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Geometry of 'standoffs' in lattice models of the spatial Prisoner's Dilemma and Snowdrift games

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HIGHLIGHTS

- Prisoner's Dilemma (PD) and Snowdrift (SD) are games used to study cooperation.
- Spatial interactions affect cooperation frequency in PD and SD.
- Certain cost–benefit ratios potentially lead to static spatial patterns (standoffs).
- Standoffs can only occur where aperiodic static patterns are possible.
- Standoffs can emerge spontaneously from non-standoff conditions.

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ABSTRACT

The Prisoner's Dilemma and Snowdrift games are the main theoretical constructs used to study the evolutionary dynamics of cooperation. In large, well-mixed populations, mean-field models predict a stable equilibrium abundance of all defectors in the Prisoner's Dilemma and a stable mixed-equilibrium of cooperators and defectors in the Snowdrift game. In the spatial extensions of these games, which can greatly modify the fates of populations (including allowing cooperators to persist in the Prisoner's Dilemma, for example), lattice models are typically used to represent space, individuals play only with their nearest neighbours, and strategy replacement is a function of the differences in payoffs between neighbours. Interestingly, certain values of the cost–benefit ratio of cooperation, coupled with particular spatial configurations of cooperators and defectors, can lead to 'global standoffs', a situation in which all cooperator–defector neighbours have identical payoffs, leading to the development of static spatial patterns. We start by investigating the conditions that can lead to 'local standoffs' (i.e., in which isolated pairs of neighbouring cooperators and defectors cannot overtake one another), and then use exhaustive searches of small square lattices (4×4 and 6×6) of degree $k = 3$, $k = 4$, and $k = 6$, to show that two main types of global standoff patterns – 'periodic' and 'aperiodic' – are possible by tiling local standoffs across entire spatially structured populations. Of these two types, we argue that only aperiodic global standoffs are likely to be potentially attracting, i.e., capable of emerging spontaneously from non-standoff conditions. Finally, we use stochastic simulation models with comparatively large lattices (100×100) to show that global standoffs in the Prisoner's Dilemma and Snowdrift games do indeed only (but not always) emerge under the conditions predicted by the small-lattice analysis.

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1. Introduction

Cooperation occurs when individuals provide a benefit to each other at a cost to themselves [1]. Cooperation among non-kin is a long-standing issue in evolutionary biology, because cooperators are vulnerable to invasion by defectors, those that accept the benefits of cooperation *from* others yet fail to provide benefits *to* others (and, in doing so, avoid the costs). Nevertheless, cooperation is both common and important in natural systems—most spectacularly in the eusocial insects and in human societies [2].

Evolutionary game theory is the main theoretical framework used to explore the evolution of cooperation [3–9]. Typically, individual cooperators and defectors interact amongst themselves and receive 'payoffs' from these interactions that influence their fitness. Payoffs depend on who interacts with whom. In the Prisoner's Dilemma, the prototypical game in cooperation studies, defection against a cooperator yields the highest payoff, followed by mutual cooperation, mutual defection, and cooperation with a defector. Regardless of what one's co-player does, it is always better to defect rather than cooperate; defection is an evolutionarily stable strategy that dominates cooperation, even though a group of cooperators has a higher mean fitness than a group of defectors [3]. Thus, the Prisoner's Dilemma is an abstraction of cooperation that evokes the inherent conflict between the interests of individuals and the interests of the populations to which they belong.

Another game with relevance to the evolutionary dynamics of cooperation is the Snowdrift game (sometimes referred to as 'hawk–dove' or 'chicken' [3,10–12]). Like the Prisoner's Dilemma, in the Snowdrift game, defection against a cooperator and mutual cooperation represent the first- and second-highest payoffs, respectively. However, in contrast to the Prisoner's Dilemma, cooperation against a defector is the third-highest payoff, with mutual defection being the worst possible outcome. This reflects the fact that in some potentially cooperative interactions, the benefit provided by a cooperator accrues not only to its co-player, but also to itself (e.g., the production of enzymes for extracellular digestion [13]). If the co-player fails to cooperate, the cooperator is stuck with paying the entire cost to receive a benefit, but so long as the value of the benefit of cooperating exceeds its cost, it is still a better outcome than mutual defection [8].

Interestingly, and counter to the Prisoner's Dilemma, in the Snowdrift game, the best strategy against a cooperator is defection and the best strategy against a defector is cooperation. Thus, in large, well-mixed populations playing the Snowdrift game, there is a stable equilibrium composed of a mixture of cooperators and defectors, with their frequencies determined by the relative costs and benefits of cooperation [4,5,11]. (In the Prisoner's Dilemma, the stable equilibrium in large, well-mixed populations is the fixation of defectors at the expense of cooperators [5].)

Several mechanisms have been proposed to explain the existence of cooperation in the Prisoner's Dilemma; to a lesser extent, the effects of these mechanisms on the prospects of cooperators and defectors in the Snowdrift game have also been examined. These mechanisms, which rely on assortative interactions among cooperators, include kin selection [14], iterated interactions [15], reputational effects [16], recognition effects (a.k.a. 'green-beard' effects [17–22]), group selection [23], and network selection [11,24–28] (see recent reviews by Nowak [1,5] and Sherratt and Wilkinson [2]). The last of these, network selection, is generalised by evolutionary graph theory [6,29], in which individuals interact with only a small subset of the entire population. In turn, this occurs due to limited social contacts or localised spatial interactions. Certain effects of localised spatial interactions (i.e., 'spatial selection') are the focus of the current study.

Spatially local interactions are most typically studied using lattice models [30]. Individual cooperators and defectors are arrayed as lattice cells with $k = 3$, 4, or 6 nearest neighbours, corresponding to the three types of regular tessellations on a plane in the context of two-dimensional geometry (i.e., those composed of tiled equilateral triangles, squares, and regular hexagons, respectively), and corresponding to regular graphs with nodes of varying degree in the context of evolutionary graph theory. Although the geometric and graph-theoretical interpretations are equivalent, here we focus on the geometrical interpretation for consistency with most previous examinations of the effects of space on the evolution of cooperation. Thus, individuals situated at a given focal cell interact with all the other individuals whose cells share a border with this focal cell; in addition, these bordering cells compose the focal cell's local neighbourhood. Furthermore, the rate of strategy replacement is proportional to the difference in payoffs between individuals situated at bordering cells.

As an aside, note that $k = 8$ lattices are also sometimes considered in studies using lattice models. In this case, space is represented by a tiled-square lattice in which cells that share a common *corner* are considered neighbours, in addition to cells that share a common *border* (i.e., the 'Moore neighbourhood' [30]). However, these are not considered here for two main reasons: First, common-corner neighbours in tiled-square lattices have a centre-to-centre distance that is greater than that of common-border neighbours by a factor of $\sqrt{2}$; in two dimensions, it is not possible for all members of an entire population to have exactly $k = 8$ equally close nearest neighbours (geometrically, this is equivalent to the fact that it is not possible to create a regular tessellation using octagons). Second, common-corner neighbours have two neighbours in common, whereas common-border neighbours have four neighbours in common. The presence of two fundamentally different types of spatial interactions greatly complicates the analyses, and also seems rather arbitrary, given that such types are not commonly considered for the other lattice types. For these two reasons, we omitted the $k = 8$ case and stuck with $k = 3$, 4, or 6.

