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Increased Costs of Cooperation Help Cooperators in the Long Run

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ABSTRACT: It has long been proposed that cooperation should increase in harsh environments, but this claim still lacks theoretical underpinnings. We modeled a scenario in which benefiting from altruistic behavior was essential to survival and reproduction. We used a spatial agent-based model to represent mutual cooperation enforced by environmental adversity. We studied two factors, the cost of unreciprocated cooperation and the environmental cost of living, which highlight a conflict between the short- and long-term rewards of cooperation. In the long run, cooperation is favored because only groups with a sufficient number of cooperators will survive. In the short run, however, harsh environmental costs increase the advantage of defectors in cooperator-defector interactions because the loss of resources leads to death. Our analysis sheds new light on the evolution of cooperation via interdependence and illustrates how selfish groups can incur short-term benefits at the cost of their eventual demise. We demonstrate how harsh environments select for cooperative phenotypes and suggest an explanation for the adoption of cooperative breeding strategies in human evolution. We also highlight the importance of variable population size and the role of socio-spatial organization in harsh environments.

Keywords: interdependence, strong selection, environmental inheritance, harsh environments, Kropotkin, agent-based.

Introduction

Altruistic behaviors benefit others at a cost to oneself. For many years, the abundance of altruistic behavior in the animal kingdom posed a serious challenge to evolutionary theorists (Harman 2010). However, extensive theoretical work has shown that altruism can evolve as long as conditions allow cooperators (altruistic individuals) to interact with one another at a sufficiently higher rate than with defectors (selfish individuals who accept the benefits of altruistic acts but do not perform those acts; Wilson and

Dugatkin 1997; Fletcher and Doebeli 2009; Bijma and Aanen 2010). Mechanisms that make this possible include kin selection (Hamilton 1963; Maynard Smith 1964), reciprocity (Trivers 1971; Axelrod and Hamilton 1981; Barta et al. 2011), spatial assortment (Epstein 1998; Koella 2000; Nowak et al. 2010), and active avoidance of selfish non-altruists (Houston 1993; Aktipis 2004; Pepper 2007; McNamara et al. 2008; Helbing and Yu 2009). In humans, the positive assortment of altruists may also be promoted by benefits related to social learning and culture (Simon 1990; Guzmán et al. 2007; Boyd and Richerson 2009) and by social institutions, such as costly punishment (Boyd and Richerson 1992; Henrich and Boyd 2001; Hauert et al. 2007), reputation (Leimar and Hammerstein 2001; Nowak and Sigmund 2005), and limited group size (Pepper 2007; Smaldino and Lubell 2011).

In many species, cooperation increases when environmental conditions are harsh, such as under increased predation (Spieler 2003; Krams et al. 2010) or when resources are scarce (Strassman et al. 2000; Callaway et al. 2002), confirming an idea first proposed by the Russian evolutionary biologist and political anarchist Peter Kropotkin (1902) that harsh environments should select for cooperation. A problem is that under circumstances of this type, unreciprocated cooperation may be more costly, or the costs of not receiving cooperation may be higher, and so the immediate payoffs to cooperators decrease relative to payoffs to defectors. Explaining why cooperation increases under harsh conditions, therefore, remains a challenge for theoretical biologists.

In this article, we investigate the evolution of cooperation in harsh environments using an agent-based model (ABM) that incorporates several important features of real organisms and ecosystems. The three most important features are (1) variable population size, in which birth and death events are decoupled, (2) an environmental cost of living, in which individuals must acquire resources in order to stay alive, and (3) a dynamic socio-spatial structure,

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in which interactions are limited by spatial structure, which, in turn, can evolve. These features are often (though certainly not always) ignored in theoretical considerations. We will demonstrate that a model with such features can give an account for increased cooperation in harsh environments.

Many evolutionary models treat the selection pressures related to cooperation as relatively weak and therefore assume that the associated benefits confer only small advantages relative to background rates of reproduction. Given the important role of cooperation in the evolution of social organisms, this may not always be the most appropriate assumption. We consider a scenario in which some interactions with cooperators are strictly necessary to acquire and maintain the resources to live, thrive, and survive. Insufficient interactions with cooperators result in death, while sufficient interactions promote survival and reproduction. Our model, broadly, is one of interdependence. Interdependence exists when two or more individuals cannot live without one another. Roberts (2005) has previously presented a formal treatment of a type of interdependence implied by pseudoreciprocity (Connor 1986) or by-product mutualism (Mesterton-Gibbons and Dugatkin 1997), in which individuals benefit simply by being in a group such that any act of cooperation that enhances the fitness of others in the group also enhances one's own fitness. Here we consider a different type of interdependence, one in which mutual cooperation is enforced by environmental adversity. This is a scenario that, up until now, has received little theoretical attention.

Our work extends research on cooperation in structured populations (Lindgren and Nordahl 1994; Wilson and Dugatkin 1997; Epstein 1998; Santos et al. 2006; Chadefaux and Helbing 2010; Nowak et al. 2010; Perc and Szolnoki 2010; Wu et al. 2010) and adds to the important but still small body of work on the evolution of cooperation in variable-size populations (Epstein 1998; Aktipis 2004; Zhang and Hui 2011; Smaldino and Schank 2012). Following a storied tradition in theoretical biology (Trivers 1971; Axelrod and Hamilton 1981; Boyd 1988; Houston 1993; Axelrod 1997; Epstein 1998; Frank 1998; Koella 2000; Doebeli and Hauert 2005; Lehmann and Keller 2006; Nowak 2006; Perc and Szolnoki 2010), we adopt the framework of the Prisoner's Dilemma (PD) game to represent interactions in which individuals can either cooperate or defect and receive payoffs accordingly. In this game, both players receive a reward, R , for mutual cooperation, but there is 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 $T > R > P \geq S$, so that defection is always the best strategy in the single-shot game, but mutual cooperation outperforms mutual de-

fection (the case where $P = S$ is sometimes called a "weak" PD). Additionally, the game requires that $2R > T + S$, so that consecutive rounds of mutual cooperation are better than individuals alternately exploiting one another.

