# Weak selection helps cheap but harms expensive cooperation in spatial threshold dilemmas

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## Abstract

Public Goods Games (PGGs) are n-person games with dependence of individual fitness benefits on the collective investment by the players. We have studied a simple PGG scenario played out by cooperating (C) and defecting (D) agents, applying the highly nonlinear threshold benefit function in an individual-based lattice model. A semi-analytical approximation of the lattice model has been developed and shown to describe the dynamics fairly well in the vicinity of the steady state. Besides the expected outcomes (i.e., the negative effect on cooperator persistence of higher cooperation costs and/or more intensive mixing of the population) we have found a surprising, counter-intuitive effect of the strength of selection on the steady state of the model. The effect is different at low and high cooperation costs, and it shows up only in the lattice model, suggesting that stochastic effects and higher order spatial correlations due to the emergent spatial clustering of cooperators (not taken into account in the semi-analytical approximation) must be responsible for the unexpected results for which we propose an intuitive explanation, present a tentative demonstration, and shortly discuss their biological relevance.

*Keywords:* nonlinear public goods, spatial pattern, stochastic replicator dynamics,

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### Highlights

- The dynamics of a spatial threshold dilemma game is studied using a lattice model.
- A semi-analytical approximation of the lattice model is developed.
- The effect of selection strength for cooperation on the dynamics is explored.
- Strength of selection is shown to act through higher order correlations of the spatial pattern

## 1. Introduction

Cooperation is certainly one of the most important types of interaction that have shaped the biosphere as we know it today. In a macroevolutionary context it may even be considered the single most important one since, without exception, all major evolutionary transitions (Maynard Smith and Szathmáry (1995)) had proceeded by the integration of cooperating entities into new entities representing higher-level units of selection. The evolutionary drive towards cooperation must have been the overwhelming fitness advantage that cooperators may harvest, in spite of the obvious short-term advantage that freeriders of cooperation by others could enjoy. One of the textbook examples of cooperation that can be (and often is) exploited by cheaters is modeled by the public goods game (PGG) (Hardin (1968); Rankin et al. (2007)). PGG is an n-person game in which cooperators invest in the production of some common good which is then shared evenly among all $n$ individuals in the group. Cheaters do not pay the (full) cost of producing the public good but enjoy the same benefit as cooperators, which is provided only by the cooperating members of the group. Thus, without mechanisms like preferential cooperation or active punishment acting against it, cheaters always outcompete cooperators (Hardin (1968)). While classical models assume that the fitness benefit of the public good increases linearly with the number of cooperators, public good benefits are almost always nonlinear functions of individual contributions (Fig. 1) in nature. In a molecular biological context such nonlinearity arises in many cases because the effects of biological molecules are often sigmoidal functions of their concentrations, due to threshold dosage effects or cooperative binding of ligands and the resulting saturation of chemical activities at higher enzyme concentrations (Cornish-Bowden (2012); Frank (2013); Zhang et al. (2013)). The nonlinear benefit of producing some extracellular material (e.g., exoenzymes) by microbes may be directly related to the nonlinear kinetics of the molecular mechanisms of their actual effects (Archetti and Scheuring (2016)). Nonlinearity is frequently modelled by the so called "threshold (or volunteer's) dilemma game" (Archetti (2009); Archetti and Scheuring (2011)), in which a certain minimum number $k$ of players have to cooperate to produce the "public good" that provides a fitness benefit $b$ for each of the $n$ players (cooperators and defectors alike), while only cooperators bear the cost $c$ of cooperation (Fig. 1). Although the threshold dilemma game is a limit case of a general sigmoid payoff function (Fig. 1), it has been shown previously that the two games yield qualitatively identical results (Archetti and Scheuring (2016)) with only quantitative differences between them, so we can safely use the threshold game as a model for sigmoid nonlinear games.

Microbes frequently form biofilms or live in a habitat (e.g., in soil) that seriously constrains individual motion. Consequently, mother and daughter cells often stay in close proximity for a long time after division, forming aggregated patches of clone-mates. However, the public goods they produce may be dispersed by diffusion or convection, so that they get diluted below the threshold level at a certain distance from where they were produced. Therefore, only cells close to the producing cells can use the product to their advantage. Social conflicts in such immobilized populations can be adequately modelled by a population of individuals living on a two dimensional grid, where neighboring individuals interact with each other in two different ways: they cooperate by sharing public goods, and they also compete for the products of cooperation which they have limited access to (see, e.g., Cremer et al. (2019), and references

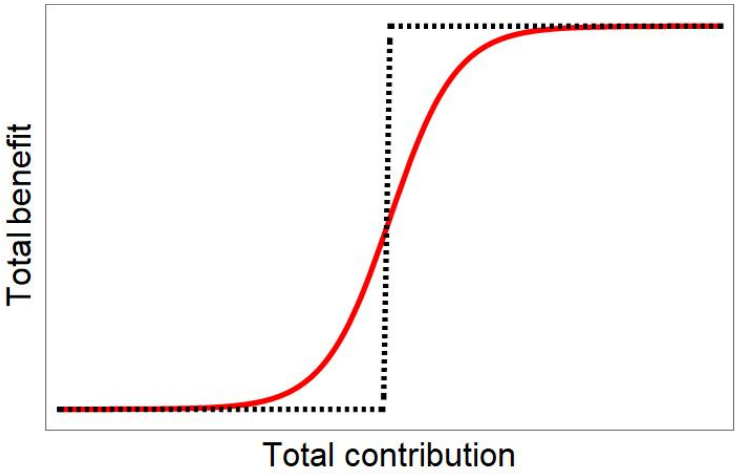

Figure 1: The total benefit of cooperation is generally a sigmoidal nonlinear function of the total contributions of the individuals (solid red line). Threshold games (dashed black line) assume that the benefit is negligible below a distinct contribution threshold above which it jumps abruptly to its highest possible value (step function).

therein). It is the competition phase of interaction that imposes selection on the population of the players. The population dynamics of growing tumor cells can be described by very similar dynamics. Cooperating cells produce growth factors which benefit all nearby cells, including non-producing cheaters (Archetti and Pienta (2019)).

