

Sixty replicates were obtained for each of these randomly distributed networks. These were then overlaid with species distributional data to analyse the number of gap species in each case. See Supplementary Information for the confidence intervals for each of the models.

Richness of protected and unprotected cells

The richness of each quarter-degree cell touching land (outside Antarctica) was calculated for all species, restricted-range species¹⁶ (occupying $\leq 50,000 \text{ km}^2$) and threatened species. Cells touching protected areas were considered 'protected'. Protected cells are significantly ($P < 0.001$) biased towards higher richness of all, restricted-range and threatened species. See Supplementary Information for a comparison of frequency distributions.

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Correspondence and requests for materials should be addressed to A.S.L.R. (a.rodrigues@conservation.org).

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Spatial structure often inhibits the evolution of cooperation in the snowdrift game

Christoph Hauert & Michael Doebeli

Departments of Zoology and Mathematics, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4, Canada

Understanding the emergence of cooperation is a fundamental problem in evolutionary biology¹. Evolutionary game theory^{2,3} has become a powerful framework with which to investigate this problem. Two simple games have attracted most attention in theoretical and experimental studies: the Prisoner's Dilemma⁴ and the snowdrift game (also known as the hawk–dove or chicken game)⁵. In the Prisoner's Dilemma, the non-cooperative state is evolutionarily stable, which has inspired numerous investigations of suitable extensions that enable cooperative behaviour to persist. In particular, on the basis of spatial extensions of the Prisoner's Dilemma, it is widely accepted that spatial structure promotes the evolution of cooperation^{6–8}. Here we show that no such general predictions can be made for the effects of spatial structure in the snowdrift game. In unstructured snowdrift games, intermediate levels of cooperation persist. Unexpectedly, spatial structure reduces the proportion of cooperators for a wide range of parameters. In particular, spatial structure eliminates cooperation if the cost-to-benefit ratio of cooperation is high. Our results caution against the common belief that spatial structure is necessarily beneficial for cooperative behaviour.

The Prisoner's Dilemma illustrates that cooperating individuals are prone to exploitation, and that natural selection should favour cheaters. In this game, two players simultaneously decide whether to cooperate or defect. Cooperation results in a benefit b to the recipient but incurs a cost c to the donor ($b > c > 0$). Mutual cooperation thus pays a net benefit of $R = b - c$, whereas mutual defection results in payoff $P = 0$ for both players. With unilateral cooperation, defection yields the highest payoff, $T = b$, at the expense of the cooperator bearing the cost $S = -c$. It follows that it is best to defect regardless of the co-player's decision. Thus, defection is the evolutionarily stable strategy, even though all individuals would be better off if they all cooperated. This outcome is a simple consequence of the ranking of the four payoff values: $T > R > P > S$. Despite this seemingly convincing argument, many natural species show altruism, with individuals bearing costs to the benefit of others: vampire bats share blood⁹, alarm calls warn from predators¹⁰, monkeys groom each other¹¹, and fish inspect predators preferably in pairs¹².

In field and experimental studies it is often difficult to assess the fitness payoffs for different behavioural patterns, and even the proper ranking of the payoffs is challenging^{13,14}. This has led to a considerable gap between theory and experimental evidence, and to an increasing discomfort with the Prisoner's Dilemma as the only model to discuss cooperative behaviour^{15,16}. The snowdrift game is a viable and biologically interesting alternative. It differs from the Prisoner's Dilemma in that the payoffs P and S have a reverse order: $T > R > S > P$. This changes the situation fundamentally and leads to persistence of cooperation.

To illustrate the snowdrift game, imagine two drivers that are caught in a blizzard and trapped on either side of a snowdrift. They can either get out and start shovelling (cooperate) or remain in the car (defect). If both cooperate, they have the benefit b of getting home while sharing the labour c . Thus, $R = b - c/2$. If both defect, they do not get anywhere and $P = 0$. If only one shovels, however, they both get home but the defector avoids the labour cost and gets

$T = b$, whereas the cooperator gets $S = b - c$. If costs are high ($2b > c > b > 0$), these payoffs recover the Prisoner's Dilemma. By contrast, if $b > c > 0$, the payoffs generate the snowdrift game, in which the best action depends on the co-player: to defect if the other cooperates, but to cooperate if the other defects. This leads to stable coexistence of cooperators and defectors in well-mixed populations.

