually dominate the entire system.

Fig 1 shows that in computer simulations I get exactly what was expected. Because the initial generations are almost completely random in the species fluctuations, they are excluded to prevent hiding of the later detail.

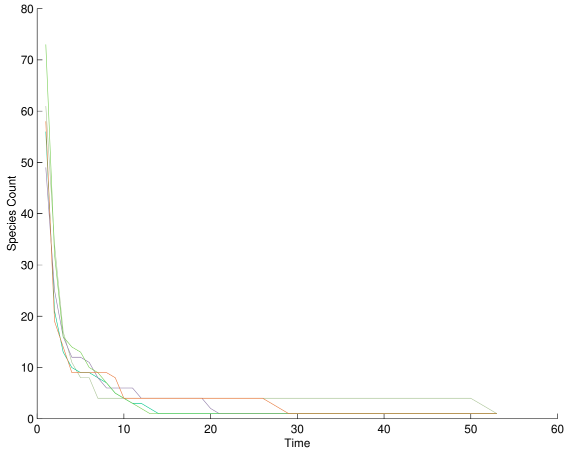

Figure 1: Species Count for five runs with no spatial structure. These we run with an initial population of 10000 species, on a 250x250 grid of sites.

3.2 Introducing Spatial Structure

So the above simulations give us no more information about the types of systems that will prevail. It was shown in Frean and Abraham [6] that spatial structure is introduced then the Mean Field becomes an attractor point. To achieve this we consider local-range dispersal, where the invader is chosen at random from the entire lattice of sites, but the invadee is chosen from the Moore neighbourhood - one of the 8 adjacent sites (rather than the entire grid).

It has been shown in Durrett and Levin [4] that with local dispersal the dynamics of the system are changed. While a species may become locally extinct, this will not necessary indicate a global extinction of the species. Also if there are competition cycles, and the lattice size is sufficiently large, then global extinction's are unlikely.

Now the Mean Field point for the species becomes an attractor point for the system. If this means that some species have to become extinct, this will happen as a natural course. The remaining species will settle into a relatively stable state, with random oscillations always being *pulled* towards the stable point, and we should see the system settle into some stable pattern of species densities.

Here we have a square lattice (250x250) of sites, each containing one species. The initial species of each site was selected at random from an initial population of 10000 species. One *epoch* consists of a number of invasions, one invasion for each site to invade one other site once, with the location of each site chosen at random. The invasion success is non-deterministic, with the probability (p_{ij} for species i invading species j) chosen at the start.

We begin the simulations with a large number of species (usually about 10000), but the first few epochs will result in most of the species becoming extinct. In the initialisation, each species will have no more than a couple of representative individuals, and the survival probability for each individual in the first generation is virtually zero. Due to this, most species become extinct within the first few generations. The initial generations are excluded from analysis to prevent this turmoil hiding smaller and more important details.

3.2.1 Binary Invasion Rates

As a simplification of the general interaction, I initially considered binary invasion rates. That is, the random invasion rates being a binary value - either 1 or 0 (i.e. always or never invade respectively). This should make little difference to the results that are obtained, but the analysis of the results will be simpler.

The first simulations allowed all types of binary relationships between any 2 given species: 0-0, 0-1, 1-0 and 1-1. Fig. 2 shows the number of each species per generation for five runs. It is easy to note here that the system quickly becomes very stable, and this is emphasised by Fig. 3, which shows that densities of each species for one run. Here the species densities are constant, which is unexpected in random environments like this.

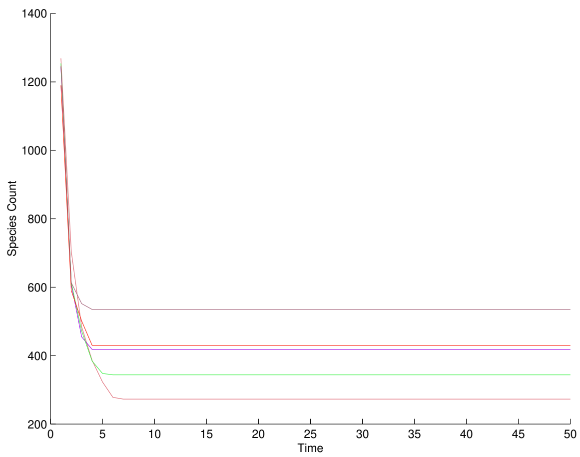

Figure 2: Species Count for five runs with binary invasion sets. These we run for 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

Fig. 4 shows the mixing of the populations, and gives us some idea of what is going on here. Of interest are islands of species, but with seemingly randomly placed individuals intermixed within the uniform groups.

The general case here quickly boiled down into completely stable interactions, where each

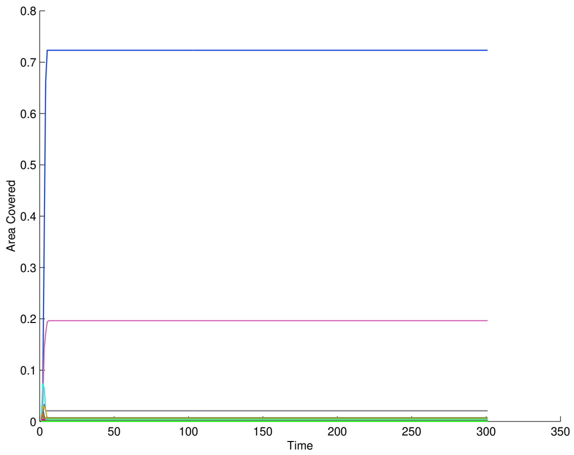

Figure 3: Species Density for one run with a binary invasion set. This was run for 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

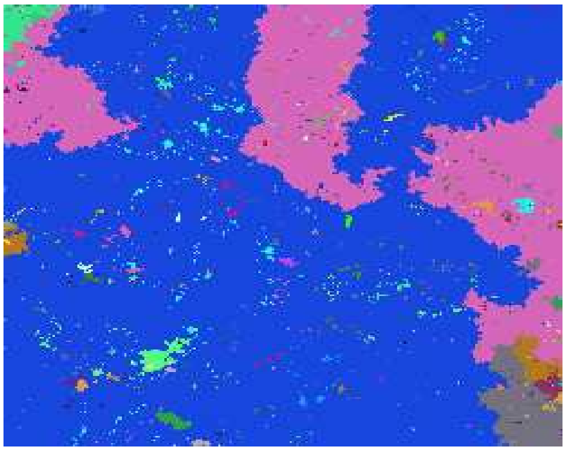

Figure 4: Simulation Surface for the above run. This was after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

site is constant. Each individual can only invade neighbouring individuals, and borders with 2 species that have the 0-0 interaction become stable. On a local scale, each individual cannot successfully invade any neighbour, and each individual remains constant with respect to its neighbours. When all interactions fall down to this state, then the simulation becomes inert. This happens even when, on a global scale, there are still interactions between species that are not 0-0, because this effect is present on the local scale of each individual.

