Static cooperator-defector patterns in models of the snowdrift game played on cycle graphs

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Evolutionary graph theory is an extension of evolutionary game theory in which each individual agent, represented by a node, interacts only with a subset of the entire population to which it belongs (i.e., those to which it is connected by edges). In the context of the evolution of cooperation, in which individuals playing the cooperator strategy interact with individuals playing the defector strategy and game payoffs are equated with fitness, evolutionary games on graphs lead to global standoffs (i.e., static patterns) when all cooperators in a population have the same payoff as any defectors with which they share an edge. I consider the simplest type of regular-connected graph, the cycle graph, in which every node has exactly two edges ($k = 2$), for the prisoner's dilemma game and the snowdrift game, the two most important pairwise games in cooperation theory. I show that for simplified payoff structures associated with these games, standoffs are only possible for two valid cost-benefit ratios in the snowdrift game. I further show that only the greater of these two cost-benefit ratios is likely to be attracting in most situations (i.e., likely to spontaneously result in a global standoff when starting from nonstandoff conditions). Numerical simulations confirm this prediction. This work contributes to our understanding of the evolution of pattern formation in games played in finite, sparsely connected populations.

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I. INTRODUCTION

The prisoner's dilemma game (PD) and the snowdrift game (SD) are the two main two-player games used to study the theoretical underpinnings of the evolution of cooperation (see, e.g., [1,2]). PD is often simplified by assuming one type of agent, cooperators, pays a cost c to provide a benefit b to their coplayer ($b > c > 0$) [3]. The other type of agent, defectors, pays no cost and provides no benefit. Thus mutual cooperation results in a net benefit of $R = b - c$ to each player, mutual defection results in a net benefit of $P = 0$ to each player, and when cooperation is played against defection, the defector receives a net benefit of $T = b$ while the cooperator receives a net benefit of $S = -c$ (i.e., a net cost of c) [3,4]. If these game payoffs are equated with evolutionary fitness, it is clear that defectors dominate cooperators in large, well-mixed populations because defection is the higher-paying strategy against both cooperators ($T > R$) and defectors ($P > S$) [5]. Thus evolutionary dynamics predicts that in the absence of mitigating circumstances (i.e., in large, well-mixed populations, with no reciprocity, kin selection, group selection, or green-beard effects; see [6,7]), defectors should wipe out cooperators, even though populations of cooperators have a greater mean fitness than populations of defectors ($R > P$) [8].

In the simplified SD, cooperation by either player results in both players receiving a benefit b. The total cost associated with providing this benefit is c, which is shared equally in the case of mutual cooperation, but paid outright in the case of unilateral cooperation (again, $b > c > 0$). Thus mutual cooperation results in a net benefit of $R = b - c/2$, mutual defection results in a net benefit of $P = 0$, cooperation against a defector yields a net benefit of $S = b - c$, and defection against a cooperator yields a net benefit of $T = b$ [4]. Thus, in contrast to PD, in SD $S > P$, meaning that cooperators can invade defectors and vice versa; in the absence of mitigating circumstances, cooperators and defectors are predicted to stably coexist with an equilibrium frequency of cooperators of $(P - S)/(R - S - T + P)$ [1,7,9]. Even though cooperators persist in the snowdrift game, the mean fitness of a mixed-equilibrium population of cooperators and defectors is still less than that of a population composed solely of cooperators (i.e., as with PD, there is still a social dilemma at play in SD [1,9]).

Evolutionary graph theory captures a particular type of population structure where individuals (represented by graph nodes) interact with others in their spatial or social neighborhood (connected by graph edges) [10,11]. In this framework, a focal individual at a particular node probabilistically adopts its neighbor's strategy according to a function of the mean payoffs of both the focal and neighbor individuals when interacting with the members of their respective neighborhoods [11]. (Such strategy updating can be interpreted as either competitive replacement or learning.) Thus, translating the results above into the parlance of evolutionary graph theory, on complete graphs, where every node is connected to every other node [12], PD predicts the extinction of cooperators, whereas SD predicts cooperator-defector coexistence.

