Variability of Cooperation in a Spatial Prisoner's Dilemma

Beryl van Gelderen[1] , **Neil Yorke-Smith**[1]

Abstract

In harsh, spatial versions of the prisoner's dilemma, a stable ratio between cooperators and defectors is sometimes reached quickly, whereas for other runs the variability of this ratio is much higher. This paper explores different patterns of this ratio over time, and compares factors that may influence these patterns. A measure based on variance is proposed to achieve this. Environmental harshness, as well as the sparsity of the environment, are found to have great influence on variability, whereas the cost of unreciprocated cooperation has little effect. The proposed measure of variability may be useful to predict population variability in the future, and help to determine when to stop a simulation.

Keywords: population dynamics, interdependence, agent-based modelling, Prisoner's Dilemma, harsh environments

1 Introduction

Altruistic behaviour seems to go against evolutionary theories, as it reduces the fitness of the altruist and therefore would be selected against. The emergence of altruism is a topic of both a philosophical nature as well as a biological and mathematical one. Axelrod and Hamilton used the prisoner's dilemma to model and study the conditions in which altruism prevails [2] in 1981. They found that, where repeated altruism yields more rewards for community at large, altruism can thrive even though egoistic behaviour yields greater rewards for the individual. As cooperation in nature often increases when environmental conditions are harsh, agent-based models have emerged that provide an explanation.

Human society is dependent on altruism and cooperation, even when it comes at a personal cost. A recent example is the covid-19 pandemic where individuals are asked to decrease their personal satisfaction for the greater good. With social distancing we ask each other to sacrifice personal happiness to protect the health of not just ourselves, but for the good of society at large. The stability of such cooperative behaviour is integral to the functioning of our society, as well as for many interdependent species in nature [3] [14].

Smaldino et al [11] proposed an agent-based, spatial model where the environmental harshness indeed increases cooperation, even when costs for unreciprocated cooperation get high. The model simulates interdependence, where agents must interact to survive. However, the variability of this cooperation over time is still unknown.

This article investigates the relation between the variability of cooperation and environmental harshness. It aims to provide a theoretical analysis of the stabilisation of altruistic and egoistic behaviours in populations in the spatial prisoner's dilemma. This is achieved by proposing a measure of cooperation variability, based on variance, where a distinction is made between low frequency variability (LFV), and high frequency variability (HFV). Then, three factors are explored: environmental harshness k, the cost of unreciprocated cooperation S, and influence of capping of the number of agents such that at least 50% of the lattice is unoccupied N*. Environmental harshness is found to be an important influence on cooperator variability, as well as sparse populations. However, a large ratio of cooperators does not necessarily correlate with low variability of cooperation.
The predictive value of the cooperation variability measures is also explored, to predict when future variability in cooperation frequency is unlikely. This is helpful to predict when a simulation can be stopped. Even though the associated experiment yields promising results, more research, with larger data sets, is needed to use population variability for this goal.

The following section provides backgrounds and definitions, followed by a description of cooperator frequency variability in section 3. Then, the exact model is described in section 4. The results of the simulations are laid out in section 5. Section 6 includes interpretation of the results, after which conclusions and recommendations for future research are provided in section 7. Section 8 discusses the reproducibility of this research.

2 Background

This section provides a theoretical background to the prisoner's dilemma, this spatial version and why was chosen for a harsher model. Afterwards, an introduction into the different variables that are explored is given.

2.1 The Prisoner's Dilemma

The prisoner's dilemma has long been used to study cooperative behaviour [4]. In this game, an agent interacts with another agent by either choosing to defect or cooperate. With each combination of choices, a payoff is associated, as seen in table 1. When both agents choose to cooperate, they receives R points (the 'Reward'). However, when one of them chooses to defect, he will gain T points (the 'Temptation'), while the cooperator gains just S points (the 'Sucker's payoff'). When both defect, the payoff is P (the 'Punishment'). The relation between these rewards is as follows [5]:

$$T > R > P > S \tag{1}$$

$$2R > T + S \tag{2}$$

Therefore, by 2, cooperation yields greater rewards for the agent community than defection, although by 1, defection yields greater rewards individually.

Axelrod and Hamilton [2] laid the groundwork for modelling the emergence of cooperative behaviour with the prisoner's dilemma, by using repeated prisoner's dilemma games. Here, each agent is able to remember their opponent's previous moves against them. They showed that more cooperative strategies fare best in this Iterated Prisoners Dilemma, thus showing a way to model the emergence of cooperative behaviour in nature.

	agent 2	
agent 1	**Cooperate**$_2$	**Defect**$_2$
Cooperate$_1$	R_1, R_1	S_1, T_2
Defect$_1$	T_1, S_2	P_1, P_2

Table 1: The payoffs for each agent, when playing the prisoner's dilemma game.