Spatially local interactions have contrasting effects in lattice models of the Prisoner's Dilemma and Snowdrift games [26]. In the Prisoner's Dilemma, local interactions allow cooperators to persist – at least when the cost–benefit ratio of cooperation is relatively low – because, by forming clusters, cooperators interact with other cooperators more than would be expected based on their relative abundance in the population alone (thereby skewing the effective payoffs associated with the different interaction outcomes [31]). In the Snowdrift game, local interactions can cause the frequency of cooperators to be greater or less than that of the mean-field predictions (with the latter outcome occurring over a wider range of cost–benefit

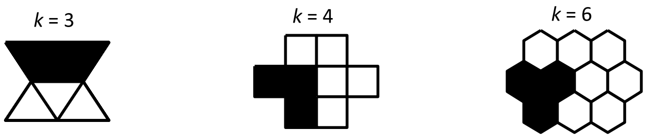

Fig. 1. Examples of the neighbourhoods surrounding the dyad C_2D_1 (middle two cells in each panel) in lattices where each cell has $k = 3$ neighbours, $k = 4$ neighbours, or $k = 6$ neighbours. Black cells are cooperators and white cells are defectors.

ratios [11,26]), although the mechanism appears to be based on limited neighbourhoods rather than spatial correlations per se [32].

Interestingly, there are some combinations of cost–benefit ratio and lattice configuration that produce 'global standoffs' (also known as 'static patterns' or 'draws' [33–35]). Global standoffs are defined as a situation where every individual in a spatially explicit population has the same payoff, or when any differences in payoffs can only lead to an unchanged spatial configuration of cooperators and defectors (i.e., because any differences in payoffs are present only between inhabitants of neighbouring cells that share the same strategy). Further, they represent the spatial situations that occur at the transition points between various dynamical 'phases' [34]. From a biological perspective, global standoffs are interesting in their own right because they can allow for the persistence of cooperators at cost–benefit ratios greater than the usual cooperator-extinction threshold. Here, we analyze the spatial configurations and model parameter values that lead to such global standoffs. We start by discussing the Prisoner's Dilemma and Snowdrift games in more formal terms. We then define local strategy configurations between pairs of interacting nodes in lattices of different degree. Next, we identify payoffs that lead to local standoffs within pairs of interacting cooperators and defectors. We then investigate the ways that such local standoffs can be 'tiled' over entire lattices to allow for global standoffs. Finally, we conduct stochastic simulation models that recapitulate many of the predicted spatial patterns for the particular standoff payoffs that we identified.

2. Prisoner's Dilemma and Snowdrift games

Generically, when two cooperators interact, they each receive the reward payoff, R. When two defectors interact, they each receive the punishment payoff, P. When a cooperator interacts with a defector, the defector receives the temptation payoff, T, while the cooperator receives the sucker's payoff, S [8].

In the Prisoner's Dilemma, cooperators pay a cost, c, in order to provide a benefit, b, to their co-player ($b > c > 0$). Defectors pay no costs and provide no benefits. Thus, for this payoff scenario, $R = b - c, P = 0, T = b$, and $S = -c$. By defining the cost–benefit ratio, $u = c/b$ (a number between 0 and 1), and by noting that relative rather than absolute payoffs are important in evolutionary dynamics, we can rescale the four payoffs as $R = 1, P = u, T = 1 + u$, and $S = 0$; this rescaling simplifies matters by defining the game in terms of a single parameter [36].

In the Snowdrift game, a benefit, b, accrues to both players, as long as at least one of them cooperates. If at least one player cooperates, a total cost c is paid (either by the sole cooperator if only one player cooperates, or shared equally by both cooperators if both players cooperate). As with the Prisoner's Dilemma, $b > c > 0$. Thus, for this payoff scenario, $R = b - c/2, P = 0, T = b$ and $S = b - c$. By defining the cost–benefit ratio of mutual cooperation, $v = c/(2b - c)$ (a number between 0 and 1), and by once again noting that relative rather than absolute payoffs are important in evolutionary dynamics, we can redefine the four payoffs as $R = 1, P = 0, T = 1 + v$, and $S = 1 - v$ [36].

3. Local spatial configurations of cooperator–defector 'dyads'

In two-player games such as the Prisoner's Dilemma and the Snowdrift game, interactions occur between pairs of players. Therefore, spatial configurations at the level of the pair are of paramount importance in the analysis of standoffs. A 'dyad', X_iY_j is defined as a pair of players playing strategies X and Y ($X, Y \in \{C, D\}$, where C and D represent cooperation and defection, respectively) that interact with one another, and which have, respectively, i and j cooperators among their k neighbours. For example, C_2D_1 is a dyad where a cooperator with two (other) cooperators in its neighbourhood interacts with a defector with one cooperator in its neighbourhood (Fig. 1).

Note that some dyads are not possible. For example, in C_iD_j dyads (i.e., those where a cooperator interacts with a defector), the focal cooperator can have *at most* $k-1$ other cooperators in its k-member neighbourhood ($0 \le i \le k-1$). Similarly, the focal defector must have *at least* 1 cooperator in *its* k-member neighbourhood ($1 \le j \le k$). Furthermore, in $k = 6$ lattices in particular, other dyads are not possible due to the fact that both members of the dyad have neighbours in common, a situation that does not exist in $k = 3$ and $k = 4$ lattices. For example, C_1D_5 is possible, but C_0D_5, C_0D_6, and C_1D_6 are not possible (Fig. 2).

Of all the possible dyads, those of the C_iD_j variety are of particular interest when addressing the phenomenon of standoffs, because they can lead to new spatial configurations (e.g., $C_iD_j \rightarrow C_{i+1}C_j$ or $C_iD_j \rightarrow D_iD_{j-1}$). By contrast, dyads of the C_iC_j and D_iD_j variety may lead to cell replacements, but these do not change the overall spatial configuration of cooperators and defectors in the lattice. Thus, it is only necessary to determine the conditions that lead to possible standoffs between cooperators and defectors.

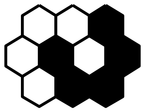

Fig. 2. In $k = 6$ lattices, the dyad C_1D_5 (*shown*) is possible (black cells are cooperators and white cells are defectors); however, C_0D_5 (*not shown*) is not possible. In order for a defector to have five cooperators in its neighbourhood, each neighbouring cooperator must have at least one cooperator in *its* neighbourhood. Likewise, C_0D_6, C_1D_6, C_4D_1, C_5D_1, and C_5D_2 are also not possible.

	D_0	D_1	D_2	D_3
C_0	0	**–1/3**	**–2/3**	**–1**
C_1	1/3	**0**	**–1/3**	**–2/3**
C_2	2/3	**1/3**	**0**	**–1/3**
C_3	1	2/3	1/3	0

(a) $k = 3$ lattices.

