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Spatial effects in social dilemmas

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Abstract

Social dilemmas and the evolutionary conundrum of cooperation are traditionally studied through various kinds of game theoretical models such as the prisoner's dilemma, public goods games, snowdrift games or by-product mutualism. All of them exemplify situations which are characterized by different degrees of conflicting interests between the individuals and the community. In groups of interacting individuals, cooperators produce a common good benefitting the entire group at some cost to themselves, whereas defectors attempt to exploit the resource by avoiding the costly contributions. Based on synergistic or discounted accumulation of cooperative benefits a unifying theoretical framework was recently introduced that encompasses all games that have traditionally been studied separately (Hauert, Michor, Nowak, Doebeli, 2005. Synergy and discounting of cooperation in social dilemmas. J. Theor. Biol., in press.). Within this framework we investigate the effects of spatial structure with limited local interactions on the evolutionary fate of cooperators and defectors. The quantitative effects of space turn out to be quite sensitive to the underlying microscopic update mechanisms but, more general, we demonstrate that in prisoner's dilemma type interactions spatial structure benefits cooperation—although the parameter range is quite limited—whereas in snowdrift type interactions spatial structure may be beneficial too, but often turns out to be detrimental to cooperation.

Keywords: Cooperation; Social dilemmas; Spatial games; Evolutionary game theory; Prisoner's dilemma; Snowdrift game; Public goods game

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1. Introduction

Social dilemmas capture the fundamental puzzle of the evolution of cooperation. Ever since Darwin (1859) the evolution and maintenance of cooperation has been a major challenge in evolutionary biology and behavioral sciences. In spite of the inherent risk of exploitation by cheaters, cooperation is abundant in nature and, in fact, it can be argued that all major transitions in evolution (Maynard Smith and Szathmáry, 1995) can be reduced to successful resolutions of social dilemmas under Darwinian selection.

Social dilemmas occur whenever conflicts of interest arise between the preferences of individuals as compared to the preferences of the community (Dawes, 1980). The simplest and most general definition of a social dilemma consists of two conditions imposed on situations where cooperators produce a valuable and publicly accessible public good b at some cost c to themselves with $b > c$ while defectors attempt to free ride on the benefits of the common resource without bearing the costs of cooperation:

(i) Groups of cooperators outperform groups of defectors because the former profits from the public good whereas the latter foregoes the opportunity of mutually beneficial interactions.
(ii) In every mixed group, defectors outperform cooperators because they avoid the costs of cooperation.

Condition (i) states that from the community perspective it is clearly advantageous to cooperate but condition (ii) dictates that individuals should opt for defection in order to maximize their profit. Hence the dilemma. Situations that meet these two conditions are abundant in nature and range from bacterial colonies to human interactions (Dugatkin, 1997). For example, yeast cells secrete an enzyme that lyses their environment, thus creating a

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publicly available food resource. Naturally, this resource can be exploited by other cells that do not produce the enzyme (Greig and Travisano, 2004). Other famous examples include alarm calls in merkats (Clutton-Brock et al., 1999), predator inspection behavior in fish (Milinski, 1987), blood sharing in vampire bats (Wilkinson, 1984) or public goods experiments with students (Fehr and Gächter, 2002).

Evolutionary game theory has long established as powerful mathematical framework to analyse social dilemmas (Maynard Smith and Price, 1973; Nowak and Sigmund, 2004). The single most famous mathematical metaphor for a social dilemma denotes the prisoner's dilemma (Axelrod and Hamilton, 1981). Other well studied models include public goods games (Kagel and Roth, 1995), which essentially represent a generalization of the pairwise prisoner's dilemma to interactions in groups of arbitrary size (Hauert and Szabó, 2003), the snowdrift game (Hauert and Doebeli, 2004; Sugden, 1986) (or chicken or hawk–dove game, Maynard Smith, 1982) as well as by-product mutualism (Connor, 1995). All these models address the problem of cooperation under different biologically plausible conditions and all are aiming at removing the apparent dilemma in social dilemmas.

Over the last decades several mechanisms have been proposed to successfully overcome the dilemma. Pioneering work goes back to Hamilton's kin selection theory (Hamilton, 1964) and Triver's concept of reciprocal altruism or direct reciprocity (Trivers, 1971). Boosted by Axelrod's computer tournaments (Axelrod, 1984) direct reciprocity attracted most attention. Only more recently alternative approaches are gaining momentum. This includes models of conditional strategies based on reputation which can establish cooperation either through indirect reciprocity (Nowak and Sigmund, 1998) or through punishment (Boyd and Richerson, 1992; Fehr and Gächter, 2002; Henrich et al., 2001; Sigmund et al., 2001), voluntary participation in social dilemmas (Hauert et al., 2002) or by introducing structured populations e.g. to account for spatial extensions (Nowak and May, 1992).

This last scenario represents the main topic of this article applied to a generalized framework of cooperation that embeds all the above models for social dilemmas. This emphasizes the common underlying structure of the different approaches and demonstrates the continuous transitions from one scenario to another when varying biologically meaningful parameters. In accordance with earlier results it turns out that spatial structure is not necessarily beneficial for cooperation and, in fact, often turns out to be detrimental as compared to well-mixed populations with random encounters.

