



Invasion and expansion of cooperators in lattice populations: Prisoner's dilemma vs. snowdrift games

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ABSTRACT

The evolution of cooperation is an enduring conundrum in biology and the social sciences. Two social dilemmas, the prisoner's dilemma and the snowdrift game have emerged as the most promising mathematical metaphors to study cooperation. Spatial structure with limited local interactions has long been identified as a potent promoter of cooperation in the prisoner's dilemma but in the spatial snowdrift game, space may actually enhance or inhibit cooperation. Here we investigate and link the microscopic interaction between individuals to the characteristics of the emerging macroscopic patterns generated by the spatial invasion process of cooperators in a world of defectors. In our simulations, individuals are located on a square lattice with Moore neighborhood and update their strategies by probabilistically imitating the strategies of better performing neighbors. Under sufficiently benign conditions, cooperators can survive in both games. After rapid local equilibration, cooperators expand quadratically until global saturation is reached. Under favorable conditions, cooperators expand as a large contiguous cluster in both games with minor differences concerning the shape of embedded defectors. Under less favorable conditions, however, distinct differences arise. In the prisoner's dilemma, cooperators break up into isolated, compact clusters. The compact clustering reduces exploitation and leads to positive assortment, such that cooperators interact more frequently with other cooperators than with defectors. In contrast, in the snowdrift game, cooperators form small, dendritic clusters, which results in negative assortment and cooperators interact more frequently with defectors than with other cooperators. In order to characterize and quantify the emerging spatial patterns, we introduce a measure for the cluster shape and demonstrate that the macroscopic patterns can be used to determine the characteristics of the underlying microscopic interactions.

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1. Introduction

The evolution of cooperation poses a fundamental challenge to evolutionary biologists (Axelrod, 1984; Maynard Smith, 1982; Nowak, 2006). Cooperators incur costs in order to benefit others while defectors reap the benefits but dodge the costs. Despite the fact that groups of defectors perform poorly as compared to groups of cooperators, Darwinian selection should favor defectors. Nevertheless, cooperation is ubiquitous in biological and social systems. The problem of cooperation represents a social dilemma characterized by the conflict of interest between the group and the individual (Dawes, 1980; Hauert, 2006).

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The two most prominent mathematical metaphors to investigate cooperation in social dilemmas are the prisoner's dilemma and the snowdrift game (Doebeli and Hauert, 2005). Both games describe pairwise interactions where each player can cooperate or defect. In the prisoner's dilemma, a cooperator incurs a cost, c , and provides a benefit, b , to its opponent with $b > c$. Defectors neither incur costs nor provide benefits. Hence, if both players cooperate, each receives $b - c$ but neither gains anything if they both defect. If a cooperator meets a defector, the defector gets the benefit and the cooperator is left with the costs. The different outcomes can be conveniently summarized in a payoff matrix:

$$\begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}. \quad (1)$$

It is easy to see that defection is dominant, i.e., it is better to defect, irrespective of the other player's decision. Consequently, the two players end up with zero instead of the more favorable

reward $b-c$ for mutual cooperation. Self-interest prevents individuals from achieving a mutually beneficial goal, which is the essence of social dilemmas.

In the snowdrift game individuals can gain access to benefits for the pair at some individual cost. Cooperators are willing to bear the costs whereas defectors are not. If two cooperators meet, both get the benefit and share the costs, $b-c/2$, and if a cooperator meets a defector, the cooperator still gets the benefit but carries the entire costs, $b-c$. For the defector, the payoffs are the same as in the prisoner's dilemma. The resulting payoff matrix is

$$\begin{pmatrix} b-\frac{c}{2} & b-c \\ b & 0 \end{pmatrix}. \quad (2)$$

The crucial difference is that the best decision now depends on the other individual: defect if the other player cooperates but cooperate if the other defects. This results in a relaxed social dilemma—cooperation remains prone to exploitation by defectors but at least they receive their share of the benefit.

The replicator dynamics (Hofbauer and Sigmund, 1998) is used to describe the evolutionary fate of cooperators and defectors in large, unstructured populations where each individual is equally likely to interact with any other one. In the prisoner's dilemma cooperation disappears and a pure defector population is the only stable outcome. In contrast, in the snowdrift game cooperators and defectors can co-exist at an equilibrium frequency of $1-c/(2b-c)$ cooperators. The fact that in the snowdrift game it is best to adopt a strategy that is different from the opponent ensures that in a population the rare type is favored and guarantees stable co-existence. Also note that the average payoff in equilibrium is lower than for a population of cooperators—another consequence of social dilemmas (Doebeli and Hauert, 2005).

In such well-mixed populations the invasion and maintenance of cooperation is trivial in the snowdrift game but additional supporting mechanisms are required for cooperation to succeed in the prisoner's dilemma. Over the last decades, much theoretical effort has been expended in order to identify different means to support cooperators (Hamilton, 1964; Hauert et al., 2002, 2007; Imhof and Nowak, 2010; Nowak and Sigmund, 1998; Trivers, 1971). One surprisingly simple way to achieve this goal is to include spatial dimensions and to consider spatial games where individuals are arranged on a lattice and their fitness is based on interactions within their local neighborhood (Hauert, 2001, 2002; Nakamaru et al., 1997, 1998; Nowak and May, 1992, 1993; Nowak et al., 2010; Ohtsuki et al., 2006; Ohtsuki and Nowak, 2008; Pacheco et al., 2006; Szabó and Töke, 1998; Tarnita et al., 2009a, b; Taylor et al., 2007). This enables cooperators to form clusters and thereby reduces exploitation by defectors. The spatial dynamics of the prisoner's dilemma has attracted increasing interest from different disciplines (for an excellent review see Szabó and Fáth, 2007).

Naturally, it is of particular importance to understand how initially rare cooperators can increase and get established in a population. According to the replicator dynamics, this never happens for the prisoner's dilemma in infinite populations but due to the inherent stochasticity in finite populations, there exists a small probability that even a single cooperator can invade and eventually take over an entire population (Nowak et al., 2004; Taylor et al., 2004). Although, this chance tends to be exceedingly small and decreases rapidly with increasing population size. However, in spatial populations, even a small patch of cooperators may trigger a successful and persistent invasion of cooperators (Ellner et al., 1998; Langer et al., 2008; Le Galliard et al., 2003; Nakamaru et al., 1997, 1998; Ohtsuki et al., 2006; Taylor et al., 2007; van Baalen and Rand, 1998).