	D_0	D_1	D_2	D_3	D_4
C_0	0	**–1/4**	**–1/2**	**–3/4**	**–1**
C_1	1/4	**0**	**–1/4**	**–1/2**	**–3/4**
C_2	1/2	**1/4**	**0**	**–1/4**	**–1/2**
C_3	3/4	**1/2**	**1/4**	**0**	**–1/4**
C_4	1	3/4	1/2	1/4	0

(b) $k = 4$ lattices.

	D_0	D_1	D_2	D_3	D_4	D_5	D_6
C_0	0	**–1/6**	**–1/3**	**–1/2**	**–2/3**	–5/6	–1
C_1	1/6	**0**	**–1/6**	**–1/3**	**–1/2**	**–2/3**	–5/6
C_2	1/3	**1/6**	**0**	**–1/6**	**–1/3**	**–1/2**	**–2/3**
C_3	1/2	**1/3**	**1/6**	**0**	**–1/6**	**–1/3**	**–1/2**
C_4	2/3	1/2	**1/3**	**1/6**	**0**	**–1/6**	**–1/3**
C_5	5/6	2/3	1/2	**1/3**	**1/6**	**0**	**–1/6**
C_6	1	5/6	2/3	1/2	1/3	1/6	0

(c) $k = 6$ lattices.

Fig. 3. Values of the cost–benefit ratio, $u = c/b$, for which cooperators with i (other) cooperators in their k-member neighbourhood (C_i, rows) have the same payoff as defectors with j cooperators in *their* k-member neighbourhood (D_j, columns) for the spatial Prisoner's Dilemma, played on (a) $k = 3$ lattices, (b) $k = 4$ lattices, and (c) $k = 6$ lattices. Dark-grey shaded areas denote unacceptable values of u (because $0 < u < 1$). Cells with bolded values represent possible spatial configurations (the others are impossible). The value of each cell is computed as $(i - j)/k$.

4. Identifying payoffs that lead to local standoffs in C_iD_j dyads

A 'local standoff' between a cooperator with i (other) cooperators among its k neighbours and a defector with j cooperators among *its* k neighbours occurs when the focal cooperator and defector have equal total payoffs, i.e., when $Ri + S(k - i) = Tj + P(k - j)$. In the Prisoner's Dilemma, this occurs when

$$u = (i - j)/k. \quad (1)$$

In the Snowdrift game, this occurs when

$$v = (j - k)/(i - j - k). \quad (2)$$

There are several constraints to these values of u and v for them to potentially allow for spatial standoffs:

First, all of i, j, and k must be integers. This confines the critical u and v values in Eqs. (1) and (2) to a small set of rational numbers.

Second, as discussed in the previous section, lattice geometry precludes certain combinations of i and j in C_iD_j dyads. This further shrinks the set of critical values of u and v.

Third, in order to be a proper Prisoner's Dilemma game, u must be between 0 and 1; similarly, in order to be a proper Snowdrift game, v must also be between 0 and 1 [36]. Given Eqs. (1) and (2), and these first three constraints, it is straightforward to identify u values and v values for which local cooperator–defector standoffs are possible in the Prisoner's Dilemma (Fig. 3) and the Snowdrift game (Fig. 4), respectively.

A value of u (or v) for which the members of *particular* C_iD_j dyads experience a local standoff is necessary, but not sufficient, for standoff conditions to prevail across an entire lattice (i.e., a 'global standoff'). For this to occur, it must be possible for *all* C_iD_j dyads in a lattice to simultaneously experience local standoffs.

	D_0	D_1	D_2	D_3
C_0	1	**1/2**	**1/5**	**0**
C_1	3/2	**2/3**	**1/4**	**0**
C_2	3	**1**	**1/3**	**0**
C_3	Parallel	2	1/2	0

(a) $k = 3$ lattices.

	D_0	D_1	D_2	D_3	D_4
C_0	1	**3/5**	**1/3**	**1/7**	**0**
C_1	4/3	**3/4**	**2/5**	**1/6**	**0**
C_2	2	**1**	**1/2**	**1/5**	**0**
C_3	4	**3/2**	**2/3**	**1/4**	**0**
C_4	Parallel	3	1	1/3	0

(b) $k = 4$ lattices.

	D_0	D_1	D_2	D_3	D_4	D_5	D_6
C_0	1	**5/7**	**1/2**	**1/3**	**1/5**	1/11	0
C_1	6/5	**5/6**	**4/7**	**3/8**	**2/9**	**1/10**	0
C_2	3/2	**1**	**2/3**	**3/7**	**1/4**	**1/9**	**0**
C_3	2	**5/4**	**4/5**	**1/2**	**2/7**	**1/8**	**0**
C_4	3	5/3	**1**	**3/5**	**1/3**	**1/7**	**0**
C_5	6	5/2	4/3	**3/4**	**2/5**	**1/6**	**0**
C_6	Parallel	5	2	1	1/2	1/5	0

(c) $k = 6$ lattices.

Fig. 4. Values of the cost–benefit ratio of mutual cooperation, $v = c/(b - c)$, for which cooperators with i (other) cooperators in their k-member neighbourhood (C_i, rows) have the same payoff as defectors with j cooperators in *their* k-member neighbourhood (D_j, columns) for the spatial Snowdrift game, played on (a) $k = 3$ lattices, (b) $k = 4$ lattices, and (c) $k = 6$ lattices. Dark-grey shaded areas denote unacceptable values of v (because $0 < v < 1$). Cells with bolded values represent possible spatial configurations (the others are impossible). The value of each cell is computed as $(j - k)/(i - j - k)$. Note that the payoff for C_k is always greater than the payoff for D_0 (i.e., their payoffs, as functions of v, are parallel when $i - j - k = 0$); at any rate, such configurations are impossible in lattice models.

5. Finding global standoffs in the spatial Prisoner's Dilemma and Snowdrift games

One way to determine the existence and nature of lattice configurations that lead to global standoffs is to consider every possible configuration of lattices of a given size. For square lattices with $N = L \times L$ individuals, the number of possible configurations is 2^N (granted, many of these are isomorphic). For this reason, the largest lattices that we could reasonably examine exhaustively were 4×4 lattices, for a total of $2^{16} = 65{,}536$ configurations. (By comparison, 5×5 lattices have $2^{25} \approx 3.36 \times 10^7$ configurations and 6×6 lattices have $2^{36} \approx 6.87 \times 10^{10}$ configurations.) Although 4×4 lattices are rather small, they are very useful in identifying the nature of spatial patterns that exist in global standoffs. In order to avoid edge effects, we considered lattices with periodic boundary conditions (i.e., tori).

Additionally, we also considered two special cases of 6×6 lattices (again with periodic boundary conditions): (1) those in which all possible 4×4 lattices are surrounded by single layer of defectors, and (2) those in which all possible 4×4 lattices are surrounded by a single layer of cooperators. These additional (larger) lattices allow for the identification of the types of standoffs that appeared to be typical in preliminary stochastic simulation models (and in other studies, such as Perc's investigation into the effect of 'cumulative advantage' in the Public Goods game [35]); i.e., those where 'islands' of cooperators (or defectors) are surrounded by a 'sea' of defectors (or cooperators).