Requejo and Camacho (2011) recently presented a model in which a well-mixed population of agents experienced environmental costs of living and could vary in size, which may on the surface appear similar to our model. Strictly speaking, their model is one not of cooperation but of parasitism. Cooperation, as usually defined in evolutionary theory, occurs when a behavior enhances the fitness of another individual relative to the absence of the behavior (Lehmann and Keller 2006). In their model, mutual "cooperation" is mathematically equivalent to the absence of any behavior. Instead, a "defector" pays a cost in order to elicit a reward from a "cooperator." Requejo and Camacho (2011) showed that, when environmental costs are high, the costs of defection (parasitism) may be greater than the benefits reaped from exploitation, and so cooperation (nonparasitism) can prevail because the payoff matrix is no longer a Prisoner's Dilemma. In contrast, interactions in our model always take the form of a Prisoner's Dilemma, and a defector always profits at the expense of a cooperator in a single interaction. Therefore, in contrast to their model, cooperation in our model can only outperform defection through positive assortment and repeated interactions. We will show that even though game interactions favor defectors in the short run, environmental costs can facilitate socio-structural dynamics that promote the success of cooperators in the long run.

We examine the influence of two factors related to environmental harshness. The first is the cost of unreciprocated cooperation. Unreciprocated cooperation corresponds to the payoff S , sardonically known as the "sucker's payoff." As S decreases, cooperators do worse in their interactions with defectors (though defectors do no better). The second factor we consider is the environmental cost of living. As stated, we assume that some interactions with cooperators are necessary to survive. We can vary this need by imposing a continuous resource drain on all individuals. A similar mechanism was proposed by Epstein (1998) but has not, to our knowledge, been explicitly implemented in PD game models. Death occurs if an individual's resource reserves fall to zero, a fate that can only be averted through regular interactions with cooperators. It is important to note that, because agents in our model are mobile and are not guaranteed to have a PD game interaction at every time step, the cost of living is not equivalent to a reduction in payoffs.

These two factors, (1) the cost of unreciprocated cooperation and (2) the cost of living, highlight a conflict between the short- and long-term rewards of cooperation.

In the long run, cooperation should be favored because only groups with a sufficient number of cooperators will survive. In the short run, however, harsh environmental costs increase the advantage of defectors in cooperator-defector interactions because the loss of resources leads to death. Increasing the cost of unreciprocated cooperation will reduce the short-term fitness of cooperators in the presence of defectors and, as a result, increase the relative short-term fitness of defectors. Increasing the cost of living raises the stakes for everyone and makes defectors increasingly dependent on the presence of cooperators. How things will work out is therefore complex and will depend on the PD game payoff matrix, the cost of living, and the frequencies and local densities of defectors and cooperators.

As an illustration, consider the limiting case of two-player groups, in which each individual has some initial amount of resources. Two defectors will perish. In a pair consisting of a cooperator and a defector, the lone cooperator will succumb even more quickly than the individuals in the defector-only dyad, since the cooperator gives all its resources to the defector and gets nothing in return. Meanwhile, the defecting partner will last only until it exhausts the resources extracted from the now-deceased cooperator. The only stable dyads will therefore consist of two cooperators. The situation, of course, becomes more complicated when populations are large and interaction partners change over time.

In the following sections, we will first describe our approach to modeling the above-described scenario. We will then formally describe the model and present its results. Finally, we will discuss some possible interpretations of our model and implications of our results.

Agent-Based Models for Structured Dynamic Populations

Our approach to modeling is similar to one first presented by Epstein (1998). His was the first study in which mobile agents played pure strategies in the PD game with neighbors and died and reproduced according to accumulated resources acquired or lost through game payoffs. It was also the first to emphasize the importance of incorporating into models generic properties of organisms, such as death, reproduction, mobility, and resource accumulation. Epstein anticipated that interesting dynamics could emerge from such a game and showed not only that spatial assortment could allow pure-strategy cooperators to endure—a result also obtained by Nowak and May (1992) and, later, others—but also that oscillatory population dynamics could emerge when defectors exploited cooperators and then grew too dense to sustain their own bloated numbers. This latter result is unique to models in which

agent birth and death events are decoupled and in which the total population size can vary.

The work presented here also exploits the conditions afforded by spatially explicit mobile agents who die and reproduce based on accumulated resources and involves a more detailed study than that presented by Epstein (1998). We systematically analyzed the influence of the cost of unreciprocated cooperation on evolutionary dynamics. We also considered the influence of the cost of living, in which agents lose energy that must be regained through game interactions. We will show that these two factors, which involve immediate costs to cooperators, have important consequences on long-term population dynamics.

Spatial structure is well known to have important consequences in the dynamics of social evolution (Epstein 1998; Szabó and Fáth 2007; Nowak et al. 2010; Perc and Szolnoki 2010), and structured populations have also been considered using analytical methods such as the pair approximation (Matsuda et al. 1992), which accounts for certain properties of spatial structure by calculating the probabilities of local neighboring pairs (Iwasa et al. 1998; van Baalen and Rand 1998; Thomson and Ellner 2003; de Aguiar et al. 2004; Hauert and Szabó 2005). This method is based on a model in which a fixed number of stationary agents are situated on a fully occupied square lattice. Models of this type, however, cannot account for many of the biologically important factors we wish to consider, including variations in population size (due to the decoupling of birth and death events), spatial heterogeneities in reproductive success due to variation in resource accumulation, agent mobility, and environmental cost of living. We therefore deem a stochastic, spatial ABM with mobile agents to be the most appropriate approach to the scenario considered in this article.