In addition to the actual form of social conflict and the spatial structure of microbial or tumor cell populations, the intensity of the competitive pressure can also play a crucial role in determining the dynamics of the selection process. Earlier works pointed out that for the prisoner's dilemma game there is an optimal strength of selection at which the equilibrium level of cooperation is highest in different structured populations including homogeneous random networks and scale-free networks (Szolnoki et al. (2009); Pinheiro et al. (2012)). The prisoner's dilemma game is probably by far the best studied two-person social conflict, but microbial interactions (as well as many other biologically realistic scenarios of interaction) involving public goods production and exploitation are certainly better modeled as multiplayer nonlinear games (see Archetti and

Scheuring (2012) and references therein). Surprisingly, the role of the strength of selection, its connection to spatial aggregation and pattern formation by players adopting different strategies has not been studied yet in nonlinear public goods games. The steady states of certain multiplayer and/or multi-strategy games have been shown to depend on selection strength for well-mixed populations in a study by Wu et al. (2013), sometimes leading to rearrangements in the equilibrium frequency ranking of strategies.

In this work we investigate the threshold public goods (or volunteer's) dilemma game (Diekmann (1985); Rapoport and Eshed-Levy (1989)) played by individuals of limited motility, competing and cooperating in a two-dimensional habitat. We focus our attention on the effect of the strength of selection on the success of cooperators, varying the cost of cooperation and the speed of motion of individuals, aiming to reveal self-organization processes shaping the local and global dynamics in a mixed population of cooperators and cheaters.

## 2. Models

### *2.1. The agent-based spatial model*

**Space, cooperation:** We consider a population of individuals on a rectangular lattice of size $L \times L$. Every site of the lattice is occupied by a single individual following either the cooperative strategy C or the defective strategy D; all individuals are identical in all other dynamically relevant respects. We assume that every individual interacts with its eight nearest neighbors by playing a nine-person threshold public goods game with them. Cooperators produce a public good at a cost $c$ which provides a benefit $b$ ($b > c > 0$) for all individuals within the interacting local group if the number of cooperators in that group is larger than or equal to $k$ ($1 \leq k \leq 9$). Without loss of generality, $b$ can be rescaled to unity ($b = 1.0$) and thus $0 < c < 1$. This simplification will be used throughout the rest of the paper. If the number of cooperators is smaller than $k$, then none of the group members benefits, but all the cooperators in the group pay the cost of cooperation even then (Table 1).

| | $\#C < k$ | $\#C \geq k$ |
|---|---|---|
| Cooperator's payoff | $-c$ | $1-c$ |
| Defector's payoff | 0 | 1 |

Table 1: The possible payoffs of cooperators and defectors as a function of the number of cooperators ($\#C$) within the local interacting group. ($0 < c < 1$). If the number of cooperators is less than $k$, then the payoff for cooperators is $-c$ and for defectors it is 0. If there are at least $k$ cooperators in the group, then cooperators receive a payoff of $1-c$ while defectors get a payoff of 1.

Table 1. shows that the defector's payoff is always higher than that of the cooperator in any particular pairwise C-D interaction within the same local group of players, thus D is the only evolutionarily stable strategy in a well-mixed (homogeneous) population (Hofbauer and Sigmund (1998)). Due to the spatial constraints arising from a) daughter agents remaining immediate neighbors after an elementary game step, b) limited motility of agents within the lattice and c) local interactions among the players in the spatial model, cooperators preferentially interact with cooperators due to "habitat viscosity", which either keeps them stably coexistent with defectors or can even drive the defector strategy extinct (van Baalen and Rand (1998);Mitteldorf and Wilson (2000); Vásárhelyi and Scheuring (2013)).

**Time, competition:** We use a random pairwise update for the competitive interaction between individuals. A pair of neighboring individuals (either orthogonal or diagonal neighbors) featuring strategies $i$ and $j$ are selected at random from the lattice, and the payoffs of these individuals are computed according to the number of cooperative strategies in their own 9-site neighborhoods. The individual playing strategy $i$ is then replaced by by a copy of the one playing strategy $j$ with probability

$$p_{ij} = \frac{1}{2} + \frac{\sigma}{2}\frac{\pi_j - \pi_i}{\Delta\pi}, \tag{1}$$

where $0 < \sigma < 1$ measures the strength of the selection; $\Delta\pi = 1 + c$ is the maximum of the possible payoff differences in the game and $\pi_i$ and $\pi_j$ are the actual payoffs of strategy $i$ and $j$. Similarly, the agent playing strategy $j$ replaces its opponent with probability $1 - p_{ij}$. We repeat this update step $L^2$ times in each time unit ("generation") with randomly chosen neighbors. This update rule leads to the classical replicator dynamics in large, well-mixed populations (Traulsen et al. (2005); Hilbe (2011)), the behavior of our agent based model is therefore directly comparable to that.

**Individual movements, diffusion algorithm:** To mimic constrained individual motility of the agents on the habitat lattice, we have deployed a simple scalable diffusion algorithm. Mixing is scaled by the diffusion parameter *Diff* ($0 < \mathit{Diff} < \infty$) which is the expected number of site swaps following each interaction step during an update. The swapped pairs of neighboring sites are also chosen at random, independently of the interacting pair.

### *2.2. The semi-analytical approximation of the agent-based model*

The update event changes the frequency of strategies if one of the strategies in the interacting pair is C and the other is a D - all other interactions are inconsequential from a dynamical point of view. To approximate the global dynamics of the system we estimate the average probabilities of D→C and C→D substitutions as functions of the actual local frequencies and the parameters of the model. In dynamical equilibrium these two updates are equally frequent, which means that the average payoff of neighbouring C and D strategies are identical.

Because of the model's geometry, neighbouring C and D strategies have common and also separate neighbours with which they interact. Depending on the relative positions (orthogonal or diagonal) of the two focal players, they have either 4 common and 3-3 separate or 2 common and 5-5 separate neighbors, besides the two focal sites which are always interacting neighbors by definition (Fig. 2). (We note here that a more homogeneous hexagonal lattice could have been chosen for the arena, in which case the orthogonal-diagonal distinction disappears, but that would have reduced the maximum neighbourhood size to 7, instead of 9, seriously constraining the range of a dynamically important model parameters.) We have calculated all the output variables for the diagonal and the orthogonal neighbourhoods separately, and averaged the results with a weight factor equal to the relative occurrence for each. The average payoff of strategy C is determined by the average frequency of C in the common neighborhood ($x_{com}$) and in its own separate neighborhood section ($x_{(C|C)}$). Similarly, the average payoff of D is determined by $x_{com}$ and by $x_{(C|D)}$, where this latter term is the average frequency of C-s in the separate neighborhood section of D. Knowing these frequencies and assuming that cooperators are selected independently around the C and D strategies with the above frequencies we can estimate the average payoff of neighbouring C and D as