It is interesting to note that few species (usually 1 to 3) become dominant, and their densities become large (> 0.2).

The 0-0 interactions of these species are unable to invade the remaining species, and the system become completely unchanging. This is not what you would expect to see in biological systems, where species ignore each other completely.

3.2.2 Restricted Binary Interactions

To get more biologically plausible systems, I attempt to prevent species from ignoring each other and force all species will have to interact in some form. To achieve this I disallow the 0-0 interaction, having only 0-1, 1-0 and 1-1 interactions. These interactions should still be enough to capture the system, but it will prevent the implausible (and uninformative) stable system from occurring.

The simulations show what we expect to see, where we have just a few species that rival each other for space. Fig. 5 shows one typical run, where the species densities have settled down into a simple pattern as predicted. The system has become stable - we have some cyclic invasion pattern that will not allow any single species to gain complete dominance. Fig. 6 shows the spatial structure for this run, and clearly shows the large groups of homogeneous individuals.

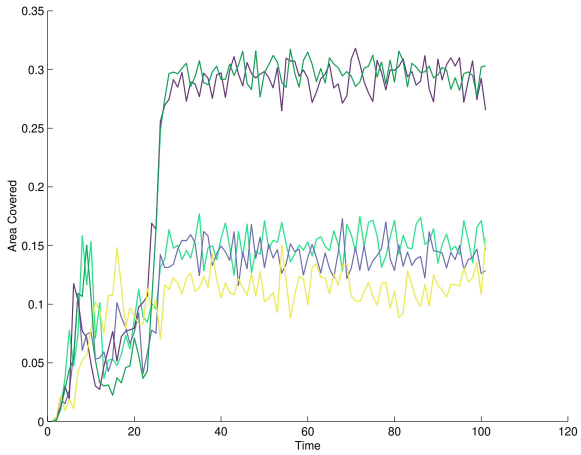

Figure 5: Species Density for one run with a restricted binary invasion set. This was run for 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

Fig. 7 gives some of the different types of binary invasion sets that came out of these simulations. [4]

3.2.3 Continuous Invasion Rates

Although the binary interactions described above should capture the system, I ran simulations with general interactions as a check. The invasion rates were allowed any value between the bounds [0..1] (with 32-bit precision). Here the 0-0 interaction are very unlikely, and this will

[4] These pictorial representations of the invasion sets can be interpreted thus: Each species is represented by a circle. The size of the circle is arbitrary and constant. The net invasion from any species to any other species is given by a line, coloured the same as the invader. The thickness of the line indicates the invasion rate, with a larger line indicating a larger probability of invasion. Since only net rates are given, there are no negative invasion rates shown, and the absence of a line indicates 0 net rate of invasion.

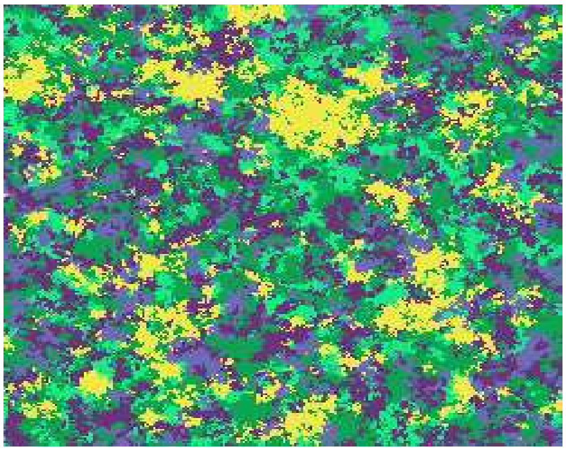

Figure 6: Simulation Surface for the above run. This was after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

not occur in sufficient amounts to cause the same effect to the system seen with the binary interactions.

Again we see that a small number of species rival each other for space. We see that we get systems with up to 7 species, but no more. Fig. 8 shows a typical run, this with 5 species, and Fig. 9 shows the spatial structure. Fig. 10 shows the invasion set that accompanies this run. The spatial structure in these simulations is similar in form to the binary simulations above.

Fig. 11 gives some of the different types of continuous invasion sets that came out of these simulations.

3.2.4 Effect Of Lattice Size

Due to the large effect spatial structure has on the stability of the system, I expect the lattice size to influence the invasion sets that occur.

A large amount of spatial structure arises when we have local interactions, and this organisation pulls the species towards the Mean Field point, where the densities of each species is stable. But random fluctuations still have an effect on the system, dragging the true densities in many different directions, including away from the Mean Field point. Due to these random fluctuations, it is still possible to have some species become extinct. This is especially likely when the stable point of a given species are close to 0.

Given that it is still possible, within a 'stable' set of species, to have extinction's, a larger lattice size will allow more individuals of each species to coexist. A larger lattice size will allow more species to recover from random fluctuations in density, and thus decreases the chance of random fluctuations removing any species. In a similar fashion, a smaller lattice size will restrict the numbers of species that can coexist under random fluctuations.