Model Description

In our model, spatially explicit agents playing pure strategies of cooperate or defect moved to find coplayers and reproduced locally after accumulating sufficient energy. The model is similar to previous ABMs of this type (Epstein 1998; Aktipis 2004; Smaldino and Schank 2012) and is unique primarily in its use of an explicit cost of living. Energy could be gained or lost via game interactions, and agents died if their energy fell to zero. Agents also incurred an energy deduction at each time step, representing environmental costs that require cooperation. There was no specific cost associated with movement other than the lack of opportunity to gain energy payoffs from a game interaction.

Interactions took place on a 100×100 discrete square grid with periodic (toroidal) boundaries. For each simu-

lation run, N agents, half cooperators and half defectors, were placed in unique, random locations and initialized with an energy level drawn from a uniform distribution of integers between 1 and 50. Each time step (or “round”), every agent that had not already played the PD game that round searched its local neighborhood, consisting of the eight closest cells, for a coplayer that had also not already played that round (fig. 1). If the agent found a coplayer, the two played the PD game and received payoffs. This differs from previous models in which agents play all neighbors simultaneously (e.g., Nowak and May 1992; Epstein 1998; Koella 2000; Ohtsuki et al. 2006; Vainstein et al. 2007; Helbing and Yu 2009; Meloni et al. 2009; Chade-faux and Helbing 2010) or play with a co-occupant of the same cell (Aktipis 2004). In our model, an agent’s life span and time to reproduce were typically much greater than the time span of a single game interaction, unlike models in which a single round of simultaneous game interactions with each of one’s neighbors represents the aggregate of every social encounter over the course of an individual’s life. Because coplayers were selected randomly from among an agent’s neighbors at each time step, an individual therefore tended to interact with many of its neighbors throughout its life even though pairwise interactions occurred one at a time.

If a coplayer 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. This is equivalent to the “naïve” agents in Aktipis (2004), which attempt movement if and only if they cannot find a coplayer, and differs from other models where agents move regardless of game interactions (Epstein 1998; Vainstein et al. 2007; Meloni et al. 2009). Although movement costs may be important, there were no explicit costs of movement other than the lack of opportunity to gain energy payoffs from a game interaction. Agents’ energy stores

were capped at 150 so that an individual could not accumulate energy without bound. If, after receiving payoffs, an agent reached 100 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. Reproduction was not attempted if the population was at its maximum carrying capacity, N^* . Each offspring was of the same type as its parent; however, the results presented below were quite robust to mutation, in which cooperators produced defector offspring and vice versa (see appendix, available online). Regardless of whether the agent played the PD game, moved, or did neither, a cost of living, k , was deducted from its energy reserve. If its energy fell below zero, the agent died and was removed from the game space. Note that the cost of living deduction is distinct from the game payoff matrix, since agents are not guaranteed to have a game interaction at each time step.

Agents were scheduled using the MASON simulation environment (Luke et al. 2005) so that the order of scheduling was randomized at each time step. We ran each simulation condition 30 times; the results reported below reflect the average cooperator frequency of $t = 10^6$ across runs. Because complex systems may have long transitory periods before settling into relatively stable long-term dynamics (Strogatz 2001), running the simulations for a large number of time steps was necessary to allow the system to settle into stable behavior. We additionally ensured this run time was sufficiently long by running several conditions out to $t = 10^7$ and noting that the long-run cooperator frequencies did not vary from $t = 10^6$. Payoffs were set as follows: $T = 5$, $R = 3$, $P = 0$. The sucker’s payoff, S , was varied, as indicated below. Unless otherwise noted, we used $N = 1,600$ and $N^* = 5,000$.

Agents’ pairwise interactions are most easily viewed as simultaneously altering the energy stores of both actors.

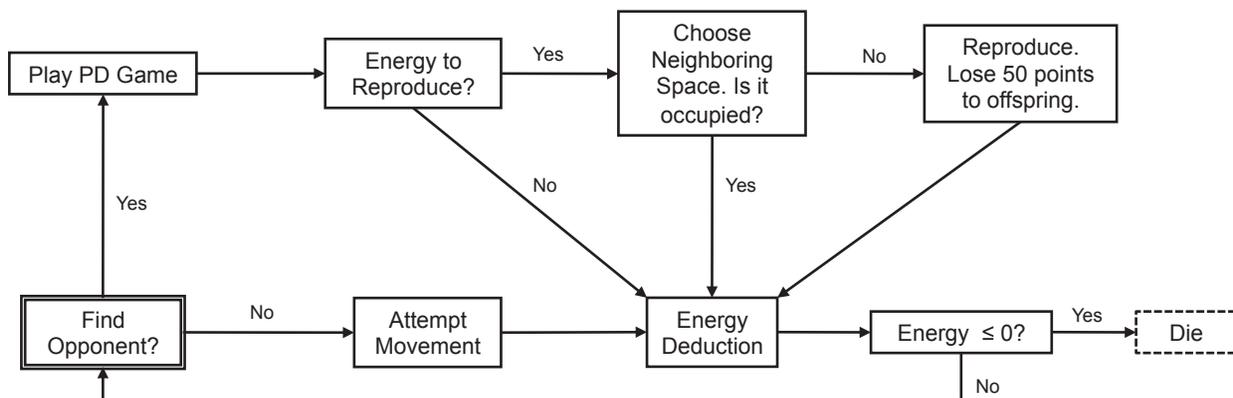


Figure 1: Flowchart depicting an agent’s behavior cycle. The first action, indicated in double-line outline, is to look for an opponent.

Due to the discrete-time nature of the model, we can alternatively assume that each discrete-time unit represents some finite but short period of time during which each of the two actors has the opportunity to cooperate with the other. While both of these interpretations exclude reciprocity over long time frames, this construction of cooperation also enables us to identify minimal conditions for cooperator success in the absence of complex memory or recognition mechanisms. Moreover, many opportunities to reciprocate do occur either simultaneously or over short time spans. For example, mobbing behavior by pied flycatchers has been described as a Prisoner's Dilemma in which cooperation reflects joining a neighbor-initiated mob and defection reflects abstaining (Krams et al. 2008). Since mobbing behavior drives off predators but is highly risky if done alone, two individual flycatchers simultaneously enhance their fitness by cooperating. Moreover, neighbors often independently initiate mobbing behavior within less than an hour of one another, allowing both individuals to take on the role of the initiator and to quickly reciprocate previous altruistic acts.

