Relating mobility interactions to population biodiversity according to rock-paper-scissor game model

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Biodiversity is a hot-topic in today's research and is vital to understanding ecosystems. In this report, the dependence of population coexistence on mobility on a spatial two-dimensional lattice grid is studied. Features of biodiversity are represented by 'rock-paper-scissors' game. This type of model for competition results in a stable coexistence of all species on the grid when allowed to evolve to a steady-state. Species mobility however plays an important role in the maintenance of biodiversity. When mobility is high, biodiversity is lost. In this report we attempt to recreate and emphasize the dependence of biodiversity on the mobility of three independent species living on a two-dimensional grid.

INTRODUCTION

Biodiversity present in nature shows a resemblance to Darwinian evolution in the sense of species competing over scarce resources and the survival of the fittest out of the species. Evolutionary games are mathematical models of Evolutionary Game Theory (EGT) which are simply applications of game theory. These games form a framework for contests/strategies that mostly have applications in biology (biodiversity/ecology/extinction). Additionally, similar games have been developed like Conway's Game of Life that formed a basis for dealing with population evolution on two-dimensional grids. These evolutionary games have helped explain altruistic behaviors in Darwinian evolution, consequently becoming of interest to politicians, ecologists, economists, philosophers, sociologists, anthropologists, and biologists. These models allow us to study and investigate a relatively new field of spatial chaos and the evolution of cooperative behavior. This field of work deals with the development of merit strategies (like tit-for-tat) to observe the outcomes of the behavioral strategies. In similar context, the rock-paper-scissors game has risen to become of interest to explain species diversity [1]. If three populations interact according to the rock-paper-scissors game, we expect that biodiversity is maintained. Each species dominates the other then being out competed be the other one, forming an endless cycle where diversity is preserved.

There are numerous examples of this phenomena in already existing ecosystems, like those found in coral reef invertebrates [2] and lizards in the inner Coast Range of California [3]. In relation to this study in particular, experiments on microbial bacteria cultures have been conducted to show the influence of spatial structure on the coexistence and diversity of species. After a study was conducted on three different specie strains of Escherichia coli in different environments, it was shown that the cyclic dominance modeled by the rock-paper-scissors game dynamics is not enough to preserve biodiversity. When the interactions between species are local (like bacteria on Petri dish), spatial interaction plays an important role in the domination of one sub population or the stable coexistence of all sub populations.

In their paper, Reichenbach, Mobilia and Frey aimed to show that biodiversity is significantly affected by the spatial mobility or migration of individuals in a sub population, which is a feature that is present in ecosystems. This mobility feature is is a constant battle with other interactions such as reproduction and selection. When there is generally low mobility, the development of species in a particular space is dominated by the interactions from neighbouring individuals from the population. The result of these interactions lead to a stable coexistence and maintenance of diversity. Also according to Reichenbach (et al), high mobility leads in biodiversity being lost. They also obtain a critical value for mobility where below this value, diversity is maintained and above this value diversity is lost and one specie emerges dominant.

This concept of mobility within species was previously visited in the island models in the context of habitat patches [4–7]. In one model, Levin studied an idealized a two-patch system and noted the critical mobility that lead to a stable coexistence of the species withing the system. Since this is a clear feature found in natural ecosystems, the method in this paper considers a stochastic approach for determining the interactions between individuals in the population. The behaviour of the stochastic models differs from the purely deterministic ones that depend on reaction-diffusion equations or couple PDEs like the Lotka-Volterra model for modeling predator prey dynamics. In this study in particular the feature of a member's mobility is explored.

We consider a group of three sub populations (A,B, and C) that are allowed to move and interact (with local neighbors) on a spatial two-dimensional lattice. The allowable interactions follow a stochastic version of the rock-paper-scissors game model developed in 1975 by Leonard and May [8]. The mobility interaction represents the ability of two neighboring members swapping positions, or an individual moving to an empty lattice