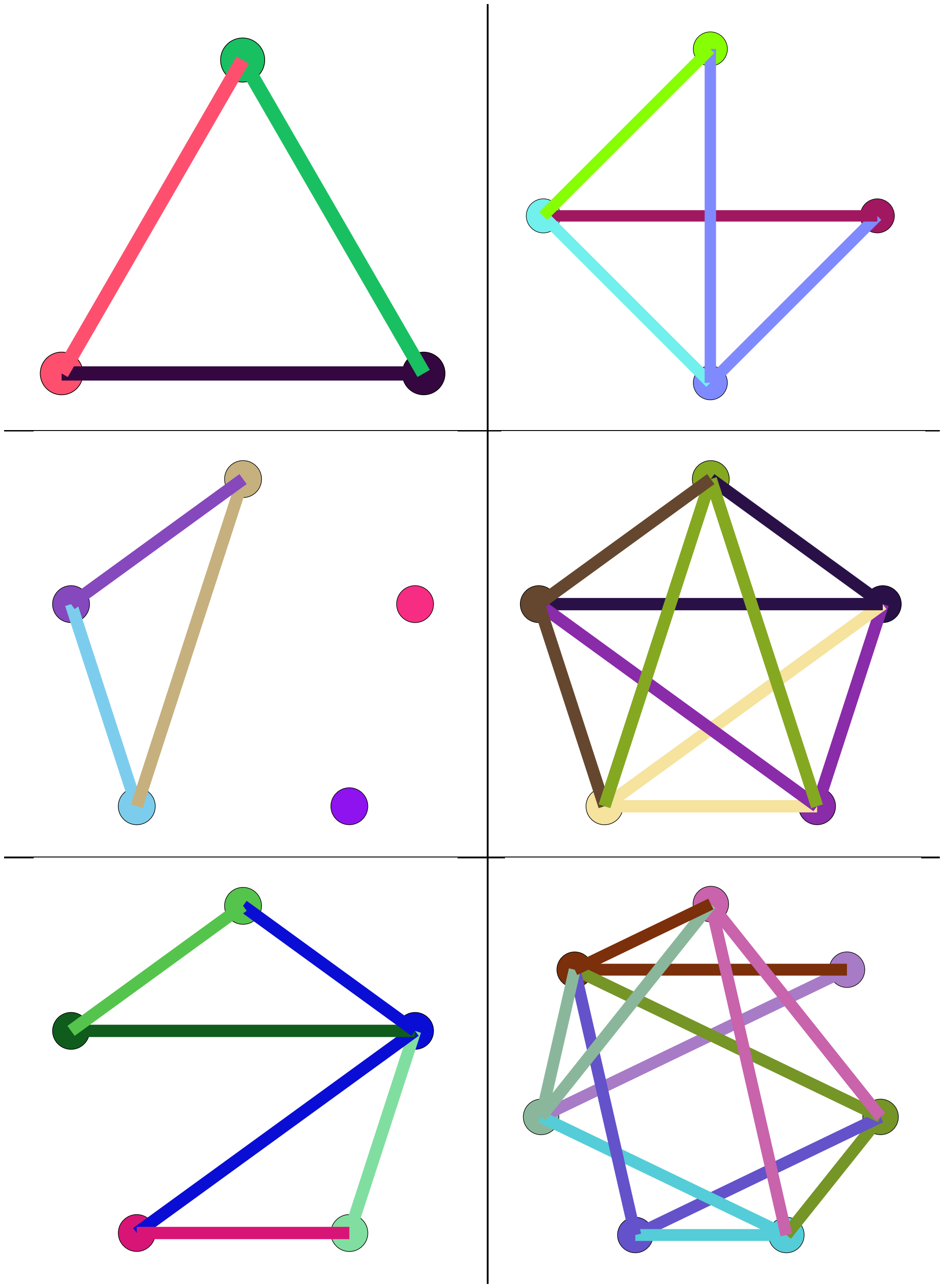

Figure 7: Some Typical simulation results (invasion sets) for restricted binary runs. These were after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

Thus we expect the stable sets of interactions that occur to be affected to some degree by the lattice size. To investigate the extent of this effect, I ran simulations similar to the ones above, but with differing lattice sizes. The results are summarised within two tables, Fig. 12 for binary invasion sets and Fig. 13 for continuous invasion sets.

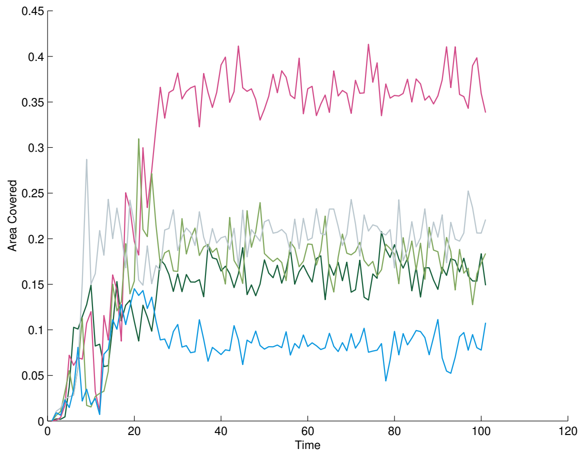

Figure 8: Species Density for one run with a continuous invasion set. This was run for 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

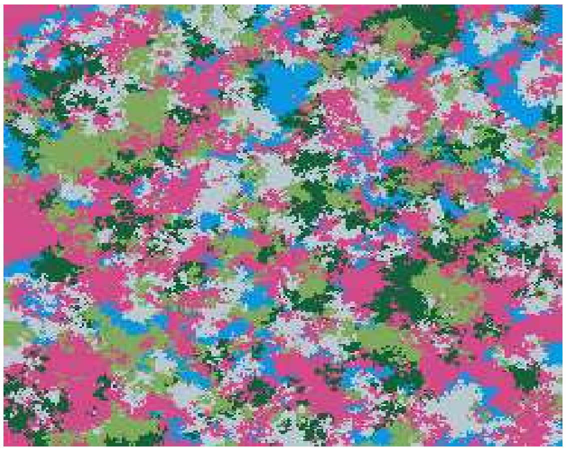

Figure 9: Simulation Surface for the above run. This was after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

With the smaller lattice size (100 by 100 sites), we have fewer species present in stable invasion sets. For both types of invasion sets (binary and continuous), we have no more than 5 species, mostly seeing 3 species. For the general case we even see some cases of complete dominance, where one species is the sole survivor. This never happened with the standard lattice size (250 by 250).

With the larger lattice size (500 by 500), we see a tendency towards more species successfully competing within the system. For both cases we see that there are more of the 5 and 7 species invasion set's, and in the binary case we even see 9 species in some invasion set's (not seen in the smaller lattice size).

This has also shown that a large increase in the lattice size gives a modest increase in the average invasion set size. This indicates that the effect of the lattice size has a minimal

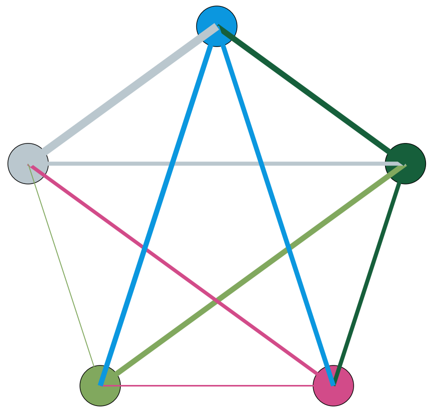

Figure 10: Simulation Invasion set for the above run. This was after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

impact on the types of invasion sets, specifically the size of the invasion sets, that we have seen in these simulations.