Simulation Results

The Cost of Unreciprocated Cooperation

We began by keeping the cost of living fixed at $k = 0.5$ and varying the payoff for unreciprocated cooperation, S .

Figure 2 illustrates the spatiotemporal dynamics for three example runs. Let us turn our attention to figure 2B, for which $S = -1$. When defectors interacted with cooperators, they quickly built up their stores of resources and reproduced. The large increase in defector numbers accompanied the death of many cooperators, and this is the state we see at $t = 200$. Not all cooperators perished, however. Some managed to cluster together and to stay alive via repeated mutual cooperation. Although the cooperators on the periphery of the clusters also interacted with defectors, sufficient interactions with fellow cooperators ensured their survival. Meanwhile, those defectors not lucky enough to be near a cluster of cooperators eventually died out, as seen at $t = 500$. The defectors on the periphery of the cooperator clusters thrived, but their offspring tended to die out due to their inability to find cooperative partners. Occasionally, through the random movement that occurred when a defector was unable to find an available interaction partner, an empty space opened up and the cooperator cluster grew via reproduction. In some instances, two or more cooperators escaped the cluster without being exploited by passing defectors, and a new cluster arose. Over time the cooperator clusters grew in size and could even consolidate, as seen at $t = 10^6$.

In figure 2A, the payoff for unreciprocated cooperation was exactly equal to the payoff for mutual defection. De-

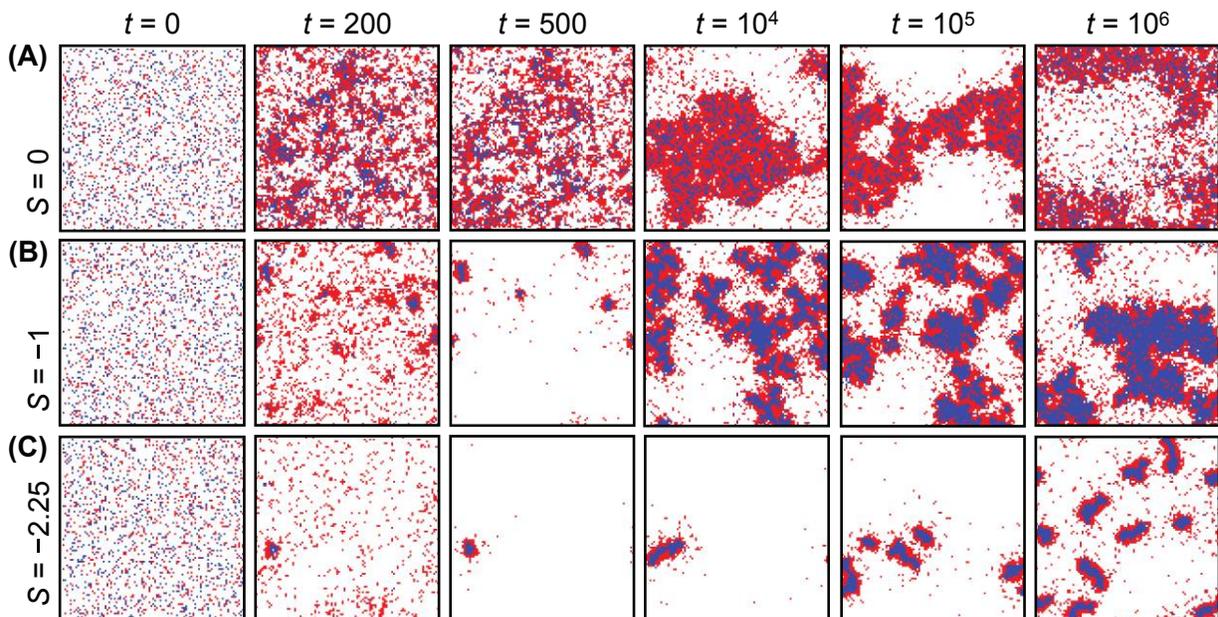


Figure 2: Spatiotemporal population dynamics for different levels of unreciprocated cooperation (the sucker's payoff, S). These spatial maps show agents' x and y coordinates at different points in time; cooperators are blue, defectors are red. For these runs, $k = 0.5$, $N = 1,600$, and $N^* = 5,000$.

