Global Cooperation Achieved Through Small Behavioral Changes Among Strangers

Cooperation in nature and human societies is paradoxical due to the apparent costs of cooperative behavior. Previous models suggest that cooperation arises most frequently when costs are recouped through reciprocity. We present a model that tracks individual players who carry a simple probability of cooperating in a spatially defined network; there are no costs for individuals to cooperate. Global cooperation in our model occurs when individuals interact, on average, with strangers (not neighbors) and are rather insensitive to how these strangers respond. We suggest that this simple model may explain the prevalence cooperation in systems as diverse as bacterial biofilms and human societies.

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INTRODUCTION

There has been a great deal of interest in the conditions that lead to the evolution and persistence of cooperative behavior. Social interactions range from mutualistic behavior, which is generally considered cooperative behavior without costs of some individual benefiting at some level, to spiteful behavior, with interacting individuals suffering costs without benefits (see [1] for examples). Perhaps the most widely studied interaction is altruism, in which individuals cooperate but are assumed to perform behaviors that accrue costs with or without the expectation of reciprocity. Cooperation may be evolutionarily stable due to indirect benefits received through helping offered by related individuals (kin selection) or due to receiving direct benefits later in time (reciprocal altruism). The rise and maintenance of cooperative behavior has been studied both theoretically, primarily through game theoretical approaches, and empirically within many disciplines, including economics, evolutionary and behavioral ecology, anthropology, sociology, and philosophy [2].

In general, approaches to understanding cooperative behavior have shared the assumption that interactions are costly. There is increasing evidence, however, that this assumption may be far from universal. For example, a frequently cited example of altruistic behavior has been vigilance, or guarding behavior, in meerkats (reviewed in [3]). Authors viewed in [3]). Authors have repeatedly suggested that sentinels stand lookout and incur the cost of the increased risk of predation. However,
Clutton-Brock and colleagues [3] have found that there is little to no cost involved with guarding behavior because these individuals have, in general, already eaten and, as sentinels, are more likely to escape predation (a selfish behavior). This model, therefore, in its absence of behavioral costs, may be argued to represent the condition of the spread of selfish behavior rather than cooperation. This seems implausible in this model, however, because selfish behavior implies the awarding of a payoff (to self), which is not included in this model. Therefore, since interactions are restricted among individuals without costs or benefits, interactions are interpreted as communicative information exchange without harm.

In human societies, there are cooperative interactions, such as the apparently culturally ubiquitous "eyebrow flash", functioning as a "hello" or a "yes to social contact" [4], that carry little to no cost. Considering the difficulty in measuring the costs and payoffs of interactions, and the likelihood that some behaviors involve little to no cost, we analyze a spatially explicit model of individuals that assumes no costs or benefits from interacting. Our model tracks the likelihood that individuals in a population, each represented as a simple probability of interacting, will continue to interact with each other. The value of this cost-free approach is to lay a foundation to better understand the stability and spread of cooperation in population networks and to reveal changes that result when costs and benefits from interactions are incorporated.

Social dilemmas, such as the standard two-player game the Prisoner’s Dilemma (PD), represent an interesting paradox because rational, or selfish, behavior (maximize individual gains) results in collective irrationality (relatively low overall gains). Analysis of the PD reveals that, in general, global cooperation is possible when interactions are repeated (iterated) with individuals expecting multiple plays [5], which is in agreement with Trivers’ [6] formulation of the role of reciprocity. Spatial models, which allow interactions to be constrained to neighborhoods, demonstrate that cooperation may break down with increasing neighborhood size because neighbors, who are likely to encounter each other repeatedly, are less likely to cheat (defection can lead to a high “suckers” payoff) [7]. Recently, however, the importance of reciprocity in nature has been challenged [8,9]. For instance, Heinsohn and Packer [10] report an interaction among female lions in which reciprocity apparently should, but does not, occur. In response to the paybacks of lion roars, female lions walk in a single line toward the sound. In a cooperative setting, different lions should lead the pride when approaching the apparent intruders. Heinsohn and Packer [10], however, found that lions did not share this responsibility (failed to reciprocate) and that the leaders did not punish the defectors, obviating the utility of models like the PD.

The simplest models generally deal with pairs of individuals. Trivers [6] first proposed that cooperation among individuals might be achieved through reciprocal altruism, where individuals interact repeatedly and incur costs from cooperative acts (e.g., those consistent with the often-cited tit-for-tat strategy). Alexander [11] further suggested that reciprocity should lead to cooperative behavior through indirect interactions in systems with more than two participants. More recently, Nowak and Sigmund [12] introduced a model that found cooperation to be facilitated by indirect reciprocity involving more than two players. Despite the widespread work on these models, their increasing complexity and limited generality make their application to real systems limited [10,13,14].