When graphs are incomplete, such that interactions occur among limited subsets of individuals, the results can be quite different [10,12–14]. Depending on the nature of the interaction graph, these differences can be qualitative (e.g., the coexistence of cooperators and defectors in PD or the extinction of cooperators in SD) or quantitative (e.g., differences in the equilibrium proportion of cooperators in SD). Here my focus is on global standoffs, i.e., static patterns that occur when all edges in a graph connect either (i) cooperator-cooperator pairs, (ii) defector-defector pairs, or (iii) cooperator-defector pairs, where the cooperator and defector have the same mean payoffs within their respective neighborhoods. In an earlier paper, my co-authors and I considered regular graphs with nodes of degree $k = 3$, 4, and 6 [15]. Moreover, these graphs represented the case where populations are arrayed on a

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two-dimensional substrate in which every individual has three, four, or six nearest neighbors (lattices), respectively. Here I consider the simpler (but, contrastingly, analytically tractable) case of graphs of degree $k = 2$ (cycle graphs). This is equivalent to interactions along one dimension where every individual in the population has a left neighbor and a right neighbor. Ohtsuki and Nowak [3] derived the cost-benefit ratios that lead to one strategy being favored over the other. I take a different tack, investigating the static graphwide patterns that occur at particular cost-benefit ratios. Thus this research contributes to a number of recent studies that have considered what happens at the transition points between different phases in evolutionary dynamical systems (e.g., [15–20]).

II. CRITERIA FOR STANDOFFS

In order for a global standoff to occur, connected cooperators and defectors must have the same mean payoff within their respective neighborhoods [15]. For every cooperator-defector pair, this means that if the cooperator is connected to i cooperators ($i \in \{0, 1\}$) and the defector is connected to j cooperators ($j \in \{1, 2\}$), then $Ri + S(2 - i) = Tj + P(2 - j)$. (Note that $i < 2$ because a cooperator connected to a defector is connected to at most one cooperator when $k = 2$; similarly, $j > 0$ because a defector connected to a cooperator is connected to at least one cooperator.) To simplify matters, in PD, we can define the cost-benefit ratio $u = c/b$ and then, noting that relative rather than absolute fitness determines the outcome of evolutionary dynamics, redefine R, S, T, and P in terms of that single parameter: $R = 1$, $S = 0$, $T = 1 + u$, and $P = u$ [4]. Substituting and solving for u, we see that in PD, the potential for standoffs only occurs when $u = (i - j)/2$. Similarly, in SD, we can define the cost-benefit ratio of mutual cooperation $v = c/(2b - c)$, redefine $R = 1$, $S = 1 - v$, $T = 1 + v$, and $P = 0$ [4], and determine that the potential for standoffs only occurs when $v = (j - 2)/(i - j - 2)$.

According to the criteria above, there are four combinations of i and j that need to be examined for both PD and SD for cycle graphs. In PD, there are no valid values of u that have the potential to lead to standoffs [Table I(a)]; PD will not be considered further here. In SD, there are two valid values of v that have the potential to lead to standoffs: $v = 1/3$ and $1/2$ [Table I(b)].

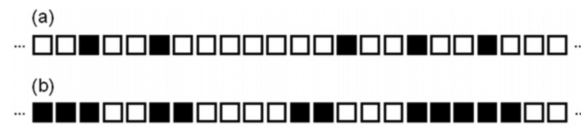

FIG. 1. Example standoffs in the snowdrift game when (a) $v = 1/3$ and (b) $v = 1/2$. Here nodes are shown as squares (black denotes a cooperator and white a defector) and edges are the borders they share. (a) For every cooperator-defector edge, the cooperator is adjacent to exactly zero other cooperators and the defector is adjacent to exactly one cooperator [see Table I(b)]. If there were longer sequences of cooperators, the terminal cooperators in the sequence would border both a cooperator and a defector. Further, if there was only one defector between two cooperators, it would by definition have two cooperators in its neighborhood. (b) For every cooperator-defector edge, both the cooperator and the defector are adjacent to exactly one cooperator [see Table I(b)].