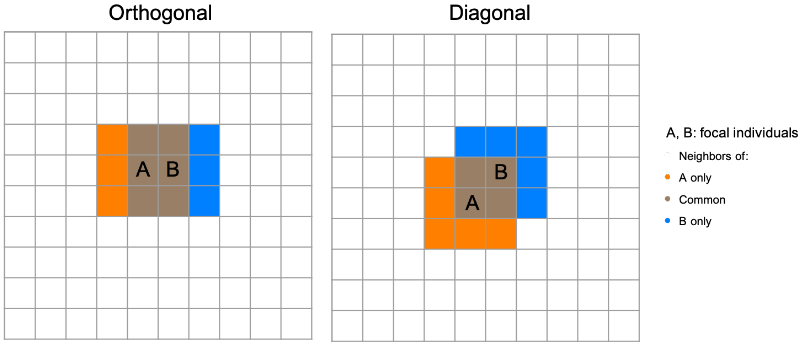

Figure 2: Separate and common neighbors of two, potentially interacting individuals (labelled A and B) with overlapping neighborhoods. left: focal individuals are in orthogonal position, right: focal individuals are in diagonal position.

$$
\begin{aligned}
\pi_C = {} & \frac{1}{2}\sum_{j=0}^{3}\sum_{i=0}^{4}\binom{3}{j}\binom{4}{i}x_{com}^{i}(1-x_{com})^{4-i}x_{(C|C)}^{j}(1-x_{(C|C)})^{3-j}\Theta(i+j+1-k)+\\
& \frac{1}{2}\sum_{j=0}^{5}\sum_{i=0}^{2}\binom{5}{j}\binom{2}{i}x_{com}^{i}(1-x_{com})^{2-i}x_{(C|C)}^{j}(1-x_{(C|C)})^{5-j}\Theta(i+j+1-k)-c\\
\pi_D = {} & \frac{1}{2}\sum_{j=0}^{3}\sum_{i=0}^{4}\binom{3}{j}\binom{4}{i}x_{com}^{i}(1-x_{com})^{4-i}x_{(C|D)}^{j}(1-x_{(C|D)})^{3-j}\Theta(i+j+1-k)+ \qquad (2)\\
& \frac{1}{2}\sum_{j=0}^{5}\sum_{i=0}^{2}\binom{5}{j}\binom{2}{i}x_{com}^{i}(1-x_{com})^{2-i}x_{(C|D)}^{j}(1-x_{(C|D)})^{5-j}\Theta(i+j+1-k),
\end{aligned}
$$

where $c$ is the cost of cooperation as before, $\Theta(i+j+1-k)$ is the Heaviside function ($\Theta(i+j+1-k)=1$ if $i+j \geq k-1$, otherwise ($\Theta(i+j+1-k)=0$).

*Well-mixed case:* By using binomial distributions in the above equations we take only the pairwise correlations between strategies into account, higher order correlations are neglected. This essentially means assuming perfect mixing of the two strategies on the lattice. As expected by intuition, if the population is well-mixed the average local frequencies of cooperators in the vicinity of C and D strategies are equal, that is, $x_{com} = x_{(C|D)} = x_{(C|C)}$. Consequently $\pi_C + c = \pi_D$, i.e, the payoff of C is always smaller than the payoff of D in eq (2), and strategy C is always excluded from the population. This, in effect, is the mean-field case.

*Spatially aggregated case:* The simplifying assumption of perfect spatial mixing clearly underestimates the real aggregation of identical strategies with limited agent motility. If diffusion is not very intense, then both C and D individuals tend to aggregate into patches, i.e., C-s can be found more frequently near other C-s than D-s: $x_{(C|C)} > x_{(C|D)}$. Individuals find themselves in patches dominated by their own clonemates, which is beneficial for cooperators but detrimental for defectors.

Since there is no method available to build the corresponding $x_{com}$, $x_{(C|C)}$ and $x_{(C|D)}$ functions from first principles, we have computed them as empirical functions fitted to the actual agent based simulations introduced above, and substituted these computed functions into (2). We have focused on the dynamically relevant parts of the lattice, so the local relative frequency $x$ of cooperators was calculated within the union of the neighbourhoods of CD pairs of competitors. CC and DD pairs are irrelevant from a dynamical point of view. Figure 3B illustrates the fitted $x_{com}$, $x_{(C|C)}$ and $x_{(C|D)}$ functions against $x$ in the dynamically relevant parts of the lattice. Note here that pairwise approximations have been used effectively in the past on regular graphs for two- (Ohtsuki and Nowak (2006))- and multi-player (Li et al. (2016);Renton and Page (2021)) games with weak selection. Due to the higher-order correlations of the links themselves within the lattices, these approximations are generally less accurate (e.g. Szabó and Hauert (2002)).

Using the fitted empirical polynomial functions we have calculated the fitness differences of C and D against $x$, determined the fixed points of the dynamics numerically, and compared this result with the dynamical behavior of the corresponding agent based simulation.

## 3. Results and discussion

We have tested the semi-analytical model using numerical simulations. The local equilibrium frequency of cooperators within the unified neighborhoods of CD-pairs, $x$, was recorded, along with $x_{com}$ (the average frequency of C in the common parts of the unions of C-D neighbourhoods), $x_{(C|C)}$ and $x_{(C|D)}$ (the average frequency of C in the respective separate parts), which were used to compute the three empirical functions of equilibrium cooperator frequency (Fig. 3B) to be applied in eq (2). Following this method for different parameter sets the semi-analytical model gives a fair but not perfect approximation of the simulated dynamics (Fig. 3A,C,D, Fig S1). Since the focal variables of the model are the local frequencies of the cooperators within C-D pairs' joint neighbourhoods and local pairwise correlations, the dynamical effects of higher order correlations (in aggregates of three, four or even more focal cooperators resulting in different C cluster geometries) are not considered. As a consequence, the effects of the aggregation of identical strategies and the spatial segregation of different strategies are underestimated in the semi-analytical model. In other words, the source of deviations between the calculated and the simulated results is that even the empirical distribution of cooperators in the separate and the common domains of the joint neighborhoods of C-D pairs fails to capture the actual distortion of cooperative help in favor of one or the other strategy due to spatial aggregation. These simplifications are responsible for the consistent inaccuracy of the semi-analytical model (Fig. S1). Previous analysis of threshold games in infinitely large populations with individuals playing the game in randomly formed local groups (random neighborhoods) and assuming