4 Cycles

Here we discuss what, out of many possible interactions between different species, will make a stable group of species.

The largest number of species seen in any of the above simulations was 9, indicating that much more than this are increasingly likely to be unstable. The exact number of species that can be sustained in this environment are affected by the lattice size, as discussed above. But what else is effecting the size and types of the invasion sets seen in these simulations?

First I discuss why we need cycles in the first place, and then I give a discussion of the types of cycles that can exist within a system, referring to the results of the above simulations.

4.1 Need For Cycles

If any one species is dominated by all other species in the system, then over time this species will be removed (made extinct, like the dodo). This should be self-evident, because if a species is invaded by all other's, and cannot invade any other species, then its total population can only decrease. Thus within some finite amount of time, the number of individuals of this species will reach 0 - this species will become extinct.

On the other hand, if any one species completely dominates all other species, then this species will eventually remove all other's from the system. Again, this is because if one species can invade all other's, and no other species can invade it, then its population can only increase. In some finite amount of time this species will cause all other species to become

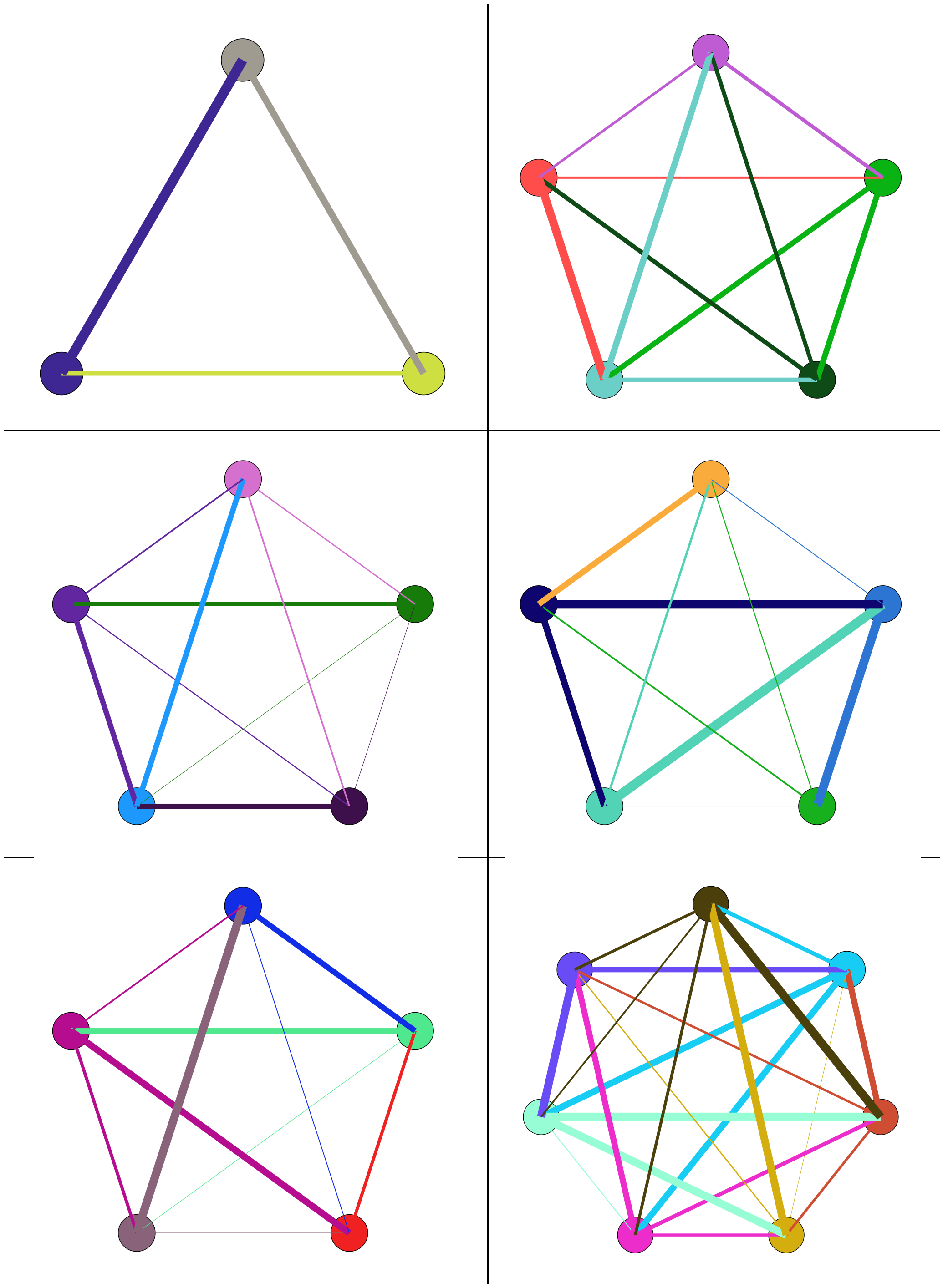

Figure 11: Some Typical simulation results (invasion sets) for continuous runs. These were after 50000 epochs, with an initial population of 10000 species, on a 250x250 grid of sites.

extinct, and control the entire system.

So the only invasion set's that will persist over the long-term are without these two types of species. There are only two ways this can occur in the system - if there is only one species; or if there is a cycle that prevents one species dominating the system. Since complete dominance of the system by one species is extremely rare (unless the lattice size is small),

Lattice Size	Invasion Set Range	Average Invasion Set
100 by 100	3 - 5	4.0
250 by 250	3 - 7	4.8
500 by 500	4 - 9	7.0

Figure 12: Effect of lattice size on the size of binary invasion sets. These we run for 50000 epochs, with an initial population of 10000 species.

Lattice Size	Invasion Set Range	Average Invasion Set
100 by 100	1 - 5	2.7
250 by 250	3 - 7	4.6
500 by 500	5 - 9	6.7

Figure 13: Effect of lattice size on the size of continuous invasion sets. These we run for 50000 epochs, with an initial population of 10000 species.

then all the other systems must contain cycles. This fact is easily confirmed by looking at the invasion sets for the simulations.

4.2 Types Of Cycles

So within stable invasion sets, cycles must exist. We now wish to get a handle on the types of interactions that can occur within a stable system.

