

# Social Structure and the Maintenance of Biodiversity

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## Abstract

Traditional ecological models assume well-mixed populations, where all members are equally likely to interact with one another. These models have been used successfully to explain competitive interactions; however, positive interactions such as intraspecific cooperation and interspecific facilitation cannot readily be captured. Previous work has highlighted the importance of spatial structure in explaining these behaviors as well as its role in maintaining biodiversity. These spatial structures have frequently been modeled using lattices, where all organisms have an equal number of interactions. Although these models capture the spatiality of interactions, natural populations are unlikely to follow such rigid patterns. There has been little work investigating the dynamics of populations with levels of social interactions that occur between these two extremes.

In this work, we investigate the dynamics of a 3-strategy non-transitive system in populations with different social structures. We first describe how extending the neighborhood of interactions in traditional lattice models diminishes a population's ability to maintain diversity. Populations are then moved to graphs where interactions are limited to cells within a defined distance of each other in Cartesian space. This method allows for a more fine-grained examination of the effects that increasing interactions have on maintaining diversity. Finally, we examine small world topologies and find that the introduction of random edges into the graph quickly disrupts the maintenance of diversity.

## Introduction

The maintenance of biodiversity has long bemused ecologists. Under most models, the number of species that can coexist within a given ecosystem is significantly less than that observed in nature. Traditional differential-equation-based models, which assume well-mixed populations, often lead to the single species with the fastest growth outcompeting all others, as demonstrated in Kerr (2007). Further, these models have difficulty capturing cooperative interactions among organisms, as these behaviors have associated fitness costs, which slow growth rates and hinder a species' ability to compete.

Ecological models that incorporate spatial structure and local interactions, such as that developed by Durrett and

Levin (1994), have been shown to more accurately describe the interactions of organisms. In these models, spatial structure is imposed by limiting the interactions of an organism to its surrounding neighbors instead of all organisms in the system. This can enable rare mutations to persist, especially if a number of these mutants exist together in close proximity. Further, if costly but beneficial behaviors are localized, the benefits of these interactions on its recipients may outweigh their costs, allowing them to spread in the population.

Allelopathic bacteria are a natural system that is frequently used to study the effects of spatial structure and cooperation, and localized interactions have been shown to contribute significantly to the coexistence of multiple strains (Kerr et al. (2002); Iwasa et al. (1998); Czárán et al. (2002)). In these systems, bacteria produce toxins called bacteriocins, which cause surrounding cells that do not express resistance to lyse. In the process, the toxin producer is killed. However, this act makes the newly-freed space and resources available to neighboring cells (ideally, the kin of the producer). Toxin production is genetically linked to resistance, so *producer* strains are also resistant to the toxin they produce. It is possible, however, to evolve resistance independent of production. Because such *resistant* strains do not pay the cost associated with production, they are able to grow faster than producer strains, while still maintaining their immunity. These strains, however, still grow more slowly than a *susceptible* strain that neither produces toxin nor is resistant. Therefore, in the absence of toxin, a resistant strain will be outcompeted by a susceptible strain. This combination of three strategies is considered a *non-transitive system*, where each strain dominates another strain, but is dominated by a third. These dynamics are captured in the classic rock-paper-scissors (RPS) game, where rock crushes scissors, scissors cuts paper, and paper covers rock.

Traditionally, spatial models of such systems have used lattices containing a fixed number of vertices, or *cells*, distributed uniformly in space. A cell is typically connected to its eight nearest cells (Moore neighborhood) by an undirected edge. To prevent boundary effects, periodic boundaries are often used, which form a toroidal grid by creat-

ing edges between cells on the periphery of the graph. This results in regular graphs in which each cell has the same number of neighbors, and the distance between any cell and its farthest neighbor is the same for all cells. This regularity indicates that any cell in the grid interacts with as many other cells as any other cell. Further, this distance property indicates that no matter where a dominant strategy begins, it must interact with the same minimum number of cells in order to spread throughout the population.