While the invasion of cooperators in the snowdrift game is trivial in well-mixed populations, it turns out that the conditions are less clear in spatial settings because in the spatial snowdrift game the limited local interactions often reduce or even eliminate cooperation (Hauert and Doebeli, 2004). Interestingly, the fact that it is better to adopt a strategy that is different from your opponent promotes cooperation and is responsible for the co-existence of cooperators and defectors in well-mixed populations, but the same mechanism often inhibits cooperation in spatial settings, because it hampers the formation of compact clusters of cooperators. Thus, in well-mixed populations establishing cooperation based on the snowdrift game is easy but unlikely for the prisoner's dilemma, whereas in spatial settings the odds seem to be reversed—space promotes cooperation in the prisoner's dilemma but not necessarily in the snowdrift game. Here we compare and contrast the microscopic and macroscopic features and characteristics of the spatial invasion process governed by these two types of social dilemmas.

2. Model

Consider a spatially extended population where each individual is situated on one site of a two-dimensional $L \times L$ square lattice with periodic boundary conditions. There are no empty sites. All individuals engage in pairwise interactions with each neighbor in their Moore neighborhood, i.e., with the eight nearest neighbors reachable by a chess-kings-move. The payoffs of all interactions are accumulated. The payoff matrices for the prisoner's dilemma and the snowdrift game can be conveniently rescaled such that they depend only on a single parameter (Doebeli and Hauert, 2005; Hauert and Doebeli, 2004; Langer et al., 2008). For the prisoner's dilemma we get

$$\begin{pmatrix} 1 & 0 \\ 1+u & u \end{pmatrix}, \quad (3)$$

where $u=c/b$ denotes the cost to benefit ratio of cooperation and for the snowdrift game

$$\begin{pmatrix} 1 & 1-v \\ 1+v & 0 \end{pmatrix}, \quad (4)$$

where $v=c/(2b-c)$ indicates the cost to net benefit ratio of mutual cooperation. With $b > c$, both u and v are constrained to the interval $[0,1]$. Note that these parameterizations are very different from the so-called weak prisoner's dilemma, which goes back to Nowak and May (1992) and actually marks the borderline between the prisoner's dilemma and the snowdrift game. However, in spatial settings a clear distinction is of particular importance because space often has the opposite effect on cooperation in the two games (Hauert and Doebeli, 2004).

The population is asynchronously updated by randomly selecting a focal individual x to reassess and update its strategy by comparing its payoff P_x to that of a randomly chosen neighbor y . The focal individual x adopts y 's strategy with a probability proportional to the payoff difference, provided that $P_y > P_x$. Specifically, the transition probability $f(P_y - P_x)$ can be written as

$$f(P_y - P_x) = \begin{cases} \frac{P_y - P_x}{\alpha} & \text{if } P_y > P_x, \\ 0 & \text{otherwise,} \end{cases} \quad (5)$$

where α denotes a normalization constant such that $f(P_y - P_x) \in [0,1]$. Here, $\alpha = k(1+u)$ or $\alpha = k(1+v)$, respectively, and $k=8$ represents the number of neighbors.

Note that this update rule, Eq. (5), is semi-deterministic, as individuals never imitate strategies of worse performing

neighbors. Alternatively, another pairwise comparison rule based on the Fermi function, i.e., $f(P_y - P_x) = 1/(1 + \exp[-\beta(P_y - P_x)])$ can be used, where β denotes the intensity of selection (Szabó and Töke, 1998; Traulsen et al., 2007). Extensive simulations have confirmed that the following results are robust with respect to such changes in the updating rule.

In order to investigate the invasion and expansion process of cooperators in the two social dilemmas, we consider initial configurations where all $L \times L$ individuals are defectors except for a small $s \times s$ cluster of cooperators ($s \ll L$) located in the center of the lattice (Langer et al., 2008). The simulation results are complemented by analytical predictions based on pair approximation (Matsuda et al., 1992; Ohtsuki et al., 2006, see Appendix). This provides important qualitative insights into the invasion dynamics but often fails to provide accurate quantitative predictions (Hauert and Doebeli, 2004; Hauert and Szabó, 2005; Szabó and Töke, 1998).

For a detailed characterization of the emerging spatial patterns we propose a measure for the cluster shape, γ , of cooperator aggregations. For each cluster i , we derive γ_i , based on the number of C–C links, I_{CC} , within cluster i and the number of C–D links, O_{CD} , that connect cluster i with the surrounding defectors:

$$\gamma_i = \frac{2I_{CC} - O_{CD}}{2I_{CC} + O_{CD}}. \quad (6)$$

The value of γ_i is constrained to the interval $[-1, 1]$. Compact clusters of cooperators have more links within the cluster than to the surrounding defectors. This is reflected in $\gamma_i > 0$ and indicates positive assortment of cooperators. Conversely, for filament like clusters there are fewer links within the cluster and more links connecting cooperators and defectors. Consequently, $\gamma_i < 0$ holds and indicates negative assortment among cooperators (or positive

assortment between cooperators and defectors). Finally, γ is obtained by averaging over all γ_i and weighted by the size of cluster i . Using pair approximation, we can estimate the cluster shape as $\gamma = q_{C|C} - q_{D|C} = 2q_{C|C} - 1$, where $q_{D|C}$ indicates the conditional probability that the neighbor of a cooperator is a defector etc. The cluster shape γ conveniently quantifies the qualitative descriptions of compact versus filament-like clusters.

3. Results

The spatial patterns generated by the invasion and expansion of cooperators sensitively depend on the type of game as well as on the parameter settings. Typical spatial configuration in the prisoner's dilemma are illustrated in Fig. 1 for increasingly hostile conditions for cooperators (larger u). In benign settings, cooperators grow in a single, contiguous cluster with embedded strands of defectors (Figs. 1a and b). Increasing u renders exploitation more attractive and defectors succeed in splitting up the cluster of cooperators into smaller parts (Figs. 1c and d). In response, cooperators form increasingly compact clusters in an attempt to minimize the cluster surface and hence reduce exploitation by defectors (Figs. 1e and f). However, if u exceeds $u_c \approx 0.15$, the extinction threshold, all invasion attempts by cooperators fail.