4.2.1 Balance Between Invaders And Invadee's

A species can only survive if it has enough invadee's that it can replace, compared to the number of invaders that replaces it. If a species has too many invaders, and not enough invadee's, then it will experience a decline in population numbers. There are two possibilities - either this species will become extinct, or enough of the invading species will become extinct so a balance is obtained. This seems to be intuitively obvious in real biological systems, and we find that the same rule to thumb applies here.

This rule can be stated more explicitly thus: For any given species i within a system, if the sum of the invasion probabilities of species invading i is greater than the sum of probabilities of species i invades, then the system is unstable (i.e. at least one species will tend to become extinct). One can also describe this more formally: *Within a system containing some species i, if $\sum_{j=1}^{M} a_{ij} < 0$ then the system is unstable and at least one species will become extinct.*

This effect will tend to prefer smaller invasion sets. With more species within a system, there is a greater chance that one particular species will have more invaders than invadee's, making the system unstable. Fewer species will reduce the chance that this will happen.

This can be seen from the stable invasion sets given earlier [5]. We see that there are few invasion sets where any species has more invaders than invadee's. The results from the continuous invasion sets are hard to analyse from these invasion diagrams, because the rate of invasion impacts greatly on the stability of a system. Many 'small' invaders (i.e. invaders with a small probability of invasion) can be counted by 'large' invadee's (i.e. invadee's with a large probability of being invaded).

It is worth checking this out in specific simulations. Here I give two simulations (of many) that show this behaviour happening (Fig. 14 and Fig. 15 for a 6 species system, also Fig. 16 and Fig. 17 for a 7 species system). In both these cases the species that is experiencing the unbalance of invaders and invadee's is the one to become extinct. Later I will discuss other options [6].

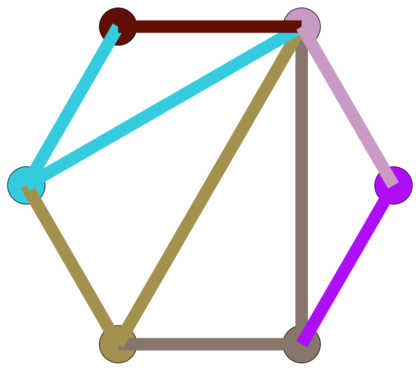

Figure 14: Unstable invasion set involving 6 species

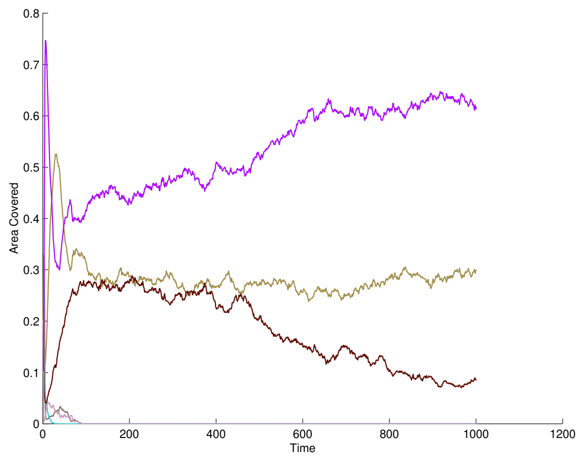

Figure 15: Species Density for the above 5 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

[5] See section 3.2.2 and section 3.2.3
[6] See section 4.2.2

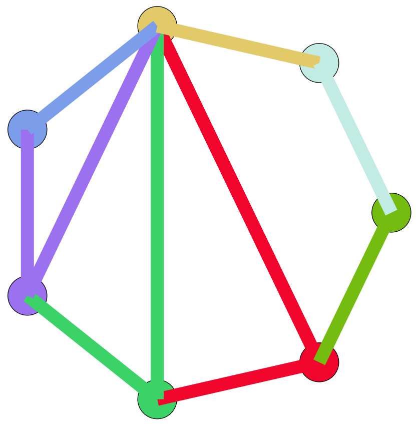

Figure 16: Unstable invasion set involving 7 species

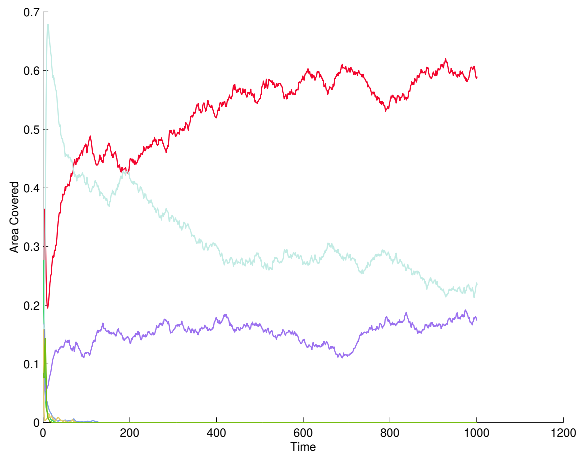

Figure 17: Species Density for the above 7 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

4.2.2 What Does Instability Mean

What do I mean by "the system will become unstable"? If any one species has more invaders than invadee's, then there are two possibilities for the system to collapse. Either the species experiencing the imbalance will become extinct, or enough of its invading species will become extinct (so the given species can reach equilibrium with respect to the invaders and invadee's).

The first effect (the species itself becoming extinct) is an obvious solution to the imbalance. But how can the other effect happen? Under what circumstances will a species be able to force the extinction of one of its invaders? Unfortunately time constraints did not allow a complete exploration of this question, but one very interesting case came to light.

Consider the following situation, where we have a system of N species (Fig. 18). Here we have one species invading two others, which are next to each other in the invasion set, the rest of the species forming the trivial cycle. You would expect that the third species, which has two invaders and one invadee, to become extinct. But actually the second species species will become extinct, leaving the other species in a trivial cycle!

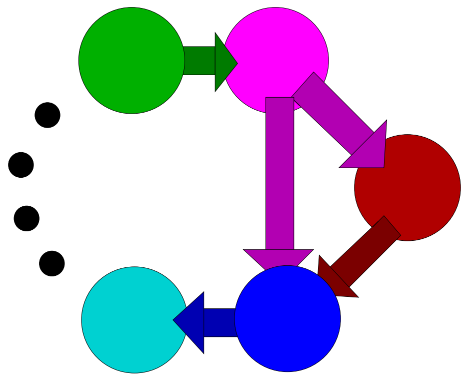

Figure 18: Unstable invasion set with an unusual extinction

Although initially counterintuitive, this effect can be reasoned thus. Species one has two invadee's, and so will be expected to have a large population. This will have a negative impact on species two and three, who are invaded by species one. Species three can offset this negative impact by invading species four, which then passes this invasion influence around the cycle. But species two only invades species three, who is still feeling the negative impact from species one. So species two is impacted by both species - first for having so many invaders in the form of species one, and secondly for having so few species to invade in the decline of species three.