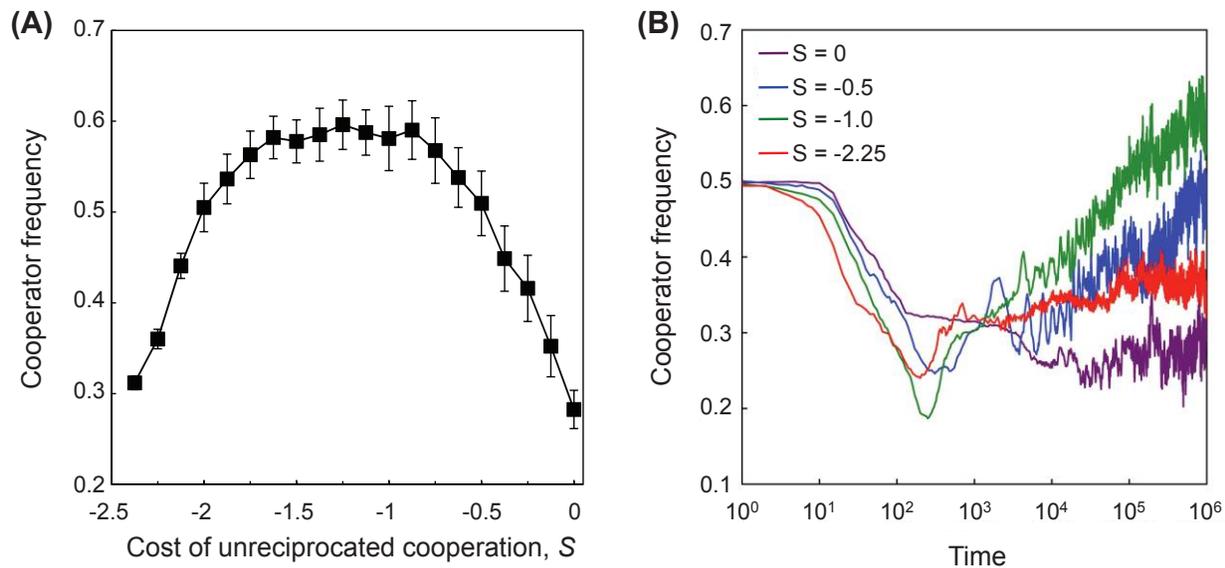


Figure 3: Population cooperator frequency for different values of the sucker's payoff, S . *A*, As the cost of unreciprocated cooperation increased (as S decreased), long-term cooperator frequencies increased, then leveled off, and then decreased again. Values are taken from $t = 10^6$, averaged across 30 runs (\pm SD). *B*, Cooperator frequency as a function of time for example simulation runs with different values of S . Short-term fitness decreases correspond to what is predicted by classic models of cooperation: higher costs of unreciprocated cooperation lead to a greater decline in cooperation. However, long-term dynamics illustrate impressive rebounds for cooperators for intermediate levels of S relative to runs with lower costs of unreciprocated cooperation. For these runs, $k = 0.5$, $N = 1,600$, and $N^* = 5,000$.

factors once again exploited cooperators and grew in number, but cooperators did not die out nearly so readily. As long as they were able to receive some minimal amount of cooperation, as occurs in very small clusters, cooperators could survive. This led to a dense mixture of small clusters of cooperators surrounded by defectors, a pattern that tended to be relatively stable over time. Importantly, cooperators never experienced the extreme early die-off and so were prevented from forming larger clusters later on.

The decimation of cooperators not situated in large clusters can therefore benefit the strategy of cooperation in the long run. However, there were limits to the benefits of a more punitive sucker's payoff for long-term cooperator success, as seen in figure 2*C*, where $S = -2.25$. As in figure 2*B*, defectors quickly exploited cooperators and then perished when unable to receive sustained cooperation, leaving only tight zones of cooperation surrounded by defectors. Because interactions with defectors hurt cooperators so much, it was much more difficult for the cluster to expand. Multiple cooperator offspring could occasionally break away and reproduce before they were besieged by defectors, as seen at $t = 10^5$ and $t = 10^6$, but the size of the clusters seems to have been limited by the harsh penalties incurred for cooperating with a defector.

The example runs point to an inverted U-shaped relationship between the long-term cooperator frequency

and the cost of unreciprocated cooperation, and this is exactly what we see when we look at the averages across many runs (fig. 3*A*). In other words, higher costs of unreciprocated cooperation do help cooperators in the long run but only up to a point: once the costs become too high, cooperators are less able to recover their numbers. Interestingly, for all values of S we tested, we saw the short-term fitness of cooperators decrease in the first hundred or so time steps, as expected by traditional models of cooperation; that is, cooperator frequency fell more dramatically with greater costs of unreciprocated cooperation. As long as S was not too low (see appendix), however, cooperator frequencies also recovered more dramatically for higher costs of unreciprocated cooperation (fig. 3*B*).

The oscillations seen in figure 3*B* are indicative of the stochasticity in agent movement, which led to the occasional flurry of cooperator expansion, followed by rapid exploitation by defectors and then an eventual defector die-off. While these oscillatory events were common, the long-term mean cooperator frequency was generally stable by $t = 10^6$. These events were due to the variability in population size as well as the fact that the carrying capacity was less than the total number of cells in the space; when N^* equaled the size of the grid, oscillatory patterns did not occur.

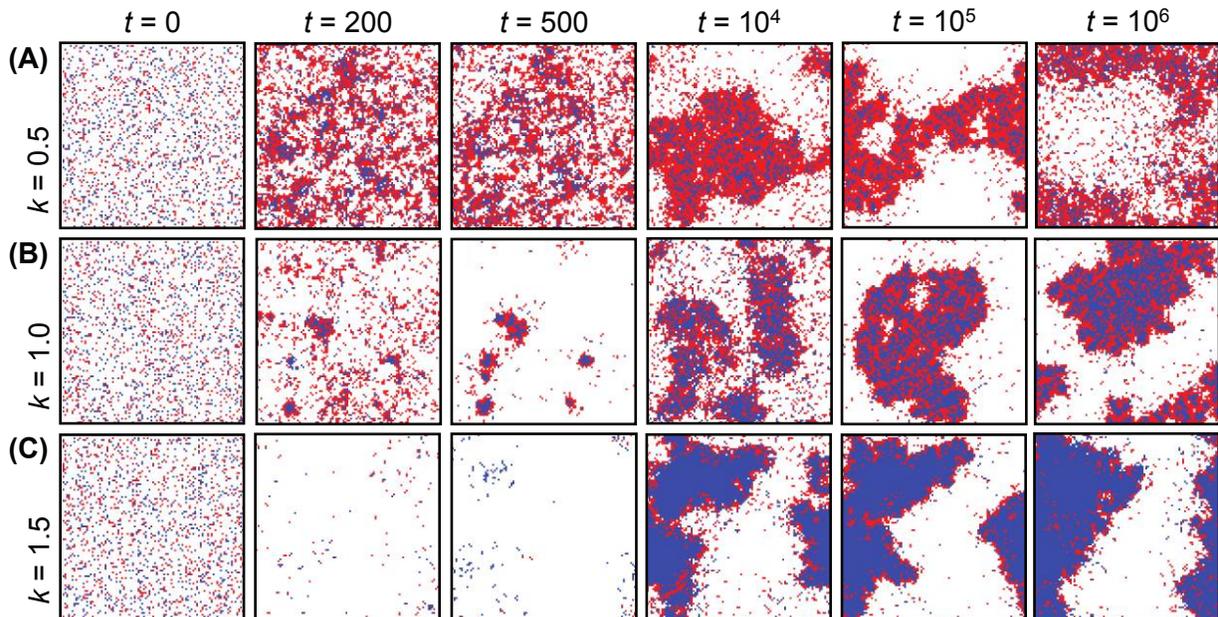


Figure 4: Spatiotemporal population dynamics for different levels of the cost of living, k . These spatial maps show agents' x and y coordinates at different points in time; cooperators are blue, defectors are red. For these runs, $S = 0$, $N = 1,600$, and $N^* = 5,000$.