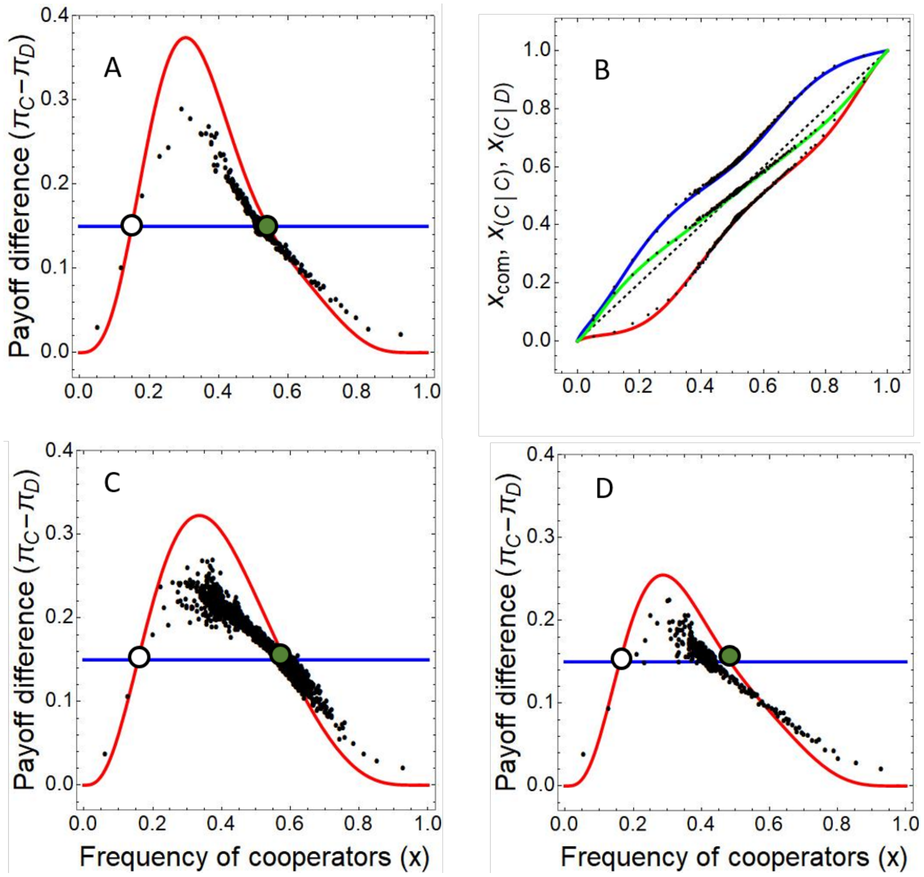

Figure 3: A,C,D: The payoff differences (red curves) and the cost (blue lines) of cooperators as functions of the average relative local cooperator frequency $x$ in the joint neighbourhoods of C-D pairs. Unstable fixed points of the semi-analytical model are denoted by empty circles and stable fixed points by green circles. Black dots represent states along two simulated trajectories, one initiated at x=0.01, the other at x=0.99. B: the empirical $x_{com}$, $x_{(C|C)}$ and $x_{(C|D)}$ data and the corresponding fitted fifth-order polynomial functions (green, blue and red lines) used to produce figure A. Parameters: A,B: $Diff = 0, \sigma = 1$. C: $Diff = 0, \sigma = 0.1$. D: $Diff = 0.2, \sigma = 1$. ($k = 4, c = 0.15$, N=90.000) everywhere.

deterministic dynamics had shown that cooperators coexist with defectors if the cost of cooperation is below, and the initial frequency of cooperators is above, a critical level (Archetti and Scheuring (2011); Archetti and Scheuring (2012)). The situation is qualitatively the same in our model as revealed by Figure 3:

at sufficiently low cooperation costs the fitness differences define a stable and an unstable fixed point (where the cost line intersects with the benefit difference function). The presence of an unstable fixed point prevents the invasion of rare cooperators in deterministic, non-spatial cases, that is, the coexistence of cooperators and defectors is possible only if the initial frequency of cooperators is above the unstable fixed point. It was also shown, however, that the spatial correlation of invading cooperators makes the unstable fixed point practically disappear in finite, spatially structured populations with a stochastic update rule (Vásárhelyi and Scheuring (2013)). Furthermore, unlike in the deterministic well-mixed model, cooperators can completely exclude cheaters at higher threshold values (Vásárhelyi and Scheuring (2013)). This latter effect has also been shown by Czárán and Hoekstra (2009). Similarly, cooperators go extinct at lower $k$ thresholds, they coexist with defectors at intermediate threshold values, and achieve fixation at higher $k$ values in the present spatial model, but, interestingly, the behavior of the system depends on the strength of selection, $\sigma$ (Fig. 4), the effect of prime interest in this study which we return to in a minute.

The fixation of cooperators seems to contradict the payoff functions, since defectors should always be capable of invading a homogeneous population of cooperators for any $1 \leq k < n$. A single invading D individual always receives payoff $b = 1.0$, while its cooperating C neighbors can get only payoff $1-c$ at most (see Table 1), so that rare defectors are always expected to spread into uniform C populations. This argument neglects pattern formation at low mixing in spatial games, as well as the stochastic nature of the dynamics. We suspect that it is the effect of these two factors that is responsible for the fixation of cooperators at higher thresholds, which will be explained in more detail later. Note that we assume no external input of agents (C or D) through invading or mutant individuals in this model - a factor that would certainly obliterate the pure C fixed point even in the spatial model. The extinction of cooperators at lower $k$-s (regardless of the initial frequency of cooperators) is again a consequence of spatial structures and stochastic dynamics, since this outcome does not exist in deterministic models without spatial aggregation (Archetti and Scheuring (2012)).

A surprising characteristic of the model is that the level of updating stochasticity (controlled by the selection coefficient, $\sigma$) modifies the steady state frequency of cooperators in a complex way. At very low motility (i.e., at zero diffusion) weak selection is detrimental for cooperators at low threshold ($k = 2$), but it is beneficial at $k > 2$. In slightly mixing populations (at $\mathit{Diff} = 0.20$) weak selection has an inconsistent effect on the steady state level of cooperators at intermediate thresholds but depresses it at both low and high $k$ values (Fig. 4).