2. Model

Recently a generalized theoretical framework to model any kind of social dilemmas in arbitrarily sized groups of N interacting individuals was introduced (Hauert et al., 2005). A summary of this framework follows to set the stage for investigations on effects arising in spatially structured populations. Each cooperator produces a benefit b that is equally shared among all N members of the group (including the individual itself). However, in groups containing several cooperators, the actual value of the accumulated benefits must not necessarily increase linearly with increasing numbers of cooperators. Instead, each additional benefit may be discounted or synergistically enhanced by a factor w. More precisely, assuming that

$$\begin{aligned} P_D(k) &= \frac{b}{N}(1 + w + w^2 + \cdots + w^{k-1}) \\ &= \frac{b}{N}\frac{1-w^k}{1-w}, \end{aligned} \tag{1a}$$

$$P_C(k) = P_D(k) - c \tag{1b}$$

states that the first cooperator provides a benefit b/N to everyone, the second increases the value of everyone's benefit by wb/N and so on to the last cooperator k augmenting the value by $w^{k-1}b/N$. Note that for defectors k runs from zero to $N-1$, whereas for cooperators k runs from one to N. If $w = 1$, all cooperators provide the same benefit b/N. For $w < 1$, the value of additional provisions of benefits is discounted. For example, in the aforementioned yeast cells, the food resource provided by the first cooperator may be vital for the survival for all group members but in particular for the cooperator itself. However, the value of additional food decreases until further increases become essentially useless because of the cell's limited capabilities of food intake. Conversely, if $w > 1$, the value of additional benefits is synergistically enhanced. This occurs, for example, in situations where cooperators produce substances for chemical reactions. The efficiency of the reaction is generally sensitive to the concentration of reactive compounds and can increase faster than linear (Fersht, 1977; Hammes, 1982). In nature, such situations can occur not only in foraging yeast and chemical reactions but essentially whenever individuals create any kind of common good (see e.g. Doebeli and Hauert, 2005), be it in the form of replication enzymes in viruses (Huang and Baltimore, 1977) or in the form of information gained from predator inspection behavior in fish (Magurran and Higham, 1988).

In well-mixed populations, interaction groups of size N are randomly formed according to binomial sampling such that the fitness of cooperators and defectors becomes

$$f_C = \frac{b}{N(1-w)}(1 - w(1 - x + wx)^{N-1}) - c, \tag{2a}$$

$$f_D = \frac{b}{N(1-w)}(1 - (1 - x + wx)^{N-1}), \tag{2b}$$

where x denotes the frequency of cooperators (Hauert et al., 2005). The growth (or decline) of cooperators is then given by the replicator dynamics (Hofbauer and Sigmund, 1998)

$$\dot{x} = x(f_C - \bar{f}),$$

where $\bar{f} = xf_C + (1-x)f_D$ denotes the average fitness of the population, such that strategies (here cooperators) that perform better than the population on average ($f_C > \bar{f}$) will increase in abundance and decrease otherwise. In the case of two strategies the replicator equation simplifies to

$$\dot{x} = x(1-x)(f_C - f_D).$$

The dynamics has two trivial fixed points $x_0^* = 0$ and $x_1^* = 1$ as well as at most one interior non-trivial equilibrium

$$x^* = [1 - (cN/b)^{1/(N-1)}]/[1-w].$$

x^* exists (i.e. lies in the interval $(0,1)$) if $1 > cN/b > w^{N-1}$ or $w^{N-1} > cN/b > 1$. It turns out that variations of the parameters b, c, N and w change the severity of the social dilemma which leads to four dynamical regions (see Fig. 1):

(a) Dominant defection ($cN/b > 1, cN/b > w^{N-1}$): Cooperators are doomed and vanish regardless of their initial frequency. x_0^* is the only stable equilibrium. This regime represents the strictest form of a social dilemma and corresponds to the prisoner's dilemma or, more generally, to public goods games.
(b) Co-existence ($1 > cN/b > w^{N-1}$): The interior fixed point x^* is the only stable equilibrium indicating a stable mixture of cooperators and defectors. This regime represents a generalized form of the snowdrift game for groups of arbitrary size. The social dilemma is relaxed because in groups of defectors it pays to switch to cooperation but groups of cooperators remain prone to exploitation by cheaters. The social dilemma is also reflected in the fact that a population at the equilibrium x^* has a lower payoff than a homogenous population of cooperators.
(c) Dominant cooperation ($cN/b < 1, cN/b < w^{N-1}$): In this regime the social dilemma is completely relaxed such that cheating no longer poses a threat to cooperation. Even though defectors continue to outperform cooperators in mixed groups, they could do even better by also switching to cooperation. In that sense, cooperation merely occurs as a by-product of an otherwise selfish act (Connor, 1995).
(d) Bi-stability ($w^{N-1} > cN/b > 1$): In this regime the two homogenous states x_0^* and x_1^* are both stable and the interior fixed point x^* is unstable. Consequentially the evolutionary outcome depends on the initial configuration of the population. For initial frequencies $x_0 > x^*$ cooperation evolves, whereas for $x_0 < x^*$ cooperation vanishes. In that situation the social dilemma presents itself as a coordination problem.

These analytical results provide a useful baseline to discuss the effects on cooperation arising in individual based models and, in particular, due to population structures leading to limited local interactions.

3. Global interactions

In individual based models, the propagation and spreading of strategies within a population can be defined in various ways. In general, Darwinian selection only requires that individuals with a higher fitness (payoff) have an increased propensity to proliferate and transmit their strategy either in terms of reproduction or through imitation by other individuals. Here we consider two basic approaches: a straightforward application of the replicator dynamics to finite populations and the Moran (1962) process applied to evolutionary game theory (Nowak et al., 2004).

In terms of the replicator dynamics, one particularly simple implementation considers a randomly selected focal individual that is updated as follows: first, the payoff of the focal individuals is determined from an interaction in a randomly formed group of size N (including the individual itself). Second, a model individual is chosen at random and its payoff is determined in the same way. Finally, the two payoffs are compared and the focal individual adopts the model's strategy with a probability proportional to the payoff difference provided that it is positive and with probability zero otherwise. Because individuals never adopt strategies of worse performing players stochastic effects are largely reduced. In fact, if the payoff of both the focal and the model individuals is determined over many interactions prior to payoff comparisons, this update rule becomes deterministic in direction but stochastic in time. A closely related approach would be that the focal individual adopts the strategy of an equally well performing model with probability $\frac{1}{2}$ and linearly increases (decreases) this probability for better (worse) performing models. In that case the dynamics becomes fully stochastic but still recovers the replicator dynamics in the limit of infinite population sizes. However, since the Moran process also leads to stochastic dynamics the latter approach will not be pursued further.