III. STANDOFFS WHEN $v = 1/3$

In SD, when $v = 1/3$, nontrivial standoffs are only possible when all cooperators have no (other) cooperators among their neighbors and have at least two defectors between them [e.g., Fig. 1(a)]. However, if a cycle graph is initialized with any two cooperators neighboring one another (i.e., a cooperator cluster), the type of standoff given in Fig. 1(a) will probably not occur. This is because at $v = 1/3$, clusters of cooperators tend to expand at the expense of clusters of defectors and cooperator singletons (i.e., single cooperators surrounded by defectors). A hypothetical example of both situations is given in Fig. 2. In the case of a cluster of cooperators meeting a cluster of defectors, the terminal member of the cooperator cluster has a mean payoff of $(R + S)/2 = 1 - v/2 = 5/6$, whereas the terminal member of the defector cluster has a (lower) mean payoff of $(T + P)/2 = (1 + v)/2 = 2/3$, leading to growth of the cooperator cluster [Fig. 2(a)]. In the case of cooperator singletons, growing cooperator clusters tend to destroy them too. When a cluster of cooperators grows through a cluster of defectors towards the cooperator singleton, there comes a time when they have a single defector between them. This defector has a mean payoff of $2T/2 = 1 + v = 4/3$, which is greater than that of either the terminal member of the cooperator cluster (5/6, as above) or the cooperator singleton ($2S/2 = 1 - v = 2/3$). Two alternatives are possible: either (i) the terminal cooperator in the cluster is taken over by a

TABLE I. Values of u and v that could potentially lead to standoffs between cooperators C and defectors D in cycle graphs in the (a) prisoner's dilemma and (b) snowdrift games, respectively. Because $b > c > 0$, both $0 < u < 1$ and $0 < v < 1$. Therefore, there are no values of u that lead to standoffs for the prisoner's dilemma, but two values of v that potentially lead to standoffs in the snowdrift game ($v = 1/3$ and $1/2$).

	(a) Prisoner's dilemma	
	D with $j = 1$ C in neighborhood	D with $j = 2$ C in neighborhood
C with $i = 0$ C in neighborhood	$u = -1/2$	$u = -1$
C with $i = 1$ C in neighborhood	$u = 0$	$u = -1/2$
	(b) Snowdrift game	
	D with $j = 1$ C in neighborhood	D with $j = 2$ C in neighborhood
C with $i = 0$ C in neighborhood	$v = 1/3$	$v = 0$
C with $i = 1$ C in neighborhood	$v = 1/2$	$v = 0$