2.2 Spatial, Agent-Based Prisoner's Dilemma

Another way to study the emergence of cooperation by using the prisoner's dilemma game, is by using a spatial environment. Here, agents do not necessarily remember their previous interactions with other agents. Instead, agents are able to move over a 2D space, and 'interact' with each other when they are in close proximity. This interaction consists of playing the prisoners dilemma game, in which points can be earned. These points are needed by the agents to stay alive, as well as enabling them to reproduce. When their energy points get below zero, they die and disappear from the lattice. Smaldino et al. [10; 11] proposed such a spatial model with just two types of agents: agents that always defect and agents that always cooperate. With this model [11], cooperators thrive in harsher environments, just as observed in nature [6], as the harshness in this model makes cooperative behaviour essential for survival.

These harsher environments were created by introducing an 'environmental cost of living', a point deduction for each round.

2.3 Cooperation Variability

I define variability of cooperation as the variance of the relative change of cooperation over time.

In the harsh environment, defecting agents cannot survive without altruistic cooperators to exploit. Cooperators die when they cannot interact with other cooperators. This leads to interesting spatial patterns: cooperators need clusters with their own kind to survive, while defectors exploit them from the edges of these clusters[10; 11; 8].

This conduces variability in the ratio between cooperators and defectors, when defectors initially thrive by exploiting cooperators, but later die when there are little cooperators left to exploit. Sometimes an equilibrium is reached quickly, where the ratio between cooperators and defectors remains about the same in the future time-steps. In other cases, the variability of this ratio varies greatly over time, and it is hard to predict if a stable ratio is ever reached.

Souza et al.[12] have laid down a framework to analyse populations in non-spatial snowdrift games. Snowdrift games are similar to the prisoner's dilemma, while [9] provide a review on group interactions, and not the pairwise interactions as defined in this prisoner's dilemma. Where Nowak provides an excellent framework for variability of cooperation with the prisoner's dilemma in a spatial environment [8], it is based on cellular automata, instead of based on moving agents.

This paper proposes a new way of measuring the variability of populations, which is suitable for the model made by Smaldino et al [11]. This measure is further explained in section 3.

3 Measuring Cooperation Variability

To categorise variability in cooperator frequency, let us first define cooperator frequency. For ease of computation and plotting, the cooperator frequency is multiplied by 1000.

$$\text{Cooperator Frequency } C_t = \frac{\text{cooperators at } t}{\text{total agent count at } t} * 1000$$

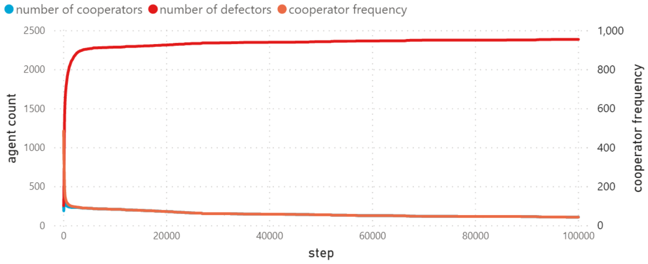
Two types of in cooperator frequency were defined. The first type of variability is High Frequency Variability, from here on called HFV. HFV describes, on the smallest scale, the variance of cooperation changes. It is calculated as described below: Let b be the bucket number, such that $0 < b \leq b_n$, with n the number of buckets, and let t be the step, with $0 \leq t < \Delta t$, where Δt depicts the bucket size.

$$\text{HFV} = \text{Avg}(\text{Var}_{b=1\ldots b_n}(C_{t=b\Delta t\ldots b\Delta t+\Delta t-1}))$$

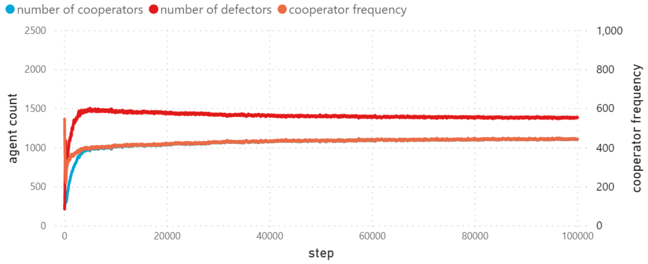
Low Frequency Variability, or LFV concerns the more high-level variability of cooperator frequency.

$$\text{LFV} = \text{Var}(\text{Avg}_{b=1\ldots b_n}(C_{t=b\Delta t\ldots b\Delta t+\Delta t-1}))$$

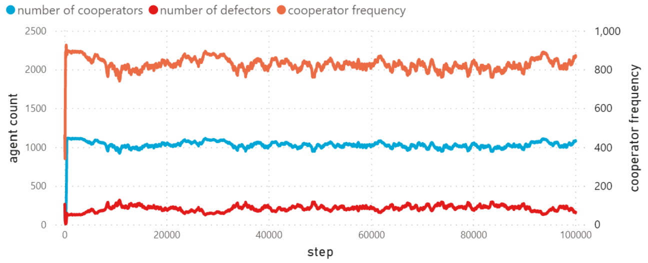
The first bucket, $b = 0$ is disregarded. During these first time-steps, most populations are still in an extremely unstable initial phase where these variability measures have little