According to the replicator dynamics¹⁷, the equilibrium frequency of cooperators in the snowdrift game is $1 - r$, where $r = c/(2b - c)$ is the cost-to-benefit ratio of mutual cooperation. Note, however, that the average population payoff at evolutionary equilibrium is smaller than the average payoff in a population of only cooperators, as in the Prisoner's Dilemma. Thus, the paradox of cooperation is also apparent in the snowdrift game.

An important insight is that spatial structure can promote persistence of cooperation. In particular, if the Prisoner's Dilemma is played in spatially structured populations, in which individuals interact only within a limited local neighbourhood, then cooperation can be maintained. Here we investigate the effects of spatial structure in the snowdrift game. To model spatial structure, we assume that individuals occupy sites on a regular lattice. Whenever a site is updated, the present occupant and its nearest neighbours compete to populate the site with their offspring. Generalizing the replicator dynamics to lattices, competitive success is determined according to differences between the payoffs that each potential parent obtained from game interactions with their nearest neighbours. Updating can be synchronous across the lattice, describing populations with discrete, non-overlapping generations, or asynchronous, describing populations with overlapping genera-

tions in continuous time (see Methods).

Intriguingly, spatial structure fails to enhance cooperation in the snowdrift game and actually tends to reduce the proportion of cooperators. Figure 1 shows equilibrium proportions of cooperators in spatial populations as a function of the cost-to-benefit ratio $r = c/(2b - c)$. Only for small r (high benefits, low costs) is the proportion of cooperators higher than the $1 - r$ expected in well-mixed populations (Fig. 1, dotted line). By contrast, spatial structure favours defectors for larger r . The threshold above which the proportion of defectors is higher than in well-mixed populations depends on the lattice geometry (Fig. 1) and decreases with increasing neighbourhood size N . In all cases, cooperation is eliminated altogether for sufficiently high r , which is again in stark contrast to the well-mixed case. Ultimately, these results are due to the small interaction neighbourhoods in spatially structured populations. Although the qualitative results do not depend on the exact number of neighbours N , some quantitative features do, such as the extinction thresholds for cooperators and defectors (Fig. 1). For example, cooperators vanish near the r value for which a single cooperator in a given neighbourhood constitutes a higher frequency of cooperation than the well-mixed expectation, that is, for which $1/N > 1 - r$.

For an intuitive understanding of the contrary effects of spatial structure in the Prisoner's Dilemma and in the snowdrift game, it is useful to look at snapshots of spatial configurations at stochastic equilibrium near the extinction threshold of cooperators (see Virtual Labs in evolutionary game theory: <http://www.univie.ac.at/virtuallabs>). In the spatial Prisoner's Dilemma, cooperators can survive by forming large, compact clusters (Fig. 2a), thus reducing exploitation by defectors. By contrast, in the spatial snowdrift game cooperators form small filament-like clusters (Fig. 2b). These spatial patterns arise from microscopic processes that are dictated by the payoff structure of the snowdrift game, which makes it advantageous to adopt strategies that are opposite to neighbouring strategies. As a consequence, an isolated cooperator acts as a seed for expanding dendritic structures, but lacks the ability to give rise to compact clusters (Fig. 2c). On average, these emergent spatial