In the Moran process, a focal individual is randomly chosen for reproduction with a probability proportional to its fitness. As above, the fitness of each individual is determined from an interaction in a randomly formed group of N individuals. Then, another randomly chosen individual (independent of its fitness) is eliminated and replaced by offspring of the focal individual. Thus, all individuals have the same average lifespan but fitter individuals tend to have higher reproductive output. This represents a specific balance between selection and drift: fitter individuals have higher chances—but no guarantee—of reproduction, whereas less fit individuals are likely—but again, no guarantee—to be eliminated.

In principle, the fact that the Moran process has two absorbing states (either all cooperators or all defectors) prohibits any other stable equilibrium states. Practically, however, transient times often become exceedingly long such that properties of meta-stable states become relevant.

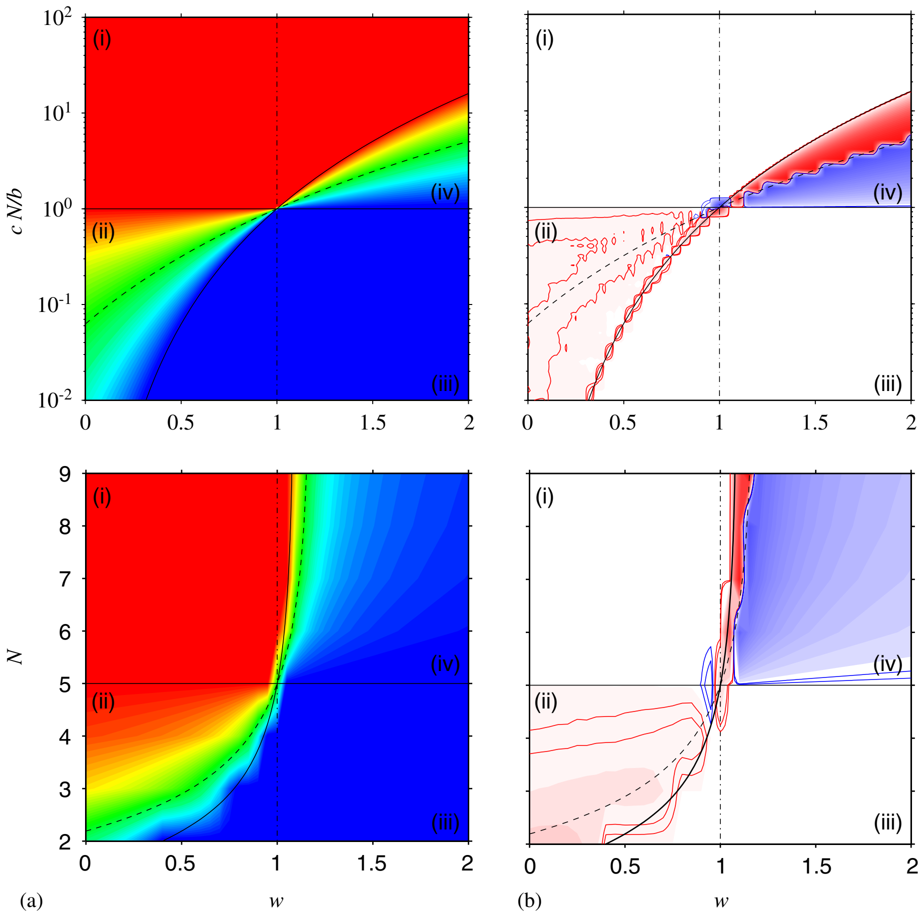

Fig. 1. Comparisons of analytical predictions and individual based simulations. The top row depicts phase-plane diagrams for the synergy/discount factor w and the cost-to-benefit ratio cN/b for a constant group size $N = 5$. The bottom row shows the phase-plane for w and the group size N for a constant cost-to-benefit ratio $c/b = 0.2$. The dash-dotted line separates discounting ($w < 1$) and synergy ($w > 1$). The phase planes are divided into four different dynamical regimes (i)–(iv), which relate to different kinds of social dilemmas: (i) dominant defection, (ii) co-existence, (iii) dominant cooperation, (iv) bi-stability (see, Section 2 for details). The solid lines delimit the regions of all cooperation and all defection. The dashed line indicates parameters for which the interior fixed point x^* corresponds to equal proportions of cooperators and defectors. x^* is stable in (ii) but unstable in (iv). (a) shows the analytically expected levels of cooperation where red indicates no cooperation, blue full cooperation and intermediate levels are indicated in orange, yellow, green and light blue for increasing fractions of cooperators. In the case of bi-stability (iv), the colors indicate the size of the basin of attraction leading to the evolutionary end states of all cooperation or all defection, i.e. bluish colors indicate that only a small fraction of cooperators is needed to establish cooperation, whereas in reddish areas a large fraction of cooperators is required. (b) illustrates the differences between the analytical results and individual based simulations inspired by the replicator dynamics. Regions where cooperators are better off in the simulations are colored blue and those favoring defectors are colored red. The saturation of blue and red indicates the strength of the effect. In addition, contour lines mark differences of ±0.5% and ±1% to highlight systematic deviations in region (ii) (see text). Parameters: random initial configuration with 50% cooperators and 50% defectors; relaxation time 5000 generations; frequencies averaged over 1000 generations; data grid 41×41 (top row) and 41×8 (bottom row).