In this paper, we examine the role social structure plays in the maintenance of biodiversity by studying the above non-transitive system on graphs with differing vertex degrees, and hence different patterns of social interactions. We use the terms spatial- and social structure interchangeably, as an organism's potential social interactions are limited to its neighbors. Our intent is to observe the dynamics of populations in the space between the regular graphs used in lattice models and well-mixed populations to determine at what point diversity breaks down. To accomplish this, we describe three models. First, we adopt the use of lattices, and the number of interactions is increased by expanding the radius of interactions surrounding each cell. This model gives us a high-level overview of the social structures in which diversity can be maintained. To achieve a more fine-grained control over a cell's interactions, we develop a method for creating graphs from a set of points in Cartesian space. Finally, we examine diversity on small world graphs, where interactions are primarily localized with the exception of some potential long-range interactions.

The spread of a two-strategy system on graphs with different properties was previously studied by Ohtsuki et al. (2006), who formulated a simple rule for the maintenance of diversity. Our work differs in that we are using a three-strategy system, and the benefits of a particular strategy are not fixed, but rather depend on the composition of each cell's neighborhood. More similar to our work, Károlyi et al. (2005) studied increases in social interactions through imperfect mixing of the spatial structure on a lattice. The primary difference is that their work used some measure of mixing, while the work presented here maintains fixed neighborhoods while differing the number of potential interactions. Finally, Buckley and Bullock (2007) used an information theoretic approach to investigate how space contributes to the complexity of a system. Although the focus of their work was different, complexity can play a large role on a population's ability to maintain diversity.

## Methods

To study the effects of social structure on biodiversity, we developed a model based on graphs. This model consisted of *cells*, which were connected to each other by undirected edges, making both cells neighbors of each other. Interactions in this system were limited to a cell and each of its neighbors. In all experiments, populations consisted of

90 000 cells. Each cell exhibited one of four possible strategies:

1. *Susceptible* cells produced no toxin, nor were they resistant to toxin production by neighboring cells. Because susceptible cells did not pay any cost to maintain such behaviors, their growth was faster than other strategies.
2. *Producer* cells produced toxin which could kill neighboring susceptible cells. Additionally, since resistance is a trait that is genetically linked with production, producer cells were also resistant to toxin produced by neighboring producer cells.
3. *Resistant* cells can be viewed as producers that cheat. They reaped the benefits provided by adjacent producer cells without themselves paying the costs of toxin production. As such, they exhibited faster growth than producer cells, but slower growth than susceptible cells due to the added cost of resistance.
4. *Empty* cells had no effect on their neighbors. When chosen, an empty cell adopted the strategy of a randomly-selected neighbor.

We refer to these different cell types as “strategies”, however they can easily be viewed as species, strains, or sub-species. At the beginning of each experiment, cells were randomly assigned one of these strategies.

Importantly, the growth of each strain was controlled by its rate of mortality. All strategies shared an intrinsic death rate, and the costs associated with resistance and toxin production manifested themselves as increases in death rate. This means that at any given time, a producer cell was more likely to die than a resistant cell, and a resistant cell was more likely to die than a susceptible cell. When a cell died, it became empty. For a cell to change from one strategy to another, it had to first die and then later adopt a neighboring strategy.

Populations were run for 10 000 *epochs*. During each epoch, 90 000 cells were chosen at random, and their states were updated asynchronously according to the rules described below. Following Kerr (2007), the probabilities of a resistant or producer cell dying during one of these updates were 0.312 and 0.333, respectively. Because the fate of a susceptible cell was tied to the presence of neighboring producer cells, its chance of death was modeled according to Equation 1, where  $\Delta_S^0$  is the intrinsic death rate for susceptible cells (0.250 in this work),  $\tau$  is the toxicity of producers (0.65), and  $f_p$  is the fraction of producers in the cell's neighborhood.

$$\Delta_S = \Delta_S^0 + \tau f_p \quad (1)$$

Studies examining the maintenance of cooperative behaviors often compare the fitness cost of a strategy with the benefits it provides (e.g., Axelrod and Hamilton (1981); Ohtsuki

et al. (2006)). In most game theoretic models, these costs and benefits are explicitly defined in payoff matrices. In our model, the costs can be viewed as the increase in mortality seen by resistant and producer cells. In this sense, the cost of each strategy is fixed and continually incurred. However, due to the spatial nature of this and most other biological systems, the benefits depend on the current distribution of strategies in a cell's neighborhood. For example, toxin production may be highly beneficial when surrounded by susceptible cells, but have no benefit when all neighbors are producers. Likewise, resistance is beneficial in the presence of producer cells, but not in the presence of susceptible or resistant cells.