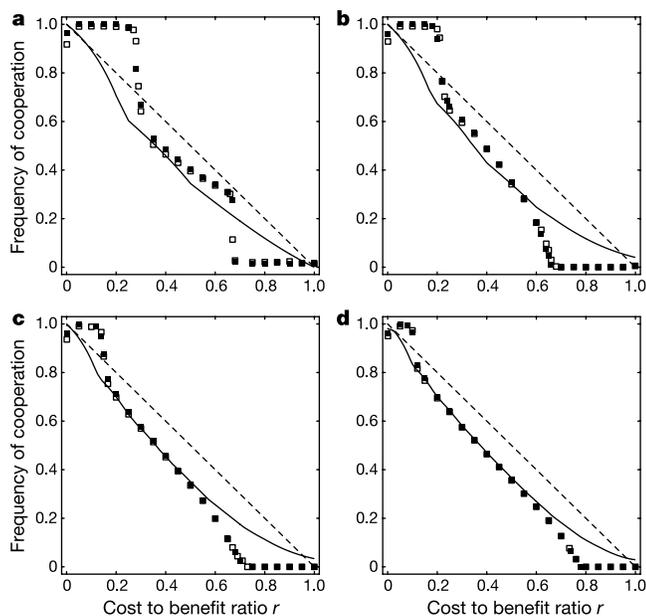


Figure 1 Frequency of cooperators as a function of the cost-to-benefit ratio $r = c/(2b - c)$ in the snowdrift game for different lattice geometries. **a**, Triangular lattice, neighbourhood size $N = 3$; **b**, square lattice, $N = 4$; **c**, hexagonal lattice, $N = 6$; **d**, square lattice, $N = 8$. For small r , spatial structure promotes cooperation; however, for intermediate and high r , the fraction of cooperators is lower than in well-mixed populations (dotted line). This result is largely independent of whether updating is synchronous (filled squares) or asynchronous (open squares). The tendency is correctly predicted by pair approximations (unbroken line), but pair approximation underestimates the effects of local configurations at high and low r . In individual-based simulations, the range of coexistence of cooperators and defectors is delimited by two threshold values: below r_1 defectors vanish, whereas above r_2 cooperators are doomed. Both thresholds correlate with the fate of local configurations: near r_1 defector pairs tend to annihilate and vanish, whereas near r_2 single cooperators and cooperator pairs cannot survive in a sea of defectors. See Methods for simulation details.

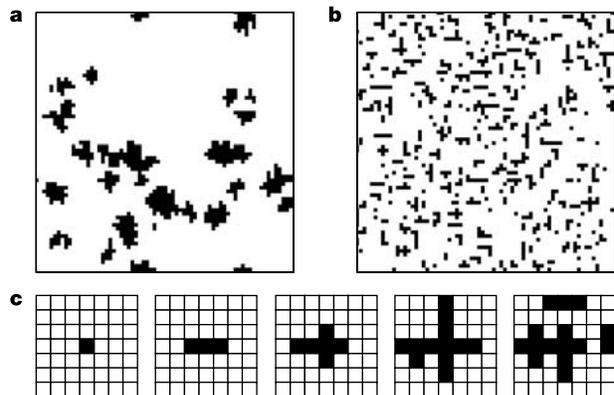


Figure 2 Snapshots of equilibrium configurations of cooperators (black) and defectors (white) in the spatial Prisoner's Dilemma and spatial snowdrift game on a square lattice with $N = 4$ neighbours near the extinction threshold of cooperators. **a**, In the Prisoner's Dilemma, cooperators survive by forming compact clusters ($R = 1$, $T = 1.07$, $S = -0.07$, $P = 0$). **b**, In the corresponding snowdrift game, cooperators are spread out, forming many small and isolated patches ($r = 0.62$; that is, $R = 1$, $T = 1.62$, $S = 0.38$, $P = 0$). This result also holds for other lattice structures (not shown). **c**, Microscopic pattern formation in the spatial snowdrift game. An isolated cooperator can grow into a row of cooperators and then form cross-like structures; however, cooperators cannot expand to compact clusters because the payoff structure protects the defectors in the corners. Eventually, cooperators form a dendritic skeleton. Occasionally, dendrites break off to form new seeds.

patterns generate an advantage for defectors, owing to increased exploitation in the fractal-like zone of contact between the two strategies. This leads to an overall reduction in cooperators as compared with well-mixed populations.

The relevant spatial pattern formation is most evident near the extinction threshold of cooperators, that is, in the parameter region in which the detrimental effects of spatial structure on cooperation are most pronounced. For lower values of the cost-to-benefit ratio r , additional mechanisms that favour cooperation start to be important. For example, despite the fact that it is always better to adopt strategies that are opposite to neighbouring strategies, it is clearly advantageous to have cooperating neighbours. Accordingly, clustering of cooperators can lead to the extinction of defectors for low r , which is in line with the established view that spatial structure should benefit cooperation. We have confirmed the results from our individual-based models using the technique of pair approximation (see Methods and Supplementary Information). Results from this deterministic approximation of the spatial dynamics (Fig. 1, unbroken line) are in good agreement with the stochastic simulations. We also note that our main findings are robust with respect to variations in lattice geometry, in synchrony of updating and in update rules (see Supplementary Information).

