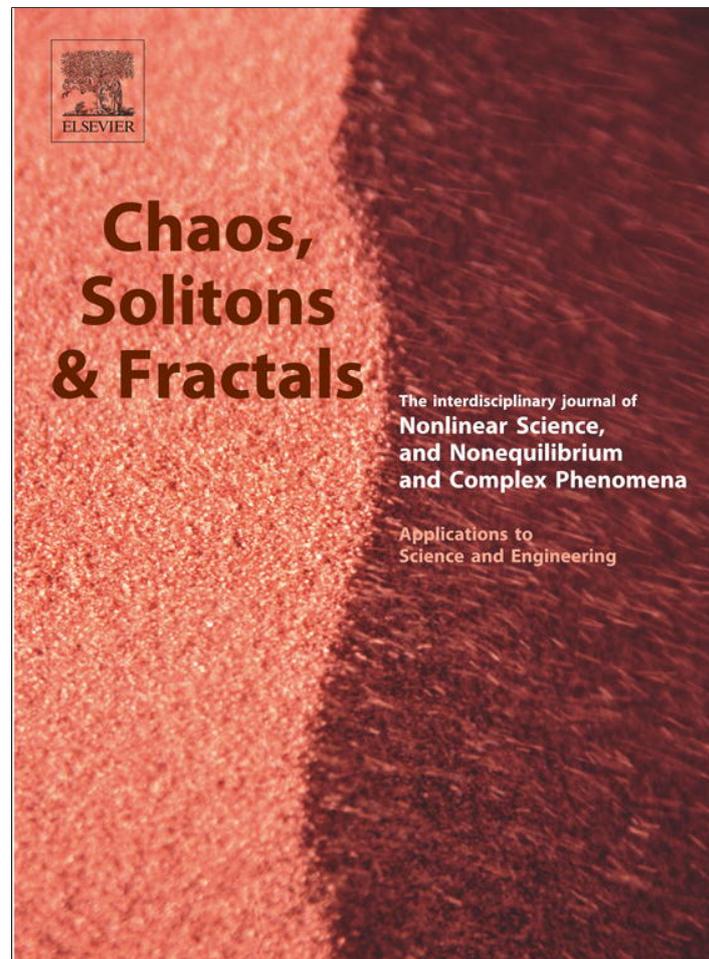


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Cooperation in harsh environments and the emergence of spatial patterns



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ABSTRACT

This paper concerns the confluence of two important areas of research in mathematical biology: spatial pattern formation and cooperative dilemmas. Mechanisms through which social organisms form spatial patterns are not fully understood. Prior work connecting cooperation and pattern formation has often included unrealistic assumptions that shed doubt on the applicability of those models toward understanding real biological patterns. I investigated a more biologically realistic model of cooperation among social actors. The environment is harsh, so that interactions with cooperators are strictly needed to survive. Harshness is implemented via a constant energy deduction. I show that this model can generate spatial patterns similar to those seen in many naturally-occurring systems. Moreover, for each payoff matrix there is an associated critical value of the energy deduction that separates two distinct dynamical processes. In low-harshness environments, the growth of cooperator clusters is impeded by defectors, but these clusters gradually expand to form dense *dendritic* patterns. In very harsh environments, cooperators expand rapidly but defectors can subsequently make inroads to form *reticulated* patterns. The resulting web-like patterns are reminiscent of transportation networks observed in slime mold colonies and other biological systems.

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1. Introduction

This paper concerns the confluence of two important areas of research in mathematical biology: spatial pattern formation and cooperative dilemmas. Emergent spatial patterns are among the most fascinating consequences of complex biological processes. Such patterns occur in all types of natural systems, living and non-living, and complex patterns may often form from simple elements obeying very simple rules [1]. Formal, generative models of pattern formation date back to Turing [2] and often revolve around reaction-diffusion (RD) processes, which are characterized by local activation and long-range inhibition [3,4]. As an illustration, consider two chemicals, A and B . A enhances the production of B , and B inhibits the production of A . A is self-produced and can maintain itself in areas of low B concentrations (local activation). B diffuses more quickly than A , so the

production of A will be inhibited away from A (long-range inhibition). This process can produce a host of patterns similar to those found in nature. Although chemical processes involving autocatalytic and diffusive compounds may explain animal patterns such as stripes and spots which appear during development, these processes do not explain a number of other patterns, such as those found in colonies of organisms such as coral and slime molds. For these systems, the natural mechanism for description may be an agent-based model, since the relevant units of the patterns are the agents themselves [3]. Jones [5] recently provided a model of pattern formation using chemotactic mobile agents that did not require RD processes, but did require a fixed population size. A remaining concern is that patterns often emerge through growth processes, and therefore require models in which population sizes can vary.