The Cost of Living

Now we turn to the environmental cost of living, k . Figure 4 shows the spatiotemporal dynamics for three example runs with $S = 0$. Note that figure 4A is identical to figure 2A for comparison purposes. When the cost of living was increased to $k = 1$ (fig. 4B), the result was reminiscent of the result in the previous subsection when $k = 0.5$ and $S = -1$. Initially, defectors exploited cooperators and reproduced rapidly, but the higher cost of living led to the demise of individuals who did not have frequent interactions with cooperators. We again see mixed clusters of cooperators and defectors, but cooperators are much more prevalent in figure 4B, since the hostile environment made more frequent interactions with cooperators necessary to survive. When the cost of living was further increased to $k = 1.5$ (fig. 4C), the effect was quite dramatic. Very few agents survived at all, and those who did had regular interactions with cooperators. This led to the existence of spatial areas with very few defectors, which allowed the cooperators in those regions to reproduce rapidly. These large cooperator clusters subsequently attracted defectors, who surrounded the group but not before cooperators dominated the population.

Long-term cooperator frequency increased across many values of S as the cost of living increased (fig. 5). Indeed, when the costs were very high, around $k = 2$, defectors all perished regardless of the cost of unreciprocated co-

operation. Figure 5 also illustrates that the inverted U-shaped curve relating long-term cooperator frequency and the cost of unreciprocated cooperation (fig. 3A) held only for a restricted range of the cost of living, $0.3 \leq k \leq 1.7$. Above this range, the cost of living influenced results so drastically that the value of S was of small consequence.

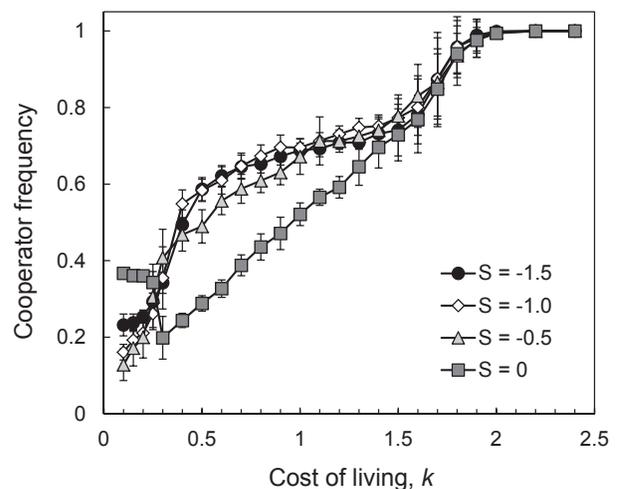


Figure 5: Population cooperator frequency (\pm SD) as a function of the cost of living, k , for several values of S . Cooperation was always increasingly favored for larger values of k when $S < 0$. $N = 1,600$, and $N^* = 5,000$.

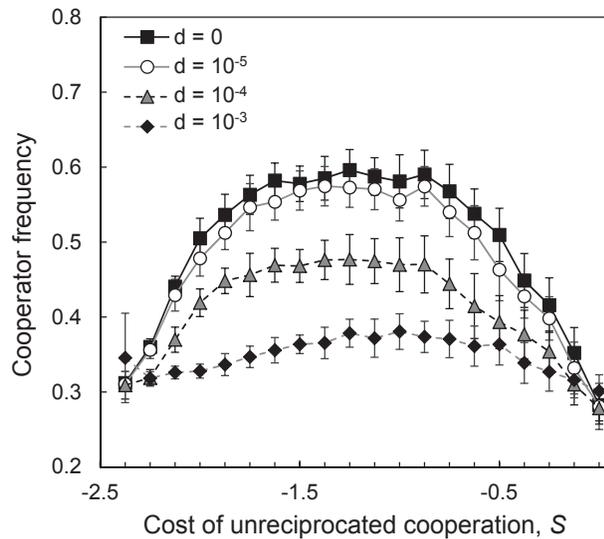


Figure 6: Population cooperator frequency (\pm SD) as a function of S for several rates of random death, d . Random death decreased cooperator fitness for intermediate values of S , but the fixation frequency of cooperators was still highest for those intermediate values. Data are taken from $t = 10^6$, averaged across 30 runs. $k = 0.5$, $N = 1,600$, and $N^* = 5,000$.

Below this range, the results held, except when S was very small (e.g., $S = 0$). In this case, the low cost of living and zero cost of unreciprocated cooperation made it so that cooperators never experienced a postboom decline as they did when costs were greater. Rather, because cooperators were not penalized for interacting with defectors, and because the cost of living required only occasional interactions with cooperators, the population stabilized rapidly. These results were robust to the introduction of random death, which is described below.

Our results also indicate that the proportions of cooperators and defectors in spatially contiguous clusters as well as the size of those clusters should be at least partly a function of environmental harshness, as seen in figures 2 and 4. The exact nature of this relationship is difficult to assess precisely due to the complexity and variability of the model, but it is an intriguing question for future research. For example, one could consider only cases in which space can be completely filled and analyze the ensuing spatial patterns using Fourier analysis or spatial information metrics (Feldman and Crutchfield 2003).