### Lattice Models with Increasing Interactions

To examine the effects of increasing social interactions in populations, we began by adopting the lattice model as used in previous work (e.g., Iwasa et al. (1998); Czárán et al. (2002); Kerr (2007)). In these models, 90 000 cells were arranged in a 300x300 grid, with each cell interacting with its 8 surrounding neighbors. Periodic boundary conditions were used in order to prevent edge effects, producing 8-regular graphs.

As a simple method for expanding a cell's interactions, we first used lattices with increasing radii of interactions. That is, with radius 1, a cell was connected to its 8 surrounding neighbors. With radius 2, a cell's neighbors were the 24 cells within a 2-hop radius. This process continued with increasing radii until diversity was no longer maintained in the populations.

### Cartesian Topology

Lattice models are well suited for studying spatial effects, but the geometric growth of neighborhood size is too fast and not necessarily representative of natural systems. In order to investigate the effects of increased neighborhood size on a finer scale, we moved from using lattice models to randomly-generated graphs that still accounted for the spatial relationships among cells.

To build these graphs, we uniformly placed 90 000 points in a unit Cartesian plane. Each point in this plane represented a cell in the world, and its neighbors consisted of the other points that fell within a circle of specified radius. Since a unit plane was used, the area of the circle was proportional to the expected number of points that it encompassed. That is, the area of a particular circle divided by the area of the plane represented the proportion of points which should, on average, fall within the circle. This construction was similar to that reported by Barnett et al. (2007), who examined how embedding space on random graphs affected various graph properties.

$$\frac{a}{1} = \frac{K}{|V| - 1} \quad (2)$$

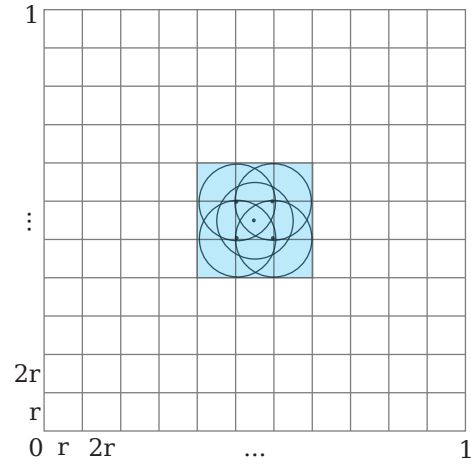


Figure 1: Unit Cartesian plane split into bins. Circles show the area where neighbors may fall, and the shaded region is the Moore neighborhood of the central bin.

In Equation 2,  $a$  is the area of a circle, 1 in the left-hand denominator represents the area of a unit plane,  $K$  is the expected average number of points within the circle (expected neighborhood size plus one for the cell the circle is centered on), and  $|V|$  is the number of cells in the world, where  $|V| - 1$  is the number of *potential* neighbors for a particular cell. Since  $a$  is the area of a circle with radius  $r$ , we can solve for the particular radius that will, on average, encompass  $K$  cells, as shown in Equation 3.

$$r = \sqrt{\frac{K}{\pi(|V| - 1)}} \quad (3)$$

This treatment also used periodic boundaries, which are achieved by allowing this circle to wrap around the edges of the plane. To reduce the running time for distance calculations, we partitioned the plane using a grid of two-dimensional *bins*, where each bin contained points that fell within a square area with side length  $r$ . Since the bins were  $r*r$  sized, any point that may have fallen in a circle of radius  $r$  around a single point could not be outside of the immediate eight bin neighbors. Figure 1 shows the bin structure overlaying the Cartesian plane and several of the extreme circles with radius  $r$ , illustrating the fact that all neighboring points must fall within the Moore neighborhood of the bin. This method dramatically reduced the number of points considered as potential neighbors. Additionally, since edges were undirected and the neighbor relation was reciprocal, once the neighbors of a point had been found, that point no longer needed to be considered. This property allowed us to proceed bin-by-bin, eliminating all points contained within the bin from further consideration after exhausting it.