Meanwhile, cooperation is among the most widely studied topics in the ecology and evolution of social organisms. Social organisms often benefit others at a cost to

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themselves, and the mechanisms which allow for cooperation to evolve and be sustained represent an enormous body of research. Much of the theoretical work on cooperation has modeled interactions using the framework of the prisoner's dilemma (PD) game, in which mutual cooperation outperforms mutual defection, but defection is always the best option in one-shot games. In this game, both players receive a reward, R , for mutual cooperation, but there is a temptation to defect, which yields a payoff of T to the defector and S to the cooperator. Mutual defection is punished with a payoff of P to both players. A PD game is defined when $T > R > P > S$ and $2R > T + S$. Among organisms which lack complex social institutions, cooperation is most easily maintained by mechanisms which promote the positive assortment of strategic individuals, such that cooperators are most likely to interact with other cooperators [6–9]. Some well-studied assortative mechanisms are kin selection [10,11] and direct reciprocity [12,13].

Spatial structure can also promote the evolution of cooperation, particularly if dispersal of offspring is limited and behavioral strategies are heritable [14–16,9,17]. In a spatially structured landscape, evolutionary models of cooperation can produce spatial patterns of cooperators and defectors. Depending on the model specifications and initial conditions, these can include web-like patterns [18], clusters [19,20], patterns resembling elaborate Persian carpets [15], and even a wide array of Turing patterns [21]. However, many of these models assume populations of a fixed size and, particularly in cases where mobility was not included, a somewhat arbitrary spatial arrangement. The relationship between the patterns that emerge from these models and those that occur in nature is therefore unclear.

To illuminate the process of pattern formation in spatial cooperation models, I studied a more biologically realistic model of cooperation among social actors, in which agents move and in which death and reproduction are de-coupled, allowing the population size to vary. Spatial patterns are generated through processes of growth, decay, and emergent spatial assortment. This means that the model may provide a generative explanation for certain types of biological patterns. The model presented here was previously investigated with a focus on the evolution of cooperation in harsh environments [22]. Here, I focus on the emergent spatial patterns produced when the population carrying capacity is equal to the number of cells on the square lattice representing the environment. In this model, agents search their immediate neighborhood for a co-player, moving randomly if one is not available and otherwise playing the PD game for energy payoffs. Accumulated energy can be used to reproduce, but agents die if their energy falls to zero. The environment is harsh, which is modeled by means of a constant energy deduction. Consequently, periodic interactions with cooperators are necessary for long-term survival. I will show that such a model can produce web-like spatial patterns similar to those found in certain biological systems. I will further show that these patterns are produced by one of two distinct processes, depending on the harshness of the environment. When the environmental harshness is relatively low, isolated clusters of

cooperators become surrounded by defectors, and gradually expand outward to produce a *dendritic* network of defectors. These networks are somewhat reminiscent of the dendritic trees produced by diffusion-limited aggregation [23], though they contain more connected loops and are not scale invariant. In harsher environments, cooperators expand rapidly, but defectors can “tunnel” in, displacing cooperators to form *reticulated* webs akin to biological transportation networks.

2. Model description

The model is identical to that studied previously by Smaldino, Schank, and McElreath [22] with the provision that the carrying capacity of the environment was set equal to the number of cells in the lattice. For convenience, the full model will be described here as well. Agents played pure strategies of cooperate or defect and reproduced offspring of the same strategy. Interactions occurred on an $L \times L$ square lattice with periodic boundaries. For each simulation, N agents, half cooperators, were placed in unique random locations and initialized with an integer energy level drawn from a uniform distribution between 1 and 50. Each time step, agents who had not already played that time step searched their local neighborhoods for a co-player who had also not already played that time step. An agent's local neighborhood consisted of the eight closest cells (its Moore neighborhood). If the agent found a co-player, the two played the PD game and received payoffs in the form of energy. If a co-player could not be found, the agent attempted to move to a random cell in its local neighborhood and was successful if that cell was unoccupied. Agents' energy stores were capped at 150 so that an individual could not accumulate energy without bound. If an agent accumulated 100 or more energy units it attempted to reproduce into a random cell in its local neighborhood and was successful if the cell was unoccupied, yielding 50 of its energy units to its offspring. Thus, when the population was very dense, agents with over 100 energy units could remain unable to produce offspring for a long time. Whether or not an agent played the PD game, a cost of living k was deducted from its energy reserve. If its energy fell below zero, the agent died and was removed from space. Since agents were not guaranteed to have a game interaction each time step, the cost of living deduction is distinct from the payoff matrix. The population carrying capacity was set equal to the size of lattice, L^2 .