Thus, for all the 4×4 lattices and the two subsets of 6×6 lattices, we screened for global standoff conditions for each unique, bolded, and non-grey-shaded value of u and v in Fig. 3 (Prisoner's Dilemma) and Fig. 4 (Snowdrift game), respectively. Out of this total of $65{,}536 \times 3 \times 41 = 8{,}060{,}928$ lattices, only 1709 were global standoffs (122 in the Prisoner's Dilemma and 1587 in the Snowdrift game).

Appendix A (supplementary data) shows these 1709 global standoffs for the small lattices examined. These results emphasise an interesting facet of global standoffs: namely, two qualitatively different types of global standoffs are possible. The first type is the 'periodic' global standoff, in which a small-scale spatial pattern is repeated ad infinitum (or at least until it can loop back on itself due to periodic boundary conditions). The second type is the 'aperiodic' global standoff, in which small-scale spatial patterns need not be repeated. Note that in our subsets of 6×6 lattices, the sea of cooperators or defectors means that it is only possible to detect aperiodic global standoffs, but the 4×4 lattices can detect both periodic and aperiodic spatial patterns (although the aperiodic patterns must still be surrounded by a sea). Importantly, while periodic global standoffs are stable by definition, they are unlikely to emerge spontaneously from a series of strategy replacements – especially in large lattices – because they require the coordination of cells' strategy types over long distances. On the other hand, aperiodic global standoffs do not require long-distance strategy coordination; rather, they only require the coordination of cells within a small local cluster.

Thus, we predicted that those local-standoff parameter values (Eqs. (1) and (2)) that lead only to periodic global standoffs (or no global standoffs at all) for certain configurations of 4×4 and 6×6 lattices should not lead to the spontaneous emergence of global standoffs in much larger lattices representing large populations of stochastically interacting cooperators and defectors. (Note that this prediction relies on the intuitive but unverified assumption that such parameter values do not admit aperiodic global standoffs whose spatial patterns are too large to fit within the confines of the 4×4 or 6×6 lattices we examined.) We further predicted that parameter values that can admit aperiodic global standoffs for certain configurations of our small lattices have the potential to lead to the spontaneous emergence of global standoffs in large mixed-strategy populations.

We tested these predictions using stochastic simulation models. The models described here are essentially those of Doebeli and Hauert [26], albeit for particular parameter values (shown as bold, un-shaded values of u and v in Figs. 3 and 4, respectively). Space was represented by a 100×100 cell lattice with periodic boundaries (i.e., a torus). At the start of each model run, cells were assigned randomly and independently to be either cooperators or defectors. The probability of initially being a cooperator was set to 0.1, 0.5, or 0.9. During each time step, a focal cell, X, was selected randomly for potential replacement by a clone of another cell, Y, selected randomly from X's k neighbours. The total payoffs to the members of this focal dyad, after playing the Prisoner's Dilemma or the Snowdrift game with each of their respective k neighbours, were designated P_X and P_Y. If $P_X \geq P_Y$ there was no replacement. However, if $P_Y > P_X$, then Y's strategy was adopted by X with a probability of $(P_Y - P_X)/(k(1 + r))$, where $r = u$ for the Prisoner's Dilemma and $r = v$ for the Snowdrift game (the denominator scales the probability between 0 and 1 in this birth–death process). There was no mutation, which naturally would tend to break up standoffs if sufficiently frequent.

A model generation was defined as 10^4 time steps, such that every individual was a focal individual and a potentially replacing neighbour once each per generation, on average. For each parameter value and each starting cooperator-frequency, 10 replicates of the models were run until (1) a global standoff was reached, (2) either cooperators or defectors went extinct (which are actually trivial sorts of global standoff, but which will not be considered global standoffs for our purposes here), or (3) 10^5 generations had elapsed, whichever came first.

6. Results

In the main text, detailed results are given for the Prisoner's Dilemma only. A summary of the major results for the Snowdrift game is given in the main text, with detailed results available in Appendix B (supplementary data).

6.1. Global standoffs in the spatial Prisoner's Dilemma

6.1.1. Prisoner's Dilemma on $k = 3$ lattices

In $k = 3$ lattices, there is only one valid value of u that produces local standoff conditions: $u = 1/3$ (Fig. 3(a)). In this case, the only possible local standoff between cooperators and defectors occurs in C_2D_1 dyads. Therefore, in order for a global standoff to occur, every cooperator–defector dyad in the lattice must be of the form C_2D_1. (Recall that cooperator–cooperator and defector–defector dyads are immaterial in the analysis of standoff conditions.) The small-lattice analysis identified three general spatial patterns that lead to global standoff conditions: (1) Parallel stripes or zigzags of cooperators and defectors, (2) clusters of cooperators surrounded by defectors, and (3) clusters of defectors surrounded by cooperators (Fig. 5). Type-(1) patterns (Fig. 5(a), (b)) are periodic, and therefore unlikely to be attracting. Type-(2) and-(3) patterns (Fig. 5(c)–(f), respectively) are aperiodic and therefore more likely to emerge spontaneously from non-standoff initial conditions. Note that type-(2) and-(3) patterns can lead to rings of defectors and cooperators (e.g., Fig. 5(e)), when observed from the perspective of the non-clustering strategy.

In the simulation models for $u = 1/3$, when the initial proportion of cooperators was 0.1, the cooperators went extinct within 18–42 model generations across the 10 replicates (Fig. 6(a)). Conversely, for the 20 replicates for which the initial proportion of cooperators was 0.5 or 0.9, a global standoff was reached within 66–120 and 107–157 model generations, respectively. When the initial proportion of cooperators was 0.5, sparse overlapping-hexagon islands of cooperators remained in a sea of defectors (i.e., aperiodic global standoffs; Fig. 6(b)). When the initial proportion of cooperators was 0.9, complex aperiodic patterns emerged (Fig. 6(c)). In accordance with our predictions, periodic global standoffs were not observed.

Ancillary simulations involving much larger lattices suggest that the variance in outcome among model runs started with varying initial proportions of cooperators may be due to finite size effects: In 10 replicates of 1000×1000 lattices with an initial proportion of cooperators of 0.1, half resulted in overlapping-hexagon standoffs, while the rest resulted in cooperator extinction (not shown).