Figure 2 shows the average distribution of neighborhood

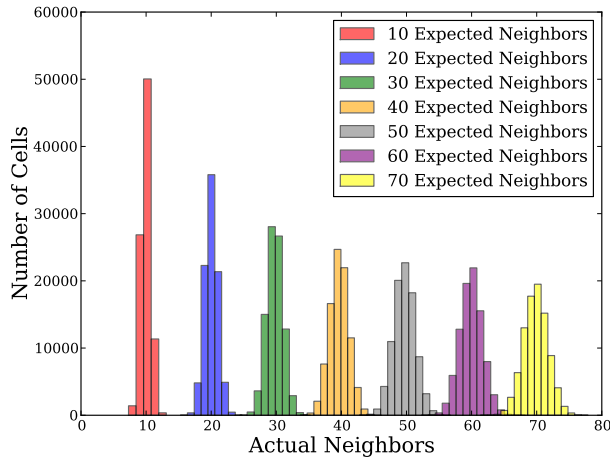


Figure 2: Histogram of the average neighborhood sizes from 20 replicates for different radii yielding expected neighborhoods from 10 to 70 cells in increments of 10

sizes when varying the expected number of neighbors from 10 to 70. The mean number of neighbors for each treatment was equal to the expected neighborhood size calculated. This method provides fine-grained control over neighborhood size while maintaining spatial interactions similar to those of lattices. Random graphs created in this way are arguably more representative of biological systems than lattice models, since the number of interactions for each organism in a population is not likely to be regular, even with explicit spatial structuring. This model allows for a distribution of neighborhood sizes around a specified expected value, as opposed to a fixed uniform neighborhood. We used this *Cartesian* method to generate random worlds with expected neighborhood sizes from 10 to 70 neighbors.

### Biodiversity in Small World Networks

Finally, we examine the stability of these strategies in small world networks, which consist primarily of localized interactions with some long-range interactions, as defined by Watts and Strogatz (1998). These interactions often result in graphs where the number of interactions separating any two cells is surprisingly small. This property is familiar to those who have played the “Six Degrees of Kevin Bacon” game, where players are able to connect any person to actor Kevin Bacon through at most six social interactions, as described in Collins and Chow (1998). Although these networks likely do not capture the highly-localized interactions of microbial populations, they have been observed to capture several natural phenomena and may offer some insight into the maintenance of biodiversity in the presence of gene flow through these long-range interactions.

To construct these graphs, 90 000 cells were arranged on

a ring, and each cell was connected to its nearest 8 neighbors. For each cell, additional interactions were created by probabilistically adding an edge to a randomly-chosen cell. At probability 0, these graphs were regular and had a diameter equal to the number of cells divided by the neighborhood size. At probability 1, the resulting graphs become random, mimicking interactions in well-mixed populations. For this work, we examine the effect that long-range interactions have on maintaining the biodiversity of this system.

### Graph Metrics

In order to compare the structure of the different graphs used in this work, their clustering coefficients and diameters were calculated using the NetworkX package from Hagberg et al. (2008). The local clustering coefficient of a particular cell, defined by Watts and Strogatz (1998), measures how well connected that cell is in its particular network, and is defined in Equation 4, where  $i$  is the vertex (cell) in question,  $k_i$  is the number of neighbors of  $i$ ,  $N_i$  is the set of  $i$ 's neighbors, and  $E$  is the set of edges.

$$C_i = \frac{2|\{e_{jk}\}|}{k_i(k_i - 1)} : v_j, v_k \in N_i, e_{jk} \in E \quad (4)$$

A clustering coefficient of 0 indicates that none of a cell's neighbors are connected to each other, while a clustering coefficient of 1 indicates that all of a neighbor's cells are connected to one another. The graph's clustering coefficient is defined as the average of the clustering coefficients of its cells. This property is important in this system, as an area with a higher clustering coefficient allows for indirect interactions such as “the enemy of my enemy is my friend”. The diameter of a graph is defined as the longest shortest path between any two cells. The diameter therefore provides an indication of how long it would take for a dominant strategy to spread to all cells in the graph.