The intuitive explanation of this somewhat surprising result is the following:

*At low thresholds* ($k = 1, 2, (3)$): The $k = 1$ case is degenerate, in fact it prescribes no cooperation, and there is no chance for self-cooperators to win the game against defectors: D is always at advantage in a C-D game by not paying the cost of cooperation. At $k = 2$, the situation is radically different: a 2-cooperator cluster has a chance of being maintained, because it always has more unsupported than supported defectors in its neighborhood (an orthogonal C doublet supports 4 out of its 10 neighbors, whereas a diagonal one supports 2 out of 12), which keeps a stable fraction of cooperators present in the steady state at low costs (Fig 4A,B) while they are more often displaced by the defectors at higher costs (Fig 4 C,D). Yet, the average frequency of cooperators remains low at $k = 2$ even at low costs due to the still substantial rate of exploitation of the cooperating doublets by surrounding D individuals (Fig 4A). Therefore, if the fitness differences between C and D players are small (i.e., $c$ and/or $\sigma$ are small), weak selection or stochastic drift may reduce C-doublets to C-singlets too often, and C-singlets are always surrounded by fitter defectors, so they are doomed to extinction (Fig 4A). Player motility ($\mathit{Diff} = 0.2$, Fig 4B) obviously acts in favor of D, pushing $x$ to zero even at stronger selection ($\sigma = 0.50$, weaker drift).

*At high thresholds* ($k = 6, 7$): Low diffusion ($\mathit{Diff} = 0.0$) leads to the aggregation of both cooperators and defectors, but with the threshold high, D clusters

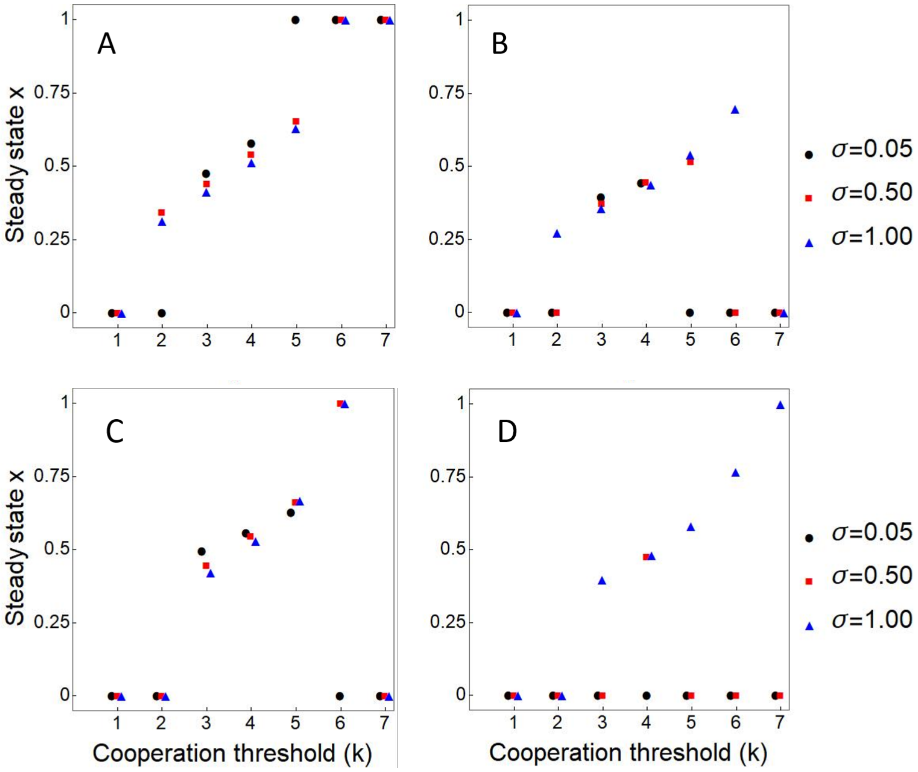

Figure 4: Steady state frequencies of cooperators as functions of the cooperation threshold $k$ at different strengths of selection $(\sigma)$ and player motilities $(\mathit{Diff})$. A,C,D: $\mathit{Diff} = 0$, B: $\mathit{Diff} = 0.2$. A,B: $c = 0.15$, C: $c = 0.20$, D: $c = 0.225$ The initial frequency of cooperators was $x(0) = 0.5$ except at $k = 7$, where it was $x(0) = 0.8$, in order to help the system start up. Data points represent the averages of the last 1.000-generations of simulations that have converged to their steady states. Symbols that would otherwise overlap are slightly offset horizontally.

cannot grow larger than a critical size, since D-s having more D neighbours than $n-k-1$ will always receive a zero payoff. Therefore, if $k$ is close to $n$, D clusters remain small. The update is stochastic, so if selection is weak ($c$ and $\sigma$ are both small, e.g., in Fig 4A) then there is a reasonable probability that these relatively small clusters disappear by chance within a short time. However, if $c$ is high, then selection is strong enough even at smaller $\sigma$ to maintain and increase the D patches and shrink the size of the C clusters below the threshold size $k$, wiping out all cooperators from the population (Fig 4C,D). We note here that since the system is finite and mutations are not allowed (all offspring inherit the strategy of their single parent) the dynamics should end up in one of the sinking states. However, if the polymorph state is a stable fixed point of the system, the fixation time increases exponentially with system size in well-mixed populations (Antal and Scheuring (2006)), which would be awfully long at our system size ($N = 90.000$). The fast fixation into the monomorph C state is a clear consequence of the emergent spatial correlations. This interpretation is supported by the fact that higher motility leads to the exact opposite outcome at high thresholds (compare Fig 4A and Fig 4B), where defectors exclude cooperators completely. This is due to the diffusive invasion of scattered D individuals into the cooperating groups of C, thereby either exploiting them, or preventing the formation of C patches of supercritical (greater than $k$) size, in both cases securing the fitness advantage of the invading defector. (Recall that a solitary D is always at advantage against its C neighbors.) Diffusion is clearly preventing higher order correlations from building up, depriving cooperators of the advantage thereof.

*At intermediate thresholds* ($k = 3, 4, 5$): These are robust cases of C-D coexistence (except at $\mathit{Diff} = 0.0$, $k = 5$, $\sigma = 0.05$ - see later), with substantial differences in the stationary $x$ values across the range of selection strengths. At the moderate, fixed cooperation cost ($c = 0.15$) assumed in the corresponding simulations (Fig 4A) it is always weak selection that is advantageous for cooperators, if higher order correlations are allowed to exist (i.e, at $\mathit{Diff} = 0.0$). The same trend is even stronger at lower costs, but it is reversed for more expensive cooperation (at $c = 0.20$ and above): the stronger the selection the higher the frequency of cooperators at the steady state (Fig 5). That is, cooperators benefit from weak selection pressure if cooperation is cheap, but it is more advantageous for them to have strong selection if cooperation is costly. We analyze this result in more detail below.