Agents were scheduled asynchronously, with the order of stepping being randomized at each time step using the MASON simulation library [24]. Aggregate data reflects averages over 50 runs for each condition. In order to ensure correct characterization of the system's long-term dynamics, simulations were run for 10^6 time steps. This length of time was generally sufficient to achieve population stability such that the numbers of cooperators and defectors did not significantly change. Payoffs were set as follows: $T = 5$, $R = 3$, $P = 0$. The payoff for unreciprocated cooperation, S , was varied as indicated. The initial population size was set to $N = 0.2 L^2$. For example runs, a lattice size of $L = 100$ was used. To reduce computing time, batch runs

used $L = 50$; the results for these runs did not differ qualitatively to those derived with a larger lattice.

3. Simulation results

Spatial patterns reminiscent of some biological systems emerged as agents filled the space and competed for resources. The ultimate pattern depended heavily on both the cost of living k and the payoff for unreciprocated cooperation S (Fig. 1), both of which can be considered measures of environmental harshness [22]. Starting with very low costs of living, the long-term frequency of cooperators increased with k . However, for each value of S there was an associated critical value of k where the dynamics of the system changed (Fig. 2). Below this threshold, clusters of cooperators could resist infiltration by defectors, leaving defectors on the periphery of cooperator clusters, which could then gradually grow outwards. This resulted in a tightly-filled space with veins of defectors that did not always connect but sometimes dead-ended, as in the upper-left portion of Fig. 1. I refer to this process as *dendritic* pattern formation.

As k increased, many defectors died early on after exploiting nearby cooperators, since they could not find

new cooperators to exploit before perishing. This led to some isolated veins of defectors, as seen in Fig. 1 when $k = 1.4$ and $S \geq -0.6$. As k increase further for a given value of S , defectors could gradually outcompete cooperators when clustered together. Initially, defectors were at a disadvantage and most died out quickly because they exploited local cooperators to death and could not find new cooperators before perishing, while cooperators that could cluster together expanded rapidly and filled most of the environment. Subsequently, however, defectors could gradually “tunnel” into a cluster of cooperators. Over time, this led to the formation of web-like patterns similar to the transportation networks seen in some slime mold colonies [5,25] as well as in other biological systems. As such, I refer to this second process as *reticulated* pattern formation.

These two different dynamical processes (dendritic and reticulated) are illustrated in Fig. 3 for systems below and above the critical threshold of k for $S = -1$. When the cost of living was relatively low (Fig. 3A), defectors exploited cooperators and multiplied rapidly. Many cooperators were overexploited and died. The cooperators who survived were those that managed to assort into spatial clusters such that the positive gains from mutual cooperation could sustain those cooperators on the periphery who