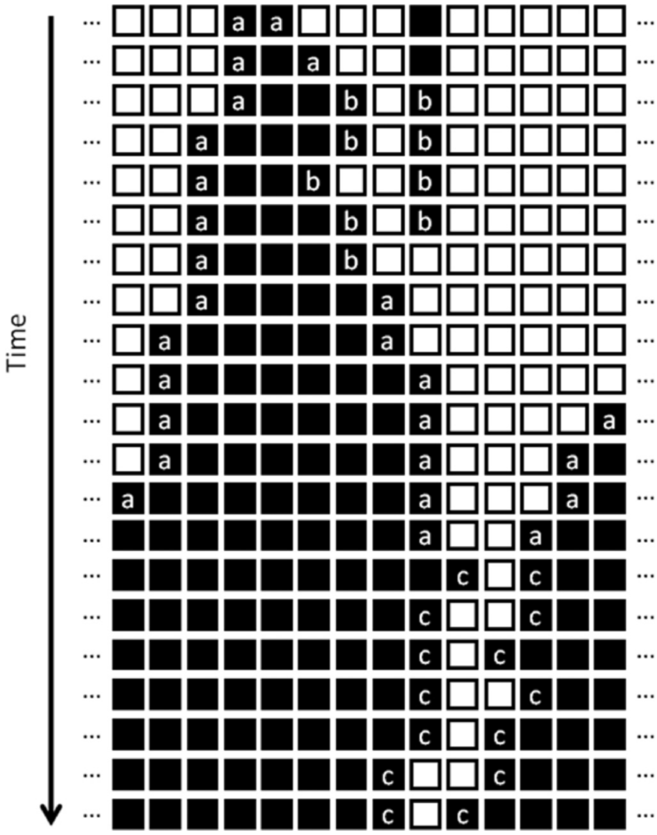

FIG. 2. Hypothetical example evolution of a graph's configuration shown through successive time steps (rows), with clones of higher-payoff nodes (squares) probabilistically and sequentially replacing the inhabitants of lower-payoff nodes (adjacent squares to the left and right), but not vice versa. Time steps in which nothing happens are omitted. (a) A cluster of cooperators (black) can grow at the expense of clusters of defectors (white) in SD when $v = 1/3$ because the terminal cooperators in the cluster have a mean payoff of $5/6$ and the terminal defectors have a mean payoff of $2/3$. (b) When a growing cooperator cluster comes close to a cooperator singleton, the defector singleton in the middle has the highest payoff ($4/3$ versus $5/6$ for the terminal cooperator and $2/3$ for the singleton cooperator). However, if the defector forms a cluster by taking over the terminal cooperator, the cooperator cluster is again at an advantage; the defectors make no further incursion. If instead the defector destroys the cooperator singleton, this opens the door for further growth of the cooperator cluster. (c) When cooperator clusters grow close to one another, they are prevented from joining by the high payoff of a single defector between them. However, this defector can never result in a defector cluster larger than two individuals. The resulting defector gap meanders between the neighboring cooperator clusters until it meets another gap; at that time, the gaps can go their separate ways or join, but they never spawn a new gap (Fig. 3). Thus, if the graph is initialized randomly, cooperators will eventually take over almost the entire graph (i.e., except for a single gap of defectors in finite graphs). This prediction was confirmed by simulation (Fig. 4).

defector, reconstituting a cooperator cluster versus defector cluster scenario in which the terminal defector is vulnerable to reinvasion by a clone of the (new) terminal cooperator, or (ii) the singleton cooperator is taken over by a defector, opening up new defector territory for further cooperator cluster growth [Fig. 2(b)].

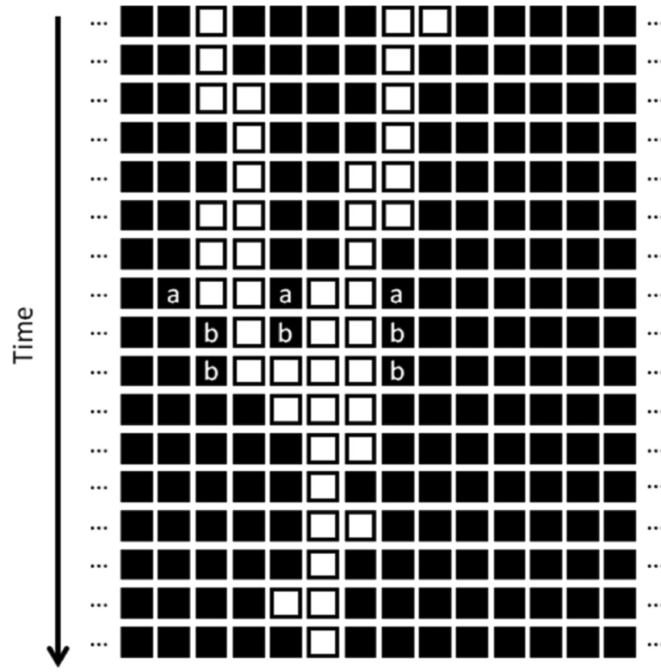

FIG. 3. Hypothetical example evolution of a graph's configuration shown through successive time steps (rows), with clones of higher-payoff nodes (squares) probabilistically and sequentially replacing the inhabitants of lower-payoff nodes (adjacent squares to the left and right), but not vice versa. Time steps in which nothing happens are omitted. (a) When two defector gaps are within one singleton cooperator of each other, the singleton cooperator and its adjacent defectors may be in temporary standoff when $v = 1/3$. (b) However, just as in Fig. 2, this standoff is vulnerable to expanding cooperator clusters from either side. Once the singleton cooperator is converted to defection, the two gaps join into one. Therefore, we expect to see the evolution towards fewer and fewer defector gaps over time.