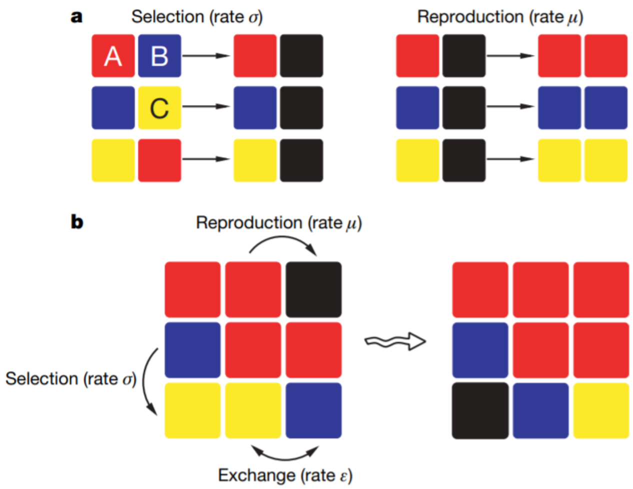

FIG. 1. (Color online) Individuals from three competing mobile sub populations A(red), B(blue), and C(yellow) live on a two-dimensional square lattice grid. (a) The individual interacts with the nearest neighbours through selection or reproduction, both occurring at random probability or at an induced/impeded rate that can be defined. Selection reflects cyclic dominance just like in the rock-paper-scissors game. A can kill B, yielding an empty black site. B can invade C, and then C out competes A. Reproduction can only occur if there is an empty lattice site next to the randomly selected cell. Mobility is also possible where the individual can swap position with a neighbor or move to an empty lattice site (exchange). (b) Example of all the three interactions on a 3x3 square lattice.

site. Although in Reichenbach and et al's paper they have used a Poisson process for an event happening at a certain rate (representing the relevant interaction), the ambiguity of the implementation was hard to recreate this exact stochastic process. For this reason, a few assumptions were taken into account to mimic the stochastic behavior generating the rate at which the interactions (selection, reproduction, and exchange) occur. A schematic for the rock-paper-scissors model (or the rules of the game) is shown in Figure 1.

For the square lattice on a two-dimensional grid, we define N as the number of sites along when length of the grid. The relation between the rate at which mobility occurs compared to the selection and reproduction processes determines the fate of the entire group whether a single species dominates the square lattice or all sub populations can coexist.

METHOD

The method used to relate the effect of mobility to species coexistence is similar in concept to the work of Reichenbach et al. A group of species (A, B, C, and empty) is randomly distributed along a lattice (matrix) of size N by N. A cell array consisting of N by N vectors, which we will call the probability array, is also initialized to store the information for the individual probabilities of the selection, reproduction, and exchange interactions to occur respectively. This part of the method is the main difference between the approach Reichenbach and et al. took and this paper. In their paper they followed a sophisticated algorithm due to Gillepsie that determined whether selection,reproduction or mobility occurred as well as the waiting time for each interaction [9]. This algorithm presents an exact method for the stochastic formulation of chemical kinetics, the time evolution of any spatially homogeneous mixture of molecular species that interact through a specified set of coupled chemical reactions. The method is a compact, computer-oriented Monte Carlo simulation procedure that is useful for modeling the transient behavior of well-mixed gas-phase systems. In our study this is analog for determining which interaction occurs along with the waiting time for the occurrence of the event.

In the stochastic lattice simulation, the three sub populations arranged on the two-dimensional square lattice were given periodic boundary conditions. At each simulation step, a random individual from the group is chosen to interact with one of the four nearest neighbors, which is also chosen randomly. Recall the probability array mentioned earlier in this section, where each cell array represents a 1 by 3 vector storing values between zero to one for the probability of selection, reproduction, or exchange to occur respectively. The highest probability in that 1 by 3 vector is chosen, and the interaction that holds the index for that highest probability will take place (selection, reproduction, then exchange). After the random cell is chosen for interaction with one of the neighbors, the probability of all three events is re-randomized to refrain from obtaining deterministic behavior of the rock-paper-scissors model. In order to promote or impede mobility in the model, an automatic assignment of the 'exchange' interaction which represents mobility is given at a rate in accordance with the time step. For example, for every 10th randomly selected individual, that individual will will perform the swap interaction regardless of the highest probability in the 1 by 3 vector obtained from the probability array. This automatic selection for the interaction will mimic a bias or obstruction for mobility, which is important to determining the effect of mobility on the diversity of the sub populations. One evolution of a generation is determined to happen when on average every individual is allowed to interact once with one of its neighbors. This constitutes one unit of time according to Reichenbach et al. After the interaction of the randomly selected individual occurs, the big matrix constituting of the whole population is updated. In this study, the big matrix representing the population is made up of numbers from one to four where one represents the first species (red), two represents the second species (blue), three represents the third species (yellow), and four represents and empty lattice site (black). For the results in Fig.2, a size 200 by 200 population is allowed to evolve over 25,000 generations. This simulation in particular took around five and a half hours to obtain the result, which will be the computational limit for the population size to study. For this reason, the main method will be applied to smaller populations and allowed to evolve over less generations due to the computational complexity and inefficient code.

RESULTS

For the results obtained in figure 2, a bias promoting mobility that was discussed in the methods section was automatically assigned at a rate that is one of every 0.025% that of the population. It can be observed that coexistence is maintained at this rate of mobility. Although the figure shows a steady-state result that looks different than that seen in Reichenbach et.al.'s, similar characteristics of the end population can also be pointed out. Sub populations or species have clumped together in near-spiral shapes. Mobility rate is high enough to have a dead-space separation that can be clearly seen, but low enough to maintain diversity and coexistence. This rate is drastically scaled with the population size however.