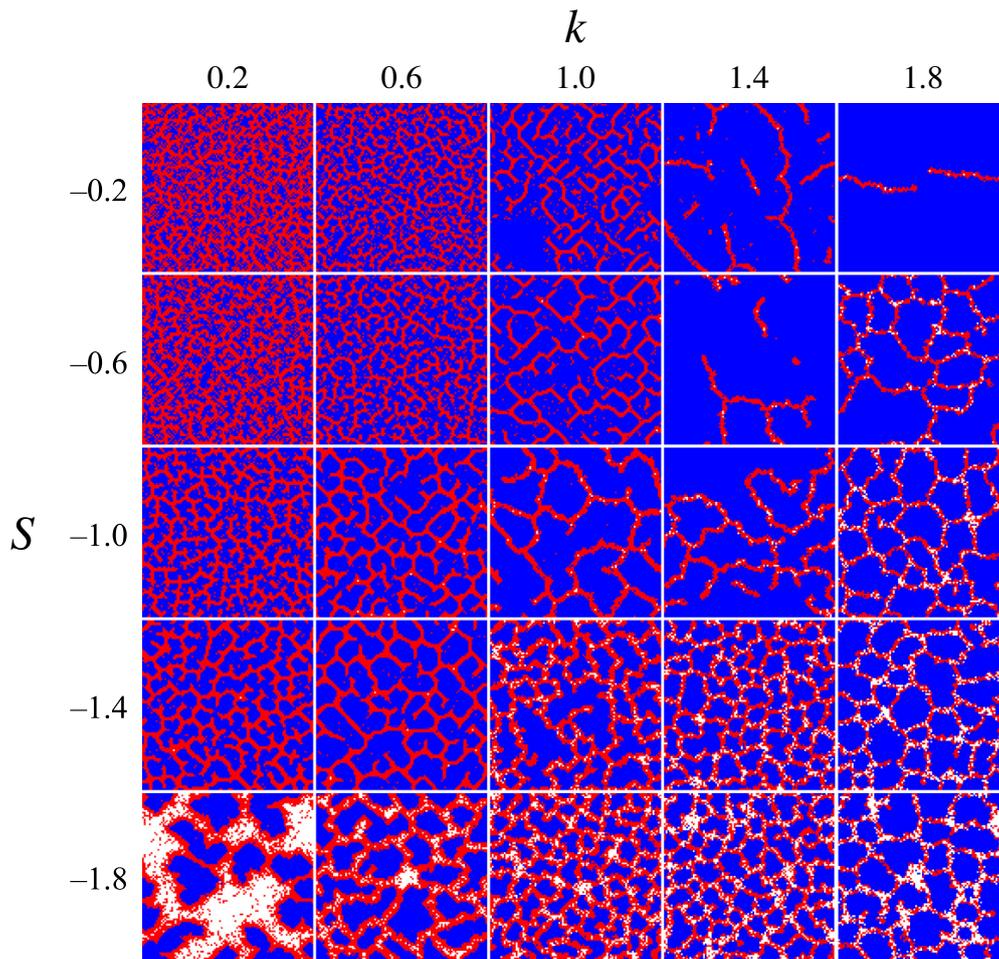


Fig. 1. Spatial patterns from example runs at $t = 10^6$ for different characterizations of environmental harshness. Blue cells are cooperators, red cells are defectors, white cells are empty. $L = 100$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

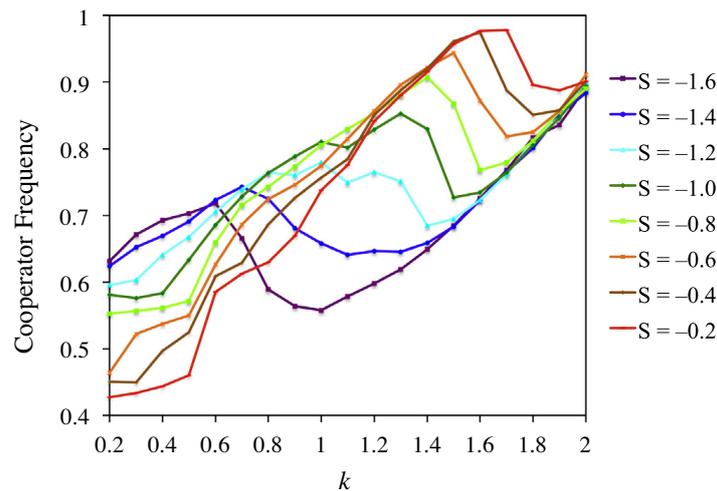


Fig. 2. Long-run cooperator frequency as a function of the cost of living, k , for different values of S . Values are taken at $t = 10^6$, averaged across 50 runs.

interacted with defectors. Those defectors without access to cooperators perished, leading to a gradual push outward from the cooperator clusters. This was driven by defectors' random movements outward, which left open spaces into which cooperators could reproduce. Eventually, a web-like structure emerged. The same basic dynamics are seen in Fig. 3B, although in this case the cost of living was higher, so that cooperator clusters needed to be larger in order to survive. Here the initial die-off of agents was more severe than in Fig. 3A. In this particular run, an opening became available for rapid expansion of cooperators in the center of the lattice, although defectors were able to expand as well, surrounding the cluster of cooperators and curbing their growth. The web of defectors gradually thinned as they moved inward to empty space and the newly-emptied locations were filled by cooperators. Because k was near the critical threshold, the dendritic patterns were not entirely stable, and the number of cooperators gradually increased – a process which continued, albeit very slowly, well after $t = 10^6$.