Given this situation where species one invades species two and species three, species two invades species three and species three invades species four (who then invades, indirectly through a cycle, species one), species two will become extinct. This will leave us with the trivial cycle of $N-1$ species.

Simulations show that this effect holds true when we have an odd number of species within the invasion set. If we have an even number of species in the invasion set. this will also hold provided there is enough instability within the system. Specifically, if the net invasion sets used consist of similar situations, but there are no 0-0 interactions (i.e. any null interactions between species are actually 1-1 interactions), then we see the extinction of the middle species.

This can be shown in the following simulations. Fig. 19 and Fig. 21 shows the 4 and 5 species system respectively, Fig. 20 and Fig. 22 showing the simulation results of these systems, and we can see that this elimination happens. The 5 species system is especially interesting, because we have two such invader eliminations (for two of these types of invasion relationships), to species 2 and 5, resulting in the Rock-Paper-Scissors cycle.

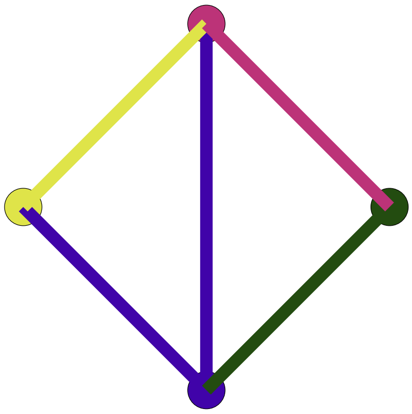

Figure 19: Unstable invasion set involving 4 species, with an unusual extinction

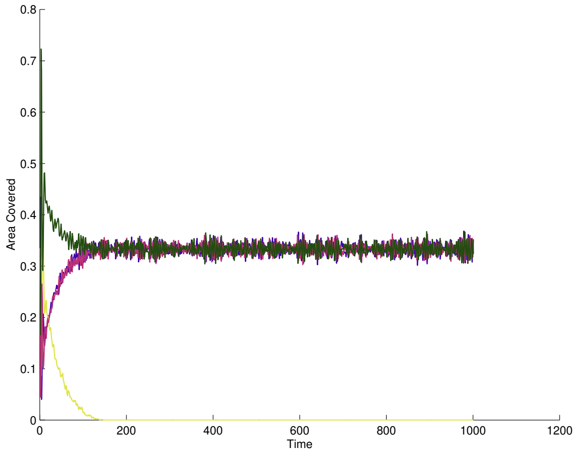

Figure 20: Species Density for the above 4 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

The five case is also interesting because the outcome, seen in the simulations, can be found by the Mean Field solutions. For the invasion set containing five species with one such situation, the Mean Field solutions are as following:

$$\begin{pmatrix} 1/4 \\ 0 \\ 1/4 \\ 1/4 \\ 1/4 \end{pmatrix}$$

When we have two such situations (like in the simulations given above), then we get the

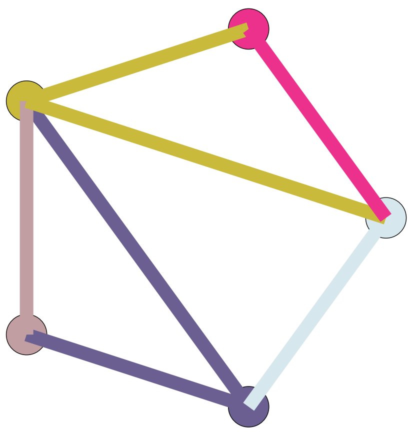

Figure 21: Unstable invasion set involving 5 species, with an unusual extinction

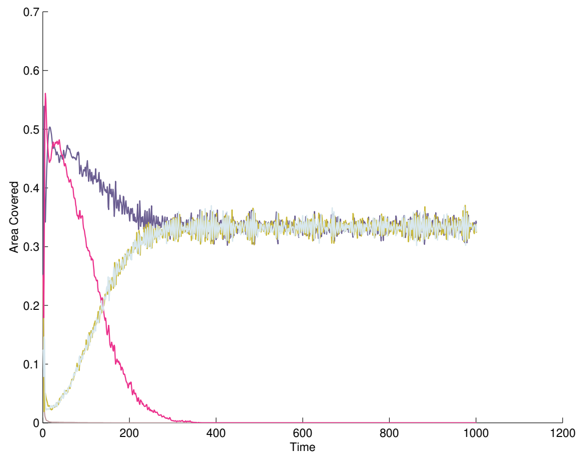

Figure 22: Species Density for the above 5 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

following solutions:

$$\begin{pmatrix} 1/3 \\ 0 \\ 1/3 \\ 0 \\ 1/3 \end{pmatrix}$$

Although these are very good results, they are rare, in the sense that this precise solution only comes about for the odd-number-of-species cases. When we have an even number of species within the invasion set then the results become rather difficult to interpret. Consider the four species case:

$$\begin{pmatrix} 1-2C \\ -1+3C \\ 1-2C \\ C \end{pmatrix}$$

where:

C is some arbitrary constant.

This constant will actually give us a entire line of Mean Field solutions. Analysing this system, we see that if C is small, then species one and three will have large values compared to species four. Species two will have a very small value compared with the rest. This implies the situations that we see within the simulations. This type of analysis for any more than four species quickly become intractable and inaccurate.

It is also worth showing this effect with an even number of species. Fig. 23 shows a 8 species system, and Fig. 24 shows the simulation results - showing that this effect also applies. Note that the net invasion set is given below, but that null (0-0) interactions are actually 1-1 interactions. Like the five species system above, we have two species in the situation described, and both species become extinct as we expect.

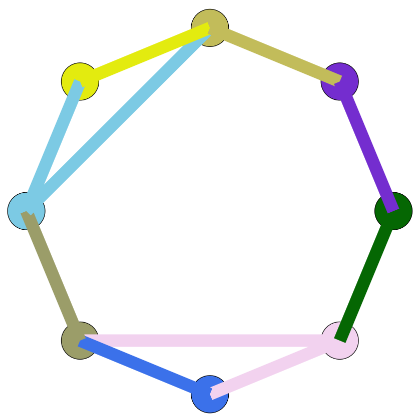

Figure 23: Unstable invasion set involving 8 species, with an unusual extinction

4.3 Biological Implications

This result has interesting and important biological implications, and seems to be undiscovered within this field of biological study. To my understanding, this effect has never been discussed in current biological literature.