In figure 3-a, a smaller population of 20 by 20 square lattice was considered. For this population, a promoted mobility at a rate of one out of every 2.5-10% of the population was high enough inhibit or distort the biodiversity. At steady state, only one sub population dominated the square lattice. For much lower mobility rates like that in figure 3-b of no induced mobility (equal probabilities of all three interactions), coexistence can be spotted. It was additionally noted that induced or promoted selection lead to the same result, when an induced selection or elimination process occurred in one of every 10% of the population on average, a single species remain dominant at steady-state (figure 3-c). Promoted reproduction (increasing reproduction rate) lead to coexistence of all species at steady-state (figure 3-d).

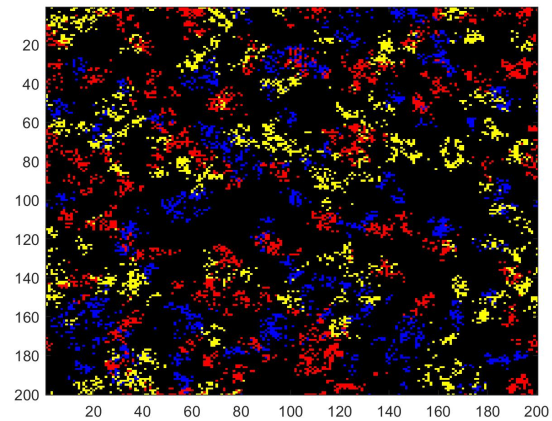

FIG. 2. (Color online) Snapshot of a 200x200 square lattice after reaching steady state. A mobility was induced at a rate of 1 of every 10 (0.025% of the grid size). This group is allowed to evolve over 25,000 generations. A slight spiral pattern can be spotted, but coexistence is clearly maintained at this mobility rate.

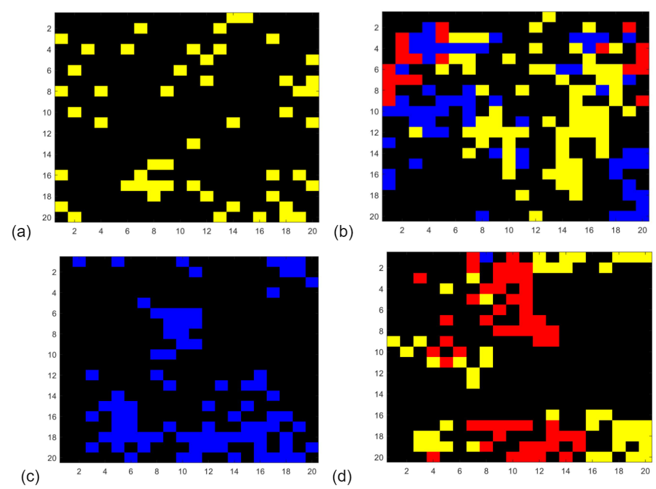

FIG. 3. (Color online) Steady-state result of stochastic rock-paper-scissors game on 20x20 populations. **a.** A single dominant species when mobility is induced. **b.** Coexistence of the three species when equal probabilities of interactions are present. **c.** Single dominant species when selection is promoted. **d.** Coexistence when reproduction is promoted.

CONCLUSION

In this paper, the mobility of species on a square lattice grid where spatial dependence is crucial is studied. A stochastic version of the rock-paper-scissors game was used to model competition of three species in a local area. For large enough grid sizes (200 by 200), computational complexity was a clear issue which did not allow for easily repeatable results. The results from such populations however like those shown in figure 2 indicate the coexistence of species at steady-state when low levels of mobility are induced, specifically at a rate of one induced exchange interaction per 0.025% of the total population or grid size. Smaller grid sizes (20 by 20) were computationally easy for a stochastic simulation of this fashion. For these population sizes, a promoted mobility clearly showed deterioration of the biodiversity, with one species remaining at steady-state (figure 3-a) at an induced mobility rate of one out of 2.5-10% of the grid size. At lower mobility rates (figure 3-b) where there is equal probability of all three interactions occurring, diversity is maintained and coexistence is clear at steady-state. Additionally, it was observed that induced selection lead to similar results for mobility while higher rates of promoted reproduction lead to coexistence of species over a long temporal development of the population.

Although a distinct critical value for induced mobility was not found, it can be said that for a 20x20 grid size induced mobility of one out of every 2.5-10% of the population was high enough to lead to jeopardizing diversity. Rates lower than that proved coexistence. These findings are analog to the results obtained by Reichenback, Mobilia, and Frey in their paper on relating mobility to biodiversity in rock-paper-scissors games [1].

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