Random Death

We tested the robustness of our results against the entropic forces of random death. In addition to death by loss of resources, at each time step agents now had a nonzero probability of dying, d , regardless of the agent's current

energy holdings. This is similar to the death mechanism used in Rendell et al. (2010), which generates more variance in agent life span than a maximum life span approach (cf. Epstein 1998). The introduction of random death somewhat inhibited the growth of cooperator clusters, primarily by allowing defectors to move into spaces vacated by dead cooperators. For very low and very high values of S , cooperation was not significantly influenced by random death, because in each of these cases, the sizes of cooperator clusters were already held in check by the other factors described above. For intermediate values of S , long-term cooperation decreased as a result of random death, but our results remained qualitatively robust: the frequency of cooperators was highest for intermediate costs of unreciprocated cooperation (fig. 6).

Extinction

Our model allows for variation in the size of the population, and our main result that long-term cooperation increases in harsh environments relies on a substantial decrease in population size followed by a recovery. Some situations, however, may be so harsh that a recovery is not possible. In these cases, spatially coherent groups of cooperators are unable to be sustained, and the population collapses. This can occur if the cost of living is too high, if the cost of unreciprocated cooperation is too severe, or if the initial frequency of cooperators is too low to generate sufficient spatial aggregation. These results are given in greater detail in the appendix. Further analyses, including demonstrations of robustness to population size, mutation, and movement strategy, as well as an extension to the Snowdrift game, are also presented in the appendix.

Discussion

Summary of Results

Under the conditions of the model—in which populations were spatially structured, individuals interacted and reproduced locally, and occasional interactions with cooperators were necessary for survival—we have demonstrated how short-term benefits to selfish individuals can lead to their own demise, while the initial exploitation of cooperators can pave the way for a dramatic recovery in which cooperation can even become the predominant strategy. These effects were enhanced when the costs of unreciprocated cooperation were increased; higher costs meant more severe losses for cooperators early on but paved the way for a more dramatic rebound. This phenomenon held up only to a point; if the cost of unreciprocated cooperation was too great, it restricted the growth of cooperative clusters. Globally applied energy costs had a more straight-

forward effect. Unless the cost of living was simply too great for any individuals to survive, increased costs tended to help cooperators in the long run, as they hastened the death of individuals not interacting regularly with cooperators.

Negative values for both S and P can also maintain cooperation in spatial models without the need for an additional cost of living, as in Epstein (1998). However, while this can lead to either stable population levels or oscillatory cycles reminiscent of predator-prey dynamics, the short-term decrease in cooperator frequency followed by a stable long-term recovery has not been found without the implementation of a nonpayoff cost of living.

A similar result—initial decreases in cooperator numbers followed by dramatic recoveries—was obtained by Chadeaux and Helbing (2010) using a spatial population of fixed size on a fully occupied lattice, in which agents could accumulate resources without bound. Their result hinged on the ability of spatial clusters of cooperation to amass great wealth via mutual cooperation and then spread, because payoffs were calculated as a proportion of accumulated wealth. At some level, this model ceased to be a Prisoner's Dilemma, because mutual cooperation could obtain a higher payoff than defection against a cooperator. Their assumptions may be valid for some human systems, in which individuals can accumulate vast wealth, although it is not entirely clear how wealth-accumulating cooperators could spawn more such individuals without limit. Our model relies instead on the need for sustained physical proximity to cooperators. Cooperators spring back not by building up large stores of resources for bursts of unrestrained expansion but simply by surviving when the harshness of the environment takes the lives of noncooperators.

Important Assumptions

Structured Populations. In a well-mixed population, cooperators cannot avoid exploitation by defectors, and the population will collapse once cooperators are extinct if the cost of living is nonzero. Real populations are rarely well mixed, however, and the importance of considering discrete, spatial populations is well established (Wade 1992; Durrett and Levin 1994). In our model, individuals are spatially located in discrete positions, move and reproduce locally, and interact with neighbors. Spatial assortment and limited dispersal promote cooperation by facilitating the positive assortment of cooperative individuals (Epstein 1998; Koella 2000; Fletcher and Doebeli 2009; Nowak et al. 2010), and sustained cooperation in our model relies on the formation and persistence of “demographic zones” of cooperation (Epstein 1998). The explicit representation of individuals who are born, live, move, and die means

that spatial organization is not constant but evolves. Limited dispersal and the tendency to sustain interactions with neighbors leads to individuals frequently interacting with parents and other close relatives. Most importantly, emergent spatial patterns that sustain cooperation persist over time and across generations.

Individuals inherit the social environments of their parents, as well as the environmental changes brought about by their parents' generation, and this shapes with whom they are likely to interact. The importance of social inheritance was recognized long ago by Wallas (1921) and is a natural extension of the recent focus on environmental (or ecological) inheritance found in the literature on niche construction (Odling-Smee et al. 2003; Goodnight et al. 2008). In humans, changes to physical and institutional infrastructure persist and influence not only our day-to-day behavior but also what is learned and enculturated through development. These structural factors influence the behaviors and social norms of the individuals involved, and those patterns also persist across generations, shaping the selective forces for both genetic and cultural evolution. Our model captures only a very simple version of this phenomenon but supports the position that spatial agent-based models with variable-size populations represent an important tool for studying phenomena related to social inheritance.

That the persistence of socio-spatial structure facilitates the long-term promotion of cooperation may also be considered in light of empirical studies indicating that inherited socio-spatial structure selects against aggressive individuals who overexploit their neighbors (Goodnight and Stevens 1997). For example, individual crop plants selected for high yield perform poorly when planted together, as they overcompete for resources (Griffing 1977). Similar results have been found when selecting hens for egg production: the individuals who produce the highest yield in diverse groups perform poorly when housed together (Muir 1996). The general principle involved here is well known: although exploitative individuals fare well among cooperators, they perform poorly when concentrated among themselves (Wilson and Wilson 2007).