When the environment was extremely harsh, as in Fig. 3C, the dynamics changed qualitatively. The cost of living was so great that most agents died within the first 100 time steps. Although defectors could exploit cooperators to survive, those cooperators died very quickly and most defectors were unable to find new cooperators to exploit before they lost all of their energy reserves. Meanwhile, the few cooperators that clustered together were able to stave off the cost of living through mutual cooperation, and subsequently were relatively unimpeded by defectors. Thus, by $t = 10^3$ (fourth frame, top level), cooperators had expanded to cover most of the available environment. However, because the cost of living was so great, repeated interactions with defectors was often sufficient to exhaust cooperators' energy reserves, which did not occur for lower values of k . Defectors were then able to spread gradually and create a web-like reticulated structure, which as noted bears a resemblance to slime mold transportation networks. Note here that the web-like patterns are rounder and less dense than those formed through the previously

described mechanism of pattern formation, and in general do not include dead ends.

Another perspective on the dynamics portrayed in Fig. 3 is shown in Fig. 4, which illustrates the temporal dynamics for a similar set of runs for $L = 50$. These simulations were run out to $t = 10^7$ to better illustrate the long-term stability of the emergent patterns. In all cases there was an initial decrease in the cooperator frequency. In the first case ($k = 0.2$), this was driven by a marked increase in defectors (as they exploited cooperators and reproduced rapidly), while in the latter two cases the entire population fell, though cooperators did so more rapidly. In all cases this population decrease was followed by an increase. In the first two cases there was a monotonic increase in the cooperator frequency as cooperators gradually replaced defectors. The opposite was true in the last case ($k = 1.8$), as defectors infiltrated the population of cooperators and formed transportation networks only after cooperators had expanded to fill most of the space. Here the relaxation phase ($t > 10^6$) was marked by greater variation in cooperato frequency due to stochastic movement in the empty spaces of the transportation networks.

If defectors always outperform cooperators on one-to-one interactions, then why weren't defectors *always* able to tunnel into clusters of cooperators? For cooperators near the boundaries of such clusters, most of their interaction partners were other cooperators. This allowed them to survive even though they lost energy through interactions with defectors. Unlike models in which all agents simultaneously interact with all neighbors, agents in this model interacted with at most one other co-player per time step. Cooperators in clusters have more neighbors and so are more likely to play. Moreover, even when they can't find a co-player, they may be unable to move, being surrounded. Defectors, on the other hand, are more likely to have a possible move: away from the cluster. In relatively low-harshness environments, these facts allow cooperative clusters to increase in size and avoid infiltration by defectors. If the environment is harsher, however, cooperators require more interactions with other cooperators to survive. The presence of a defector can then