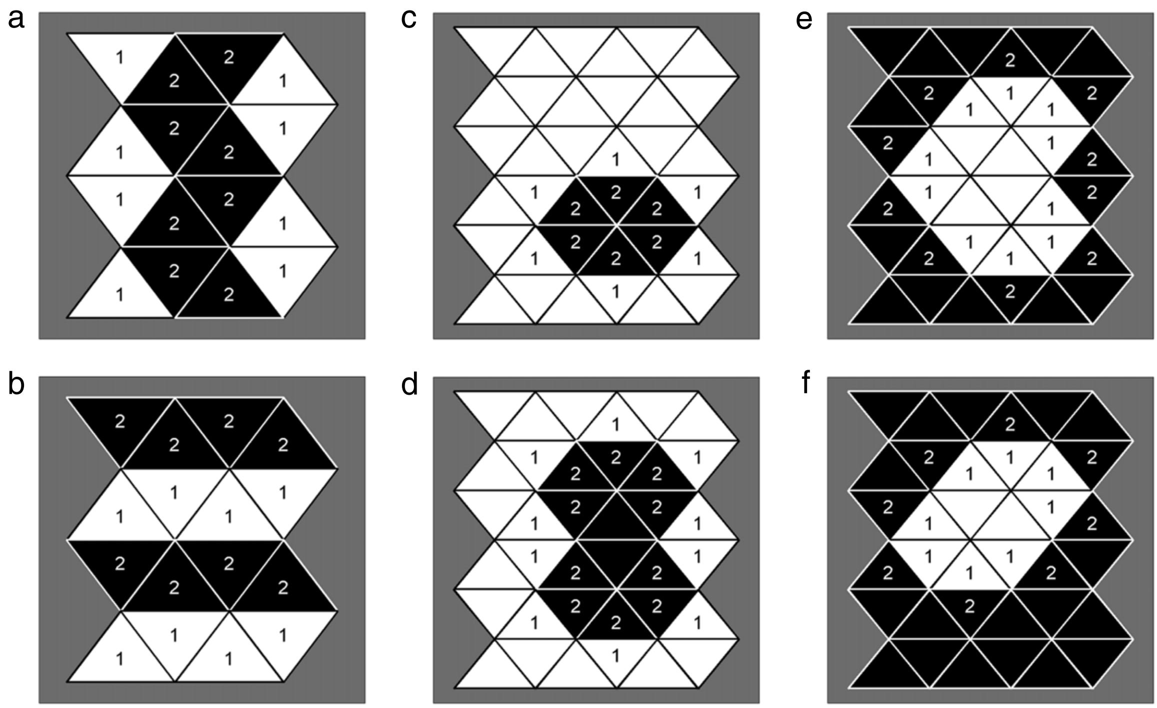

Fig. 5. Examples of global standoffs in the Prisoner's Dilemma when $k = 3$ and $u = 1/3$ (with periodic boundary conditions). Black cells are cooperators and white cells are defectors. Note that every cooperator that shares a border with a defector (black cells with numbers) has exactly two neighbouring cooperators and that every defector that shares a border with a cooperator (white cells with numbers) has exactly one neighbouring cooperator, as predicted in Fig. 3(a). (Cooperators that do not share a border with a defector have exactly three neighbouring cooperators and defectors that do not share a border with a cooperator have exactly zero neighbouring cooperators; however, these are not involved in any lattice-configuration changes.) (a), (b) Examples of periodic patterns (zigzags or stripes). (c)–(f) Examples of aperiodic patterns, where clusters of cooperators or defectors are surrounded by rings of defectors or cooperators, respectively. For all the possible global standoffs that occur in 4 × 4 or the examined subsets of 6 × 6 lattices, see Appendix A.

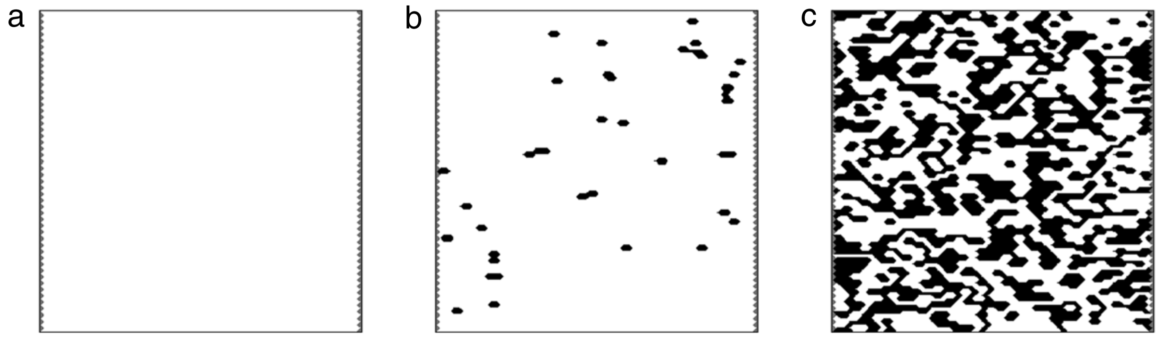

Fig. 6. Examples of outcomes of stochastic simulation models for the Prisoner's Dilemma when $k = 3$, $u = 1/3$, and the initial proportion of cooperators was (a) 0.1, (b) 0.5, or (c) 0.9. There are a total of 10,000 cells (100 × 100); black cells are cooperators and white cells are defectors. (b) and (c) are global standoffs between cooperators and defectors; (a) is a trivial standoff in which cooperators have gone extinct.

6.1.2. Prisoner's Dilemma on $k = 4$ lattices

In $k = 4$ lattices, there are two values of u that produce local standoff conditions: $u = 1/4$ and $u = 1/2$ (Fig. 3(b)). In the case of $u = 1/4$, there are two possible cooperator–defector dyads that can result in local standoffs: C_2D_1 and C_3D_2. Therefore, in order for a global standoff to occur, every cooperator–defector dyad in the lattice must either be of the form C_2D_1 or C_3D_2. The small-lattice analysis demonstrated two main ways that this can occur: (1) single cell-width stripes of cooperators or defectors (Fig. 7(a), (d)), or (2) 2 × 2 squares of cooperators surrounded by defectors, or defectors surrounded by cooperators (Fig. 7(b), (c)). The former case is periodic, and therefore unlikely to be attracting; however, the latter case is aperiodic and therefore has the potential to lead to the spontaneous emergence of global standoffs in mixed-strategy populations that start with non-standoff conditions.