The traditional formulation of the Moran process represents a birth–death process. Conversely, one could assume a death–birth process where first a randomly selected individual is eliminated and only then another individual is randomly chosen for reproduction with a probability proportional to its fitness (Ohtsuki et al., 2005). It is quite obvious that the two processes become identical in the limit of infinite population sizes. Interestingly, however, considerable differences occur between birth–death and death–birth processes in structured populations. In fact, it turns out that the death–birth process tends to support cooperation. Similar distinctions have been made referring to fertility versus mortality selection (Irwin and Taylor, 2001; Nakamaru et al., 1997, 1998).

One major difference between the approach based on the replicator dynamics and the Moran process is that the latter requires global information. What matters in the replicator dynamics is the performance of a strategy as compared to the average population payoff. In the individual based formulation, however, the average population payoff does not explicitly enter the calculations. Instead, the average population payoff is estimated by randomly sampling a single model member and comparing the focal individual's payoff to the payoff of the model. Obviously this sampling process could be improved by comparisons to an increased number of model members. However, in biological settings, increases of sampling size would often be associated with costs e.g. in terms of searching time. In contrast, strictly speaking, the Moran process requires complete information of every individual's fitness in order to randomly select one for reproduction. This is certainly a very strong requirement but in return it makes certain problems such as fixation probabilities analytically tractable (Imhof et al., 2005; Lieberman et al., 2005; Nowak et al., 2004; Taylor et al., 2004).

The simulation results for all three processes (local replicator update, the birth–death and the death–birth processes) are in excellent agreement with the analytical predictions. In Fig. 1 this is illustrated for the local replicator update. Weak but systematic deviations occur in region (ii) where cooperators and defectors co-exist. Individual based simulations return slightly lower equilibrium fractions of cooperators than analytical predictions. This difference can be related to different selection gradients above and below the equilibrium composition in finite populations (Ficici and Pollack, 2000). The results for the two Moran type processes are essentially identical except for minor deviations along the boundary of region (ii) where either cooperators or defectors persist only at very low frequencies and occasionally disappear due to fluctuations.

Fig. 1 highlights the smooth transitions between the different social dilemmas. For example, given a prisoner's dilemma type interaction (region (i)), decreasing the group size N relaxes the dilemma and transforms it to a snowdrift type interaction (ii). Further decreases of N increase the equilibrium fraction of cooperators and eventually may transform the interaction to by-product mutualism. Similarly, reducing the discounting (increasing w) promotes cooperation and transforms a snowdrift type interaction (ii) into by-product mutualism (iii) for $cN/b<1$ and a prisoner's dilemma type interaction (i) into a coordination game (iv) for $cN/b>1$. Note that neither co-existence nor bi-stability are possible for $w=1$. This is important, because the traditional formulation of public goods interactions corresponds to $w=1$.

4. Local interactions

Assuming well-mixed populations with random formation of interaction groups has the significant advantage to allow for analytical solutions. For more realistic approaches, however, it is important to take population structures into account which result in limited local interactions rather than random global interactions. In the simplest case this can be modeled by considering lattice populations where every individual is confined to one lattice site. Individuals interact and compete only within their respective local neighborhood. For example, consider a rectangular lattice where each individual interacts with its eight neighbors reachable by a chess-kings-move (Moore neighborhood). The update rules introduced above for well-mixed populations can be easily adapted to structured populations with local interactions by two simple changes: (i) to determine each individuals fitness, the $N-1$ other members of the interaction group are randomly selected among the individual's neighbors. Naturally, the neighborhood size puts an upper bound on the size of the interaction group, e.g. $N\leqslant 9$ for the Moore neighborhood. (ii) The model individual is a randomly chosen neighbor of the focal individual. For an intuitive understanding of the evolutionary dynamics of games in structured populations, the VirtualLabs (Hauert, 2005) provide a collection of interactive on-line tutorials on the evolutionary game theory in general, and synergy and discounting, in particular. It is easy to see that the complete graph, where every individual is connected to every other member of the population, recovers the process described in well-mixed populations.

In structured populations the death–birth process slightly favors cooperation as compared to the birth–death process (Irwin and Taylor, 2001; Nakamaru and Iwasa, 2005). The intuitive reason is that in the birth–death process a cooperator–defector pair competing for reproduction are necessarily neighbors which means that the cooperator has directly contributed to the fitness of its defecting competitor and thus decreased its own chances to produce offspring. Conversely, in the death–birth process, cooperators and defectors compete to recolonize a vacant site and hence they are usually not direct neighbors, which largely prevents cooperators from nourishing their opponents.

Population structures generally favor the evolution and persistence of cooperation because this enables cooperators to form clusters, thereby reducing exploitation by defectors. This has been confirmed by extensive studies based on the prisoner's dilemma or public goods games (Hauert and Szabó, 2003; Killingback et al., 1999; Nowak et al., 1994; Nowak and May, 1992). However, it is important to keep in mind that the clustering advantage is rather limited. For example, persistence of cooperation in the spatial prisoner's dilemma generally requires that the net benefits of mutual cooperation exceed the tenfold costs with some variation depending on the update rule (Doebeli and Hauert, 2005; Szabó and Hauert, 2002). In addition, recent results indicate that under the relaxed conditions for cooperation in the snowdrift game, spatial structure is often even detrimental resulting in lower equilibrium frequencies of cooperators than expected from well-mixed populations (Hauert and Doebeli, 2004).