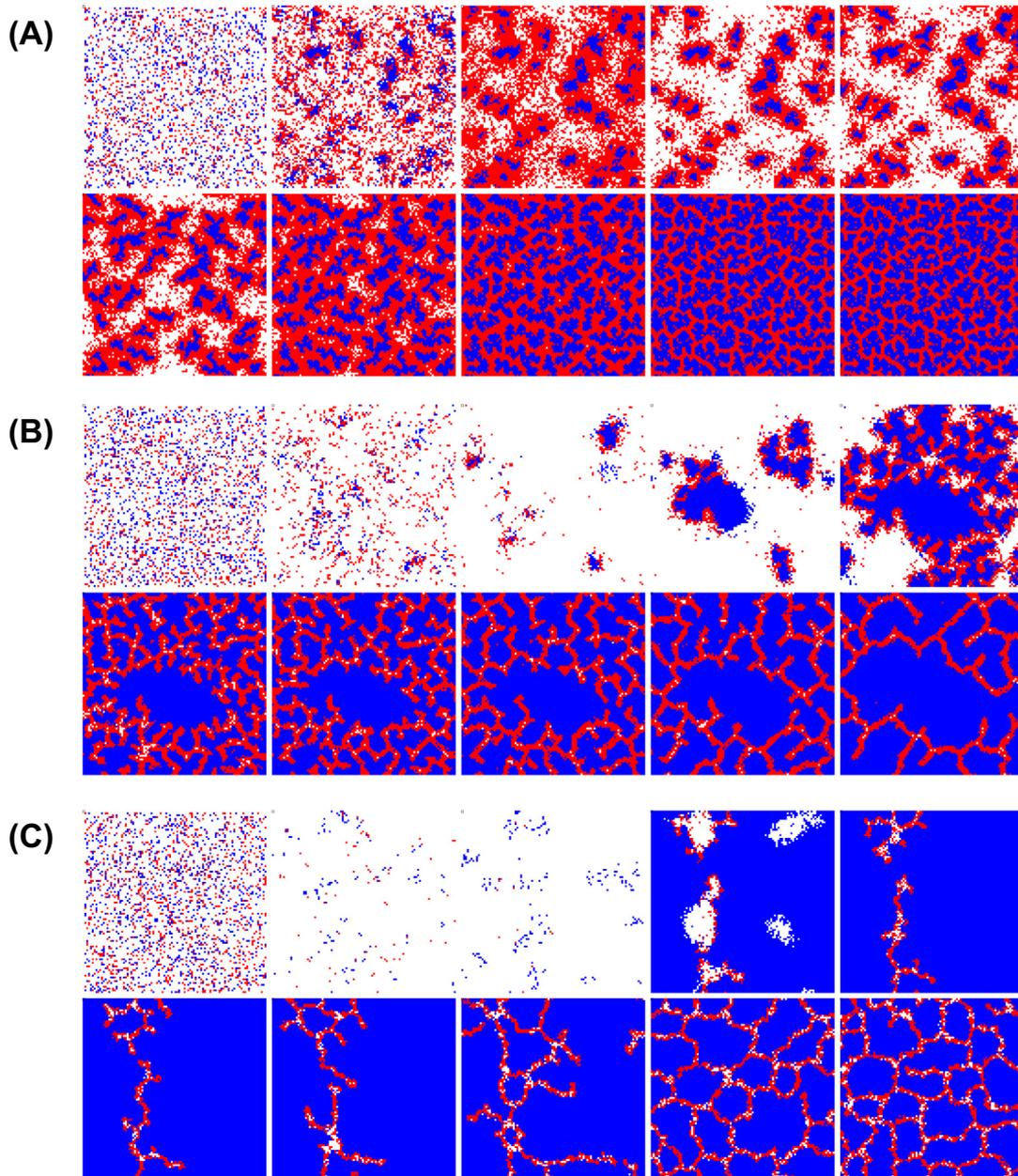


Fig. 3. Spatiotemporal population dynamics for three different values of the cost of living k : (A) Dendritic pattern formation, $k = 0.2$; (B) dendritic pattern formation nearer the critical threshold, $k = 1.0$; (C) reticulated pattern formation, $k = 1.8$. In all cases $S = -1$ and $L = 100$. Blue cells are cooperators, red cells are defectors, white cells are empty. For each figure, time moves left to right, top to bottom, taking on the following values in each case: $t = \{0, 10^2, 3 \times 10^2, 10^3, 3 \times 10^3, 10^4, 3 \times 10^4, 10^5, 3 \times 10^5, 10^6\}$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

be enough to kill off a cooperator, creating an empty space for defectors to move into.

Because this paper focuses on pattern formation, I have presented only those runs in which a mixed population of cooperators and defectors persisted. However, mixed populations did not always result. In intermediately harsh environments, defectors could sometimes exploit cooperators too quickly for the cooperators to cluster, leading to a collapse of the entire population. As environmental harshness increased further, defectors could exhaust their nearby cooperator neighbors so fast that they were unable to find new cooperators to exploit before they themselves perished, and in some cases this led to a world of all cooperators without any defectors. The occurrence of both of

these scenarios became more frequent as the payoff of unreciprocated cooperation (S) became more punitive, because interactions with defectors could kill cooperators more quickly (Fig. 5). It should be noted that the model analyzed in this paper did not include mutation. Mutation was previously shown to not affect qualitative results for mixed populations in a version of this model in which the carrying capacity was less than L^2 [22]. However, the inclusion of mutation in this case would preclude cooperator-only worlds from remaining so, as it has been shown here that a few defectors could increase their numbers in very harsh environments by “tunneling.” Finally, the population would always collapse if the cost of living exceeded the benefit of mutual cooperation, i.e., if $k > R$.