When studying cooperation, it is often useful to allow for continuously varying degrees of cooperative behaviour, which can be achieved by considering mixed strategies describing an individual's propensity to cooperate. This approach has been often applied to the hawk–dove game^{3,18}, a version of the snowdrift game traditionally used in behavioural ecology: when competing for resources or mates, hawks escalate conflicts, whereas doves are conciliatory. When two doves meet they share the resource β and

both get $R = \beta/2$, but when facing an escalating hawk the dove takes flight ($S = 0$) and the hawk gets the whole resource ($T = \beta$). If two hawks meet, they escalate until one is injured and incurs a fitness loss γ ($\gamma > \beta$). Escalation thus yields, on average, $P = (\beta - \gamma)/2 < 0$. With $b = (\beta + \gamma)/2$ and $c = \beta$, this game is equivalent to the snowdrift game in the sense that the payoff matrices only differ by a constant, so that update rules based on payoff differences yield identical results. In particular, for the replicator dynamics in well-mixed populations, the evolutionarily stable mixture consists of r hawks and $1 - r$ doves, where $r = \beta/\gamma$. This game can be viewed as a mixed strategy game, in which one individual adopts the behavioural patterns of hawk and dove with specific probabilities¹⁹. In correspondence with the pure strategy game, the evolutionarily stable mixed strategy plays dove with a probability $1 - r$.

We have investigated the mixed-strategy hawk–dove game in spatially structured populations (see Methods). For synchronously updated populations (Fig. 3, filled squares), spatial structure systematically lowers the probability to show dove-like behaviour. In particular, cooperation vanishes for high r , for which all conflicts escalate. For $N = 3$ this happens for $r \geq 0.8$ (Fig. 3a), whereas the corresponding well-mixed populations (Fig. 3a, dotted line) support up to 20% dove-like behaviour. This effect decreases for increasing N , such that results for $N = 8$ (Fig. 3d) are essentially indistinguishable from well-mixed populations. With asynchronous updating (Fig. 3, open squares), the effects of spatial structure are negligible, independent of the lattice geometry and neighbourhood size.

Our results show that spatial extension generally fails to promote cooperative behaviour in the hawk–dove or snowdrift game. In fact, with the exception of small cost-to-benefit ratios, spatial structure tends to reduce the level of cooperation. In contrast to the Prisoner's Dilemma, the snowdrift game is a simple model for the evolution of cooperation when defection is not an evolutionarily stable strategy. We therefore conclude that spatial structure may be rarely beneficial, but often detrimental, to cooperation in such schemes.

It is generally thought that any form of associative interactions, such as those that are due to kinship²⁰, discrimination²¹ or "population viscosity"²², which includes spatial structure, would favour the evolution of cooperation (see refs 23, 24, for some exceptions). Such associations can lead to the formation of clusters of cooperators that can maintain cooperation against defecting invaders at the cluster boundaries²⁵. However, this mechanism does not operate in the spatial hawk–dove and snowdrift games. Ironically, the ultimate reason for this is that cooperation is already maintained in the well-mixed versions of these games, because the payoffs are such that it is best to adopt strategies that differ from the strategies of the opponents. This hinders cluster formation of cooperators in spatial populations.

Even though determination of payoff matrices in real systems is notoriously difficult, our results may be relevant for many natural populations. For example, predator inspection in sticklebacks is an often cited application of the Prisoner's Dilemma¹², but only the payoff ranking $T > R > S$ has been experimentally confirmed¹³. If P turns out to be less than S , predator inspection would actually be a snowdrift game. Similarly, RNA phages engage in Prisoner's Dilemma interactions in cells¹⁴, but selection alters the payoff structure, leading to stable coexistence of cooperating and defecting types in a snowdrift game²⁶. Other well-known examples of potential snowdrift or hawk–dove games include alarm calls in meerkat¹⁰ and fighting in large ungulates²⁷. Cooperation seems to be ubiquitous in meerkat, whereas serious escalations of fights seem to be common in musk ox. Because costs of alarm calls seem to be small¹⁰, whereas costs of forgoing reproduction are high, both observations are in agreement with our results that space should benefit cooperation for low cost-to-benefit ratios, but should lead to more frequent escalations for high ratios.