These general results remain valid for interactions in social dilemmas for groups of larger sizes. For public goods or prisoner's dilemma type interactions ($cN/b>1, cN/b>w^{N-1}$), defection dominates in well-mixed populations but the clustering advantages arising from the spatial structure enables cooperators to survive. However, the clustering advantages are limited which confines persistence of cooperation to a small area of the parameter range. This is illustrated in parameter region (i) of Figs. 2–5 for the different update rules referring to the replicator approach as well as the birth–death and death–birth approaches based on the Moran process. The differences between the

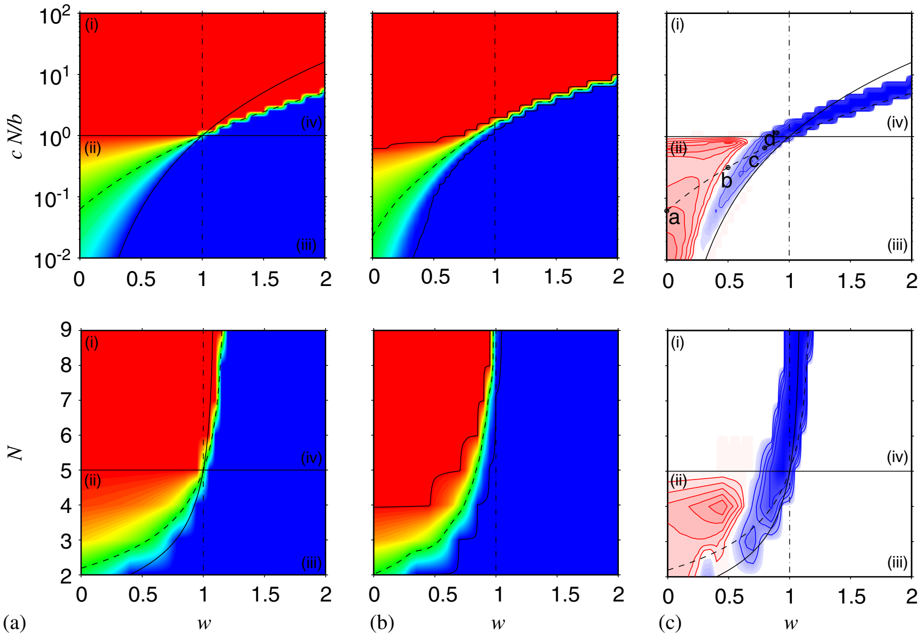

Fig. 2. Effects of spatial structure on cooperation in social dilemmas for population updates based on the replicator dynamics. Top and bottom row depict the phase-plane diagrams of two transects through parameter space (see legend to Fig. 1 for details). Column (a) shows the equilibrium fraction of cooperators in individual based simulations for well-mixed populations. Red indicates no cooperation, blue full cooperation and orange, yellow, green and light blue specify intermediate levels of cooperation. The solid and dashed lines indicate the analytical predictions and separate the dynamical domains relating to different kinds of social dilemmas (see legend to Fig. 1 for details). The middle column (b) shows the frequency of cooperators derived from simulations with local interactions on rectangular lattices. Each individual has eight neighbors (Moore neighborhood) which form the basis for randomly sampling $N-1$ interaction partners. The solid lines indicate the 1% and 99% levels of cooperation and along the dashed line equal proportions of cooperators and defectors are observed. Finally, column (c) shows the difference between the previous two, i.e. emphasizes the effects of spatial structure. In reddish areas, space reduces the equilibrium fraction of cooperators and in bluish regions space promotes cooperation by increasing the equilibrium fraction. The saturation indicates the strength of the effect. In addition, red contours mark the reduction of cooperators in increments of 2% and blue contours the increase of cooperators in increments of 10%. In the top row, the dots marked a, b, c and d refer to the respective snapshots of the lattice as depicted in Fig. 3. The right column clearly shows that in regions (i) and (iv), spatial structure has considerable effects and leads to substantial increases of cooperation. In particular, spatial structure alone enables cooperators to thrive in prisoner's dilemma type interactions (region (i)). In contrast, for the relaxed conditions of snowdrift type interactions, the effects of space are less clear. While space can still be favorable for cooperation under milder conditions (less discounting, larger w), it often turns out to be detrimental and actually reduces the equilibrium fraction of cooperators. For dominant cooperation (region (iii)) nothing changes. Parameters: 100 × 100 lattice with periodic boundary conditions; other parameters same as in Fig. 1.

three update types are quite striking in this region as illustrated in Figs. 3d and 6d. The panels show a typical snapshot of the spatial configuration of the lattice for equal parameters. For the replicator approach roughly one-third are cooperators clumped in fairly large compact clusters (Fig. 3d). In contrast, for the birth–death process, only around 18% cooperators are able to survive, whereas for the death–birth process 90% cooperate leaving only patches of defectors (Fig. 6d). The effects of spatial structure are summarized in the frequency distribution of the number of cooperators in each interaction group for the replicator approach. Cooperators interact significantly more frequently in groups of all cooperators than expected from random binomial sampling. Similarly, defectors have substantially less chances to exploit cooperators and often forgo the benefits of the common enterprise in interactions among defectors only (Fig. 3d).

In the other extreme where cooperation dominates ($cN/b<1, cN/b<w^{N-1}$), which relates to by-product mutualism, spatial structure does not affect the equilibrium state and cooperation continues to dominate. This situation refers to parameter region (iii) of Figs. 2, 4, 5 again for the three different update rules.