(a) $LFV = 144$, $HFV = 1$

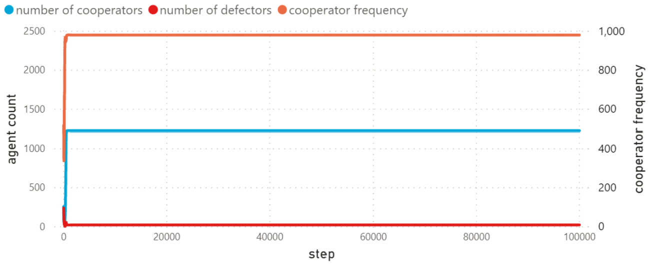


(b) $LFV = 137$, $HFV = 5$

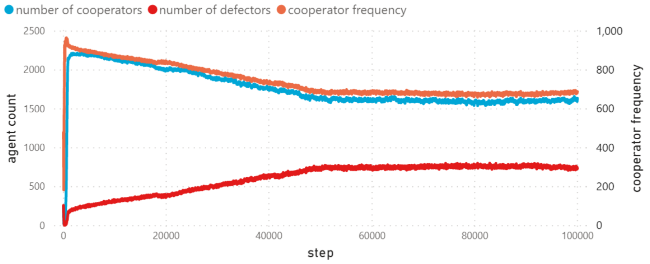


(c) $LFV = 312$, $HFV = 375$

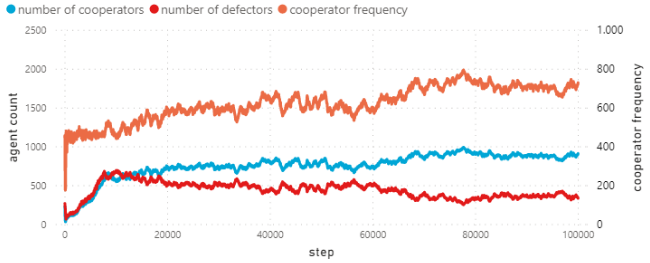
Figure 1: Examples of different values for High Frequency Variability (HFV). These plots all have similar LFV.



(a) $LFV = 0$, $HFV = 0$



(b) $LFV = 5005$, $HFV = 36$



(c) $LFV = 5592$, $HFV = 519$

Figure 2: Examples of Low Frequency Variability (LFV).

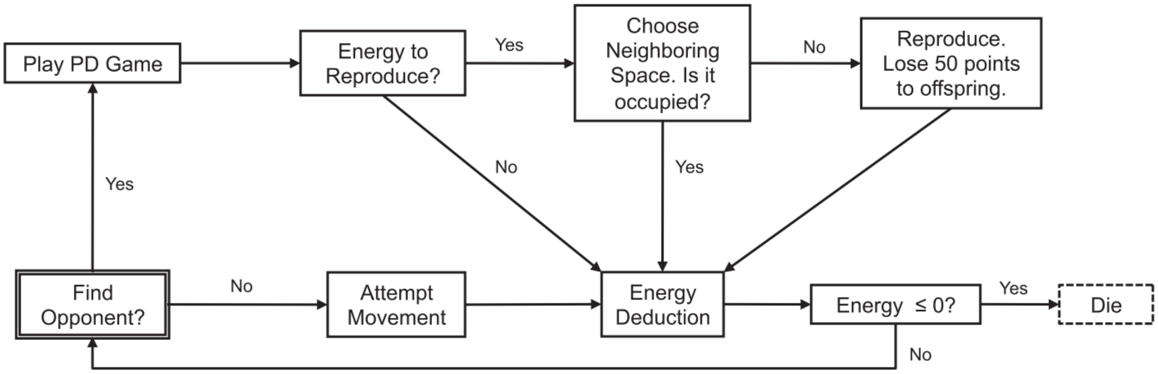


Figure 3: Reprinted from [11]. The behaviour cycle of an agent.

predictive value over the rest of the run. Examples to illustrate different values of HFV and LFV can be found in figure 1 and figure 2.

The advantage of these measures is that their use of variance makes them comparable over multiple types of runs, with differing population sizes or maximum time-step.

4 Model Description

The model is built on the model proposed and studied by Smaldino, Schank, and McElreath [11]. For an in-depth discussion and a theoretical background, I refer to their paper [11].

This spatial, agent-based model, has agents interact on a $L * L$ lattice. This lattice is configured with a Moore neighbourhood that wraps around the edges. There are just two agent types: those that always cooperate and those that always defect. At initialisation, N agents, half cooperators and half defectors, are placed in random locations. For all experiments conducted here, $N = 500$ There is a maximum of one agent at each location. Each agent is initialised with a random amount of energy points between 1 and 50. At each time step, every agent goes through a sequence that is described in figure 3. First, an opponent is selected from the agent's 8 neighbouring cells. If an opponent is found, the prisoner's dilemma game is played and payoffs are added or deducted to the agent's energy points. If no opponent is found, because no neighbouring agent exists, or because the neighbouring agents have already played during this time-step, a movement is attempted to any unoccupied neighbouring cell. Each agent energy store is capped at 150 energy points. An agent can attempt to reproduce at 100 energy points, success depends on the availability of an empty neighbouring location. If an agent is able to reproduce, it loses 50 energy points. The newborn agent has the same strategy as it's creator, and is initialised with 50 energy points. At the end of each agent's behaviour cycle, the cost of living k is deducted from its energy store. If the energy store gets to or below 0 energy points, the agent dies and disappears from the lattice.