Overall, our results indicate that spatial extension of natural

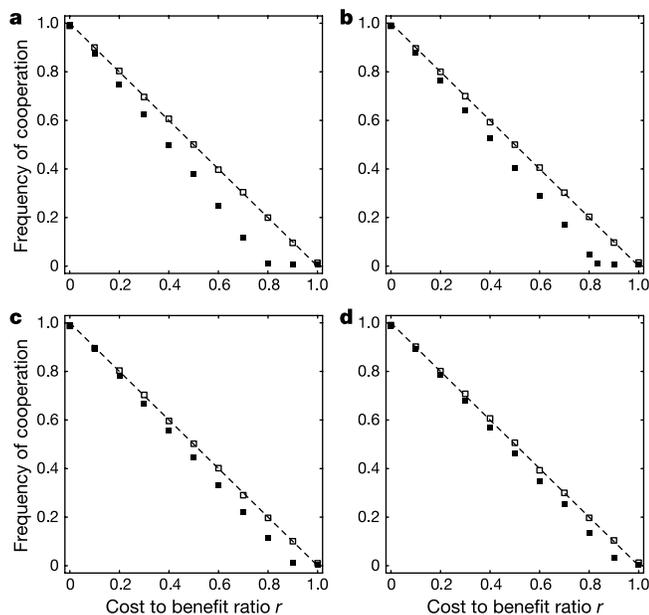


Figure 3 Average mixed strategy at stochastic equilibrium in the spatial hawk–dove game as a function of the parameter $r = \beta/\gamma$ for different lattice geometries. **a**, Triangular lattice, neighbourhood size $N = 3$; **b**, square lattice, $N = 4$; **c**, hexagonal lattice, $N = 6$; **d**, square lattice, $N = 8$. For synchronous updates (filled squares), spatial structure systematically increases the frequency of hawk-like behaviour as compared with well-mixed populations (dotted line). This effect becomes more pronounced for smaller N . By contrast, spatial structure barely affects the equilibrium strategy for asynchronous updates (open squares). See Methods for simulation details. Note that the equilibrium proportion of hawk-like behaviour in the mixed-strategy case is generally different from the equilibrium proportion of hawks in the pure strategy case (see Fig. 1). This contrasts with well-mixed populations, where the evolutionarily stable equilibrium is the same in both cases.

populations may decrease cooperation and lead to more frequent escalations of conflicts in situations in which cooperation persists in well-mixed populations. Thus, spatial structure may not be as universally beneficial for cooperation as previously thought. □

Methods

Spatial structure

In our spatially structured populations, individuals are confined to sites on regular 100×100 lattices with periodic boundary conditions, and interact with their neighbours. We used square lattices with $N = 4$ and $N = 8$ neighbours, hexagonal lattices ($N = 6$) and triangular lattices ($N = 3$). Whenever a site x is updated, a neighbour y is drawn at random among all N neighbours; the chosen neighbour takes over site x with probability $w_y = f(P_y - P_x)$, where the function f translates payoff differences into reproductive success, reflecting natural selection based on relative fitness. The site x remains unchanged, with probability $1 - w_y$. Lattice updating can be either synchronous or asynchronous. For synchronous updates, first all individuals interact in their respective neighbourhood and then all sites are updated simultaneously through competition with a randomly chosen neighbour. For asynchronous updates, only a single, randomly selected focal site is updated at each simulation step: first the payoffs of the focal individual and a random neighbour are determined, after which these two individuals compete to re-populate the focal site. See Supplementary Information for the case where competition involves all neighbours, rather than just a randomly chosen one.