For each of the treatments described above, 20 replicate populations were studied. Each replicate started with a different random seed, which led to differences in the structure of the graphs used in the Cartesian and small world treatments, the initial distributions of strategies, the stochastic processes of cell death, and the selection of random replacements for empty cells. These differences allowed populations to follow different trajectories.

### Results

In all treatments, we found that diversity quickly declined with increasing neighborhood size. Increasing the radius of interactions in Moore graphs allowed us to observe this, however at a coarse granularity. The generated Cartesian graphs provided more insight into the maintenance of diversity, most importantly in intermediate ranges. Finally, small world graphs highlighted the significant effect that long-range interactions can have in these systems. Next, we discuss each of these results in detail.

## Expanded Radius of Interaction on Lattices

As the radius of interaction was increased in lattices, diversity quickly diminished. As Figure 3 shows, at radius 3, several populations were unable to maintain all three strategies, while at radius 4, none did.

Due to the nature of this system, the loss of one strategy will break the non-transitivity of the system, which quickly leads to the loss of a second strategy. As an example in rock paper scissors, if no paper remained, rock would outcompete scissors, as rock no longer faced competition. Alternatively, if scissors were lost, paper would dominate rock.

As is common in this type of system, in cases where all three strategies were able to coexist, the strategies remained in patches, as is shown in Figure 4.

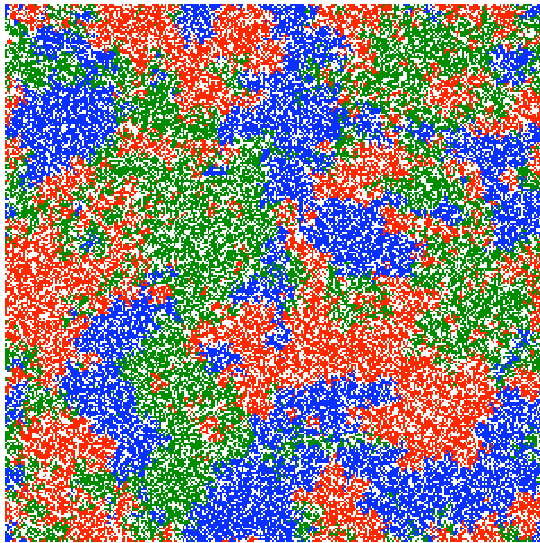


Figure 4: Spatial patterns observed in typical populations. When diversity is present, strategies exist in clusters. Sensitive cells are colored blue, resistant are green, and producer cells are red.

Although these experiments allowed us to investigate the role that the number of interactions has on diversity, the geometric increases in neighborhood size prohibited studying these features in detail. Table 1 highlights the effects that increasing the radius of interactions in a Moore neighborhood has on the structure of the resulting graphs. The sharp decrease in diameter allows a faster-growing strategy to spread quickly, outcompeting competitors regardless of their capabilities. This corresponds with Figure 3(d), where the sensitive strategy quickly eliminates the other strategies.

## Increasing Interactions in Cartesian Space

The Moore topology provided only one treatment in which some runs maintained all three strategies while others collapsed to a single strategy, and the spread between conditions did not allow us to more closely examine the rate at

Table 1: Properties of Lattice Graphs Studied

Neighbors	Diameter	Clustering Coefficient
8 ( $r=1$ )	150	0.429
24 ( $r=2$ )	75	0.522
48 ( $r=3$ )	50	0.543
80 ( $r=4$ )	38	0.551

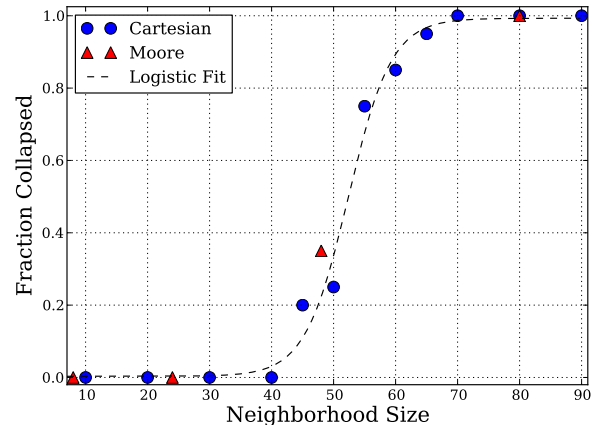


Figure 5: Fraction of runs (out of 20 replicates) that collapsed to a single strategy across different expected neighborhood sizes -  $F$  value 247.62 ( $p \ll 0.001$ ), adjusted  $R^2$  0.985