When two growing cooperator clusters come together at $v = 1/3$, they eventually have a single defector between them; this lone defector has a higher mean payoff ($4/3$, as above) than either terminal member of the two cooperator clusters ($5/6$, as above). Thus the lone defector can grow to a cluster of two; however, it can grow no further (and, indeed, is liable to shrink back to a lone defector) because it is now a defector cluster versus two cooperator clusters. Thus there remains a one- or two-defector gap between clusters that are growing towards one another [Fig. 2(c)]. The positions of these gaps migrate as random walks between the cooperator clusters that define them.

Thus, in SD when $v = 1/3$ on cycle graphs with initial cooperator clusters, we inevitably reach a point where all the clusters have grown close to one another with short, meandering defector gaps between them. When these defector gaps meet, they tend to coalesce (Fig. 3). Given enough time, therefore, finite cycle graphs initialized with at least one cooperator cluster should be left with a single large cooperator cluster and a single small defector gap, but not a standoff.

Stochastic simulations confirm this prediction. I investigated the evolution over 10^5 time steps of 50-node cycle graphs that were initially populated with a random assortment

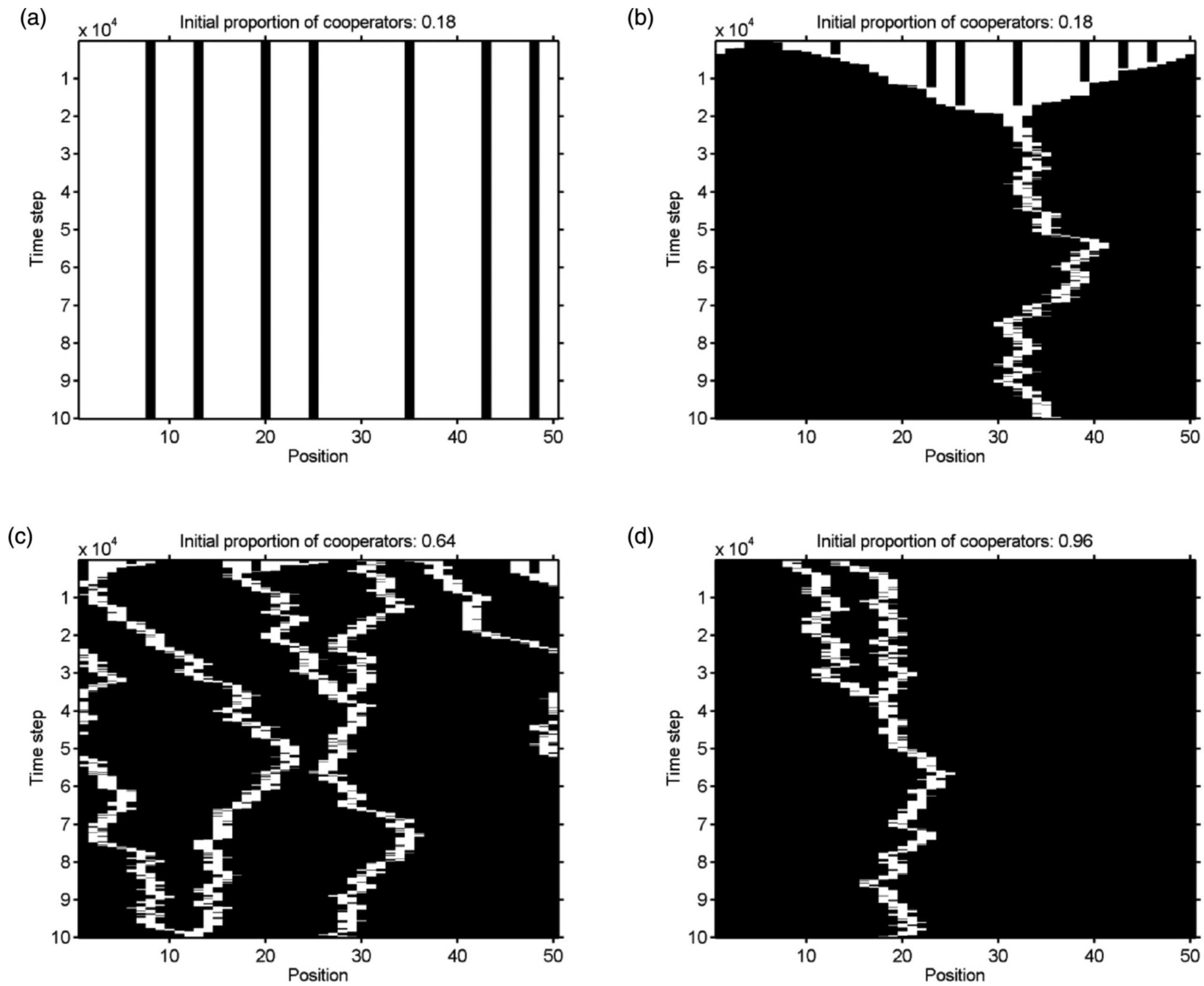

FIG. 4. Four example simulation outcomes for the evolution of 50-node cycle graphs (positions 1 and 50 are neighbors, as are any positions within 1 of one another) that initially had a random assortment of cooperators (black) and defectors (white), with $v = 1/3$ (snowdrift game). The configurations of the graphs are shown across 10^5 time steps (rows). (a) When there are no cooperator clusters initially, the graph becomes a standoff. (b)–(d) In contrast, when there are any cooperator clusters initially, they tend to grow and take over almost the entire graph.