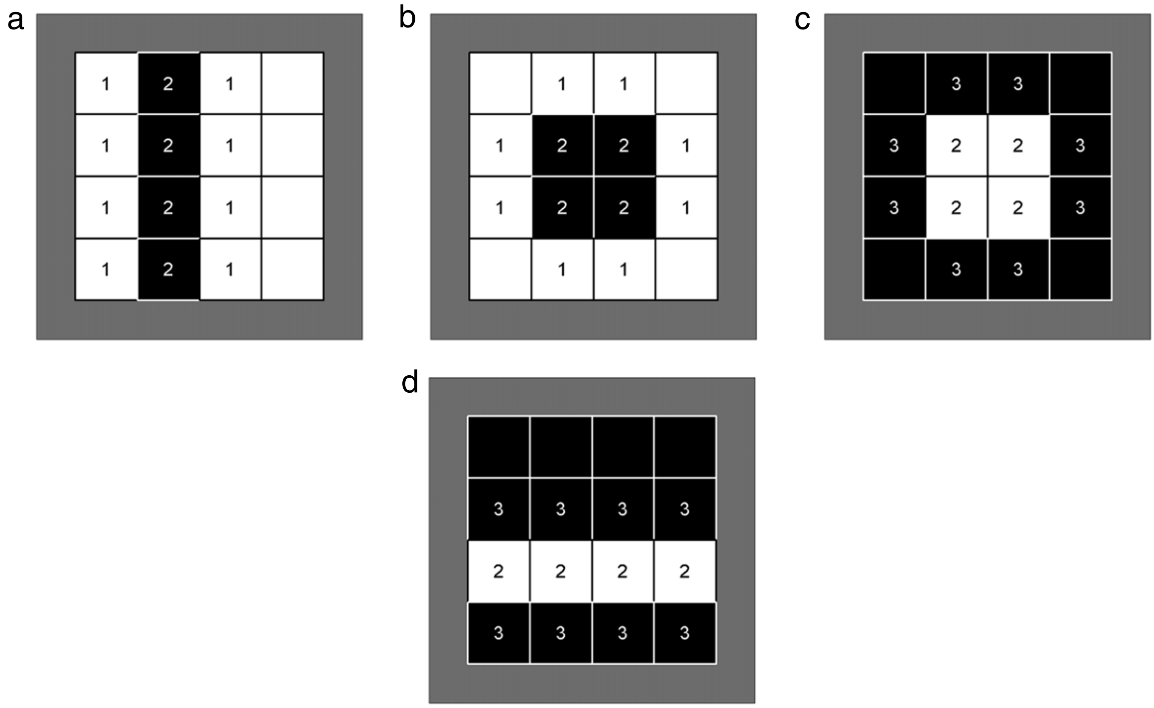

Fig. 7. Examples of global standoffs in the Prisoner's Dilemma when $k = 4$ and $u = 1/4$ (with periodic boundary conditions). Black cells are cooperators and white cells are defectors. Note that every cooperator–defector dyad is either of the form (a), (b) C_2D_1 or (c), (d) C_3D_2, as predicted in Fig. 3(b). (a) and (d) are examples of periodic patterns (stripes), whereas (b) and (c) are examples of aperiodic patterns (2 × 2 squares of cooperators surrounded by defectors of defectors surrounded by cooperators). For all the possible global standoffs that occur in 4 × 4 or the examined subsets of 6 × 6 lattices, see Appendix A.

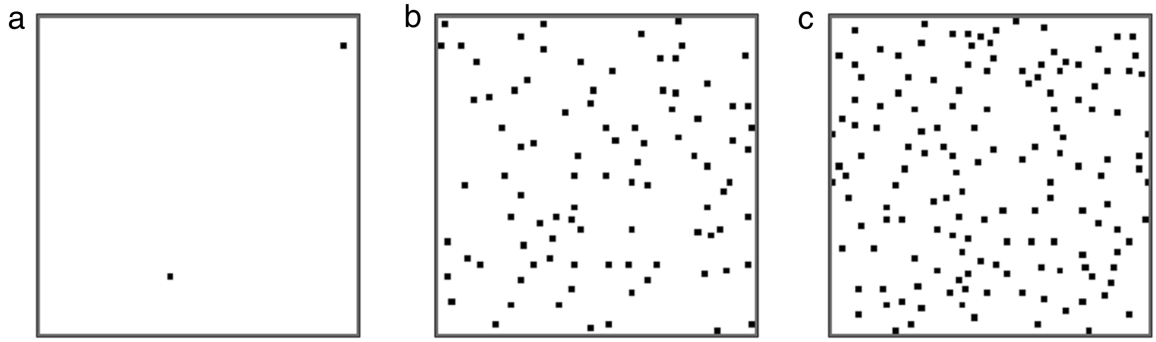

Fig. 8. Examples of outcomes of stochastic simulation models for the Prisoner's Dilemma when $k = 4$, $u = 1/4$, and the initial proportion of cooperators was (a) 0.1, (b) 0.5, or (c) 0.9. There are a total of 10,000 cells (100 × 100); black cells are cooperators and white cells are defectors. All three panels depict global standoffs between cooperators and defectors (black squares are 2 × 2 cooperator clusters). Note that the outcome in panel (a) was one possible outcome; starting with a proportion of cooperators of 0.1 cooperator extinction also occurred frequently.

All thirty of the stochastic simulations for $u = 1/4$ reached a global standoff (or cooperator extinction) within 21–44, 179–321, and 446–681 model generations for initial proportions of cooperators of 0.1, 0.5, and 0.9, respectively. When the initial proportion of cooperators was 0.1, the cooperators sometimes went extinct (six of 10 replicates), but in other cases held out in a very small number of 2 × 2 islands in a sea of defectors (i.e., global standoffs; Fig. 8(a)). When the initial proportion of cooperators was 0.5 or 0.9, the cooperators persisted 10 out of 10 times each, but again as 2 × 2 islands (Fig. 8(b), (c)). As predicted, periodic global standoffs were not observed in the stochastic simulation models.

In a similar manner to what we noted in $k = 3$ lattices, the frequent extinction of cooperators that we observed in 100 × 100 lattices with $k = 4$, $u = 1/4$, and a starting proportion of cooperators of 0.1, was much rarer in 1000 × 1000 lattices with equivalent starting conditions; indeed, in 10 replicates of these larger lattices, all 10 resulted in 2×2 cooperator-island standoffs, rather than cooperator extinction (not shown).

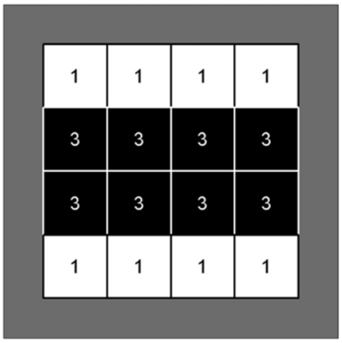

Fig. 9. An example global standoff in the Prisoner's Dilemma when $k = 4$ and $u = 1/2$ (with periodic boundary conditions). Black cells are cooperators and white cells are defectors. Note that every cooperator–defector dyad is of the form C_3D_1, as predicted in Fig. 3(b). The only global standoff patterns that can exist under these conditions are periodic ones; specifically those of alternating parallel stripes of cooperators and defectors of a thickness of at least two cells. For all the possible global standoffs that occur in 4×4 or the examined subsets of 6×6 lattices, see Appendix A.

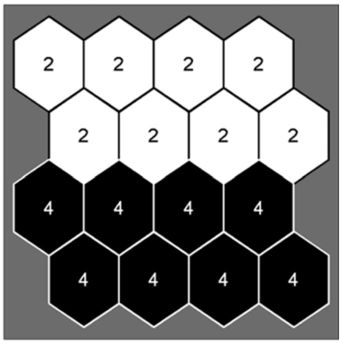

Fig. 10. An example global standoff in the Prisoner's Dilemma when $k = 6$ and $u = 1/3$ (with periodic boundary conditions). Black cells are cooperators and white cells are defectors. Note that every cooperator–defector dyad is of the form C_4D_2, one of the configurations predicted in Fig. 3(b). The only global standoff patterns that can exist under these conditions are periodic ones; specifically those of alternating parallel stripes of cooperators and defectors of a thickness of at least two cells. For all the possible global standoffs that occur in 4×4 or the examined subsets of 6×6 lattices, see Appendix A.