Clearly, the most intriguing effects of spatial structure occur for the parameter range where cooperators and defectors co-exist ($1>cN/b>w^{N-1}$). This corresponds to generalizations of snowdrift type interactions to groups of arbitrary size and refers to parameter region (ii) of Figs. 2, 4, 5. For stronger discounting (w small) as well as upon increasing costs or decreasing benefits (cN/b approaching one) spatial structure is detrimental to cooperation, i.e. shifting the equilibrium fraction of cooperators in favor of defectors as compared to unstructured, well-mixed populations. All these changes increase the severity of the social dilemma. This is equally reflected in the decreasing frequency of cooperators in well-mixed populations, but spatial structure further amplifies the deleterious effects. On the other hand, for weaker discounting (w approaching one) and more favorable cost-to-benefit ratios, spatial structure is again beneficial and the frequency of cooperators is enhanced as compared to well-mixed populations. These general patterns are observed for all three update

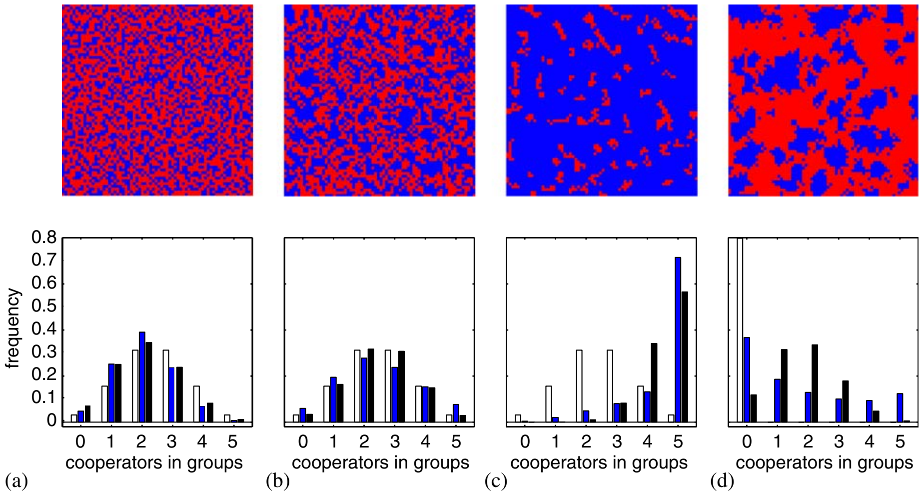

Fig. 3. Snapshots of typical equilibrium lattice configurations of cooperators (blue) and defectors (red) together with the corresponding probability distribution for the number of cooperators in each interaction group. (a)–(c) refer to region (ii) where cooperators and defectors co-exist (c.f. Fig. 2). In well-mixed populations, all three parameter combinations result in equal proportions of cooperators and defectors. In (a) spatial structure decreases the fraction of cooperators to about one-third, (b) leaves the fraction of cooperators essentially unchanged and in (c) cooperators thrive and leave only patches of defectors. (d) refers to region (i) and corresponds to prisoner's dilemma type interactions. In well-mixed populations cooperators go extinct but spatial structures enable cooperators to form clusters thereby reducing exploitation by defectors. The probability distribution of finding a certain number of cooperators in a group (bottom row) illustrates that spatial structure can lead to assortative or disassortative interactions among the two strategic types—the former enhances cooperation, whereas the latter inhibits cooperation. The histograms depict the actually observed fraction of interactions with certain numbers of cooperators (blue), the binomial distribution for the observed frequency of cooperators (black) and, as a reference, the binomial distribution for equal proportions of cooperators and defectors (white). (a) Disassortative interactions are indicated by the bias towards fewer cooperators as well as the sharper peak (blue) than the binomial distribution (black). (b) Even though the strategy frequency is unaffected by the spatial structure, interactions are clearly assortative, i.e. the distribution (blue) is considerably wider and homogenous groups occur substantially more frequently than in binomial sampling (black). (c) The pronounced peak at five (blue) again indicates assortative interactions. (d) Assortativity is most pronounced in prisoner's dilemma type interactions as indicated by the U-shape distribution (blue) as compared to the unimodal binomial (black). Parameters: 70×70 lattice, periodic boundaries; Moore neighborhood, $N = 5$; (a) $w = 0, cN/b = 0.0625$; (b) $w = 0.5, cN/b = 0.316$; (c) $w = 0.8, cN/b = 0.656$; (d) $w = 0.9, cN/b = 1.15$ (marked in Fig. 2c).

rules but the deleterious effects are less pronounced for the derivatives of the Moran process and actually almost vanish for the death–birth process (see Fig. 5).

Typical snapshots of equilibrium lattice configurations are shown in Figs. 3, 6a–c for parameters where theory predicts equal proportions of cooperators and defectors in well-mixed populations. For the replicator approach, spatial structure can lead to filament like cluster formation that results in an overall decrease of cooperation (Fig. 3a), leave the equilibrium frequencies essentially unchanged (Fig. 3b) or promote cooperators (Fig. 3c). In contrast, for the same parameters, the Moran type updates invariably promote cooperation (Fig. 6a–c)—an effect that is marginally more pronounced in the death–birth approach.

Finally, for bi-stability ($w^{N-1} > cN/b > 1$), spatial structure is clearly in favor of cooperators. For all three update types, the basin of attraction of cooperators is considerably enhanced.

5. Conclusions

The evolutionary success of cooperators in social dilemmas is substantially altered in spatially extended settings with limited local interactions. For the most stringent form of social dilemmas, as represented by prisoner's dilemma (or public goods) type interactions, spatial structure enables cooperators to thrive by forming clusters and thereby reducing exploitation by defectors. However, this clustering advantage is rather limited. To illustrate this, consider the net cost to net benefit ratio of mutual cooperation r: the net benefits are given by $P_C(N)$ and the net costs by $-P_C(1)$. Note that the latter must be positive for prisoner's dilemma type interactions (c.f. Eq. (1a)). For $w = 1$ this ratio becomes particularly simple with

$$r = \frac{N-1}{N-\frac{cN}{b}} - 1. \tag{3}$$

The condition for dominant defection requires $cN/b > 1$ and the simulation results (region (i) in top row of Figs. 2, 4, 5) indicate that for $N = 5$ cooperators survive only if $cN/b \lesssim 2$ holds. Thus, persistence of cooperation requires $0 < r < \frac{1}{3}$, i.e. the net benefits of cooperation must exceed the threefold net costs, or similarly, this restricts feasible cost and benefit values to a small parameter range $\frac{1}{5} < c/b < \frac{2}{5}$. Note that the upper bound of r varies with N and may become as small as $\sim \frac{1}{10}$ for pairwise interactions (Doebeli and Hauert, 2005). At the same time, it is only marginally affected by the microscopic update mechanism.