**METHODS**

Our approach to modeling cooperative behavior involves tracking only individual probabilities \( p_i \) of cooperating. Populations consist of immortal and immobile individuals on a two-dimensional square toroidal lattice. Simulations have fixed neighborhood sizes in which individuals potentially interact. Neighborhoods range in size from local (eight nearest neighbors) to global. Individuals that interact are, in essence, open to communication and are considered cooperative. Individuals with low \( p_i \) values interact infrequently and, if \( p_i = 0.0 \), function as pure defectors (never interact). Simulations end either when there is a single individual in a population with \( p_i = 0.0 \) or when all individuals have \( p_i = 1.0 \) (all individuals always cooperate, which is referred to as “global cooperation”). Simulations are terminated with the presence of a single pure defector \( (p_i = 0.0) \) because these individuals, without mutation, do not change, thus precluding such simulations from achieving global cooperation. Our model lacks costs or benefits of cooperative or noncooperative behavior.

We also investigate how individual reactions to neighbor behavior influence the emergence of global interactions. This is done by varying the parameter \( s \), the amount each cooperater’s \( p_i \) is changed in response to play, Individuals \( (i) \) are systematically chosen to play. Play consists of choosing a uniformly distributed pseudo-random number \( 0 \leq r \leq 1 \). If \( r < p_i \), the target individual \( i \) cooperates and seeks a neighbor with which to play. If \( r \geq p_i \), the individual \( i \) is considered a defector and play moves to the next target individual.
We choose a random neighbor \((k)\) and determine whether the neighbor cooperates or defects (if a new \(r < p_k\)). If the chosen neighbor cooperates, the target individual has its \(p_i\) increased by \(\varepsilon\); otherwise it is decreased. The value of \(\varepsilon\) is set at the beginning of each simulation and is tested over a range from 0.01 to 0.5. No change is made in \(p_k\) at this time.

Individuals that are not pure defectors \((p_i > 0)\) change their probability of cooperating only after interacting with neighbors. Whether an individual’s \(p_i\) value goes up or down depends on neighbor behavior. Interactions with cooperative neighbors raise an individual’s probability of cooperating in the next time step while a neighbor’s defection decreases the target individual’s probability of cooperating. Therefore, individuals that have cooperative neighbors will, on average, increase their probabilities of cooperating in the future while individuals in neighborhoods with low average \(p\) values will tend to become less cooperative. Individual \(p_i\) values are updated simultaneously after all individuals have had the opportunity to interact.

We ran simulations with different initial distributions of \(p_i\) (all either set to a constant \(p_{init}\) or normally distributed about a mean \(p_{init}\)). Lattice size \(L^2\) was varied from \(L = 41\) to \(L = 1001\) but was set at \(L = 501\) for most runs. We also tested the effect of mutation, where each individual with a probability of 0.001 had their \(p_i\) value increased or decreased by 0.01, within the constraint 0 \(\leq p_i \leq 1\). This model differs from game theoretical models such as the PD because it lacks payoffs and resulting costs. In the PD, individuals that cooperate with defectors are punished and receive a “sucker’s payoff,” generally the lowest possible return. In our model, suckers simply reduce their probability of cooperating in the future.

**RESULTS**

Communities that begin with \(p_{init} < 0.5\) always end with a population of defectors (Figure 1). Global cooperation (all individuals having \(p_i = 1\)) is possible only when the initial mean probability of cooperating \((p_{init}) \geq 0.5\). As \(\varepsilon\) gets smaller and \(n\) gets larger, cooperative communities become more likely (Figure 2). This suggests that cooperation is most likely when individuals interact with strangers and react little in response to neighbor behavior.

Individuals within small neighborhoods tend to converge to similar \(p_i\) values, resulting in the emergence of clusters of either cooperators or defectors (compare simulations with small neighborhoods in Figure 3(a) and (c) against larger neighborhoods in Figure 3(b) and (d)). Defector clusters, when neighborhoods are small, tend to grow as neighboring cooperators attempt interaction and ultimately have their \(p_i\) values reduced. Small neighborhood size, therefore, leads to spatial variance in individual \(p_i\) values with defined regions of cooperators and defectors, with the latter tending to grow over time, increasing the probability that individual \(p_i\) values reach the absorbing state of 0 (Figure 3).

When neighborhood size is small, \(p_{init}\) needs to be larger than in simulations with large \(n\) to achieve global cooperation (Figure 2). Larger neighborhoods make global cooperation both more likely and more robust because, scattered defectors are unlikely to be chosen repeatedly by individual cooperators. Instead, individuals perceive the mean of a larger neighborhood that, if \(p > 0.5\), causes individual \(p_i\) values to increase, leading to global cooperation.