For the snowdrift game, the emerging patterns are rather different as illustrated in Fig. 2. Again, under hospitable conditions (small v), cooperators expand in a single contiguous cluster with embedded defectors but now they form isolated specks (Figs. 2a and b). Increasing v reflects more hostile conditions and the cluster of cooperators gradually breaks up into smaller filament-like clusters (Figs. 2c–e) and eventually

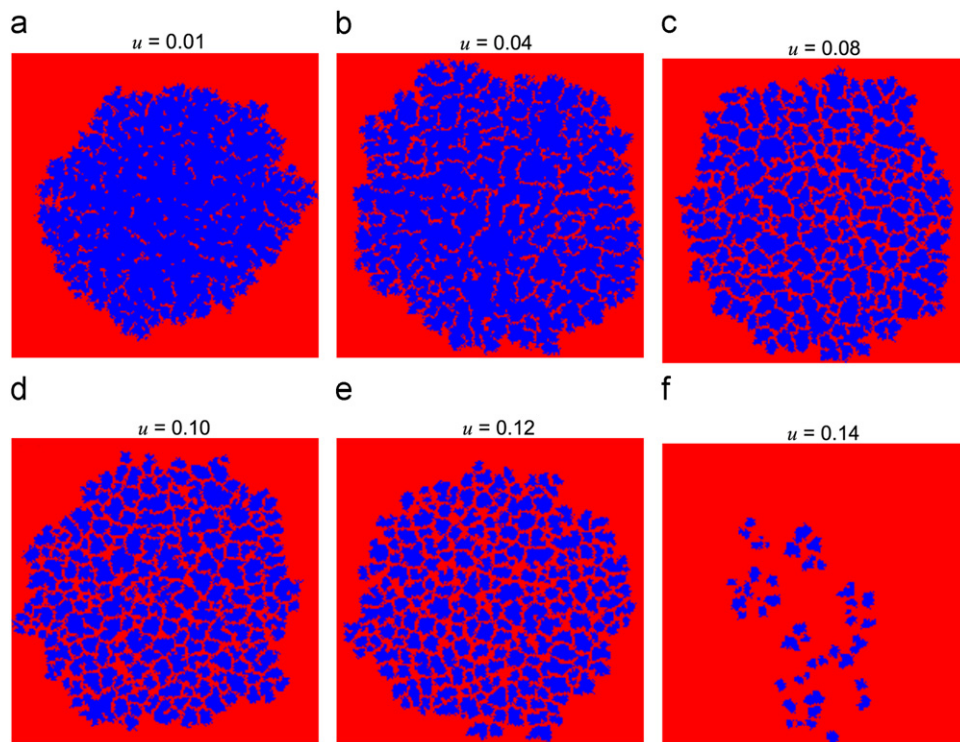


Fig. 1. Typical snapshots of the invasion of cooperators (blue) in a world of defectors (red) for the prisoner's dilemma under increasingly hostile conditions. The snapshots are taken when the first cooperator reaches the boundary of a 200×200 lattice with an initial 5×5 cluster. Under hospitable conditions [$u < 0.06$, panels (a) and (b)], cooperators expand as a single contiguous cluster interspersed with strips of defectors. Whereas under less favorable conditions [$u > 0.06$, panels (c)–(e)], cooperators separate into numerous small compact clusters. Near the extinction threshold, $u_c \approx 0.15$, [$u = 0.14$, panel (f)], a minimal cluster size of about 60 is necessary for cooperators to survive. All snapshots can be reproduced using the *VirtualLabs* (Hauert, 2009). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

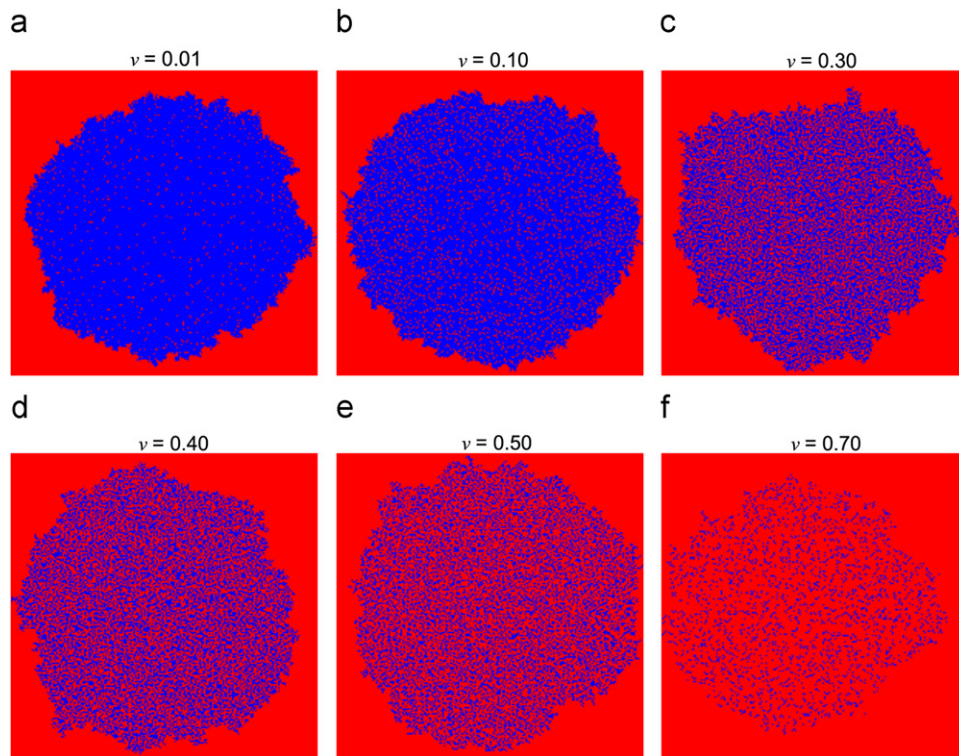


Fig. 2. Typical snapshots of the invasion of cooperators (blue) in a world of defectors (red) under increasingly hostile conditions for the snowdrift game. The initial configuration is the same as in Fig. 1. Under benign conditions [$\nu < 0.35$, panels (a)–(c)], cooperators expand as a single contiguous cluster with embedded specks of defectors. While under less favorable conditions [$0.35 < \nu < 0.7$, panels (d) and (e)], cooperators separate into numerous smaller dendritic clusters where they on average interact more with defectors than with other cooperators. Near the extinction threshold, $\nu_c \approx 0.78$, [$\nu = 0.7$, panel (f)], one- and two-cooperator clusters are mostly observed. In contrast to the prisoner's dilemma (c.f. Fig. 1) the snowdrift game prevents the formation of compact clusters. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most clusters consist of merely a few cooperators (Figs. 2f). For large ν , the structure of the snowdrift game prevents the formation of compact clusters because it is always better to adopt a strategy that is different from those of the opponents. For this reason, individuals arrange such as to maximize the interface between cooperators and defectors, which is reflected in filament-like cluster shapes that then result in an overall decrease of cooperation. In analogy to the prisoner's dilemma, all invasion attempts fail for sufficiently large $\nu > \nu_c$. In the snowdrift game a single cooperator can survive in a sea of defectors provided that its payoff $[8(1-\nu)]$ is no less than that of the surrounding defectors $[1+\nu]$ (Hauert, 2001). Based on this condition we can estimate the extinction threshold $\nu_c = \frac{7}{9} \approx 0.78$. Near the extinction thresholds of cooperators the differences in the microscopic invasion patterns generated by the two games become most apparent (c.f. Figs. 1f and 2f).