Consider a trivial cycle of some number of species, where each species invades the one below it and is invaded by the one above it. If a species evolves to attack (invade) the species

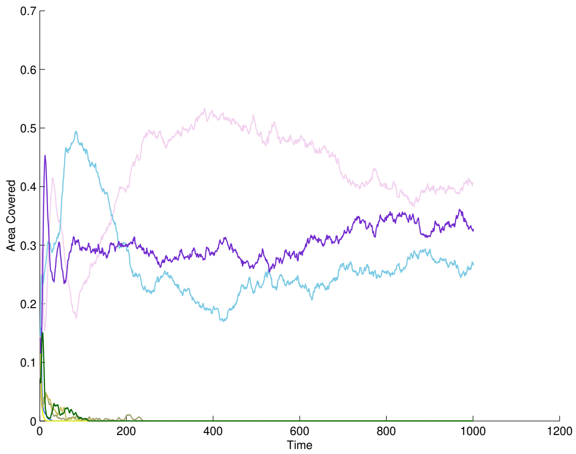

Figure 24: Species Density for the above 8 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

two down the chain (i.e. the species below the one it currently invades), then this will throw the system into imbalance. Specifically, this will force the extinction of the species caught in the middle.

Not only will this decrease the number of species within the system, but will also retain the chances of survival of the evolving species (because it will now only be invading one species, when it had just evolved to invade two separate species).

As an example, consider a system containing species one, who invades species two, who in turn invades species three (who then through a cycle of species indirectly invades species one). Now species one undergoes what would seem to be a favourable evolution to invade species three, increasing its food supply and thus its chances of survival. But as a consequence of this change in the system, species two will become extinct. Removing this species will return the system into a stable state (baring any more evolutions), and also return species one to a similar state it was before the evolutionary change.

Note that this effect is not seen if species one invades any other species other than species three. But given that this species is the closest to species one in the chain, and thus most similar to species one, this evolutionary change would be most likely.

What would seem to be a likely and favourable evolution of a species will not result in a net gain for that species. It will result in the extinction of another species, but this species is one of the invadee's of the given species, and thus return the original species to the current state. The system has one less species within the invasion set, but otherwise has not fundamentally changed as a result of the evolution.

Of course repeated evolutions of this nature will erode the number of species within the system, and thus is an effective way to keep biological diversity to a minimum.

4.4 One Interesting Invasion Set

There is one other interesting invasion set that it is worth mentioning. This involves 4 species, in the following system of invasions (Fig. 25). This is worth mentioning because we have 2 species here that fill in the role of one within the system.

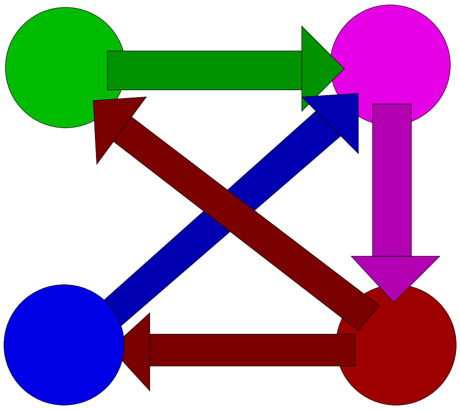

Figure 25: Unique invasion set involving 4 species

What we have here is two Rock-Paper-Scissors cycles, involving two species that cannot directly affect each other. This system is unstable, but in a most curious way. Here, even though two species (species one and four) cannot directly affect each other, their species density at any given moment is completely dependent on the other species density. One can see this easily from the species densities for one run, with the above system (Fig. 26 and Fig. 27).

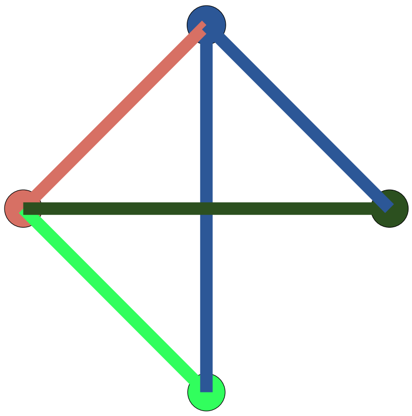

Figure 26: Invasion set involving 4 unique species

There is some logical reasoning about why this dependency happens. Both these species invade, and are invaded by, the same two species within the system (species two and three respectively). This means that whatever effect one of the species is experiencing will be

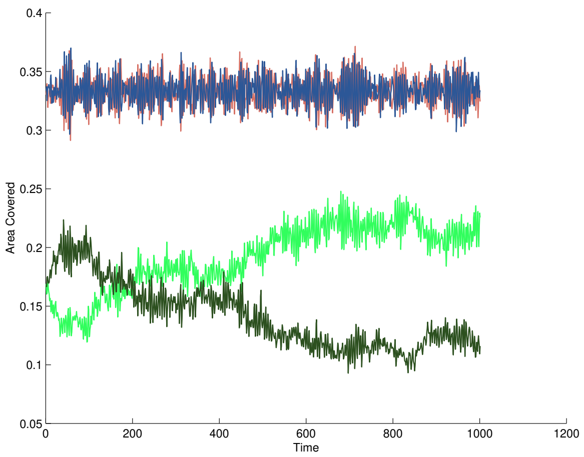

Figure 27: Species Density for the above unique 4 species system. This was run for 5000 epochs, on a 250x250 grid of sites.

felt by the other species. Since these species must share the same space normally filled by one species within the Rock-Paper-Scissors invasion set, they act as one species within the system. When one species experiences an increase in their density the other will experience an decrease in density, by exactly the same magnitude.

The changes in density of each of these species seem to be arbitrary, having little guiding forces. It seems very similar to the random changes seen in simulations where spatial structure was not allowed (where there are no attractor points for the species densities) [7]. For this reason, after some finite amount of time one of these species will become extinct, and the system will be reduced to the true Rock-Paper-Scissors invasion set described earlier.

As above, one can actually see this result from the Mean Field solutions. They are:

$$\begin{pmatrix} 1/3 - C \\ 1/3 \\ 1/3 \\ C \end{pmatrix}$$

where:

C is some arbitrary constant.

