Exploring the effects of spatial structure in EGT-games

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Abstract

Evolutionary Game Theory is an important tool to investigate biological evolution. The two most classic games to simulate the behavior of animals are the Hawk-Dove game and the Prisoner's Dilemma. In these games the players contest over a sharable resource. Because both models follow different payoff schemes, it is important to know how a simulation model reacts to different settings. Knowing the relevance of particular parameters can enhance simulations of biological processes. In this study, we explored how spatial structure and different cost-to-benefit ratios affect the frequency of cooperation in simulated populations. Furthermore we simulated variable neighborhood-sizes and a mutation-rate. The simulations were programmed with NetLogo and plotted in R. In the NetLogo models, the probabilities for different behaviors were calculated according to the payoff matrices of the games. We compared the simulations by recording the frequency of cooperators and the cost-to-benefit ratio. Our main finding is that spatial structure does not automatically enhance cooperation in evolutionary games. In the Prisoner's Dilemma spatial structure allows for cooperation at low cost-benefit ratios whereas spatial structure mostly lowers the frequency of cooperation in the Hawk-Dove game. Neighborhood size and cost-benefit ratio are the two most important variables determining whether a stable ratio of cooperators can persist in a population or not.

1 Introduction

1.1 Evolutionary Game Theory

In 1944 the economic scientists Neumann and Morgenstern (Von Neumann and Morgenstern 1944) developed the theory of games as an economic model. Much later, in the 1970s, the evolutionary game theory originated. Instead of playing the game once, like in the game theory, the game in evolutionary game theory is played over and over again by biologically or socially conditioned players. In most cases a player is randomly drawn from a large population and has a specific behavior (Weibull 1997) Our study compares these non-spatial games in well-mixed populations with spatial games and varying variables.

Two of the most popular and most intensively studied games are the "Prisoner's Dilemma" (Axelrod and Hamilton 1981) (abbreviated "PD") and the "Hawk-Dove Game" (Sugden 1986) ("HD"). In general the Prisoner's Dilemma and the Hawk-Dove game have the following notation for a two player game with the two strategies "cooperation" or "defection". R, T, S and P are the payoffs of the game.

	C	D
C	R	S
C	T	P

(R: Reward; T: Temptation; S: Sucker's reward; P: Punishment; C: Cooperator; D: Defector)

1.2 The Prisoner‘s Dilemma:

	C	D
C	b-c	-c
D	b	o

(b: benefit, c: cost)

In a PD defection is the evolutionarily stable strategy. The defector gets the benefit b when he plays with a cooperator, who gets a punishment: The cost c. The relationship between payoffs is $T > R > P > S$. When cooperation is mutual, both have the benefit $R = b - c$, but pay a cost for that. Mutual defection results in Payoff $P = 0$ for both players. Because of the punishment of the cooperator, when the other player defects, it is best to defect, regardless of the co-players' decision (Hauert and Doebeli 2004). Though, in nature there are examples which prove, that not only defection can be evolutionarily stable. Alarm calls warn other animals from predators. It seems to be that cooperation only works when the cost-to-benefit ratio is not too high and spatial structure exists (Clutton-Brock et al. 1999).

1.3 The Hawk-Dove game:

	C	D
C	b-c/2	b-c
D	b	o

Field and experimental studies had problems with the PD as the only model to discuss behavior of "players". Its difficult to estimate proper fitness payoffs. That caused various problems between theory and field - and experimental studies. Scientists needed another model for the payoffs of cooperative behavior (Milinski et al. 1997; Nowak and May 1992). In the HD mutual cooperators are better off, because they share the cost of cooperation and receiving the whole benefit. Although cooperation gets rewarded, not punished by playing with a defector. The payoffs P and S have a reverse order in the HD which differs from the PD. P becomes the value $b - c$, so P and S have the reverse order. The new payoff matrix ($T > R > S > P$) leads to persistence of cooperative players beside defectors except for very high costs ($2 * b > c > b > o$) which would recover the PD. When $b > c > 0$ the best action in the Hawk-Dove game depends on the co-player. In case that players always play the opposite strategy of their game partner, you have stable coexistence of cooperators and defectors in well-mixed populations - thus, an equilibrium of cooperators and defectors (Hauert and Doebeli 2004).