which biodiversity was lost. With just these data points, any number of possible curves could be drawn with equally good fit. The Cartesian topology allowed us to more closely investigate the effect of neighborhood size on the proportion of populations that lost biodiversity. The properties of the resulting graphs are listed in Table 2. It should be noted that several of the graphs generated with expected neighbor size of 10 were disconnected, as one might expect in a natural population with limited interactions. Figure 5 plots these proportions for a range of neighborhood sizes, where we focused on the range that produced intermediate loss of biodiversity. The logistic curve of best fit is highly significant, with an  $F$  statistic of 247.62 ( $p \ll 0.001$ ), and an adjusted  $R^2$  of 0.985.

The cell count plots for varying radii of this topology look similar to those in Figure 3, thus they are not included. Instead, we provide simplex phase planes for runs with different radii. A simplex phase plane depicts the proportion of strategies that were in the population at a given time and the trajectory the population took over all. The three corners of the triangle represent the three strategies, producer (P), sensitive (S), resistant (R), and the relative distance from each corner depict the proportion of the population the strategies

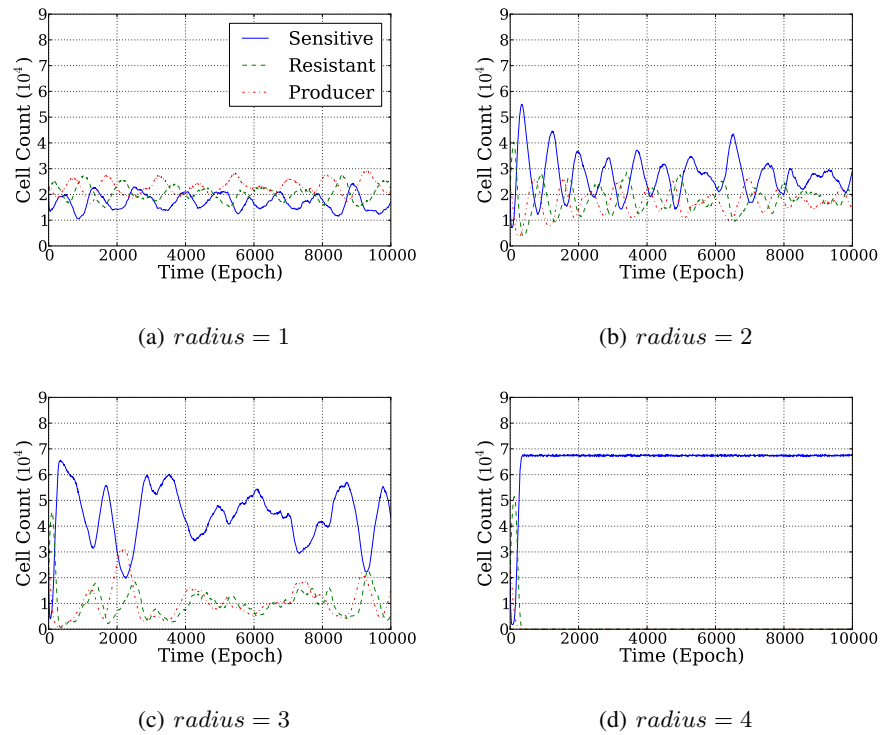


Figure 3: Strategy counts over time for different neighborhood sizes from sample runs. All three strategies remain in all replicates when neighborhood radius is 1 (a) or 2 (b). At radius 3 (c), diversity was maintained in 13/20 replicates, while diversity did not persist at radius 4 (d).

Table 2: Properties of Cartesian Graphs Studied

Expected Neighbors	Diameter	Clustering Coefficient
10*	45.5	0.585
20	83.25	0.587
30	57.25	0.588
40	51.5	0.589
50	59.0	0.588
60	53.0	0.586
70	49.0	0.587
80	45.0	0.587
90	38.0	0.591

comprise. Thus, a point in the center of the simplex would have equal frequency of each strategy, and a point at the P corner of the triangle would represent a population completely composed of producers.