of cooperators and defectors [for each replicate, the initial proportion of cooperators was drawn from the uniform random distribution $U(0, 1)$]. In each time step, a focal individual and one of its neighbors were chosen randomly. Their mean payoffs from playing SD within their neighborhoods, p_f and p_n, respectively, were then compared. [The cost-benefit ratio of mutual cooperation was set to $v = 1/3$; see Table I(b).] If and only if $p_n > p_f$, a clone of the neighbor took over the position occupied by the focal individual with probability $(p_n - p_f)/(1 + v)$; the denominator, being the difference between the maximum and minimum mean payoffs, ensures that this probability is between 0 and 1 [9], although note that there is actually no way for a maximum-payoff individual (a defector between two cooperators) to be beside a minimum-payoff individual (a defector between two defectors). This update procedure is usually called the replicator rule, due to its convergence with replicator dynamics in large, well-mixed populations [11,21]. Other update procedures are possible [11,22]; however, in order for true standoffs to occur, it is necessary to adopt a rational update procedure such that replacement never occurs when $p_n \leqslant p_f$.

Over 100 replicates, two patterns were noted. When the initial graph had no cooperator clusters, which happened only rarely, and only then when cooperators were initially rare, it became a standoff [Fig. 4(a)]. However, when the initial graph did have cooperator clusters (as was typical), cooperators took over almost the entire graph, except for surviving defector gaps, which tended to join together and become less numerous over time [Figs. 4(b)–4(d)]. Thus, even though $v = 1/3$ can admit standoffs in SD, they do not necessarily evolve from nonstandoff conditions; i.e., cooperator-defector standoffs may be stable, but not attracting, depending on the starting configuration.

Interestingly, though, there are some very specific initial graph configurations that are not standoffs themselves, but that can lead to standoffs. Specifically, when pairs of cooperator