1.4 Problem and Gap of Knowledge

A lot of researchers of social, economic and biological science worked on the evolutionary game theory. It has become a powerful tool to investigate the emergence of cooperation in groups (Hauert and Doebeli 2004). However, there is an increasing with the PD currently being the simulation model almost exclusively used as basis to discuss cooperative behavior in natural populations. The HD is an interesting alternative for describing some behavioral patterns discovered in field studies(Milinski 1987). The underlying theoretical processes have been discussed several times before (Nowak and May 1992; Milinski 1987), but the HD has never been simulated extensively. To find out the different performance of the PD and the HD, we compare the results of various simulations. For example we want to find out whether the common knowledge that spatial structure supports cooperation in the PD game (Nowak and May 1992) is also true for the HD game or whether mixed playing strategies influence the outcome of a game. Our results may deepen the theoretical work that has been published on HD games so far and help other scientists choose the right model for describing natural processes. Choosing the right model to describe natural processes is a big challenge for scientists.

1.5 Our approach and specific questions

In our study we test the following **hypotheses**:

- Spatial structure benefits cooperators especially in the PD.
- Neighborhood-size has an influence to the effect of spatial structure.
- Mixed-strategies change the effect of spatial structure.

For testing the Hypotheses we simulated different HD and PD games with NetLogo 5.1.0 (Wilensky 1999) and performed them with varying variables. The results of the three experiments were fitted and visualized in R (R Core Team 2014) to make them comparable. The main focus of the experiments was put on the frequency of cooperators with varying cost-to-benefit ratios.

2 Methods

2.1 Non-spatial PD and HD

The first step for our model was to calculate the average payoff for cooperators and defectors in the non-spatial PD and HD. We used p for the probability of players being defectors (probability of cooperators is $1-p$). Due to the payoff matrix of the HD game we used $P_c = 0.5 * (1-p) * c + b - c$ and $P_d = p * b$. For the PD average pay-off for cooperators changes: $P_c = (1-p) * b - c$. These average Payoffs reduce or increase the fitness of the single players. In an iterated game fitter players reproduce and get a higher percentage of the population - in our case cooperators or defectors. For the next iteration (reproduction) of the game p is now calculated by comparing the fitness of defectors with the fitness of all players.

2.2 Spatial structure and neighborhood size

In our spatial games we used a 50 x 50 square lattice. Every patch represents one player. The whole lattice was updated synchronically. We introduced different neighborhood-sizes from four to 24 neighbors in our model. Therefore we worked with four different sizes of radius (1, $\sqrt[2]{2}$, 2, $2 * \sqrt[2]{2}$, caliber of players as unit) around the players for five neighborhood-sizes (4, 8, 12, 24). Instead of using p, which was the probability to be a defector in the non-spatial game, we inserted a local probability p_l in the average payoff terms. These were calculated with the neighbors' probabilities to be a cooperator or defector. Herewith fitness of the players is calculated again facing the neighborhood. As opposed to the non-spatial game the change of the strategy in the next round of the game was not calculated for the whole population, it was calculated for the single player (in our simulation patch). The players randomly chose neighbors for the competition. Then the transition probability (probability to change strategy) was calculated with $p_c = Z/\alpha$. Z is the difference between the fitness of the competitor F_c and the own fitness F. α is the maximum difference between the payoffs, and equals $\alpha = T - P = b$ in the HD game and $\alpha = T - S = b + c$ in the PD. This correction term ensures p_c values between 0 and 1. If $Z > 0$, the player changed the strategy with the probability p_c, which represents a reproduction of the fitter players.