Figure 6 depicts four simplex phase planes for different neighborhood sizes roughly corresponding to those from the Moore topology. The oscillatory dynamics observed in Figure 3 are also present in this topology, and are distinguishable by the circular path within the phase plane in Figure 6(a). Similarly, the large swings in cell counts with increased neighborhood sizes form the larger circular paths depicted in Figure 6(b) and 6(c).

Several runs that maintained biodiversity despite having larger neighborhood sizes (such as in Figure 6(c)) exhibited drastic transient dynamics, where the population of one or more strategies came dangerously close to being eliminated. It is these initial transient dynamics that stochastically led to population collapse as the mean neighborhood size increases. That is, in those runs that survive the transient dynamics, the population ends up in a *safer* region of phase space, one that is less susceptible to stochastic extinction. Of course, as the neighborhood size continues to increase, so does the magnitude of oscillations, and eventually all populations will collapse to a single strategy as the others are driven to extinction, as is shown in 6(d).

These transient dynamics are due to initial conditions where each cell strategy (including empty cells) is uniformly distributed throughout the world. As depicted in Figure 4, clusters of strategies emerge, and it is during the transition between the initial and self-organized states that populations often collapse. Essentially, we are starting the population in a random state with respect to clusters of strategies. While this approach biases the population towards larger cycles, it means our estimates for the collapse of biodiversity are conservative.



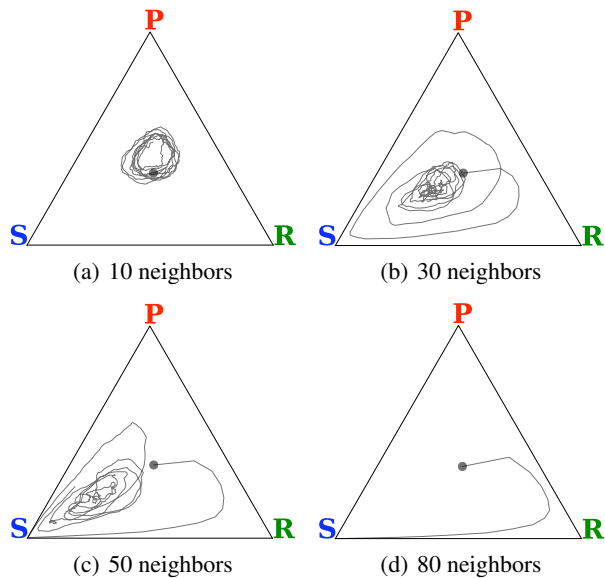


Figure 6: Simplex phase planes for Cartesian topology runs with increasing number of neighbors. The initial distribution of strategies is indicated with a dot.

### Interactions in Small World Graphs

Finally, we evaluated the effect of long-range interactions on diversity. As shown in Figure 7, even a small probability of such interactions had a dramatic effect on the system. We found that diversity quickly waned when the probability of adding these interactions was between 1% and 2%, which resulted in an additional 900 and 1800 pairs of interactions, respectively, on average. These additional interactions decreased the diameter of the resulting graphs to an average of 54.5 when the probability was 1% and 32.3 when the probability was 2%. The clustering coefficients for these configurations were uniformly 0.631 and 0.620, respectively. The difference in dynamics between systems at 1% and 2% edge creation possibility is shown in Figure 8.

Considering the small diameters typical of small world graphs, it is perhaps not surprising that diversity is quickly lost when long-range interactions are added. In the absence of these long-range interactions, the diameter of these graphs is 11 250. Adding additional edges with probabilities between 1% and 2% quickly shrank the diameters in these environments, which made the formation of clusters of strategies difficult. Nonetheless, these experiments provide a dramatic insight into how small increases in interactions can hinder diversity.