While the strength of selection only rescales the time units in deterministic models of well mixed populations (Traulsen et al. (2005); Antal et al. (2009); Hilbe (2011)), it can have a significant effect on the model's behavior if the dynamics is stochastic (Wu et al. (2015)) or in structured populations in two person prisoner's dilemma game (Vukov et al. (2006); Szolnoki et al. (2009);Pinheiro et al. (2012)). The results of the model presented in Figure 4 clearly show that the strength of selection has an effect on the dynamics of the spatial threshold game at different threshold values. Therefore, below we focus our attention on how the strength of selection and the cost of cooperation interact in determining the dynamics of the spatial threshold game. We have found that at cooperation costs below a critical level increasing selection decreases the equilibrium frequency of cooperators, while this trend turns around above a critical

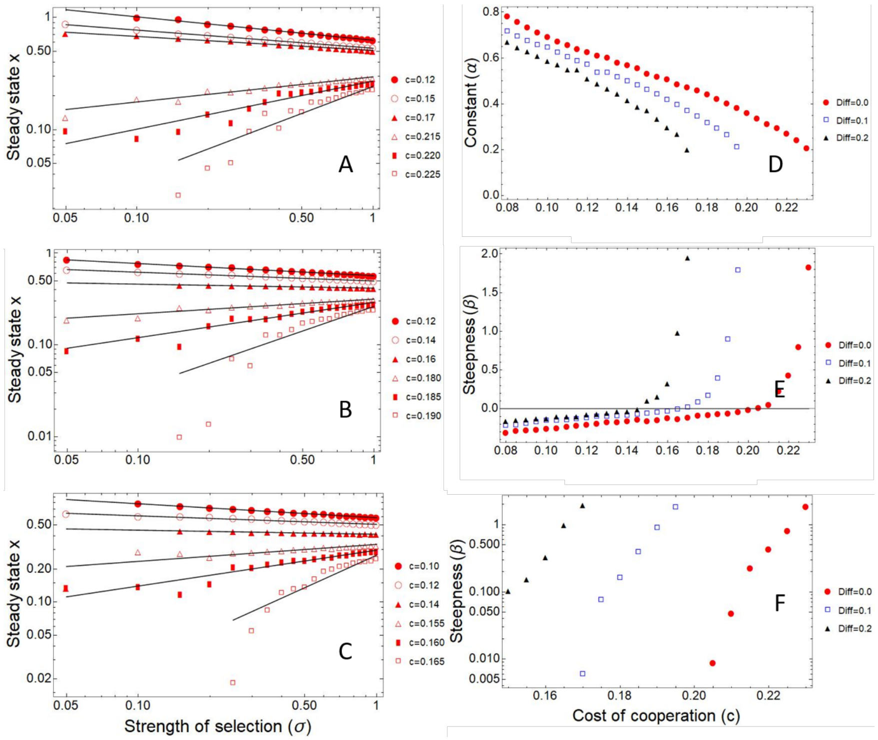

Figure 5: The effect of selection strength and cost of cooperation on the equilibrium cooperation level. A-C: The equilibrium frequency of cooperators at different strengths of selection follows a power law function ($\alpha\sigma^{\beta}$). Trends are measured at different diffusion rates (A: $Diff = 0$, B: $Diff = 0.1$, C: $Diff = 0.2$). The parameters of the power law functions follow monotonous trends in function of the cost (D, E). Steepness increases exponentially in the high cost range (F) ($k = 4$, $N = 90.000$).

level of the cost (Fig. 5 A-C). Moreover, Figure 5 A-C demonstrate that the power law function $\alpha\sigma^{\beta}$ is a good fit to the stationary state versus strength of selection ($\sigma$) data points at any given level of cost $c$. The constant of the power law function ($\alpha$) and the steepness of it ($\beta$) depend on $c$ following clear trends (Fig. 5 D-F). In accordance with intuition, increasing the cost of cooperation decreases the equilibrium frequency of C players (Fig. 5 A-C), and modifies the slope of the dependence of $x$ on $\sigma$ in a monotonic but non-linear way (Fig. 5 D-F). At the low-cost range the decreasing trend of equilibrium cooperator frequency with increasing $\sigma$ weakens as the cost of cooperation increases (Fig. 5 E), whereas above a critical cost level the slope increases in an exponential fashion (Fig. 5 F). Comparing the results at different diffusion rates it is clear that increasing diffusion reduces both the equilibrium frequency of cooperators and - slightly - its $\sigma$ dependence (Fig. 5 E,F), which supports the idea that it is spatial correlation that is responsible for the observed phenomenon. Results are demonstrated for the $k = 4$ case here, but we observed qualitatively similar relations for lower and higher thresholds ($k = 3, 5$) (see supplementary Fig S2). Notice that for higher diffusion rates (about $Diff > 0.30$, at $c > 0.15$, $k = 4$, and practically any positive strength of selection) cooperators are always excluded by defectors (as the system approaches the mean-field case).

To reveal the reason for the equilibrium frequency of cooperators being dependent on $\sigma$ and this trend being a function of $c$ we have visualized the spatial patterns of the strategies in dynamical equilibrium at different combinations of $\sigma$ and $c$ values (Fig. 6.). Increasing the strength of selection seems to have a consistent effect on the dispersion of the strategies: higher $\sigma$ decreases the average patch size for both, but at low cost of cooperation( $c = 0.10$) this dispersion helps the defector (D) whereas at higher cost ($c = 0.22$) it is beneficial for the cooperator (C). The obvious effect of higher cooperation cost decreasing cooperator frequency needs no explanation, but two more, less trivial questions arise: 1) why does stronger selection fragment large patches into many smaller ones, and 2) why does this fragmentation always help the rarer strategy as selection becomes stronger (i.e., D at $c = 0.10$ and C at $c = 0.22$)?

The fragmentation effect of increasing $\sigma$ is easy to explain for rare D agents attacking larger C patches which is a common event at small or moderate costs ($c \lessapprox 0.15$ (see. Fig. 5 E and Fig 6, upper row)): according to (1) the actual fitness advantage of a solitary defector is proportional to $c\sigma$ if it is surrounded by at least $k$ C agents, so the higher the $\sigma$ the more probable that the solo defector sticks and spreads locally, resulting in many small D patches. These patches cannot grow large, because larger D patches are easily eroded by successful cooperators from outside, as a C backed by at least $(k-1)$ other C agents enjoys a fitness advantage $(1-c)\sigma$ over D with less than $k$ C neighbours, i.e., in and around larger D clumps. That is, small D patches are born and eliminated stochastically at a fast pace at higher $\sigma$ values, resulting in a dynamical spatial equilibrium of many small D islands in the ocean of C agents.