2.3 Effect of mixed strategies in the spatial and non-spatial Hawk-Dove game

In our simulation for the HD with mixed strategies every player was characterized by the probability p to show dove-like behavior which in turn was subject to a small mutation rate to allow for evolution in the game. The initial heterogeneity of the players was randomly chosen from a normal distribution. The mean of the normal distribution was the equilibrium strategy of well-mixed populations $p_w = (1 - c/(2*b - v))$, calculated from the cost-to-benefit ratio. The standard deviation was set to 0.02. The boundaries of the distribution were set to 0 and 1 to get a fitting value for the probability. The following procedure was the same as for the models with spatial structure, but with different mathematics to introduce the mutation. The average payoff $P_{mix} = p_w * p_n * (b - (0.5 * c)) + p_w * (1 - p_n) * (b - c) + (1 - p_w) * p_n * b$ was P with p_n as the mean strategy of all interacting neighbors. More generally the term is $P_{mix} = p_w * p_n * R + p_w * (1 - p_n) * S + (1 - p_w) * p_n * T + (1 - p_w) * (1 - p_n) * P$, which means that the payoff differences between neighboring individuals are very small. The update rule for pure strategies had a very small probability of change, which made the simulation very slow. For that reason a non-linear term was introduced for the change-probability: $p_{cmix} = [1 + exp(-z/k)]^{-1}$.

2.4 Simulations with NetLogo, plots with R

The simulations were programmed agent-based with NetLogo (Wilensky 1999). The modeling of the non-spatial and the spatial HD and PD with different neighborhood-sizes were ran with the Behavior Space of the program. For having robust results we ran the simulation 10 times for 5000 time-steps with varying costs and benefit set to 1. The costs we calculated according to the replicator dynamics, the equilibrium frequency of cooperators in the HD with $r = c/(2 * b - c)$. Therefore $c = (2 * r/(1 + r))$ with a sequence for r from 0 to 1 with an 0.05 step. The population had the size of 50 x 50 patches, that means 2500 players. The mixed strategy games ran for 10.000 time-steps to make sure that we the equilibrium level. To compare the models we plotted the results in R (R Core Team 2014) with the frequency of cooperation on the y-axis and the cost-to-benefit ration on the x-axis.

3 Results

3.1 Effect of spatial structure in PD and HD games

In our first simulation experiment, we compared the effect of spatial structure on the persistence of cooperators in the PD and HD games. For the **PD game** we were able to reproduce the theoretical prediction that spatial structure enables cooperators to persist, even if cooperation is not an evolutionarily stable strategy in well-mixed populations. Our simulated spatial PD population with neighborhood size = 8 could maintain an average of 66.5% cooperators (±1.12%) at a cost-benefit ratio of $r = 0.05$. For higher cost-benefit ratios, however, cooperation was not evolutionarily stable at this neighborhood size and ceased within the 5000 time steps. If cooperation did was cost-free, the proportion of cooperators remained close to its initial value. See figure 3.1 for a comparison of the frequency of cooperation in spatial and nonspatial PD games.
In the spatial **HD game** we found a quite contrary effect of spatial structure. When simulating a well-mixed population we could reproduce the theoretical prediction that the equilibrium frequency of cooperators is $f(wm) = 1 - r$. However, adding spatial structure to the model reduced the frequency of cooperators as compared to the non-spatial version for most r values (figure 3.1).