The payoffs for the prisoners dilemma interactions are described in table 2. Except for the price of unreciprocated cooperation S (see also section 2.1), payoffs were fixed. Lattice size was set at $L = 50$. As [10] notes, this lattice size does not produce different results with regards to the emerging spatial patterns or ratio's between populations such as patterns or ratio's, compared to runs with a larger lattice size.

Simulations were run in NetLogo, which randomises the order in which each agent behaviour cycle is initiated during each time-step [1]. The NetLogo Behaviorspace functionality was used to generate batch runs.

	agent 2	
agent 1	**Cooperate**$_2$	**Defect**$_2$
Cooperate$_1$	$3, 3$	$S, 5$
Defect$_1$	$5, S$	$0, 0$

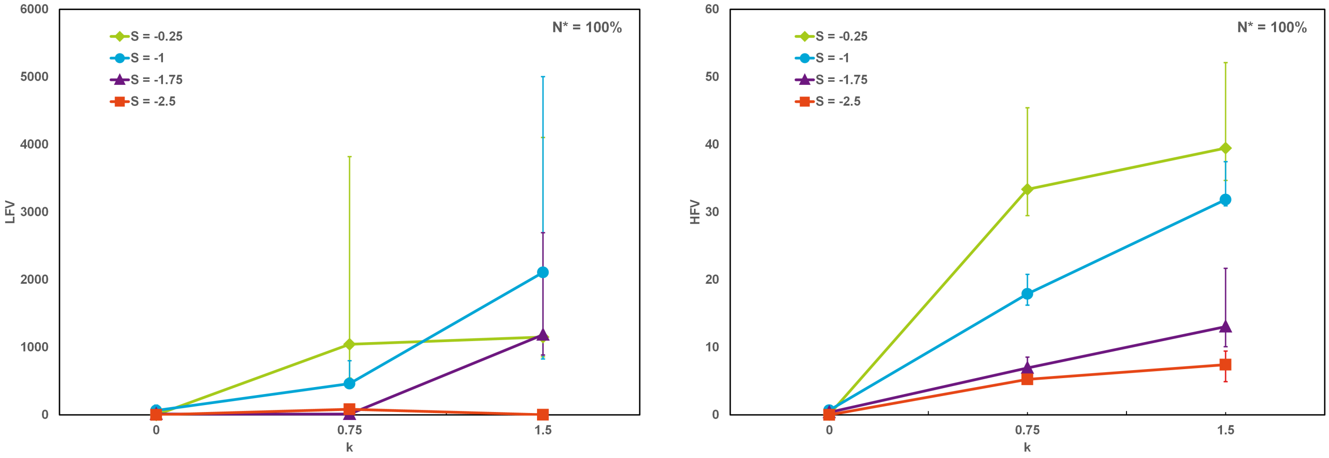
Table 2: The payoffs for each agent, as used in this model, in the form (payoff agent 1, payoff agent 2)

5 Simulation Results

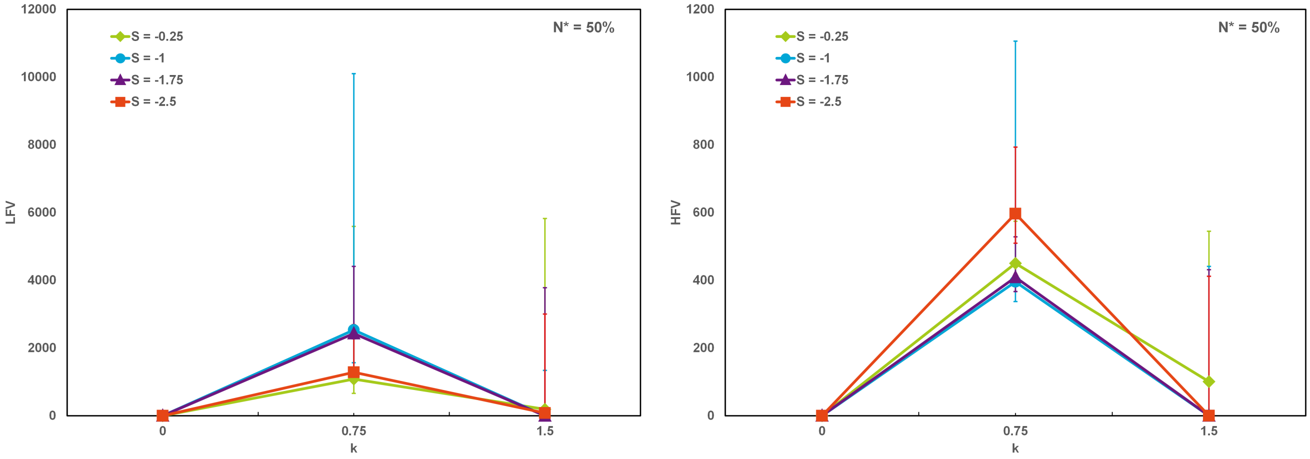
Two experiments were conducted.