The success or failure of an invasion attempt not only depends on the details of the game but may also hinge on the initial number and the spatial arrangement of the pioneering cooperators. An invasion is assumed to be successful if cooperators reach the boundary of the $L \times L$ lattice. The survival probability of a small island of $s \times s$ cooperators ($s \ll L$) in a sea of defectors is shown in Fig. 3 for the prisoner's dilemma and the snowdrift game. In the prisoner's dilemma, the initial cluster size plays a crucial role in determining the evolutionary fate of cooperators. It becomes increasingly important under more hostile conditions (larger u) and especially when approaching the extinction threshold, $u_c \approx 0.15$ (see Fig. 3a). For increasing s , the survival probability approaches a step function with the threshold u_c (Fig. 3a). For $u < u_c$ all invasion attempts succeed with certainty for sufficiently large s .

In contrast, in the snowdrift game, the survival probability of cooperators is independent of the initial cluster size because for $\nu < \nu_c$ even an isolated cooperator can survive and for $\nu > \nu_c$ all invasion attempts fail regardless of s (Fig. 3b). Note the excellent agreement between our analytical approximation for $\nu_c \approx 0.78$ and the simulation data. For both games, pair approximation confirms that cooperators are able to invade but the extinction threshold is overestimated in the prisoner's dilemma and none exists in the snowdrift game (Fig. 3).

3.1. Invasion and expansion

The spatial invasion and expansion process in the prisoner's dilemma and the snowdrift game is shown in Fig. 4. In both games, increasingly hostile conditions (larger u or ν , respectively) oppose the propagation of cooperation and thus lower the speed of invasion (Figs. 4a and d). The invasion process is characterized by two distinct dynamical phases: local equilibration followed by uniform expansion (Langer et al., 2008). The initial island of cooperators needs to achieve a local equilibrium with nearby defectors. During this equilibration process, the global abundance of cooperators increases very slowly, but the local configuration of cooperators changes rapidly as reflected in the local clustering of cooperators, $q_{C|C}$, (Figs. 4b and e) as well as in their cluster shape γ (Figs. 4c and f).

During the subsequent uniform expansion process, the frequency of cooperators, p_C , grows quadratically, while $q_{C|C}$ and γ hardly change. This indicates that, in the wake of the invasion front, the local equilibrium between cooperators and defectors is already established. The quadratic growth of cooperators is a

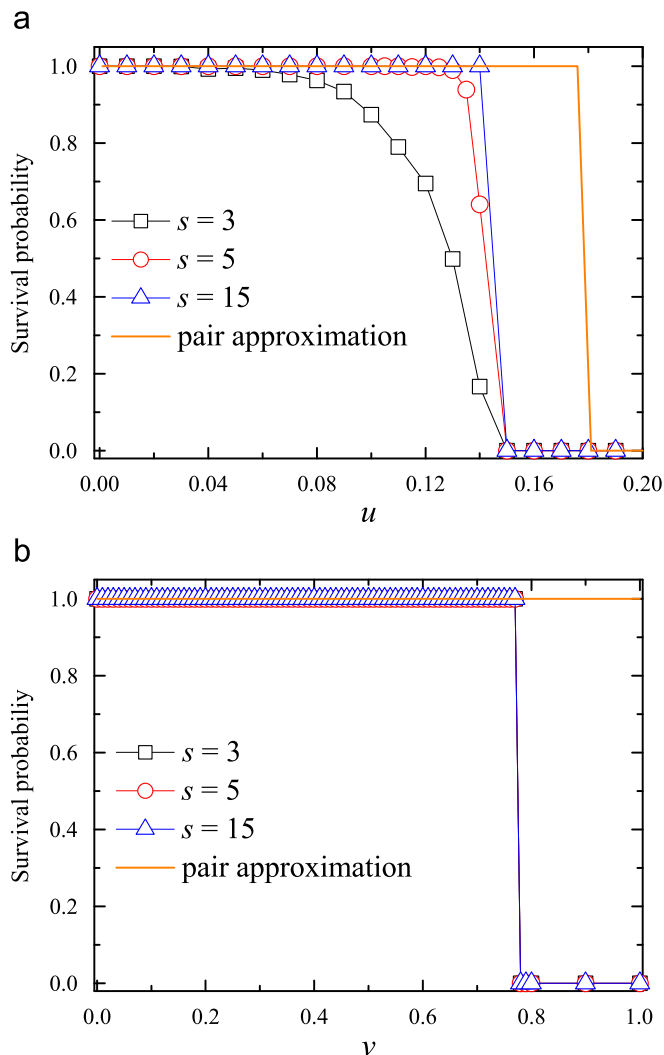


Fig. 3. Survival probability, σ_c , of cooperators for (a) the prisoner's dilemma and (b) the snowdrift game for different sizes of the initial $s \times s$ cluster (\square : $s=3$, \circ : $s=5$, \triangle : $s=15$). Under hospitable conditions (small u , v), cooperators survive with certainty, whereas under harsh conditions (large u , v), invasion attempts of cooperators invariably fail. In the prisoner's dilemma, the size of the initial cluster is an important determinant for the success of an invasion attempt and becomes particularly pronounced near the extinction threshold. In contrast, the initial cluster size has no effect in the snowdrift game. σ_c is determined from 1000 independent runs on a 125×125 lattice. Cooperators are assumed to survive if they reach the boundary. The solid lines are analytical predictions from pair approximation.

simple consequence of the two-dimensional lattice space. Once the boundary of the lattice is reached, the frequency of cooperators saturates at the equilibrium level (Figs. 4a and d).