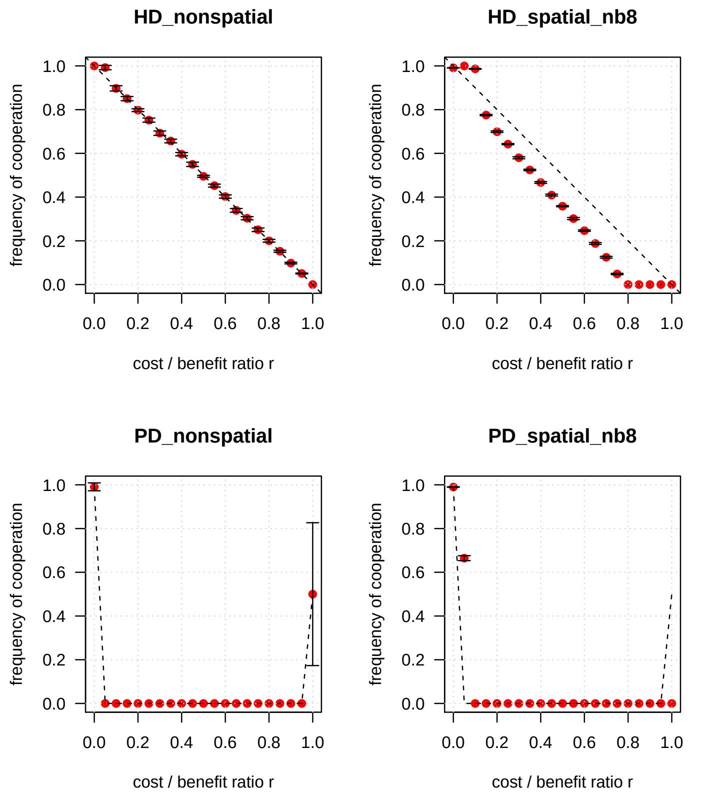


Figure 1: Comparison of HD and PD game simulations, both with and without spatial structure. [t = 5000, i = 10, error bars with 95% confidence]

The higher the r value, the bigger the relative disadvantage of cooperators was. For $r \geq 0.8$ cooperation completely vanished from the population. Only at very low cost-benefit ratios, cooperators in the HD game profited from spatial structure. The threshold r value up to which cooperators profited was 0.1 for a neighborhood size of 8.

3.2 Effect of neighborhood size

In the second simulation experiment we varied neighborhood size in the spatial PD and HD games and investigated whether changes in neighborhood size would change the effects of spatiality. Except for neighborhood size, the HD simulations were run with the exact same parameter set as before. In the first PD game simulation spatial structure only came into effect at very small r-values. To achieve a reasonably high x-axis resolution in the most relevant section, we lowered the r-stepwidth from 0.05 to 0.01 for r-values < 0.1 in the second PD experiment.

Spatial Hawk-Dove games

Varying neighborhood size in the HD game yielded three main observations:
In the spatial HD game with eight neighbors, cooperators profited from spatial structure at low cost-benefit ratios and suffered at higher r-values. This also goes for different neighborhood sizes. However, the threshold r-value at which benefit turns into disadvantage varies with neighborhood size: It is higher for small neighborhood sizes and decreases with increasing neighborhood size.
In addition to the increased benefit from spatial structure at small r-values, smaller neighborhood sizes (4 neighbors) had another effect in the second HD experiment: The detriment of spatial structure in comparison to well-mixed populations increased faster for r-values above the threshold r-value. In contrast, bigger neighborhoods (> 8 neighbors) were less detrimental to cooperators at high r-values.
At the upper end of the range of r-values, another effect of neighborhood size became apparent: The r-value above which total extinction of cooperators becomes likely changed with neighborhood size. The smaller the neighborhood, the more likely cooperators are to die out completely. With N being the average number of neighbors, cooperators were likely to die out completely if $1/N > 1 - r$. The effects of varying neighborhood sizes in the HD game are illustrated in figure 2.