First, to investigate cooperator frequency variability's relation to environmental harshness, population sparsity and the cost of unreciprocated cooperation, simulations were run on the model as described in the following section 5.1.

Second, to investigate the predictive value of HFV and LFV, a number of runs were conducted that continued to 10^6 time-steps. The outcome of this experiment is described in section 5.2.



(a) LFV, $N^* = 100\%$ (b) HFV, $N^* = 100\%$



(c) LFV, $N^* = 50\%$ (d) HFV, $N^* = 50\%$

Figure 4: The range of LFV and HFV, with differing cost of unreciprocated cooperation S and differing cost of living k

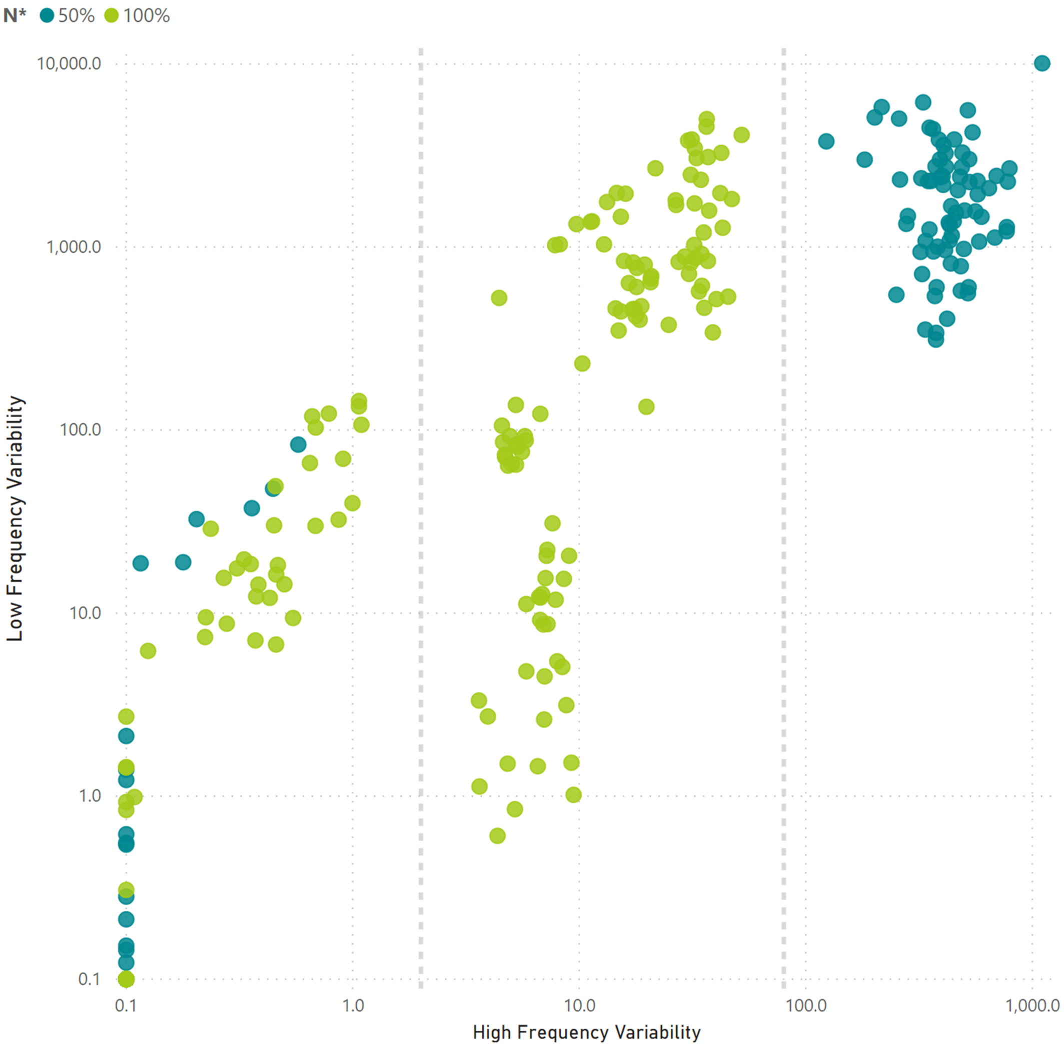


Figure 5: N*, the sparsity of the environment, has a large influence on the HFV of the cooperation frequency variability. The dotted lines, at HFV = 2 and HFV= 80, surround a region where there are regular, very small changes, or 'jitters', in the ratio of cooperators.