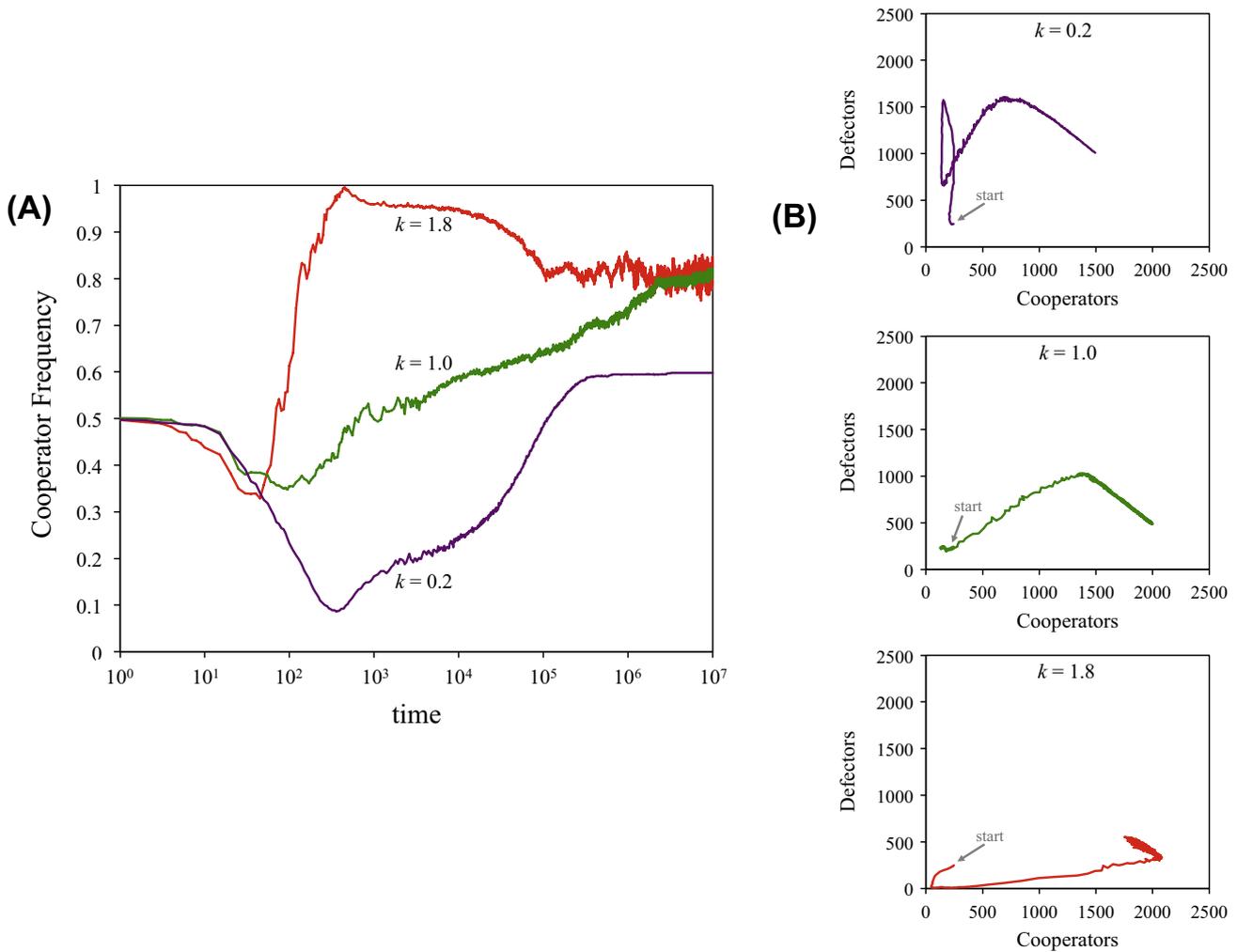


Fig. 4. Dynamics of example runs with three different values of k , for $S = -1$, run out to $t = 10^7$. Values are taken from runs with a lattice of size $L = 50$. (A) The cooperator frequency as a function of time for the three runs. All three runs show an initial decline in cooperators as they are outcompeted by defectors, followed by a recovery. Note that for values of k below the critical threshold ($k \approx 1.4$), the cooperators frequency increases monotonically following the recovery, while this is not the case for $k = 1.8$. (B) Trajectory plots in phase space showing the number of cooperators and defectors for the same three runs. In the first two cases, the run ends with a gradual decrease in defectors and an increase in cooperators. In the last case, the opposite is true.