Under the relaxed conditions for cooperation as described by snowdrift type interactions, spatial structure

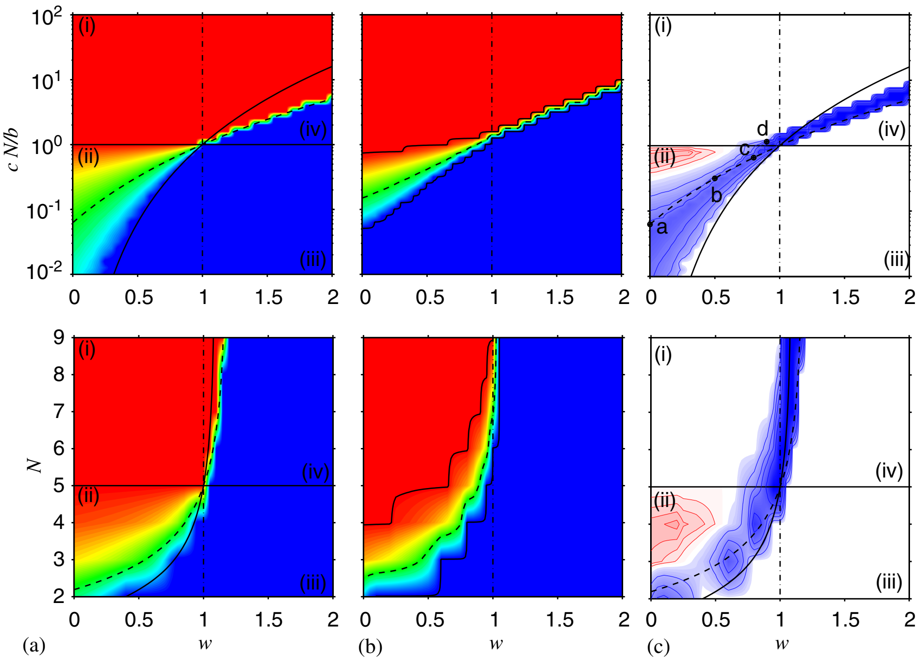

Fig. 4. Effects of spatial structure on cooperation in social dilemmas for population updates based on the Moran process and implemented as a birth–death process. As in Fig. 2, the top and bottom row display the phase-plane diagrams of two different transects through parameter space. The equilibrium fraction of cooperators is depicted as a function of the discount/synergy factor w and the cost-to-benefit ratio cN/b (top) with $N = 5$ fixed and as a function of w and the group size N (bottom) with $c/b = 0.2$ fixed. For further details, see legend to Fig. 2. (a) shows the fraction of cooperators in well-mixed populations, (b) their frequency in lattice populations and (c) displays the difference between the two, emphasizing the changes arising from local interactions and the spatial arrangement of the individuals. The results are very similar to those for the update based on the replicator dynamics (c.f. Fig. 2): spatial structure increases the parameter range where cooperators thrive (shades of blue) in regions (i) and (iv), has no effect in region (iii) and may either favor or hinder (shades of red) cooperation in region (ii). Quantitatively, cooperators draw less profit from the spatial structure in regions (i) and (iv) for the birth–death process. At the same time, the birth–death process supports cooperation in the region of co-existence (ii) and significantly decreases the region where spatial structure has detrimental effects on cooperation. To illustrate this Fig. 6 depicts typical snapshots of the equilibrium configuration of the lattice for the parameters indicated by the points labeled a, b, c and d in the top panel of the right column.

can both enhance or inhibit cooperation as compared to the equilibrium fraction of cooperators in well-mixed populations with random group formation. This observation cautions against the traditional viewpoint that local interactions always benefit cooperation (Hauert and Doebeli, 2004). Moreover, the equilibrium state of the spatial system sensitively depends on the underlying local update mechanism. The replicator approach results in a large parameter range where spatial structure reduces cooperation, whereas for the death–birth process the deleterious effects almost vanish. The intuitive reason why cooperation is promoted in the case of the death–birth process is based on the fact that by first eliminating an individual, i.e. vacating a site, the relation among the competitors changes. More precisely, competing cooperators and defectors are generally not nearest neighbors themselves but rather separated by the vacant site. Thus, and in contrast to the other mechanisms, the benefits produced by the cooperator do not accrue to the defector, i.e. cooperators no longer support their competitors and thus become better competitors themselves.

The detrimental effects of spatial structure do not extend into the realms of by-product mutualism or bi-stability. For by-product mutualism, cooperation continues to dominate and remains unaffected by the population structure. For bi-stability, spatial structure again benefits cooperators by substantially increasing the basin of attraction of the cooperative state, i.e. a much smaller initial fraction of cooperators is required in spatial settings to end up in a state with all cooperators than in well-mixed populations.

In summary, the problem of cooperation in any kind of social dilemma can be phrased in terms of four biologicallly meaningful parameters: costs and benefits of cooperation, interaction group size as well as a factor determining the discounted or synergistically enhanced value of accumulated benefits (Hauert, 2005; Hauert et al., 2005). This unifying framework encompasses various types of cooperative interactions that have been traditionally studied separately. For spatially extended systems the results confirm that limited local interactions and clustering opportunities tend to reduce exploitation and thereby support and promote cooperation. However, they also caution against the common belief that spatial structure is necessarily beneficial for cooperation because the clustering benefits are limited to a small parameter range and, moreover, for snowdrift type interactions spatial structure may even become detrimental to cooperation.