5.1 Which Factors Influence Cooperator Frequency Variability?

The model's setup was as follows:

- Run stops until a populations goes extinct, or at 10^5 time steps
- range of S (cost of unreciprocated cooperation): -2.25 to -0.25, with steps of 0.75
- range of k (cost of living): 0 to 2.25, with steps of 0.75
- range of N^*: 50% and 100% of capacity $L * L$ ($N^* = 2500$ or $N^* = 1250$)
- 480 runs in total, 15 of each combination of variables
- Bucket size Δt: 5000 time-steps.

These values were chosen to replicate the harsh environments in which cooperators thrive, as noted by Smaldino et al [11].

The Effect of Population Sparseness on Cooperator Variability

N^* has a strong effect on variability. The sparser environment $N^* = 50\%$ has, on average, a much larger variability than $N^* = 100\%$. This holds for both the HFV as well as the LFV, as seen in figure 4. Especially when looking at HFV, $N^* = 50\%$ does not produce any runs where there are regular, small changes in the population sizes of cooperators and defectors. These small 'jitters' are found in abundance in $N^* = 100\%$. $N^* = 50\%$ has either very little HFV, below $HFV < 2$, or a lot of large, irregular changes in it's cooperator frequency, resulting in values above $HFV > 80$, as shown in figure 5.

The Influence of Environmental Harshness on Cooperator Variability

k has a large effect on variability. This holds for both LFV and HFV. With regards to LFV: In general, a larger k increases variability. The lowest value of $k = 0$ resulted in the smallest LFV. However, there is a difference to be noted here between $N^* = 100\%$ and $N^* = 50\%$. On average, $N^* = 50\%$ has a much larger LFV than $N^* = 100\%$. For $N^* = 50\%$, the largest LFV is found around $k = 0.75$, whereas $N^* = 100\%$ has the largest LFV around $k = 1.5$.

The effect of k on HFV is even more pronounced. It follows the same pattern as the LFV, with maxima at $N^* = 50\%$ at $k = 0.75$ and $N^* = 100\%$ at $k = 1.5$. These effects are shown in figure 4.

Note that all agents die at $k = 2.25$, which is further discussed in further on in this section under Extinction.

The Influence of Unreciprocated Cooperation on Cooperator Variability

S has little influence on both LFV and HFV. Although some of the smaller variability values are found at smaller values of S, especially at $N^* = 100\%$, the correlation is weak.

Extinction

A run was ended when a population went extinct, i.e. when all agents with a certain strategy died. This took place in 197 runs out of the 480. Almost all of these extinctions enfolded during the first 5000 steps, except for two runs ($N^* = 2500$, $k = 0$, $S = -2.5$ or $S = -1.75$). All runs with the largest cost of living, $k = 2.25$, ended in extinction. In this experiment, two types of extinction can be identified:

1. Both populations die together. More strictly defined: the total agent count < 250 at time of extinction.
2. Cooperators go extinct while defectors thrive, or, more strictly: at time of extinction, more than 250 defecting agents are alive. In practice, the total agent count, consisting of only defectors, was ≥ 975 at time of extinction.

Extinctions where cooperators had a larger agent count than 250, did not take place within these runs.

k is a strong predictor for the type of extinction. All extinctions of type 1, where both agent types die in large numbers, happened when $k \geq 0.75$, whereas all extinctions of type 2, where defectors drive away cooperators, took place in environments with $k = 0$, as is illustrated in 4.

Although S has little influence on variability, it does have influence on the frequency of extinctions, as well as on the type of extinctions. When $S = -0.25$, the only type of extinction is type 1. The number of type 2 extinctions increases as S goes down.

	k			
S	**0.00**	**0.75**	**1.50**	**2.25**
-0.25	0%	0%	13%	100%
-1.00	100%	7%	13%	100%
-1.75	100%	7%	20%	100%
-2.50	100%	27%	20%	100%

(a) $N^* = 50\%$. Number of runs: 240.

	k			
S	**0.00**	**0.75**	**1.50**	**2.25**
-0.25	0%	0%	7%	100%
-1.00	0%	0%	7%	100%
-1.75	7%	0%	20%	100%
-2.50	27%	7%	33%	100%

(b) $N^* = 100\%$. Number of runs: 240.

Table 3: Percentage of extinctions, per k and S. Total number of runs: 480.

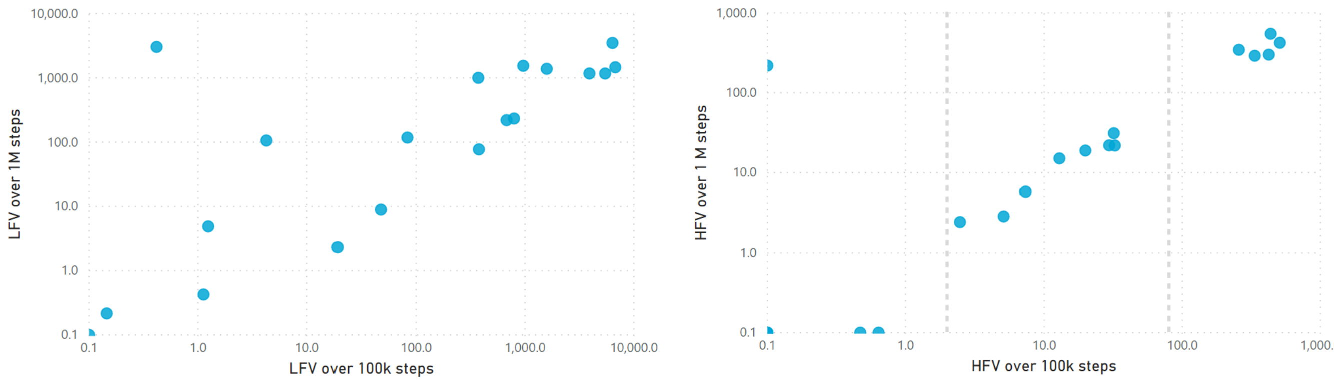
	k			
surviving population	**0.00**	**0.75**	**1.50**	**2.25**
defectors	50	0	0	0
cooperators	0	0	0	0
surviving agents <250	0	7	20	120