The simulation results are complemented by pair approximation using identical initial conditions, i.e., $p_c(0)$ and $q_{c|c}(0)$ are determined based on $s=5$ and $L=125$ as used in the simulation setup (Fig. 4). Pair approximation does not incorporate spatial dimensions and hence the quadratic growth of p_c cannot be observed. The initial changes of $q_{c|c}$ and γ are larger and more abrupt than in the simulations. In particular, the heavy initial drop of $q_{c|c}$ suggests that the local initial configuration, as reflected in $q_{c|c}(0)$, has little or no effect on the results. This is a consequence of the fact that pair approximation assumes infinite populations. In contrast, for the prisoner's dilemma, the configuration of the initial cluster is crucial (Hauert, 2001). However, pair approximation confirms that local equilibration is fast compared to the expansion process. Moreover, increasing u (or v , respectively)

invariably decreases the values of p_c , $q_{c|c}$ and γ at equilibrium. Interestingly, the change in $q_{c|c}$ and γ is much more pronounced in the snowdrift game than in the prisoner's dilemma.

3.2. Emerging patterns

The previous section established that in the wake of the invasion front cooperators and defectors quickly reach a local equilibrium. For this reason we can analyze the macroscopic features of the emerging patterns once the population has reached the global equilibrium. Fig. 5 shows the cluster size and cluster count under increasingly hostile conditions in the prisoner's dilemma and the snowdrift game. In both games, this leads to a decrease of the cluster size and the cluster count exhibits a maximum close to the extinction threshold. As illustrated by the snapshots (Figs. 1 and 2), cooperators expand as a single contiguous cluster under favorable conditions, but split into numerous smaller clusters in hostile settings. For the snowdrift game, the sharp drop in cluster size is accompanied by a steep increase in the number of clusters (Fig. 5b). In contrast, in the prisoner's dilemma the cluster size decreases more slowly as u increases and reaches a minimum of about 60 at the extinction threshold u_c (Fig. 5a). Consequently, the cluster count can be more than an order of magnitude larger in the snowdrift game than in the prisoner's dilemma. Also note that the minimum cluster size required to secure the survival of cooperators in the prisoner's dilemma turns out to be surprisingly large and may further challenge cooperation.

The frequency of cooperation, p_c , and the cluster shape, γ , in equilibrium are shown in Fig. 6 under increasingly hostile conditions. In the prisoner's dilemma, the frequency of cooperators p_c exhibits three phases (Fig. 6a): for $u < 0.1$, p_c decreases slowly with increasing u and cooperators dominate the population ($p_c > 0.5$); for $0.1 < u < u_c$, p_c drops quickly and for $u > u_c$ cooperators disappear. In the snowdrift game, p_c shows four phases (Fig. 6c): for $v < 0.1$, spatial structure promotes cooperation ($p_c \approx 1$); for $0.1 < v < v_c$, spatial structure inhibits cooperation and often lowers p_c by more than 0.1 as compared to the co-existence equilibrium in the replicator equation (Hauert and Doebeli, 2004); near the extinction threshold ($0.68 < v < v_c$), p_c decreases with a larger slope than that at $v < 0.68$; and finally, for $v > v_c$, spatial structure eliminates cooperation altogether. Note the intriguing parallels between the cluster size (Fig. 5) and the frequency of cooperators, p_c (Fig. 6).

The cluster shape γ reveals further interesting aspects characterizing the differences in the invasion patterns generated by the prisoner's dilemma and the snowdrift game. In both games, γ is close to one under benign conditions and then gradually decreases as conditions deteriorate and the setting becomes increasingly hostile. In the prisoner's dilemma, positive assortment and hence the formation of compact clusters is essential for the survival of cooperators (Pepper and Smuts, 2002). However, as u increases defectors perform better and force cooperators to form smaller clusters, which leads to a decrease of γ . Nevertheless, $\gamma > 0.5$ always holds, which means that each cooperator interacts with at least three times more cooperators than defectors and represents substantial positive assortment (Fig. 6b).

In contrast, in the snowdrift game γ changes from positive to negative values for increasing v (Fig. 6d). The change occurs near $v_0 \approx 0.32$ such that for $v < v_0$ a cooperator more frequently interacts with another cooperator than with a defector (positive assortment), but for $v > v_0$ cooperators interact more often with defectors than with cooperators. In spatial settings, such negative assortment can be realized by the formation of filament-like clusters.

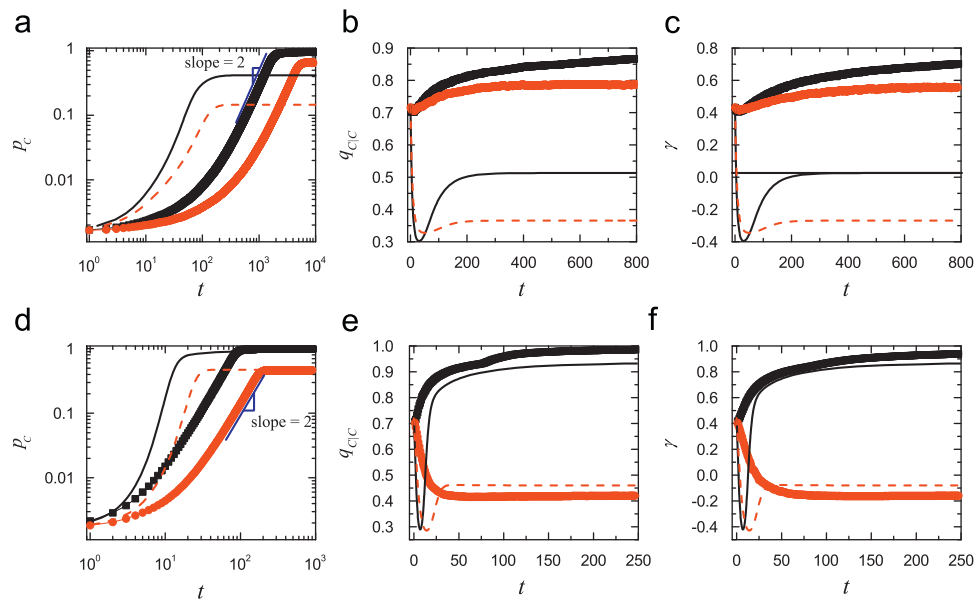


Fig. 4. Spatial invasion dynamics as characterized by the global density of cooperators p_C (left), the local density of cooperators $q_{C/C}$ (middle), and the cluster shape γ (right) for the prisoner's dilemma (top row) and the snowdrift game (bottom row). For both games, rapid local equilibration between cooperators and defectors is followed by a uniform quadratic expansion process. The speed of the expansion of cooperators decreases under less favorable settings (increasing u , v). $q_{C/C}$ and γ rapidly converge toward an equilibrium state. Once local equilibrium is achieved, p_C increases quadratically. For the prisoner's dilemma results are shown for $u=0.02$ (■) and $u=0.10$ (●) and for the snowdrift game for $v=0.05$ (■) and $v=0.40$ (●). The expansion process is shown for a 5×5 cluster on a 125×125 lattice averaged over 100 runs. The lines indicate results based on pair-approximation (upper solid, $u=0.02$, upper dashed, $u=0.10$; lower solid, $v=0.05$, lower dashed, $v=0.40$). The γ value is averaged over all cooperator clusters weighted by their cluster size.