4. Discussion

I have presented a generative model for the emergence of spatial patterns similar to those found in some biological systems, such as corals and slime mold colonies, using an evolutionary model of cooperation. The mechanism is similar to that found in RD processes in that it relies on local activation and long-range inhibition. Moreover, the interactions between defectors and cooperators in the present model are in many ways similar to a relationship between predators and prey. Indeed, a previous RD model of predators and prey [26] showed that spatial organization could produce Turing patterns. The present model produces spatial patterns with agents rather than continuous distributions, and does not require continuous diffusion. However, it should be noted that the present model does not produce as broad a range of patterns as more general RD models.

The model is highly stochastic, which reduces the capacity for rigorous mathematical analysis. For example, I was unable to calculate a precise formula for the values

of S and k corresponding to the domains in which the two different processes of pattern formation were dominant. Nevertheless, a stochastic agent-based model may capture important consequences of individual behavior in a spatial environment that may be missed by analytical approximations [22,27]. A positive consequence of using such a model is that I have identified processes of pattern formation that stem from increasingly realistic properties of biological agents – agents that are mobile, occupy finite space, reproduce, and die.

The world we inhabit is full of twisting, twining patterns of cooperation and exploitation, of connecting paths and dead ends. A complete understanding of all of those twists and turns is likely to be beyond the capability of the human mind. Nevertheless, I hope that the model and analysis provided in this paper help to shed a modicum of light on the myriad puzzles of social and biological life. The model is necessarily a simplification, but all explanatory science must contain such fictions as long as, in the words of Valentino Braitenberg [28], “our brains are only minuscule fragments of the universe, much to

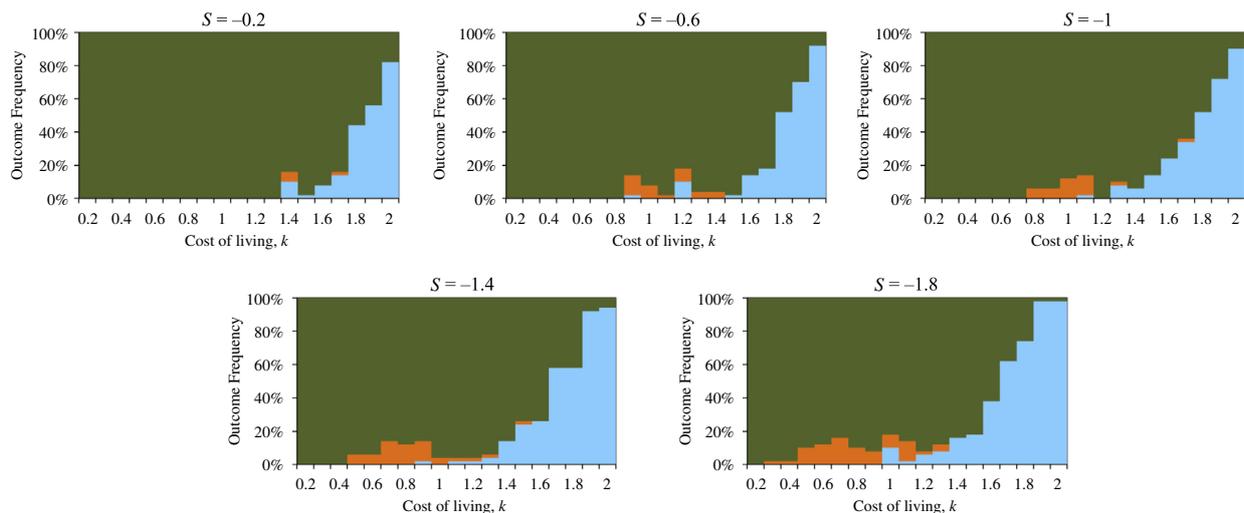


Fig. 5. The frequency of outcomes of runs which ended in a mixed population (green), all defectors and a population collapse (orange), or all cooperators (blue). Results are shown as a function of the cost of living k for several values of the payoff for unreciprocated cooperation, S . Outcomes are based on 50 runs for each condition, $L = 50$. Non-mixed outcomes were less common when $L = 100$, but the qualitative patterns were quite similar. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

small to hold all the facts of the world by not too idle to speculate about them.”

Acknowledgments

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