The mechanism for the reverse pattern at $c = 0.22$ (and at high cooperation costs in general, see Fig. 5 E) is less obvious. At high cooperation costs the cooperator has a chance to persist only if the cooperation threshold is high (typically $k > 3$ see Fig 4 C,D). This means that relatively large C clusters have to be maintained in spite of the ongoing external attacks from defectors, because only relatively large $k$ allows for cluster geometries with sufficient self-support inside C patches and no support for neighboring defectors. More compact patches with convex surfaces are better at resisting invasion by D agents, since then the invading D-s are less likely to be supported by C agents from within the C cluster under attack (Szabó and Fáth (2007);Pinheiro et al. (2012)). Obviously, D agents with a sufficient number of C in their separate neighborhood domains could also easily invade even compact C clusters, but at high cooperation costs this situation is relatively rare, because C patches are rather scattered anyway.

Increasing selection pressure (larger $\sigma$) has two counteracting effects on C clusters: 1) It tends to keep them compact and close to $k$ in size, because outlying C agents not supported by the critical number of cooperators will probably have a fitness disadvantage of $-c\sigma$ against surrounding D-s and they may get eliminated - only the compact “core” of the C cluster is safe, and it is safer at high $\sigma$ precisely because of the isometric (i.e., of roughly equal extension in all spatial directions) cluster shape it provides Fig 7.

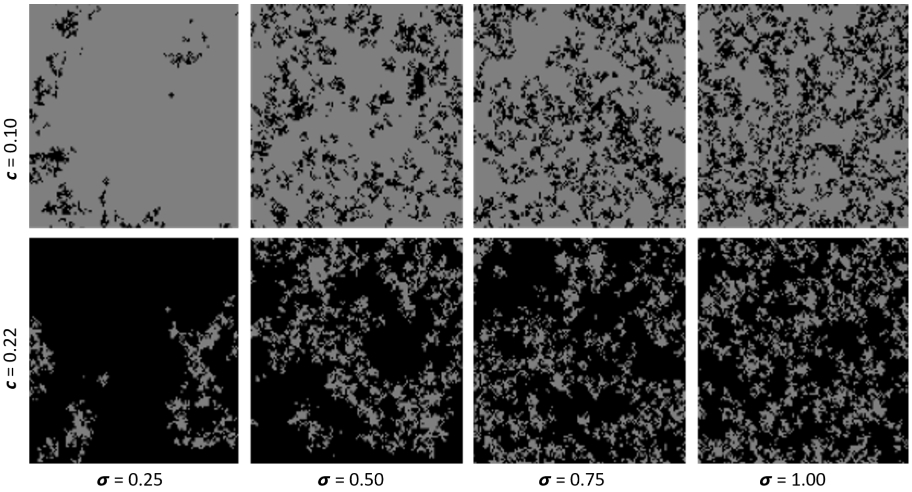

Figure 6: Spatial patterns of steady state C-D communities at different cooperation cost $c$ and strength of selection $\sigma$ values, at fixed cooperation threshold $k = 4$ and diffusion $\mathit{Diff} = 0.00$. The less frequent strategy benefits from stronger selection. Gray: cooperator (C), Black: defector (D)

This effect can be considered as the "surface tension" of the C clusters of size $k$ or larger (Zhang et al. (2000)), which scales with the strength of selection. 2) Yet, increasing $\sigma$ also tends to disintegrate larger C clusters by defectors intruding mostly through the flat or concave surfaces of the clusters and thus cutting them in smaller pieces, making use of the cooperative support from the many surrounding cooperators and their fitness advantage $c\sigma$ thereof. Strong selection tends to keep C clusters relatively isometric until they grow large enough for the fractions that they eventually get cut into to still remain above the cooperation threshold and start growing again. At weaker selection pressures C clusters remain more "wobbly" (of less surface tension), growing appendages which can be cut off by D agents attacking at concave sections of the surface, separating them from the core of the cluster. Most of these separated C cluster fragments remain under the cooperation threshold and thus vanish easily. That is, expensive cooperation is helped by strong selection through the division of isometric C clusters to “daughter” clusters of relatively even and viable sizes, whereas weak selection allows defectors to eliminate the smaller fragments after uneven cluster divisions (see Supplementary Material, videos SV1-SV3).

## 4. Conclusion, further directions

We have introduced a semi-analytical model for describing the dynamics of a spatial threshold dilemma game. This model provides relatively accurate estimates for the equilibrium frequency of the C strategy when compared to the outcomes of the corresponding individual-based spatial simulations. However, since the semi-analytical approximation relies only on the average pairwise correlations of the strategies, and the dynamics of the simulations is, to a large extent, determined by higher order spatial correlations and by the geometry of the interacting patches, it is not surprising that the approximation cannot accurately describe the dynamics in all detail. That said, the numerical model still gives a fair approximation for the stable fixed point of the lattice model if $k$ is not too small ($k = 2$) or high ($k > 6$) (Fig 3, Fig S1).

Not surprisingly, diffusion suppresses cooperators and benefits defectors in the simulation model (see Fig. 4,5). This is not a new observation for two-person cooperative games (Számadó et al. (2008); Smaldino and Schank (2012)), but the diffusion effect has not been studied for multiplayer game interactions before. We have demonstrated the underlying mechanism: the cost of cooperation is balanced by the fitness advantage arising from more frequent aggregation of cooperators around cooperators than around defectors. Diffusion disrupts the aggregated clusters of cooperative individuals and thus benefits defectors.