Pair approximation provides good predictions of γ in the snowdrift game below the extinction threshold v_c . Near v_c and for larger v the quantitative prediction is unsatisfactory primarily because pair approximation is unable to reproduce the extinction threshold. In the prisoner's dilemma, pair approximation yields poor predictions for γ . The main reason for this failure is the inability of pair approximation to account for social loops such as if two neighboring individuals share common neighbors. Such loops become particularly important in compact clusters and hence pair approximation works much better in the snowdrift game where positive assortment among cooperators is weaker or even disassortative. The improved pair approximation (IPA) method (Satō et al., 1994; Morita, 2008), which takes triplet correlations into account, is still only capable of predicting trends, although with marginal improvement (Fig. 6). Note that for the prisoner's dilemma, IPA underestimates the equilibrium values as well as the critical points (Figs. 6a and b); while for the snowdrift games, IPA predicts an overestimated critical point (Figs. 6c and d).

4. Discussion

For the problem of cooperation the most important evolutionary question is how cooperators manage to gain a foothold in a population and increase in abundance when initially rare. In the present work we approach this challenge by investigating the spatial invasion and expansion of cooperators in a world of defectors. In particular, we compare the characteristic features of the invasion process as well as of the emerging spatial patterns in the two most prominent social dilemmas, the prisoner's dilemma and the snowdrift game. In both games the invasion of cooperators succeeds for sufficiently benign conditions but fails if cooperation entails high costs or benefits are low. This is of particular importance in the snowdrift game because for this type of interaction the replicator equation (Hofbauer and Sigmund,

1998), which models well-mixed populations with random encounters of individuals, predicts that cooperators and defectors can co-exist. Hence, spatial structure may inhibit or even eliminate cooperation in the snowdrift game (Hauert and Doebeli, 2004). In contrast, spatial structure promotes cooperation in the prisoner's dilemma because it enables cooperators to form compact clusters. This leads to more frequent interaction of cooperators with other cooperators, reduces the exploitation by defectors and prevents their extinction.

Successful invasion attempts, initiated by a small cluster of cooperators, exhibit two distinct phases: rapid local equilibration of cooperators and defectors is followed by a uniform expansion process—a 'wave of cooperation' expanding into defector territory. In the wake of the invasion front characteristic spatial patterns emerge. The macroscopic features reflect the microscopic interactions following the principle that form follows function.

We should point out that the presented spatial invasion dynamics of cooperation is analogous to the general contact process that predicts a continuous transition from the active ($p_C > 0$) to the absorbing state ($p_C = 0$) (Hinrichsen, 2000; Marro and Dickman, 1999). Using the updating rule based on the Fermi function in physics, previous studies have revealed that the extinction of cooperators in spatial games falls into the universality class of directed percolation on square lattices (Szabó and Hauert, 2002; Hauert and Szabó, 2005). Although a quantitative characterization of such critical phenomena goes beyond the scope of our present study, we confirm that our results are robust to variations in updating rules. The systems behavior near critical points, albeit modified by the intrinsic features of the chosen updating rule (i.e., only imitate better performing neighbors) and spatial geometry (i.e., Moore neighborhood), is qualitatively similar to that of the general contact process (see the snapshots in Figs. 1f and 2f).

In empirical situations it is often difficult to distinguish the prisoner's dilemma from the snowdrift game. Turner and Chao (1999) demonstrate that RNA phages are trapped in a prisoner's

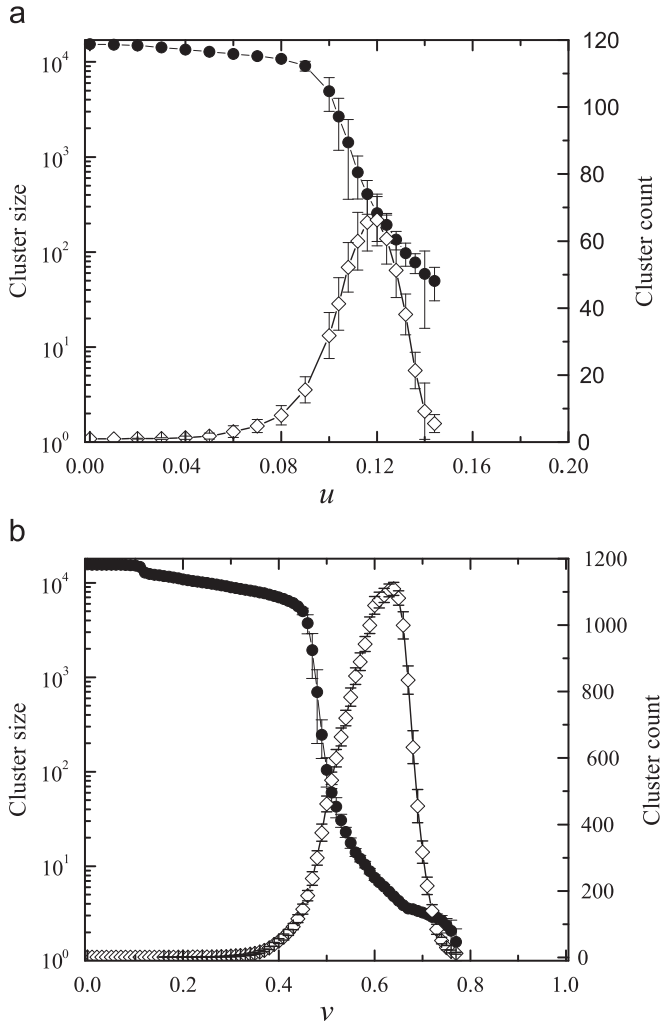


Fig. 5. Macroscopic characteristics of the invasion dynamics of cooperation: cluster size (●) and cluster count (◇) for (a) the prisoner's dilemma and (b) the snowdrift game. In both games, the cluster size reduces when increasing the game parameters and the cluster count reaches a maximum near the extinction threshold. In the prisoner's dilemma, a minimum cluster size of about 60 is required for cooperators to survive, in sharp contrast to the snowdrift game where even an isolated cooperator is able to persist. For an initial cluster of 15×15 cooperators, the cluster size and count are determined when the system reaches equilibrium on a 125×125 lattice and averaged over 100 runs. The cluster size is averaged over all existing cooperator clusters weighted by their size. The error bars mark one standard deviation.

dilemma—but they fail to cooperate. However, selection alters the payoff structure and the game turns into a snowdrift game (Turner and Chao, 2003). Other famous experiments on cooperation include predator inspection behavior in sticklebacks (Milinski, 1987; Milinski et al., 1997) or enzyme production in yeast (Greig and Travisano, 2004; Gore et al., 2009). While it is clear that individuals are facing a social dilemma in all cases, the data is either insufficient to differentiate between the prisoner's dilemma and the snowdrift game or the evidence seems to be in favor of the latter.