Again we have a family of solutions. This family implies the solutions we find in the simulations. The densities for species one and four must always sum to 1/3, and there is one single constant in both species densities. This means that when one species experiences an increase in their density, the other species must have an equal and opposite decrease. The other two species will have a reasonably constant species density around 1/3. This is exactly what we see in the simulations.

[7]See section 3.1

5 Conclusions

I have considered systems of competing individuals, where individual species compete with each other for one resource - space. Different restrictions were enforced on the simulations in an effort to get informative results, and when this was obtained I attempted to give some analysis of the types of systems that we see.

To this end, the mathematical Mean Field solutions was considered first, where the lattice of available sites was not limited. Given a system of species, where it is expected that none will become extinct, then the Mean Field solutions will give the final densities of each species. But this mathematical model does not handle negative species densities very well, in that species with negative densities will continue to impact the system without having any presence within the system.

Limiting the number of sites within the model, with no spatial structure (where interactions can take place over any distance), the trivial system of one single species will occur in all simulations, due to the lack of an attractor point. If local interactions are enforced to give some spatial structure, then stable systems of species will emerge over time. To simplify the analysis of the types of invasion sets that occur, simulations only allowing binary (0 or 1) interactions were run, as well as continuous invasion rates.

Given simulation results patterns begin to emerge. A system of invasions will only be stable if there exists some cycle, and also no species has more invaders than invadee's. If there is one species that has more invaders than invadee's, then either that species will become extinct or enough invaders will be removed from the system to balance the system. In a surprising (and counterintuitive) result I showed that if we have some middle man scenario - where species one invades species two and three, species two invades species three and species three invades (through some arbitrary number of species), in a cycle, species one - then the middle species (species two) will become extinct, forced out by the other two species.

This seems to be a *non-trivial and previously undiscovered result* in this field of biological study. It implies that if a species undergoes what would seem a likely and positive evolutionary change to invade a new species, the system may react to remove the species caught in the middle, resulting in no gain for the species that underwent evolutionary change. This is a major contribution of this paper.

6 Future Work

The above Mean Field model consists of linear equations. For a given set of species, we can solve this set of simultaneous equations to find the stable densities of each species. I showed that if there are density values ≤ 0 in the final solution then this method will not suffice, and that to find the correct solution quickly becomes intractable.

So we included the assumption that all the final densities are greater than zero (i.e.

$\forall i : d_i > 0$). But if we are able to solve the quadratic set of linear equations $\vec{d}(\mathbf{A} \cdot \vec{d}) = \vec{0}$ then we can ignore this assumption. Solutions with some ≤ 0 final densities can still be solved to find the stable set of species.

The species with densities that are equal to, or less than, 0 cannot survive. They will become extinct over some finite time. In order to get the stable solutions to this set of equations, one can eliminate the species with the most negative density (ties can be broken arbitrarily), and recalculate the stable points. We only remove the species with the lowest density, not all species i with $d_i \leq 0$, because the species that are removed may have a detrimental effect on some of the surviving species. With this species removed the surviving species will have a different final density that may be greater than 0. The species with the lowest density is removed because it is reasoned that this species will be removed from the environment the quickest (i.e. will become extinct sooner than the other species).

Thus when we have final densities all greater than 0 we can say, ignoring any extinction's due to (ill) luck, this will be the densities of all the species within the system after a long time. Currently, due to our lack of knowledge of general solutions to quadratic linear equations, most systems are unsolvable in this manner.

References

[1] M. T. Burrows and S. J. Hawkings. Modelling patch dynamics on rocky shores using deterministic cellular automata. *Marine Ecology Progress Series*, 167:1–13, 1998.

[2] Charles R. Darwin. *The Illustrated Origin of Species*. Faber and Faber Ltd, 1979.

[3] Rick Durrett. Stochastic spatial models. Technical report, Cornell University Department of Mathematics, 1999.

[4] Rick Durrett and Simon Levin. Spatial aspects of interspecific competition. *Theoretical Population Biology*, 53:30–43, 1998.

[5] Rick Durrett and Simon A. Levin. Stochastic spatial models: A user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London*, 343:329–350, 1994.

[6] Marcus Frean and Edward R. Abraham. Rock-scissors-paper and the survival of the weakest. *Proceedings of the Royal Society (London), Series B*, 268:1323–1327, 2001.

[7] Michael E. Gilpin. Limit cycles in competition communities. *American Naturalist*, 109, No. 965:51–60, 1975.

[8] Garrett Hardin. The competitive exclusion principle. *Science*, 131:1292–1298, 1960.

[9] Garrett Hardin. The tragedy of the commons. *Science*, 162:1243–1248, 1968.

[10] Alan Hastings. *Population Biology Concepts and Models*. Springer-Verlag, 1998.

[11] Josef Hofbauer and Karl Sigmund. *Evolutionary Games and Population Dynamics*. Cambridge University Press, 1998.

[12] Jef Huisman and Franz J. Weissing. Fundamental unpredictability in multispecies competition. *The American Naturalist*, 157 No. 5, 2001.

[13] C. R. Johnson. Self-organising in spatial competition systems. http://life.csu.edu.au/esa/esa97/papers/johnson/johnson.html, 2000.

[14] Clarence L. Lehman and David Tilman. *Competition in Spatial Habitats*, chapter Eight, pages 185–203. Princeton University Press, 1997.

[15] C. E. Paquin and J. Adams. Relative fitness can decrease in evolving asexual populations of s. cerevisiae. *Nature*, 306:368–371, 1983.

[16] Bill Shipley. A null model for competitive hierarchies in competition matrices. *Ecology*, 74, No. 6:1693–1699, 1993.

[17] Karl Sigmund. *Games of Life: Explorations in Ecology Evolution and Behavior.* Oxford University Press, 1993.

[18] B. Sinervo and C. M. Lively. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature*, 380:240–243, 1996.

[19] Gyorgy Szabo and Tamas Czaran. Phase transition in a spatial lotka-volterra model. *Physical Review E*, 63, 2000.

[20] Gyorgy Szabo and Tamas Czaran. Defensive alliances in spatial models of cyclical population interactions. Personal Communication - Unpublished Manuscript, 2001.

[21] Y. Takeuchi. *Global Dynamical Properties Of Lotka Volterra Systems.* World Scientific Publishing Company, 1998.

[22] F. J. Weissing. Evolutionary stability and dynamic stability in a class of evolutionary normal form games. In R. Selten and Reinhard, editors, *Game Equilibrium Models I: Evolution and Game Dynamics*, pages 29–97. Springer-Verlag, 1991.