### Conclusions

Understanding how the interactions among organisms affects biodiversity is critical to building a more complete picture of the forces that shape ecosystems. As such, this knowledge can inform conservation efforts and help to

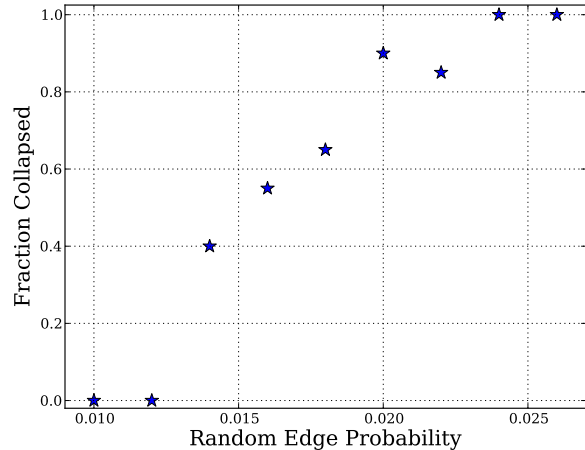


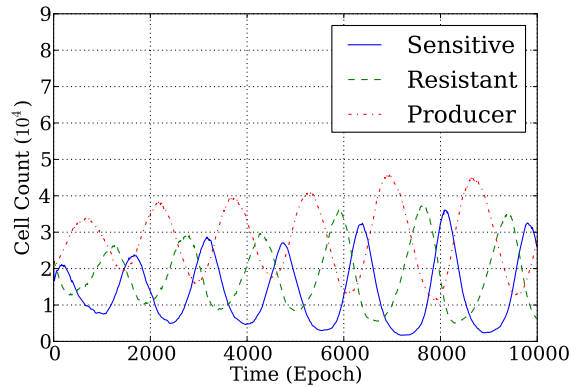
Figure 7: Fraction of runs (out of 20 replicates) that collapsed to a single strategy in small world networks with increasing probabilities additional random interactions

understand the ramifications of living in an increasingly-connected world.

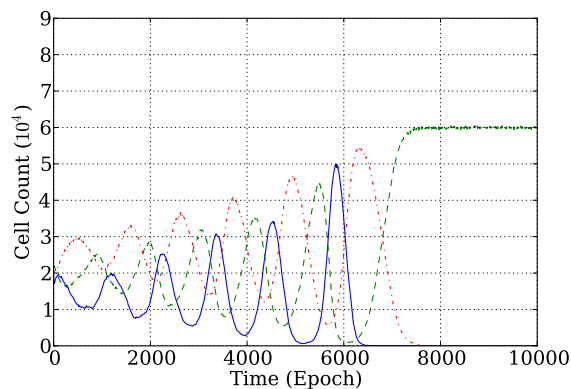
This work has demonstrated the strong effect social structure has on the maintenance of biodiversity in a model non-transitive system. Specifically, we have seen in three different models that as the number of interactions among cells increases, the magnitude of oscillations between the different strategies increases and quickly leads to the loss of diversity. Further, we have observed in small world networks that when a small number of long-range interactions are added, diversity is quickly lost, perhaps necessitating the use of kin discrimination or other mechanisms to promote the maintenance of diversity and cooperative behaviors in higher-order species.

Extending this model to include independent subpopulations and migration between them would allow the effects of gene flow to be examined, which could significantly change the dynamics of these populations. For example, this flow could enable the persistence of so-called “fugitive” species, which are not able to outcompete other species, but are able to persist through quick reproduction and constant migration. Although we claim that the long-range links in the small world networks studied in this work could represent gene flow between clusters of cells, this feature does not necessarily capture the effects of having multiple independent subpopulations.

It is worth noting that this work examined the maintenance of biodiversity from a purely ecological perspective. Allowing cells to mutate and change their strategies through the evolutionary process can have significant effects on a population’s diversity. Previous work has examined the effects on populations when mutations allow a cell



(a)  $p = 0.01$



(b)  $p = 0.02$

Figure 8: Strategy densities over time in small world networks. (a) At 1% probability of creating a random edge, biodiversity is maintained. (b) At 2%, diversity is lost.

to change its investment in a particular strategy (Prado and Kerr (2008), Czárán and Hoekstra (2009)) or to change its strategy completely (Mobilia (2010)). These works examined biodiversity in regular and well-mixed populations, respectively. Variations to social structure, as presented in this paper, could present different dynamics in evolutionary studies, and therefore lends itself to investigation in the presence of evolution.

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