In the well-mixed model of stochastic replication dynamics of $2 \times 2$ games, changing the intensity of selection only rescales time for the dynamics, leaving the fixed points unaffected (Traulsen et al. (2005); Antal et al. (2009); Hilbe (2011)). Earlier papers have studied the effect of the strength of selection on the equilibrium frequency of cooperators for the stochastic Prisoner’s Dilemma game in structured populations ( Vukov et al. (2006); Szolnoki et al. (2009);

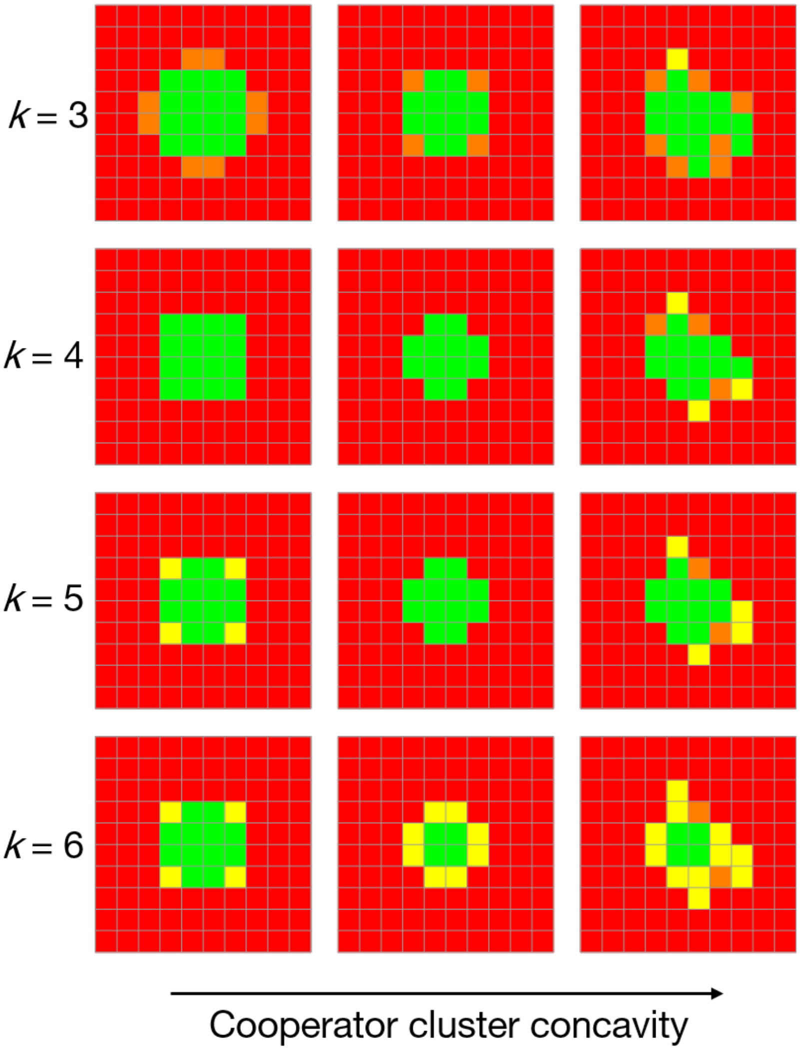

Figure 7: Schematic illustration of the "surface tension" effect of the cooperation threshold $k$ on cooperator clusters of different shapes, assuming strong selection. More concave sections of the surface of a C cluster are easier to attack for D individuals, resulting in a higher chance of the cluster becoming more isometric. Green cells: supported C; Yellow cells: unsupported C; Orange cells: supported D; Red cells: unsupported D. The payoff order is: Yellow<Red<Green<Orange (cf. Table 1).

Pinheiro et al. (2012)) and for the PGG extended with a cooperating punisher strategy (Wu et al. (2013)). All studies found that there is an intermediate selection level at which the frequency of cooperators or cooperating punishers is the highest, independently of the parameters and the population structure of the model. We have not experienced this type of optimal selection level in our spatial N-person nonlinear game; instead, we have found that weak selection helps cooperators at low costs of cooperation, while it helps defectors if $c$ is above a critical level. It is clear that the change in steady states along the strength-of-selection axis in the simulations is the consequence of spatial structure. We have provided an intuitive explanation for the dependence of the $\sigma$ effect on $c$, i.e., that strong selection is beneficial for expensive cooperation, but weak selection helps maintaining cheap cooperation.

The biological relevance of these results lies in the fact that threshold PGGs played out in relatively static spatial structures are frequent in microbial communities, especially, but not exclusively, in biofilms (Allison et al. (2010)). Possible examples include the microbiome of soils (Yadav et al. (2020)), that of human or, in general, mammalian guts (Macfarlane (2008)) - all these microbial habitats are spatially constrained, thus offering more chance for cooperating strains to withstand attempts of exploitation and exclusion by cheating genotypes. Similarly, the cooperation dilemma of certain types of tumor cells can be considered as a spatial threshold PGG in which the cooperator cells produce extracellular growth factors while defectors exploit the product of cooperators (Archetti et al. (2015); Archetti and Pienta (2019);Renton and Page (2021)). In this study we have shown that - besides the all-important cost/benefit ratio of cooperation - the relative difference in the fitness of cooperators and defectors, i.e., the strength of the selection pressure between them is also a significant factor in setting the steady state frequency of cooperators in spatially constrained populations. The effect of the strength of selection is usually quantitative, and it acts through the higher order correlations of the spatial pattern of C-D interactions, shifting the steady state frequency of cooperators in coexistent cases, but occasionally it may also change the outcome of selection in the qualitative sense, helping one or the other strategy to achieve fixation. A straightforward interpretation of the strength of selection is the relative effects of noise (i.e., environmental or demographic stochasticity) compared to deterministic trends on the dynamics under study. In this picture, strong habitat or demographic stochasticity (i.e., weak selection) helps cheap cooperation, whereas stable habitats or deterministic demographic trends (strong selection) favour more expensive cooperation. The former case, which is typical of microbiomes colonising ephemeral habitats, is consistent with intuition. The latter case is the more surprising one which may, for example, apply to cancer cells in a stable tissue environment. A possible, admittedly somewhat remote but potentially important inference could be that even cancer cells using expensively produced growth factors can be viable.

A possible direction for future research along the lines initiated here would be to attempt finding a direct and quantified connection between the emergent topology of the spatial strategy pattern and the corresponding key parameters of the model $(\sigma, c, k)$ (Li et al. (2016); Stenseke (2021)). Interesting implications may be expected from investigating the effect of selection strength in similar threshold games on graphs of different topologies (Lieberman et al. (2005); Szabó and Fáth (2007)). Since n-person cooperative games are often used to model situations involving the diffusive spread of public goods cooperatively produced by biological agents, it would be certainly worthwhile to consider the reaction-diffusion limit case of the model (Durrett and Levin (1994); Wakano et al. (2009)).

## Acknowledgement

C.T. was supported by the National Research, Development and Innovation Office (NKFIH) under Grant Number K119347. I.S. was supported by the National Research, Development and Innovation Office (NKFIH) under Grant Number K128289 and by the European Union's Horizon 2020 research and innovation programme under grant agreement No 952914.

The authors wish to thank Balázs Király for his detailed, accurate and helpful comments on the first draft of the manuscript, which, we believe, resulted in significant improvements. The authors also thank three anonymous reviewers for their helpful and thoughtful comments.

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