Our study offers a rule of thumb to discriminate between the two types of interactions based on the characteristics of the emerging spatial patterns, which might be particularly relevant for experimental evolution in microbial populations. The emergence of compact patches of cooperators points towards the prisoner's dilemma, whereas filament-like or fractal cluster shapes serve as an indicator that the underlying interaction is governed by a snowdrift game.

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Appendix A. Pair approximation

Let p_C and $p_D = 1 - p_C$ denote the fraction of cooperators and defectors and p_{CC} , p_{CD} , p_{DC} and p_{DD} represent the fractions of CC, CD, DC and DD pairs, respectively. The probabilities of all larger configurations are expressed and approximated in terms of pair configuration probabilities—hence the name pair approximation (Matsuda et al., 1992; Nakamaru et al., 1997, 1998; Satō et al., 1994). Then, $q_{X|Y} = p_{XY}/p_Y$ with $X, Y \in \{C, D\}$ specifies the conditional probability that the neighbor of an individual of type Y has type X . Using normalization ($p_{CC} + p_{CD} + p_{DC} + p_{DD} = 1$) and symmetry ($p_{CD} = p_{DC}$), the two dynamical variables, p_C and $q_{C|C}$ fully determine the dynamics of the system.

Let us first consider the case that a randomly selected focal D -player switches to C . The D -player has k_C cooperators and k_D defectors ($k_D = k - k_C$) in its neighborhood on a regular graph with connectivity k . The frequency of such configurations is

$$\frac{k!}{k_C!k_D!} q_{C|D}^{k_C} q_{D|D}^{k_D}$$

and the payoff of the focal D -player is $P_D(k_C, k_D) = c \cdot k_C + d \cdot k_D$ using the general payoff matrix

$$\begin{pmatrix} a & b \\ c & d \end{pmatrix}. \quad (7)$$

Similarly, the payoff of a neighboring C -player is $P_C(k_C', k_D') = a \cdot k_C' + b \cdot (k_D' + 1)$, where k_C' and k_D' are the numbers of C - and D -players among the $k - 1$ remaining neighbors besides the focal D -player. The frequency of this configuration is

$$\frac{(k-1)!}{k_C'!k_D'!} q_{C|C}^{k_C'} q_{D|C}^{k_D'}$$

where $q_{X|YZ}$ gives the conditional probability that a player next to the YZ pair is in state X (here X, Y , and Z denote C or D). The probability that the D -player switches to C can be written as

$$W_{D \rightarrow C} = \frac{k_C}{k} \sum_{k_C' + k_D' = k-1} \frac{(k-1)!}{k_C'!k_D'!} q_{C|C}^{k_C'} q_{D|C}^{k_D'} f(P_C(k_C', k_D') - P_D(k_C, k_D)),$$

where the transition probability $f(P_C(k_C', k_D') - P_D(k_C, k_D))$ (see Eq. (5) in main text) is weighted by the configuration probability of the C -player's neighborhood and summed over all possible configurations. Consequently, p_C increases by $1/N$, where N denotes the population size, with probability

$$\text{Prob}\left(\Delta p_C = \frac{1}{N}\right) = p_D \sum_{k_C + k_D = k} \frac{k!}{k_C!k_D!} q_{C|D}^{k_C} q_{D|D}^{k_D} W_{D \rightarrow C}. \quad (8)$$

At the same time, the number of CC pairs increases by k_C and thus p_{CC} increases by $2k_C/(kN)$ with probability

$$\text{Prob}\left(\Delta p_{CC} = \frac{2k_C}{kN}\right) = p_D \frac{k!}{k_C!k_D!} q_{C|D}^{k_C} q_{D|D}^{k_D} W_{D \rightarrow C}. \quad (9)$$

Similarly, the probability that p_C decreases by $1/N$ is given by

$$\text{Prob}\left(\Delta p_C = -\frac{1}{N}\right) = p_C \sum_{k_C + k_D = k} \frac{k!}{k_C!k_D!} q_{C|C}^{k_C} q_{D|C}^{k_D} W_{C \rightarrow D}, \quad (10)$$