Pure strategies

With pure strategies, each individual is either a cooperator or a defector. Lattices are initialized randomly with equal proportions of the two strategies. $f(z) = z_+/\alpha$ determines the transition probabilities, where z_+ is equal to z if $z > 0$ and 0 otherwise, and where $\alpha = T - P$ in the snowdrift game and $\alpha = T - S$ in the Prisoner's Dilemma, ensuring that $f(P_y - P_x) \leq 1$. In well-mixed populations this implements the replicator dynamics¹⁷. Equilibrium frequencies of cooperators and defectors are obtained by averaging over 1,000 generations after a relaxation time of 5,000 generations.

The individual-based spatial models are complemented by deterministic pair-approximation (ref. 28 and see Supplementary Information). This approach correctly predicts a decrease in the frequency of cooperators in spatially structured populations, but it underestimates the effects of local correlations: for larger r the fragility of cooperative clusters is underrated, as is the ability of cooperators to displace defectors for small r (Fig. 1). Near the extinction thresholds, interesting symmetrical dynamics occur: tiny patches of defectors (cooperators) meander in a sea of cooperators (defectors). Occasionally they divide into pairs or collide and vanish. This resembles a branching and annihilating random walk, which suggests that there are critical phase transitions and points to interesting relationships between game theory and condensed matter physics²⁹.

Mixed strategies

For mixed strategies in the hawk–dove game, an individual is characterized by the probability p to show dove-like behaviour. Exploration of this continuous strategy space requires mutations. Whenever an individual with strategy p reproduces, a mutation occurs with a small probability (0.01) that assigns the offspring the strategy $p + \xi$, where ξ denotes a gaussian-distributed random variable with a mean of 0 and an s.d. of 0.002. To speed up simulations, the lattice is initialized with random strategies drawn from a normal distribution with a mean corresponding to the equilibrium strategy in well-mixed populations and an s.d. of 0.02. The simulation results are insensitive to the initialization details.

An individual in x with strategy p interacting with a neighbour with strategy q gets an average payoff $P_x = pqR + p(1 - q)S + (1 - p)qT + (1 - p)(1 - q)P$. The small difference in the strategies of parents and mutant offspring leads to small payoff differences $P_y - P_x$ between neighbouring individuals. Thus, the update rule for pure strategies returns small probabilities for a strategy change, which slows down the simulations. We therefore used the nonlinear function $f(z) = [1 + \exp(-z/\kappa)]^{-1}$, in which κ is a noise term that reflects uncertainties in assessing the payoffs. This nonlinearity greatly speeds up the simulations and introduces an interesting and realistic form of error, whereby a worse performing player occasionally manages to reproduce. For $\kappa \rightarrow \infty$, errors in assessing the payoffs increase until no information is left and the players randomly adopt neighbouring strategies. We used $\kappa = 0.1$ in our simulations. The equilibrium levels of dove-like behaviour were determined by evolving the lattice over 10,000 generations and then averaging the mixed strategies over another 1,000 generations.

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Correspondence and requests for materials should be addressed to C.H. (hauert@zoology.ubc.ca).

Emergence of cooperation and evolutionary stability in finite populations

Martin A. Nowak^{1,2}, Akira Sasaki⁴, Christine Taylor^{1,5} & Drew Fudenberg³

¹Program for Evolutionary Dynamics, ²Department of Organismic and Evolutionary Biology and Department of Mathematics, ³Department of Economics, Harvard University, Cambridge, Massachusetts 02138, USA

⁴Department of Biology, Kyushu University, Fukuoka 812-8581, Japan

⁵Department of Mathematics, MIT, Cambridge, Massachusetts, 02139, USA

To explain the evolution of cooperation by natural selection has been a major goal of biologists since Darwin. Cooperators help others at a cost to themselves, while defectors receive the benefits of altruism without providing any help in return. The standard game dynamical formulation is the 'Prisoner's Dilemma'^{21–11}, in which two players have a choice between cooperation and defection. In the repeated game, cooperators using direct reciprocity cannot be exploited by defectors, but it is unclear how such cooperators can arise in the first place^{12–15}. In general, defectors are stable against invasion by cooperators. This understanding is based on traditional concepts of evolutionary stability and