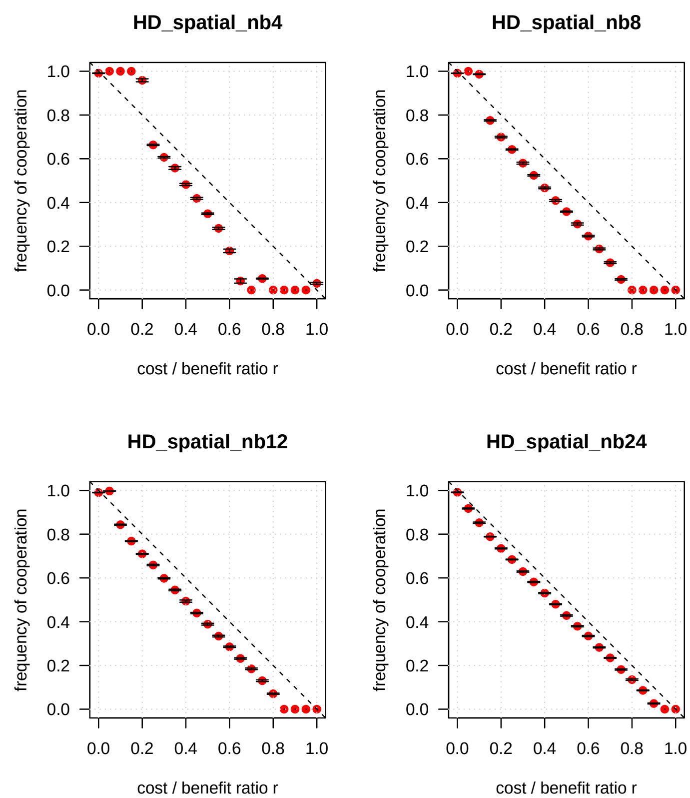
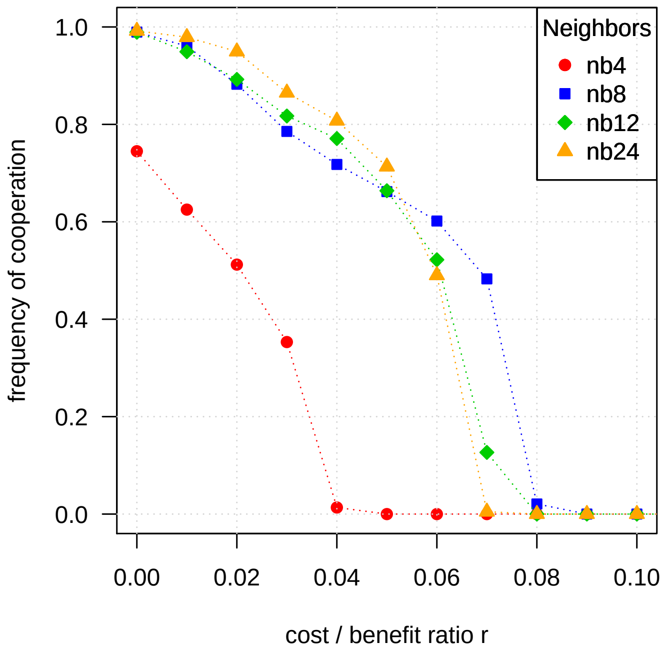


Figure 2: Effect of varying neighborhood size in the HD game. The red dots represent the mean simulated values for the spatial HD game with 95% confidence intervals. The dashed line represents cooperation frequency in a well-mixed population. [t = 5000, i = 10]

Spatial Prisoner's Dilemma games

For all simulated neighborhood sizes, we could reproduce our finding from the first experiment: Spatial structure allows for the evolution of cooperation in PD games. Nonetheless, our second experiment revealed some constraints to this finding:



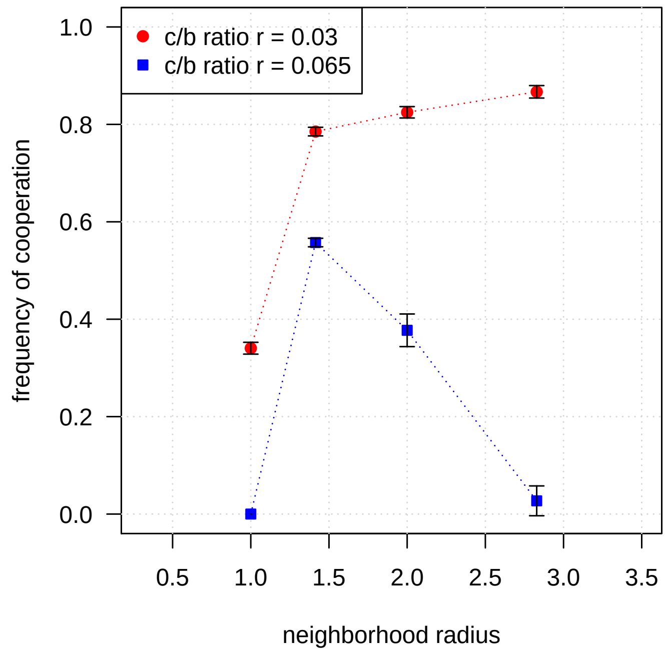


Figure 3: Spatial PD game simulations with different neighborhood sizes. The X-axis is cut off at 0.1 as for all higher r-values, the frequency of cooperation was 0. [t = 5000, i = 10]

Figure 4: Spatial PD game simulations with fixed cost-benefit-ratio and different neighborhood sizes. Radius 1 is adequate to 4 neighbors, radius 1.4 = 8 neighbors, radius 2 = 12 neighbors and radius 2.8 = 24 neighbors. [t = 10000, i = 10]

Firstly, cooperation is only evolutionarily stable for r-values ≤ 0.09, for bigger r-values it disappears from the population. Secondly, neighborhood size has a big influence on a population's ability to maintain cooperation.
In very small neighborhoods (4 neighbors), cooperators are generally much less likely to persist and therefore make up for smaller ratios of the population than in bigger neighborhoods (see figure 3). The extinction threshold for cooperators is at $r = 0.04$ and thereby significantly lower than in bigger neighborhoods.
For neighborhood sizes of 8 or more neighbors, however, the results are ambiguous: Up to a threshold of $r = 0.05$, bigger neighborhoods result in slightly higher numbers of cooperators. At r-values between 0.05 and 0.08 however, the order inverts so that populations with neighborhood size 8 can maintain more cooperation than those with neighborhood size 12 or 24.
Figure 4 better illustrates this anomality: We ran the spatial PD game for two fixed r-values below (0.03) and above (0.065) the tipping point and at the same time varied neighborhood size. When looking at the results, it becomes apparent that at r-values close to the extinction threshold, the population with neighborhood size = 8 constitutes an optimum for cooperators whereas populations with bigger neighborhood size can not maintain the high ratio of cooperators they supported at lower r-values.

3.3 Effect of mixed strategies in the Hawk-Dove game

In our third experiment, we implemented mixed strategies in the HD game in order to compare the effect of spatial structure in the mixed-strategy HD game with that in the pure-strategy game. In the pure-strategy HD game, spatial structure lowers the ration of cooperators, except for very small r-values where it benefits them. In mixed-strategy HD games however, this ambivalence does not exist. For any r-values the probability to play cooperator is reduced in comparison to the non-spatial version of the game. However, the detriment of spatial structure on cooperators is not as severe as in the pure-strategy HD game, especially at high r-values (figure 5).
The general effect of varying neighborhood size is similar to the pure-strategy HD game: Bigger neighborhoods reduce the detriment of spatial structure to cooperators. As the frequency of cooperators in the mixed-strategy HD game is very close to their $1 - r$ frequency in well-mixed populations anyway, the change induced by varying neighborhood size becomes negligibly small.