In the case of $u = 1/2$, there is only one cooperator–defector dyad that results in a local standoff: C_3D_1 (Fig. 3(b)). The only way this can occur is through perfectly straight cooperator–defector borders; specifically, lattices composed of alternating parallel stripes of cooperators and defectors of a thickness of at least two cells (Fig. 9). This is a periodic pattern and therefore unlikely to be attracting.

In accordance with this, in all thirty of the stochastic simulations for $u = 1/2$, the cooperators went extinct within 18–24, 30–49, and 70–94 model generations for initial proportions of cooperators of 0.1, 0.5, and 0.9, respectively (the resulting all-defector lattices are not shown).

6.1.3. *Prisoner's Dilemma on $k = 6$ lattices*

In $k = 6$ lattices, there are two values of u that produce local standoff conditions: $u = 1/6$ and $u = 1/3$ (Fig. 3(c)). When $u = 1/6$, there are four possible cooperator–defector dyads that can result in local standoffs: C_2D_1, C_3D_2, C_4D_3, and C_5D_4 (Fig. 3(c)). Therefore, in order for a global standoff to occur, every cooperator–defector dyad in the lattice must be in one of those four forms. No possible standoffs occurred in the exhaustive search of 4×4 lattices or the subsets of 6×6 lattices. (However, see Section 7 for two periodic global standoffs found in an ad hoc manner for 8×8 lattices.)

As predicted by the small-lattice search, no global standoffs emerged spontaneously in stochastic simulations. In all thirty of the stochastic simulations for $u = 1/6$, the cooperators went extinct within 26–59, 2261–7454, and 4517–7416 model generations for initial proportions of cooperators of 0.1, 0.5, and 0.9, respectively (the resulting all-defector lattices are not shown).

When $u = 1/3$, there are three possible cooperator–defector dyads that can result in local standoffs: C_3D_1, C_4D_2, and C_5D_3 (Fig. 3(c)). In the exhaustive search of small lattices, the only way this was found to occur is through perfectly straight cooperator–defector borders of type C_4D_2; specifically, lattices composed of alternating parallel stripes of cooperators and defectors of a thickness of at least two cells (Fig. 10). This is a periodic pattern and therefore unlikely to be attracting.

Once again as predicted, no global standoffs were observed for $u = 1/3$. In all thirty of the stochastic simulations for $u = 1/3$, the cooperators went extinct within 18–26, 41–64, and 135–189 model generations for initial proportions of cooperators of 0.1, 0.5, and 0.9, respectively (the resulting all-defector lattices are not shown).

6.1.4. Summary of global standoffs in the spatial Prisoner's Dilemma

In accordance with our prediction, global standoffs emerged in the simulations only when aperiodic patterns were found to be possible in the analysis of small lattices. Specifically, this occurred in $k = 3$ lattices when $u = 1/3$, in $k = 4$ lattices when $u = 1/4$, and not at all in $k = 6$ lattices (see Appendix A for details). In most cases, the spatial patterns that accompanied global standoffs in the Prisoner's Dilemma were composed of small, isolated cooperator clusters (e.g., Fig. 6(b), 8); However, in $k = 3$ lattices with $u = 1/3$, lattices initialised with mostly cooperators produced highly convoluted standoff mixtures of cooperators and defectors (e.g., Fig. 6(c)).

A summary of the Prisoner's Dilemma results is given in Fig. 11, including potential standoff conditions, compared with the non-standoff conditions across the entire range of possible values of u (in increments of 0.01). This comparison yields a number of interesting observations:

(1) When $k = 3$ and $u = 1/3$ (Fig. 11(a)), non-trivial standoffs were observed except when the starting cooperator frequency was low (0.1), in which case trivial standoffs were observed (i.e., cooperator extinction). Non-trivial standoffs allowed cooperators to persist at a much greater frequency than at near-by values of u (e.g., $u = 0.33$ and 0.34; Fig. 11(a), line). In addition, the standoff value of $u = 1/3$ is also the maximum value of u for which cooperators can persist at all; above this value, defectors dominate (Fig. 11(a)).

(2) A similar link between a potential standoff value of u and the critical value of u for cooperator persistence is noted for lattices with $k = 6$, $u = 1/6$ (Fig. 11(c)). These links are unsurprising, given that standoff values of u are also the exact (and only) values of u where competitive reversals occur (e.g., for $k = 6$, the payoffs of the different spatial configurations are ranked $D_6 > C_6 > D_5 > C_5 > D_4 > C_4 > D_3 > C_3 > D_2 > C_2 > D_1 > C_1 > D_0 > C_0$ for $0 < u < 1/6$, $D_6 > C_6 = D_5 > C_5 = D_4 > C_4 = D_3 > C_3 = D_2 > C_2 = D_1 > C_1 = D_0 > C_0$ for $u = 1/6$, and $D_6 > D_5 > C_6 > D_4 > C_5 > D_3 > C_4 > D_2 > C_3 > D_1 > C_2 > D_0 > C_1 > C_0$ for $1/6 < u < 1/3$; also see the discussion of 'transition points' in Refs. [33,37], 'phase transitions' in Ref. [38], 'draws' and 'static patterns' in Ref. [34], and 'superpersistence' in Ref. [35]).

(3) When $k = 4$ and $u = 1/4$ (Fig. 11(b)), non-trivial standoffs were observed except in six of the 10 model runs for which initial cooperator was low (0.1), in which case cooperator extinction was observed (although, as noted above, this appears to be a finite size effect). The non-trivial standoffs occurred in a region of u-values that otherwise did not allow for cooperator–defector coexistence; other than at $u = 1/4$, cooperators are dominated by defectors at values of u above approximately 0.07 (Fig. 11(b)).

6.2. Global standoffs in the spatial Snowdrift game

As with the Prisoner's Dilemma, in the Snowdrift game, and once again in accordance with our prediction, non-trivial global standoffs emerged in the simulations only for those cost–benefit ratios for which aperiodic standoff patterns were possible in the analysis of small lattices (e.g., Fig. B.14). However, the reverse was often not true: In a number of cases, even though aperiodic standoff patterns were possible, global standoffs did not emerge spontaneously from non-standoff conditions. The reason for this is that for many critical cost–benefit ratios, the long-term frequency of cooperators in the lattice remains either too high or too low for a particular global standoff to be possible. For example, for $k = 3$ lattices with $v = 1/2$, aperiodic global standoffs whose C–D dyads are of the form C_0D_1 are possible (Fig. 4(a)). This can occur via the very simple spatial pattern where single cooperator islands are isolated in a sea of defectors (Appendix A). Nevertheless, in the majority of cases, standoffs did not occur under these conditions in the simulation models (Fig. B.5(a)–(c)). In this case, the long-term frequency of cooperators is typically too high to allow such an isolated-cooperator pattern to occur. This assertion is supported by the exception to the trend of no global standoffs in $k = 3$ lattices with $v = 1/2$, which only occurred when the starting proportion of cooperators was sufficiently low (0.1) to allow them to be isolated, and even then only occasionally (Fig. B.5(d)).