Table 4: Runs that ended in extinction, categorised by type of extinction and the value of k, cost of living.

Cooperator Variability over Time

5.2 Cooperator Variability as a Predictor of Future Cooperator Variability and Frequency

To study if HFV and LFV are useful as a predictor of future changes in cooperator frequency, another experiment was conducted. The setup of the model was similar to the prior experiment, as described in 5.1, with the most important difference that simulations were stopped at 10^6 instead of10^5. Be-



(a) LFV, until 10^5 and until 10^6

(b) HFV, until 10^5 and until 10^6

Figure 6: The relation between Cooperation Variability until 10^5 and until 10^6. The outlier is described in figure 7.

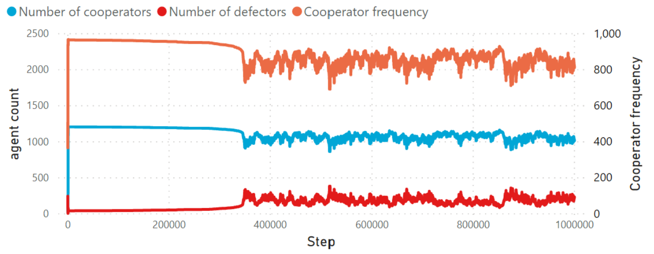


Figure 7: The outlier, with $S = -1.75$, $N = 50\%$ and $k = 1.5$

cause of computational constraints, only 1 run of each combination of variables was performed. This resulted in 32 runs in total. 13 of these had extinctions. They all went extinct before 10^5. 19 runs ran to the maximum time-step of 10^6.

Both HFV and LFV did not seem to change much from $t = 10^5$ to $t = 100^6$. This is shown in figure 6. There was one notable difference. This run, with $S = -1.75$, $N = 50\%$ and $k = 1.5$, initially seemed to have little cooperator variability, but started showing large cooperator variability at around $t = 344000$, as shown in figure 7. For all other runs, the correlation was strong.

Cooperator Frequency Changes over Time and Variability

The difference in cooperator frequency was measured by taking the absolute difference between the average cooperator frequency for $0.95 * 10^5 \leq t < 10^5$, and the average cooperator frequency for $t = 0.995 * 10^6$ and $t = 10^6$.

LFV has a strong correlation between the difference in cooperator frequency and LFV, except for one run. This was the same outlier that was described in the previous paragraph. Except for this run, there were no large changes in cooperator frequency observed when LFV is low. With exception of the outlier, changes in cooperator frequency were small.

6 Discussion

In the result section, it was shown that a larger cost of living generally increases both HFV and LFV. Sparser environments may lead to higher HFV. The cost of unreciprocated cooperation has little influence on HFV and LFV. HFV and LFV usually do not change much after the roughly the first 10^5 time-steps. Except for one run, where this was not the case.

This chapter provides a discussion of the underlying assumptions, as well as for the results.

6.1 Important assumptions

Length of runs

In a previous experiment, changes in cooperator frequency were noted after 10^5 time-steps [10], although the same paper asserts that 10^6 time-steps is sufficiently long "to allow the system into stable behaviour", from "running several conditions out to $t = 10^6$ and noting that the long-run cooperator frequencies did not vary from $t = 10^6$. As cooperator frequency may still change between 10^5 and 10^6 time-steps,

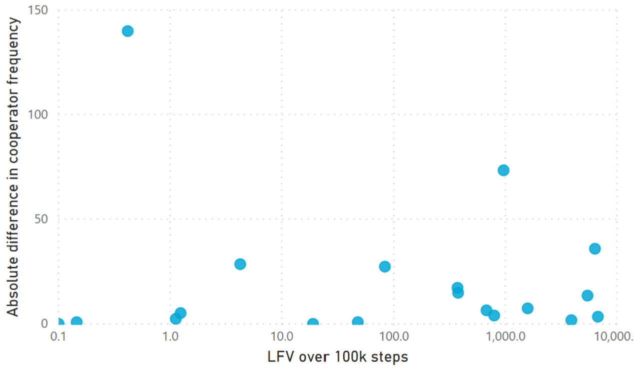


Figure 8: The relation between LFV until $t = 10^5$ and the difference in cooperator frequency over time. The difference in cooperator frequency was measured by taking the absolute difference between the average cooperator frequency for $0.95 * 10^5 \leq t < 10^5$, and the average cooperator frequency for $t = 0.995 * 10^6$ and $t = 10^6$. The outlier is described in figure 7.

variability may behave differently as well. Because of computational limitations, most runs were set to $t = 10^5$ as their last time-step. In the small sample of 19 runs that ran to $t = 10^6$, one run was detected that changed in LFV, HFV and cooperator frequency after $t = 10^5$. All other runs did not change much after the first 10^5 time-steps, both with regards to LFV and HFV, as well as their cooperator frequency.