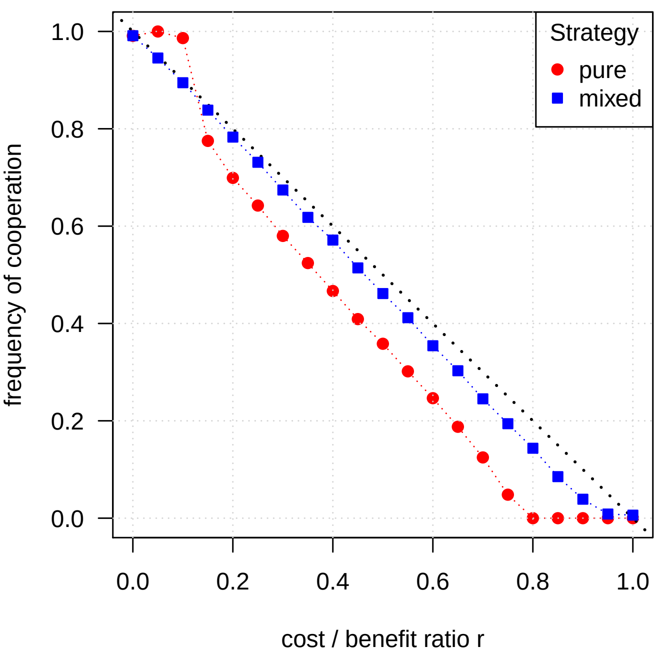


Figure 5: Spatial HD game simulations with neighborhood size = 8 and different strategies. The dotted black line depicts the frequency of cooperation in non-spatial HD games which equals $1 - r$ for both pure- and mixed-strategy games. [t = 10000, i = 10]

4 Discussion and Conclusions

4.1 Spatial structure

If the **Prisoner's Dilemma** is played in well-mixed populations, cooperation is not an evolutionarily stable strategy. However, previous research has shown that associative interactions, such as spatial structure can allow for the evolution of cooperation (Nowak and May 1992; Doebeli and Knowlton 1998; Killingback et al. 1999). In our simulations, we could reproduce this finding: In spatial PD games, cooperators form spatial clusters that reduce the exploitation by defectors. However, cooperation could only be maintained at very low cost-benefit ratios ($r < 0.1$). At higher r-values, defectors "eat up" the clusters from their borders so that the cooperators vanish from the population. Our finding matches well with the results of Ohtsuki et al. (2006) who investigated different ratios of $benefit/cost$ found a threshold value: If b/c is bigger than the average number of neighbors, cooperation can evolve.

In the **Hawk-Dove Game**, the effect of spatial structure is more ambiguous. Due to the payoff structure of the HD game, it is most beneficial to use different strategies than neighboring cells. For this reason, even well-mixed populations maintain a ratio of $1 - r$ cooperators. The same mechanism, however, inhibits the emergence of larger clusters. Instead, clusters in the shape of crosses or filaments are formed. Especially at higher r-values where the natural proportion of defectors is high, cooperators are much more prone to exploitation in the contact zones where they encounter adjacent defectors. As a consequence, the ratio of cooperators is lower than in well-mixed population for most (higher) r-values. Unlike in the well-mixed population, cooperation can vanish completely at high r-values.

At very low r-values, we found that cooperators profit from spatial structure. A possible explanation could be that even if the co-player defects, in the HD game the benefit of cooperation can still outweigh the cost. Furthermore, cooperators profit from cooperating neighbors, which are much more frequent at low r-values (Hauert and Doebeli 2004).

4.2 Different neighborhood sizes

Our simulations on the effect of varying neighborhood sizes again produced very different results for PD and HD games. In the **HD game**, both benefits and disadvantages through spatial structure were most pronounced in the small neighborhood (4 neighbors). The bigger the neighborhood, the curves leveled out and converged towards the linear $1-r$ relationship from the non-spatial HD game. We think that this effect is caused by the fact that in the HD game, spatial structure only works over very small distances because there are no larger clusters of the same strategy. When the co-player for the next round is drawn, in bigger neighborhoods the ratios of the different strategies are closer to the population average. Besides the fact that spatial structure has a larger effect in small neighborhoods, we found that the extinction threshold for cooperators also varies with neighborhood size. This confirms the findings of Hauert and Doebeli (2004).

Regarding the effects of different neighborhoods in the **PD game**, our results leave more room for interpretation. In our simulation, bigger neighborhoods resulted in higher frequencies of cooperation for r-values ≤ 0.05. For higher r-values this effect partly reversed so that a neighborhood size of 8 was optimal. At r-values ≥ 0.09 cooperation died out for any neighborhood size (see figure 3). We think that these somewhat ambiguous findings result from two different mechanisms that came into play at the same time:

Already in the first simulation, we were able to reproduce the common opinion that spatial structure favors cooperators in the PD game. The survival of cooperators in this case is facilitated by the formation of clusters: Patches in the center of a cluster receive the full benefit of cooperation at every time step. If the cost-benefit ratio is sufficiently low and the neighborhood sufficiently large, cooperating patches on the border of a cluster can profit from interaction with interior cells and compensate the loss that they suffer from adjacent defectors (Szabó and Fath 2007).