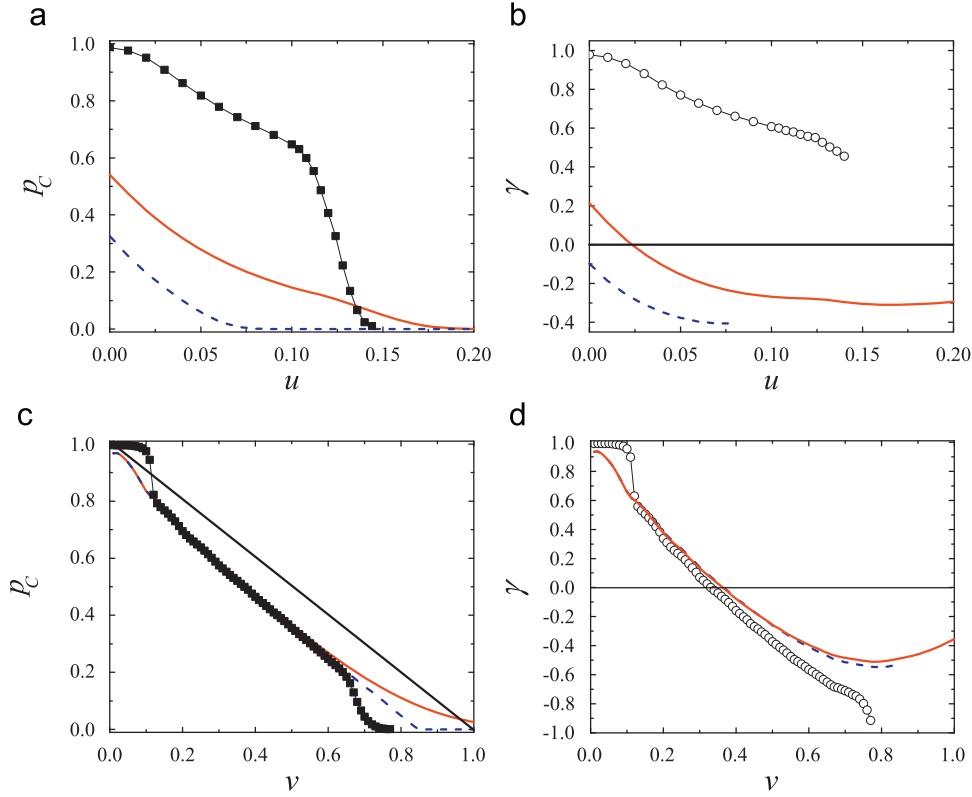


Fig. 6. The equilibrium fraction of cooperators, p_C , (left) and cluster shape, γ , (right) in the prisoner's dilemma (top row) and the snowdrift game (bottom row) as a function of the game parameters u , v , respectively. Symbols show simulation results, solid lines show the corresponding results based on pair approximation, and dashed lines show the corresponding results based on improved pair approximation (see Appendix). In the prisoner's dilemma, $\gamma > 0$ always holds, which indicates positive assortment of cooperators. In the snowdrift game, γ is positive under hospitable conditions but becomes negative in hostile settings, which indicates negative assortment such that cooperators interact more often with defectors than with other cooperators—a consequence of the filament-like cluster shapes. As a reference, the diagonal line in panel (c) indicates the equilibrium frequency of cooperators, $1 - v$, in well-mixed populations. The initial configuration is the same as in Fig. 5.

where $W_{C \rightarrow D}$ denotes the probability that the focal C-player switches to D, i.e.,

$$W_{C \rightarrow D} = \frac{k_D}{k} \sum_{k_C + k_D = k-1} \frac{(k-1)!}{k_C! k_D!} q_{C|DC}^{k_C} q_{D|DC}^{k_D} f(P_D(k_C', k_D') - P_C(k_C, k_D)). \quad (11)$$

And p_{CC} decreases by $2k_C/(kN)$ with probability

$$\text{Prob}\left(\Delta p_{CC} = -\frac{2k_C}{kN}\right) = p_C \frac{k!}{k_C! k_D!} q_{C|DC}^{k_C} q_{D|DC}^{k_D} W_{C \rightarrow D}. \quad (12)$$

In the limit of large population sizes we obtain

$$\dot{p}_C = \lim_{N \rightarrow \infty} \frac{\Delta p_C}{1/N} = \text{Prob}\left(\Delta p_C = \frac{1}{N}\right) - \text{Prob}\left(\Delta p_C = -\frac{1}{N}\right), \quad (13)$$

$$\begin{aligned} \dot{p}_{CC} &= \lim_{N \rightarrow \infty} \frac{\Delta p_{CC}}{1/N} \\ &= \sum_{k_C=0}^k \frac{2k_C}{k} \left[\text{Prob}\left(\Delta p_{CC} = \frac{2k_C}{kN}\right) - \text{Prob}\left(\Delta p_{CC} = -\frac{2k_C}{kN}\right) \right]. \end{aligned} \quad (14)$$

Setting

$$M_C = \frac{1}{p_C} \left\{ \text{Prob}\left(\Delta p_C = \frac{1}{N}\right) - \text{Prob}\left(\Delta p_C = -\frac{1}{N}\right) \right\} \quad (15)$$

$$M_{CC} = \frac{1}{p_{CC}} \left\{ \sum_{k_C=0}^k \frac{2k_C}{k} \left[\text{Prob}\left(\Delta p_{CC} = \frac{2k_C}{kN}\right) - \text{Prob}\left(\Delta p_{CC} = -\frac{2k_C}{kN}\right) \right] \right\} \quad (16)$$

and using $q_{C|C} = p_{CC}/p_C$, we find

$$\dot{p}_{CC} = \dot{q}_{C|C} p_C + \dot{p}_C q_{C|C} = (M_C q_{C|C} + \dot{q}_{C|C}) p_C = M_{CC} p_{CC} = M_{CC} p_C p_{C|C}$$

and thus,

$$\dot{p}_C = M_C p_C, \quad (17)$$

$$\dot{q}_{C|C} = (M_{CC} - M_C) q_{C|C}. \quad (18)$$

The above equations require a 'moment closure' by approximating $q_{X|YZ} \approx q_{X|Y}$. This means that only first order pair correlations are taken into account and hence termed pair approximation. However, the predictions can be improved by considering higher order correlations. One possibility is to consider the improved pair approximation (IPA), which takes triplet correlations into account when estimating $q_{X|YZ}$ in spatial lattices (Satō et al., 1994; van Baalen, 2000; Morita, 2008). Based on the Kirkwood approximation, Morita (2008) gave the following equations to approximate $q_{X|YZ}$:

$$q_{C|CD} = (1-\theta) q_{C|C} + \theta \frac{q_{C|C}}{q_{C|C} + q_{D|D}}, \quad (19)$$

$$q_{D|CD} = 1 - q_{C|CD}, \quad (20)$$

$$q_{D|DC} = (1-\theta) q_{D|D} + \theta \frac{q_{D|D}}{q_{C|C} + q_{D|D}}, \quad (21)$$

$$q_{C|DC} = 1 - q_{D|DC}, \quad (22)$$

where θ is the clustering coefficient, i.e., the probability of finding the triplet in closed form. Alternatively, van Baalen (2000)

considered the correlation of the triplets as follows:

$$q_{C|CD} = q_{C|C} \left[(1-\theta) + \theta \frac{p_{CD}}{p_C p_D} \right], \quad (23)$$

$$q_{D|CD} = 1 - q_{C|CD}, \quad (24)$$

$$q_{D|DC} = q_{D|D} \left[(1-\theta) + \theta \frac{p_{CD}}{p_C p_D} \right], \quad (25)$$

$$q_{C|DC} = 1 - q_{D|DC}. \quad (26)$$

We found that taking clustering coefficient into account results in marginally better predictions (see Fig. 6). In principle, better approximations can be obtained by including higher order terms, i.e., by going from pair to n -point approximations (Szabó et al., 2005), or by including other measures such as the correlation coefficient (van Baalen, 2000).

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