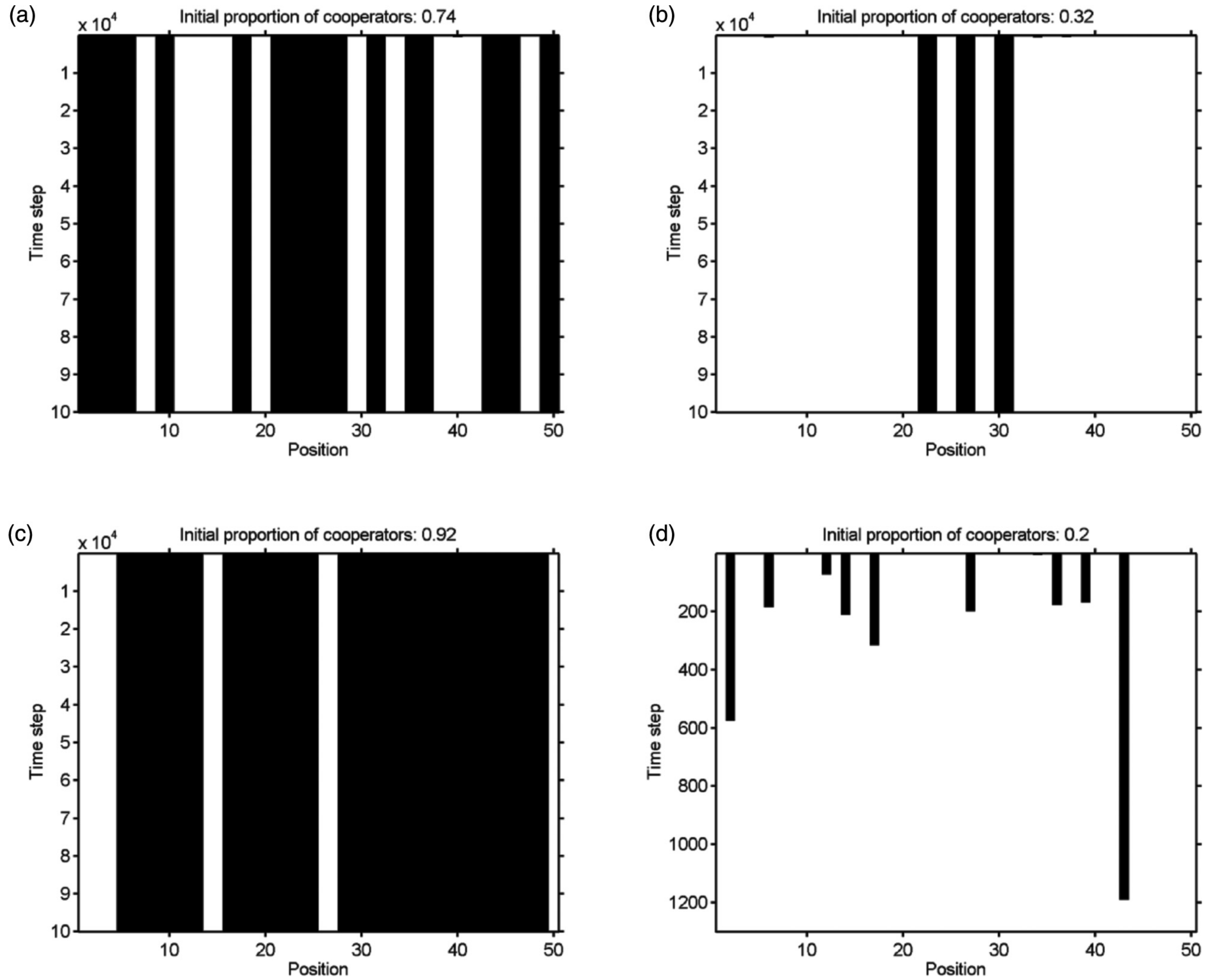

FIG. 5. Four example simulation outcomes for the evolution of 50-node $k = 2$ graphs (positions 1 and 50 are neighbors, as are any positions within 1 of one another) that initially had a random assortment of cooperators (black) and defectors (white), with $v = 1/2$ (snowdrift game). (a)–(c) The configurations of the graphs are shown across 10^5 time steps (rows), except for (d), which is shown across 1300 (the entire graph was taken over by defectors at time step 1190).

singletons have a defector singleton between them, the defector singleton can overtake one of the cooperator singletons, leading to a defector cluster and a remaining cooperator singleton. This is what occurred in the model run in Fig. 4(a). In addition to the seven cooperator singletons that persisted until the graph reached a standoff, there were also initially cooperator singletons at positions 10 and 23, two positions away from other cooperator singletons at positions 8 and 25, respectively. The cooperator singletons at positions 10 and 23 lasted for 44 and 23 time steps, respectively, not long enough to be visible in Fig. 4(a). Thus, once the cooperator singleton at position 10 was converted to a defector, this graph became a standoff.