The general mechanism of cluster formation works the better the larger the neighborhood of a single cell is: Larger clusters are formed and higher proportions of cooperators are maintained. Cooperator patches on the border of a cluster are less exposed to defectors the bigger a cluster is. In comparison, populations with very small neighborhoods (4 neighbors) can only form small clusters. Because the payoff of a small cooperator's cluster does not sufficiently exceed that of defectors, smaller clusters cannot reduce exploitation from defectors as efficiently as bigger clusters (Wang et al. 2012). We think that this mechanism explains the effect of neighborhood size found for r-values ≤ 0.05.

Although populations with bigger neighborhood sizes are very stable for low r-values ≤ 0.05 and maintain high rates of cooperators, the do not remain stable at higher r-values (figure 4). We think that this seemingly unexpected phenomenon is caused by the second mechanism: As our simulation lattice is only 50 x 50 patches large, the two biggest neighborhoods are prone to mean-field-type behavior. For low r-values, defection is not influential enough yet, but once the cooperating clusters start to struggle with high r-values, more defectors emerge and the cooperators die out due to the mean-field mechanism. We base our interpretation on the findings of Wang et al. (2012), who recorded a very similar pattern in their PD simulations on regular lattices.

4.3 Mixed strategies in the Hawk-Dove game

In the mixed-strategy HD game, patches do not adopt one fixed strategy but rather inherit a certain probability to play either of the two strategies. In the pure-strategy non-spatial game, the evolutionarily stable frequency of cooperators is $1 - r$. In the mixed-strategy non-spatial game, the evolutionarily stable probability to play cooperator in the next round is also $1-r$, which results in the same proportion of cooperators for both mixed and pure strategies. Once spatial structure is added to the model, the outcomes of mixed- and pure-strategy HD games differ though. In general, spatial structure in the mixed-strategy HD game lowers the evolutionarily stable probability to cooperate. However, the detriment of spatial structure on cooperators is not as severe as in pure-strategy game. We think that this is because the mixed strategy adds another random element to the patches' strategy determination which counteracts the formation of spatial structures on the lattice. In both mixed- and pure-strategy HD games, very high r-values lead to an extinction of cooperators (doves respectively) because there are so many defectors (hawks respectively) that almost any encounter leads to an escalating conflict (Hauert and Doebeli 2004).

4.4 Final conclusions, applications and further research

Based on our results, we conclude that spatial structure does not automatically enhance cooperation in the PD and HD games. In fact, this common belief only applies under certain conditions:

In the **Prisoner's Dilemma**, where cooperation is not evolutionarily stable in well-mixed population, spatial structure enables cooperation to persist at low cost-benefit ratios. Medium-large neighborhoods amplify this effect.

In the **Hawk-Dove game** however, spatial structure mostly reduces the frequency of cooperation which usually levels out at $1 - r$ in well-mixed populations. Only in the rare case of pure-strategy games with small neighborhoods and very small r-values, cooperators can profit from spatial structure.

We find that neighborhood size and cost-benefit ratio (r) are the two most important variables determining whether a stable ratio of cooperators can persist in a population or not.

When applying Evolutionary Game Theory to natural populations, correctly measuring the payoffs is usually the most tricky part. If for example a high rate of cooperation is maintained in a population, it could either be the result of a spatial PD with small neighborhood size and low cost-benefit ratio, or just the cooperation rate naturally maintained in HD games - all depending on the payoff ranking. For this reason we aim to study more natural examples of PD and HD games and refine the available techniques for payoff measurement.

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Appendix

All Netlogo models and R scripts we created and used for this report can be accessed on the projects' github page at https://github.com/peterantkowiak/EGT_course.

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