Strong Selection on Cooperation. Many evolutionary models of cooperation assume that only weak selection pressures operate on the outcomes of (potentially) cooperative interactions. Two standard assumptions of weak selection, that the population size is large and stable and that differences in fitness among different behavioral phenotypes are small (Wild and Traulsen 2007), do not hold in the scenario considered here, in which population size can vary and fitness is highly dependent on cooperative interactions. Weak selection also implies frequency independence over a wide range of conditions (Ross-Gillespie

et al. 2007), an implication that runs counter to a fundamental assumption of our model. Boyd (1982) has shown that weak selection models can also hide influences in fecundity from local differences in population density and the spatial organization of behavioral phenotypes. More generally, the assumption of weak selection ignores phenotypic effects that lead to organismal death and thereby omits a key criterion for the evolution of complex organizational structures (Wimsatt and Schank 2004). While weak selection may be a valid assumption for some evolutionary systems, we stress the importance of investigating models that assume strong selection on cooperation.

In our model, an implication of the strong selection assumption was that population size was variable. If the population size is fixed, then evolution only occurs by changes in strategy frequencies and excludes any potential influences of explicit group sizes. In such cases, individuals with higher payoffs are favored to reproduce, and lower S , for example, always translates to lower fitness for cooperators. In contrast, the decoupling of birth and death allows population size to vary, which here provided cooperators with the opportunity to recover their numbers following an initial decline.

Fixed Behavioral Phenotypes. Our model assumes that individuals have genetically fixed behavioral phenotypes and therefore cannot account for individual changes in behavior in response to opponent behavior, as in models of reciprocity (Trivers 1971; Axelrod and Hamilton 1981), or as a result of rapid changes in the environment. A recent model has suggested that, in cases of rapid change in environmental harshness, individuals may adaptively respond to the increased uncertainty about future resource availability by increasing cooperation (Andras et al. 2007). Our model nevertheless indicates a mechanism for how long-term cooperation could flourish more in harsher environments even when unreciprocated cooperation is more costly. Importantly, our results do not require any sophisticated abilities to detect resource availability or to act contingently in response to social behaviors. Although the behavioral repertoire of individuals in our model was highly constrained, we included many general properties of biological organisms that are often absent from other models, including explicit death and reproduction, mobility, and resource accumulation, all of which were influenced by numerous events throughout the life span. By incorporating more elements of ecology and life history in agent-based PD game models, the scope of possible explanations and conditions for the evolution of cooperation is broadened.

Interpretations

Interdependence, Environmental Harshness, and Cooperative Breeding. Kropotkin (1902) proposed more than a century ago that harsh environments should select for cooperation. Our model corroborates that evolutionary pressures may select for an increase in cooperation when the cost of living increases.

In nature, there are several instances in which organisms provide aid in circumstances that would otherwise lead to mutual demise, such as food sharing (e.g., Wilkinson 1984; Jaeggi and van Schaik 2011). Another example is the prevalence of cooperative breeding among social species, wherein individuals contribute to the rearing of offspring other than their own. Although cooperative breeding often occurs among related individuals, it has become apparent in recent years that kin selection alone is not generally sufficient to explain cooperative breeding and that much of the benefit is instead derived from direct reciprocity (Bergmüller et al. 2007). While this relationship does not necessarily imply the kind of interdependence at work in our model, recent evidence suggests that interdependence may have driven cooperative breeding behavior in the case of human evolution. A large body of research indicates that humans have historically raised their young collectively rather than in biparental care (Hrdy 1999, 2009; Mace 2000; Sear and Mace 2008; Hill and Hurtado 2009; Walker et al. 2011), and it has been proposed that the adoption of cooperative breeding strategies played a large role in the evolution of human cognition (Burkhart et al. 2009). A possible reason for this adoption was the interdependence necessitated by living in large communities, coupled with the nutritional requirements for developing young (a cost of living). Indeed, Hill and Hurtado (2009) studied two South American hunter-gatherer societies and found that not only were cooperative breeding practices prevalent but also husband-and-wife pairs were physically incapable of procuring enough food for their offspring and themselves without help from other individuals, who included nonrelatives. Our model shows how, in such a case, cooperative strategies could be strongly selected for. There are, of course, many complex factors involved in the evolution of human cooperative breeding, including mating practices and family structures, which our model admittedly does not capture. We are currently working on developing mathematical and computational models to examine the role of cooperative breeding, mate choice, and family structure in human evolution (e.g., Smaldino et al. 2011). The model presented here, however, provides strong evidence that interdependence will favor reciprocity as long as socio-spatial structure emerges and can be at least loosely maintained.

Competing Goals for Socio-spatial Organization. The introduction of random death compromised the integrity of the emergent cooperative clusters by allowing defectors to infiltrate gaps left by dead cooperators. Although the qualitative character of our results—that long-term cooperation could increase even as the costs of cooperation also increased—held even for relatively high rates of random death, overall long-term cooperation decreased as more individual deaths increased the spatial disorganization. If, however, cooperators had been able to move quickly outward to fill those gaps along the cluster peripheries, defectors would have been unable to effectively capitalize on the spatial disorder produced by random death. This suggests that, at the group level, there may be increased selection for compensatory mechanisms against entropic forces that compromise the socio-spatial clustering of cooperative individuals. Cooperators might plausibly engage in active boundary defense, move inward to maintain tight aggregations, or even collude to retaliate against defectors as a form of selective punishment, in which case we should also expect defectors to curb the growth of cooperators and exist at the socio-spatial peripheries. An interesting direction for further research will be the investigation of coevolutionary competition between cooperators' need to increase socio-spatial organization and defectors' need to decrease it.

Concluding Remarks

When the cost of living requires cooperation, increased costs to cooperators can, perhaps counterintuitively, increase the long-term prevalence of cooperative strategies. A consequence, however, is a dramatic shrink in the population size during the period before the cooperative recovery. This should give us pause before we celebrate situations that increase the struggle for existence.

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