Appendix B provides details of the Snowdrift game results.

7. Caveats

There are at least four caveats to consider:

First, if the values of u or v do not exactly balance the payoffs of cooperators and defectors, or if these values fluctuate over time, then the spatial configuration of a population will be unstable. However, if competitive replacement (or strategy-updating due to social learning) is positively related to the difference in the payoffs between members of a dyad, then values of u or v close to the balance point would cause a population's spatial configuration to change very slowly (i.e., a 'pseudo-standoff'). For instance, such patterns are seen in Ref. [33].

Secondly, if the topology of interactions is not described by a lattice, but rather by a regular or regular-random network, small-world network, or some other social network of average degree k [6,29], then it will be difficult to predict whether standoff conditions are likely, without considering each pair of connected nodes separately. However, this does not imply that standoff conditions cannot exist in such networks—indeed, they can; it merely means that the methods described here would need to be extended in order to analyze them.

Thirdly, (1) if individuals are motile, rather than sedentary, (2) if they experience occasional strategy mutations, or (3) if they sometimes undergo 'irrational' strategy change even when $P_X \geq P_Y$, then standoff conditions are likely to be broken

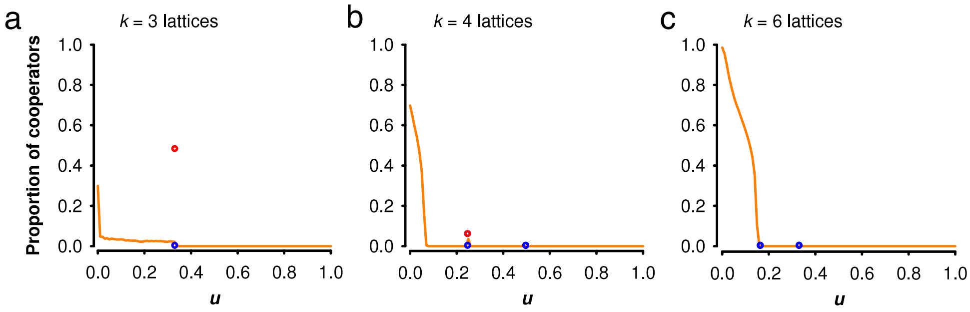

Fig. 11. Symbols give the proportion of cooperators at the ends of model runs for possible standoff values of the cost–benefit ratio, u for the Prisoner's Dilemma when (a) $k = 3$ ($u = 1/3$), (b) $k = 4$ ($u = 1/4$, $1/2$), or (c) $k = 6$ ($u = 1/6$, $1/3$); see Fig. 3, main text. Each critical value of u has a pair of symbols associated with it: Upper symbols for each value of u show the maximum percentage of cooperators across 30 model runs (with varying starting proportions of cooperators); lower symbols show the minimum percentage of cooperators across 30 model runs. (In some cases the upper and lower symbols overlap.) Red symbols accompany those values of v for which a non-trivial standoff was reached (i.e., for some model runs of $k = 3$, $u = 1/3$ and $k = 3$, $u = 1/4$ only). Blue symbols accompany those values of u for which a trivial standoff was reached (i.e., cooperator extinction). For comparison purposes, orange lines show the mean proportion of cooperators between generations 5000 and 6000 (5 replicates) for u in increments of 0.01 (starting with cooperator frequency of 0.5). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

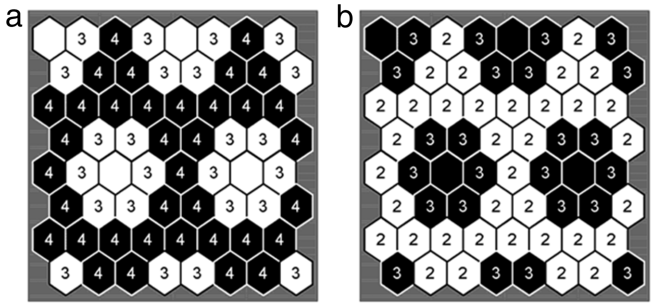

Fig. 12. Examples of global standoffs in the Prisoner's Dilemma when $k = 6$ and $u = 1/6$ (with periodic boundary conditions). Black cells are cooperators and white cells are defectors. Note that every cooperator–defector dyad is either of the form (a) C_4D_3 or (b) C_3D_2, among the possibilities predicted in Fig. 3(c). Both are periodic patterns.

up by individuals swapping locations with one another, by individuals moving to entirely new locations, or by individuals randomly adopting a new strategy. Thus, the analyses described here are most consistent with populations of sedentary organisms attached to a two-dimensional substrate with rare mutation and mostly deterministic replacement. However, depending on the relative rates of interaction, movement, mutation, and irrationality, spatial standoffs could occur in motile, mutation-prone, or irrational populations too—at least temporarily.

Fourthly, there may be larger-scale standoffs then the methods presented in Section 5 are able to detect (e.g., periodic 8 × 8 pattern in Fig. 12). Nevertheless, given the results in Section 6, if these larger-scale standoffs exist, and if they are aperiodic, they are apparently very improbable lattice configurations in stochastically interacting populations that are randomly initialised.

8. Conclusions

Spatial population structure is thought to be one of the main ways that the mean-field predictions of the Prisoner's Dilemma can be circumvented, allowing for cooperators to persist despite the ever-present temptation to defect [24–26,33,37]. Additionally, spatial structure can also greatly affect the long-term proportion of cooperators and defectors in another important game used to study the evolution of cooperation, the Snowdrift game [11,26,32]. Here, we considered the cost–benefit ratios of cooperation that have the potential to lead to global standoffs in lattice models of the Prisoner's Dilemma and the Snowdrift game, and then showed that this potential is often realised by the spontaneous emergence of global standoffs in lattices that were randomly initialised with the cooperator and defector strategies and stochastically updated. However, in many other cases, these critical cost–benefit ratios were insufficient to ensure that a global standoff actually arose in stochastic models; in such cases, either (1) lattice geometry precluded any global standoffs from occurring (i.e., there is no way to tile the necessary local configurations over the entire population), (2) standoffs were not precluded by lattice geometry, but were necessarily periodic in nature and therefore unlikely to be attracting, or (3) aperiodic standoffs were possible but could only occur when the frequency of cooperators was greater or less than what was actually experienced by populations at the particular cost–benefit ratio in question. Altogether, our research contributes to the wider goal of understanding how local interactions that occur at the neighbourhood scale can produce a range of static and dynamic spatial patterns at the population scale. Subsequent research should include investigations into whether, and under what circumstances, other types of population structure (i.e., non-lattice networks) and other games (e.g., N-player games like the Public Goods game [39]) admit the spontaneous formation of global standoffs.

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Appendix. Supplementary data

Supplementary material related to this article can be found online at http://dx.doi.org/10.1016/j.physa.2013.04.008.

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