**Figure 1**

Without space (global neighborhood size) and with small changes in individual \(p_i\) values \((\varepsilon = 0.01)\) simulations with initial probability of cooperation \((p_{init}) < 0.5\) communities move toward global defection while \(p_{init} > 0.5\) leads to global cooperation. When \(p_{init}\) is exactly 0.5 (at reference line), cooperation and defection are equally common due to stochasticity. Note that the rate of change is asymmetric, with cooperators moving faster than defectors (cooperators play more often and therefore can change their \(p_i\) values more frequently). Lattice size \((L) = \text{neighborhood size} (n) = 501\).
With small \( \varepsilon (=0.01 \text{ or less}) \), simulations with \( p_{\text{init}} = 0.5 \) are equally likely to go to global cooperation or defection. Use of a normal distribution for players’ initial states (\( p_{\text{init}} \pm \text{random deviate} \)), rather than beginning simulations with all individuals having the same \( p_i \) value, does not alter the results, although relatively large standard deviations produce trivial initial communities containing pure defectors (\( p_i = 0 \)) that, in the absence of mutation, never change and prevent the system from achieving global cooperation. Therefore, \( p_{\text{init}} = 0.5 \) defines a saddle between stable points of global defection (\( p = 0 \)) and global cooperation (\( p = 1 \)) (Figure 1). Below this saddle point, global defection is guaranteed, while above this point global cooperation is possible, although not guaranteed.

We tested the stability of globally cooperative communities by introducing a single defector (\( p_i = 0 \)) into communities with varying \( \varepsilon \) and neighborhood sizes. Without mutation and with large neighborhoods, these communities remain cooperative, although the defector remains frozen. Simulations with small neighborhoods end in global defection as neighbors around the defector decrease their \( p_i \) values. With mutation, however, pure defectors are increased from \( p_i = 0 \) to 0.01. When neighborhood size is large, defectors are “rescued” by the surrounding cooperators.

When \( \varepsilon \) is large, individuals are relative “hot-heads,” with simulations resulting in noncooperative communities. This occurs because, by chance, some individuals will drift toward the absorbing state of \( p_i = 0 \). There exists a critical value for \( \varepsilon (\varepsilon_{\text{crit}} \approx 0.35) \) where all communities, even those of pure cooperators with low mutation rates, quickly collapse to communities of defectors as the probability of any single individual having a \( p_i = 0 \) increases toward 1. The value of \( \varepsilon_{\text{crit}} \) is dependent on lattice size, decreasing with increasing lattice size (when \( L > 1000 \)). This suggests that bistability does not exist in an infinite lattice where globally cooperative communities subjected to mutation are likely to lead to at least one pure defector (see [15]). In this infinite system, reducing the value of \( \varepsilon \) should only increase the waiting period for an individual to drift to \( p_i = 0 \), ultimately producing a system of defectors. In the finite space and discrete time of this model (tested with \( L = 1000 \) for 10,000 iterations), small \( \varepsilon (0.01) \) leads to robust communities of cooperators in which mutation reduces mean \( p \) only slightly from 1.0 and is balanced by the increases in \( p \) caused by interactions among cooperative neighbors, a condition producing bistability.

**DISCUSSION**

The results from this model suggest that global cooperative behavior is most likely when neighborhoods are large (individuals generally play with strangers) and individuals change their probability of cooperating (\( p \)) little in response to neighbor behavior (small \( \varepsilon \)). When neighborhoods are small, individuals with relatively low probabilities of cooperating tend to reduce the \( p \) of neighbors, a pattern that spreads over time and eventually leads to global defection. As individuals become more reactive to neighbor behavior (increasing \( \varepsilon \)) the probability of any individual \( p \) becoming 0, a state where global cooperation becomes impossible, increases to 1.

These results are counter to previous results found using cost-based models such as the PD in which cooperation is most likely when play is repeated.
among neighbors. Our model suggests that the emergence of cooperation is not dependent on this cost assumption and that the simple rule of tracking one's own probability of cooperating based on past experience is sufficient to lead to global cooperation.

This model may be thought to represent a simple behavior in a society where individuals use a probabilistic rule that defines how they interact with neighbors. Individuals that cooperate either increase their likelihood to cooperate in the future if neighbors are amicable or reduce their likelihood to cooperate if neighbors are disagreeable. The amount of change individuals make in response to neighbor behavior influences the likelihood the simulations reach the state of global cooperation. An example of this type of behavior might be the exchange of greetings, such as an “eyebrow flash” or smile to passing strangers. Such behaviors represent a type of interaction without apparent cost, offer no direct payoff, and may be offered to individuals that will never again be encountered (a large interaction neighborhood).