IV. STANDOFFS WHEN $v = 1/2$

The other possible value of v that leads to standoffs in SD on cycle graphs is $v = 1/2$ [Table I(b)]. In this case, standoffs are only possible when all cooperators are in clusters (no cooperator singletons) and all such clusters are separated by at least two consecutive defectors [no defector singletons; see, e.g., Fig. 1(b)]. Unlike the $v = 1/3$ case, in the $v = 1/2$ case, such standoffs tend to emerge spontaneously from random initial configurations of the graph. When $v = 1/2$, in contrast to when $v = 1/3$, cooperators never have a higher payoff than a defector with whom they share an edge; the best they can do is a tie when a cooperator cluster abuts a defector cluster. In this case, the terminal cooperator has a payoff of $(R + S)/2 = 1 - v/2 = 3/4$ and the defector has a payoff of $(T + P)/2 = (1 + v)/2 = 3/4$. Thus defector singletons and clusters must necessarily take over all cooperator singletons until the graph is entirely composed of cooperator and defector clusters. In addition, we should expect the proportion of cooperators in the standoff to be very closely related to proportion of cooperators in the initial configuration of the graph.

Stochastic simulations confirm both of these predictions. When the models above were rerun for $v = 1/2$, standoffs were reached rapidly in every replicate [Figs. 5(a)–5(c)], except when the initial proportion of cooperators was sufficiently low that every cooperator was a singleton [in this case, the

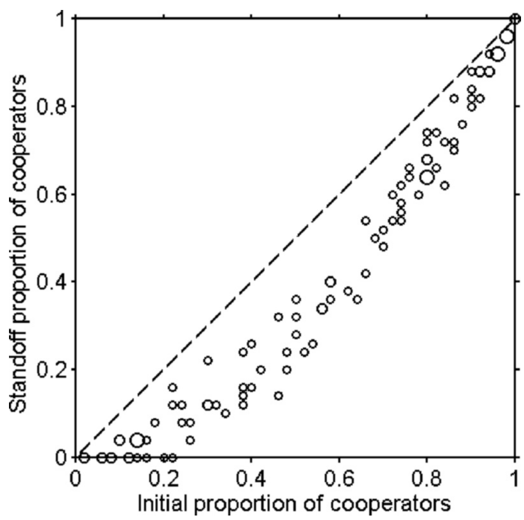

FIG. 6. For 100 simulations runs on 50-node cycle graphs, with $v = 1/2$ (snowdrift game), the standoff proportion of cooperators was significantly positively correlated with the initial proportion of cooperators (Spearman rank correlation: $r_S = 0.99$, $P < 0.0001$, and $n = 100$). The initial arrangement of cooperators and defectors was random. The symbol area is proportional to the number of overlapping points at particular coordinates. The 1:1 line is shown for visual reference; because cooperators can never overtake defectors under these conditions, all points must be on or below this line.

cooperators were rapidly wiped out by the defectors; see Fig. 5(d)]. In Fig. 5(b), the initial purging of cooperator singletons can barely be seen; in Fig. 5(d), the vertical axis has been scaled so that this purging is obvious. Additionally, the proportion of cooperators when the standoffs were reached was strongly positively correlated with the initial proportion of cooperators (Fig. 6).

V. CONCLUSIONS

Thus, to summarize, the determination of cooperator-defector standoffs in PD and SD played on cycle graphs is analytically tractable. For costs c and benefits b ($b > c > 0$), there are no valid values of $u = c/b$ (i.e., those that are between 0 and 1, exclusive) that can potentially produce a global standoff in PD [Table I(a)]. By contrast, there are two valid values of $v = c/(2b - c)$ that can potentially produce a global standoff in SD, $v = 1/3$ and $1/2$ [Table I(b)]. When $v = 1/3$, simple pattern analysis and numerical simulation demonstrate that cooperator-defector standoffs will only emerge from nonstandoff conditions if there are no initial cooperator clusters [Figs. 1(a) and 4(a)]; if there is even one cooperator cluster, it will take over almost the entire cycle graph, except for a small defector gap that cannot be eliminated [Figs. 2, 3, and 4(b)–4(d)]. Therefore, when $v = 1/3$, global standoffs are typically nonattracting. In contrast, when $v = 1/2$, the presence of any cooperator clusters leads to an attracting standoff because the terminal cooperator in a cluster will have the same payoff as the terminal defector of the defector cluster that abuts it [Figs. 1(b), 5, and 6]. Overall, this work contributes to our understanding of the evolution of pattern formation in games played in finite, sparsely connected populations.

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