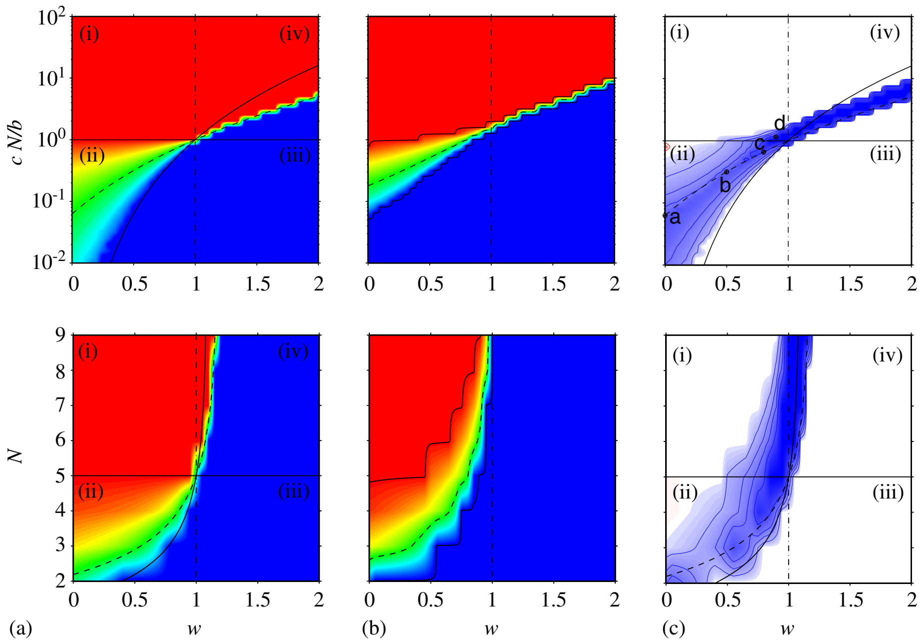

Fig. 5. Effects of spatial structure on cooperation in social dilemmas for population updates based on the Moran process and implemented as a death–birth process. The same transects through parameter space are shown as in Fig. 2 for the update rule based on the replicator dynamics and in Fig. 4 for the birth–death process. (a) shows the frequency of cooperators in well-mixed populations, (b) in spatially structured lattice populations and (c) shows the difference between the two. The previous qualitative results remain unchanged by the death–birth update rule but quantitatively it is clearly the most favorable for cooperators. Not only does it lead to the most pronounced increases of cooperator frequency (shades of blue) in regions (i) and (iv), but also the parameter range where spatial structure is deleterious (shades of red) in the region of co-existence (ii) is essentially displaced by substantial increases of the parameter range that benefits cooperation. This shift in favor of cooperators is also illustrated in Fig. 6 depicting snapshots of typical equilibrium lattice configurations with parameters as indicated by the points labeled a, b, c and d in the top panel of the right column.

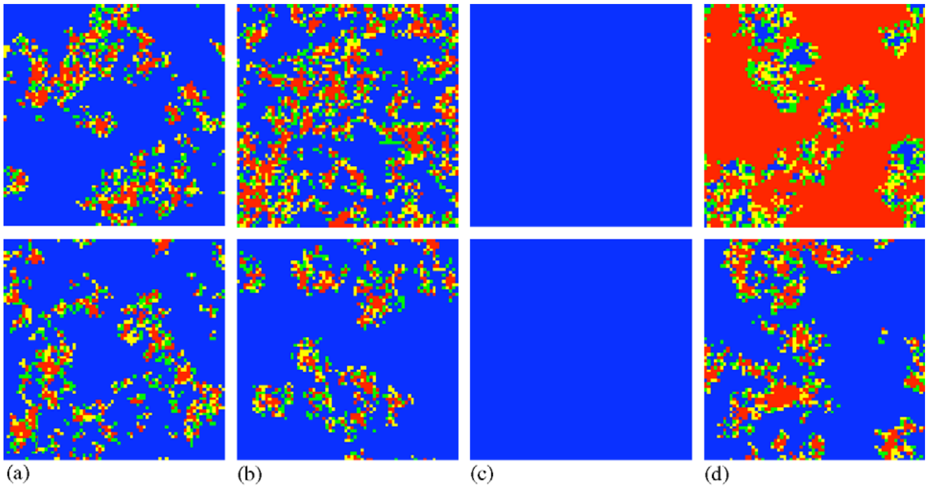

Fig. 6. Snapshots of typical equilibrium configurations for update rules based on the Moran process. The upper row shows the results for the birth–death process and the lower row for the death–birth process. (a)–(c) refer to the region of co-existence (ii) and in well-mixed populations these parameter settings would lead to equal proportions of cooperators and defectors. The results for the two processes are essentially indistinguishable but as compared to well-mixed populations they both substantially enhance cooperation. In (a) the contrast is even more striking when comparing to the update rule based on the replicator dynamics (c.g. Fig. 3a), where spatial structure had detrimental effects on cooperation. (d) refers to region (i) for prisoner's dilemma type interactions. Because the persistence of cooperators crucially hinges on the cooperators' ability to reduce exploitation through cluster formation, their success is particularly sensitive to changes in the update rule for this strictest form of social dilemmas. Here the favorable effects of the death–birth process on cooperation result in around 90% cooperators as compared to around 18% for the birth–death process. Same parameters as in Fig. 3 and as marked in Figs. 4c and 5c.

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