Our model suggests that if individuals interact locally, perhaps only within their family group and a few friends, the society is more likely to collapse to global defection than if individuals have larger social networks. This situation might occur when an individual, within a small neighborhood, rarely presents friendly greetings. This might lead others in the neighborhood to avoid exchanging pleasantries and eventually lead to a spread of this behavior among subgroups.

Our results are consistent with the evolution of metazoans (multicellular organisms), although change in our immortal individuals does occur over time. This differs substantially from how natural selection operates. For such life forms to arise, we can imagine the simplest scenario with some form of information exchange, or the production of byproducts, available among potentially interacting cells without necessarily invoking costs and payoffs. Our model suggests that for cooperation to be sustained among such cells, information exchange should occur over relatively long distances (e.g., diffusion of compounds through a medium). There is support for this occurring. Bacterial biofilms are formed by cell-cell communication [16]. Some bacteria secrete an intercellular homoserine lactone molecule that functions to provide information on local density. In addition, a suite of peptides also are secreted, which are collectively referred to as “quorum sensors,” that accumulate in proportion to the abundance of bacteria. Bacteria must reach sufficient densities (large neighborhoods) for sensor concentration to activate gene expression for biofilms to form [16,17]. Whether sensor production incurs significant cost remains to be determined, but the fact that bacteria secrete these substances independent of biofilm formation suggests that costs may be low.

In another bacterial system bistability of two strains of Escherichia coli has been found empirically [18] and corroborated theoretically [19,20]. Strains generally either produce or are sensitive to the allelopathic toxin colicin (effectively, defectors and cooperators, respectively) with a cost in growth rate being accrued by producers. Adding spatial structure allows colicin producers (defectors) to invade communities of the colicin-sensitive strains (cooperators). This is similar to our model in which defectors can invade cooperative communities only when there is spatial structure; otherwise both defector and cooperator communities are locally stable. Slowly adding spatial structure to cooperative communities reduces local stability until, in the limit, a pure cooperative community is an unstable equilibrium point. Unlike the model of Durrett and Levin [19], our model produces these results without attaching costs to interactions.

Filamentous cyanobacteria are a one-dimensional life-form contain specialized, nitrogen-fixing heterocysts cells that are located intermittently within strands of photosynthetic cells [21]. The location of these heterocysts is dependent on a decreasing nitrogen gradient.
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away from other heterocysts. At certain thresholds of nitrogen availability, cells along the filaments differentiate into heterocysts [21]. This is consistent with our model, which suggests that when information is transmitted over relatively long distances, systems tend toward global cooperation. Our model suggests that communication over relatively long distances (beyond neighboring cells) may also help to coordinate cooperation and organization within organisms that have two- and three-dimensional structures.

To address the maintenance of cooperation in human societies Nowak and Sigmund [12] present a model that incorporates indirect reciprocity. Their model shows that cooperation may be achieved when individuals assess the behavior of potential players. Interestingly, the model of Nowak and Sigmund [12] and our model both suggest that cooperation may be achieved through interactions among strangers. The difference between the result of Nowak and Sigmund and our result is that cooperation in our model requires no complex assessment rules of player behavior but rather emerges through maintaining a simple probability of cooperation for each individual. Although indirect reciprocity may increase the likelihood of cooperation, our results suggest that simple pairwise interactions among individuals in a population are sufficient to achieve global cooperation.

An important question is whether cooperation can evolve in this model from the state of global defection. It seems quite improbable that individuals will somehow mutate over the saddle of a mean $p$ of 0.5 and, therefore, is unlikely to emerge and impossible to evolve gradually in large communities. The state of global defection, however, may not represent the proper null scenario. As suggested by the example of biofilm-forming bacteria, communication may occur as a simple byproduct. Therefore, it may be more appropriate to consider that, in the absence of costs of cooperating, individuals have probabilities of interacting (individual $p$ values) that are randomly distributed ($0 \leq p \leq 1$), with a mean near 0.5. This could then lead to the formation of cooperative networks among individuals and would suggest that the emergence of such cooperative communities over evolutionary time would be inevitable.

In our simple model, global cooperation is most likely to arise in systems where individuals interact with many other individuals in large neighborhoods where the probability of repeated plays is low and where individuals change their own behavior little in response to these interactions. Achieving global interaction, therefore, is possible without invoking either direct or indirect reciprocity (i.e., future payback of altruistic, or costly, behavior). In addition, such a system appears to have at least some natural analogues, ranging from the grouping of bacteria into biofilms, the maintenance of different bacterial strains, to human behavior.

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