Stochastic nature of the model

The model, as well as agent-based modelling in general, is highly stochastic. This makes generalising the observed correlations complicated. I have been unable to find a reliable formula to predict variability of the ratio's between. However, the properties of agent-based models have advantages that other methods of analysis lack. The generative and stochastic nature of the model helps to simulate the logic and consequences of individual behaviour and the interdependence between agents. Agent based modelling enables the analysis of mechanisms that change behaviour of low-level entities to create circumstances for change at a higher level of abstraction, with a flexibility that more rigorous mathematical approximation lacks [7].

6.2 Population sparseness and HFV

The differences in HFV between $N^* = 50\%$ and $N^* = 100\%$ are partially explainable by the nature variance, on which HFV is based on, itself. With smaller populations, any small change in the populations results in a larger difference in cooperation frequency. The larger oscillatory patterns, where $HFV > 80$, are absent in a fully filled lattice. This has been noted by Smaldino et al. [11], as “indicative of the stochasticy in agent movement, which led to the occasional flurry of cooperator expansion, followed by rapid exploitation by defectors and then an eventual defector die off.”

The same source continues with: “These events were due to variability in population size, as well as the fact that the carrying capacity was less than the total numbers of cells in the space.”[11] My observations do not fully agree here. Many runs that do show larger oscillatory patterns, where $HFV > 80$ and $N^* = 50\%$, do not have much variation in population size at all, whereas runs with smaller oscillatory patterns, where $2 < HFV < 80$, and $N^* = 100\%$, much more often have empty spots remaining unfilled after a time-step. Many of these large oscillations were not related to a large decrease in population size. Although some sudden drops in population size were observed in the $N = 50\%$, those were often absent while the large oscillatory patterns continued. And even when those sudden drops were observed, they usually were not very large.

6.3 Cooperator Frequency and its Impact on Variability

Before conducting this experiment, I expected that a high ratio of cooperators would decrease variability, as cooperators are needed by both other cooperator, as well as defectors, to stay alive. As noted in the results sections, a large number of cooperators never coincided with extinction of the defector population. But the converse is not true: many simulations with a majority of defectors do not end in extinction. When looking at cooperator frequency variability in the simulations without extinction, many runs with a high rate of defectors showed very little variability in cooperation frequency, both for HFV and LFV. Moreover, many runs with a high ratio of cooperators do have a large HFV and LFV. Therefore, cooperator frequency has little effect on the variability itself.

6.4 Predictive Value of Variability

Variability of cooperation may be useful to predict when a run can be stopped. Of the 19 runs, 18 had little change in cooperator frequency, and if they had, their variability measures were higher. However, one run behaved differently, and it should not be disregarded just yet, as the changes in frequency were large, and LFV and HFV were both very small. As Strogatz describes [13], complex systems may take a long time before entering a phase of stable behaviour. Therefore, more research is needed to determine if the variability measures are useful to determine when the cooperator frequency will not change much in the future.

7 Conclusion & Future work

The proposed measures of HFV and LFV are useful to describe the level of variability of the ratio between two populations in a simulation. The strongest influence on cooperator variability was the harshness of the environment. Although cooperators usually fare better in harsher environments, a higher prevalence of cooperators did not reduce cooperator variability. An enforced sparseness of populations has a large influence on cooperator variability. Generally, the proposed variability measures correlate well with future variability. However, it does not provide a definitive prediction if the simulation has entered into stable behaviour. Future research is needed to examine the predictive qualities of cooperator variability.

8 Responsible Research

Because of the stochastic properties of agent-based modeling, and of this model in particular, repeating this experiment may yield slightly different results. However, a detailed description of the model is provided in chapter 3. The original model, the resulting data sets and the data analysis can be found at https://gitlab.com/BEvanGelderen/Variability_Cooperation.

References

[1] NetLogo 6.1.1 User Manual: Programming Guide.

[2] R Axelrod and W. Hamilton. The evolution of cooperation. *Science*, 211(4489):1390–1396, 3 1981.

[3] C. Baan, R. Bergmuller, D.W. Smith, and B. Molnar. Conflict management in free-ranging wolves, canis lupus. *Animal Behaviour*, 90:327–334, 2014. cited By 21.

[4] A.R.A.M. Chammah, A. Rapoport, A.M. Chammah, and C.J. Orwant. *Prisoner's Dilemma: A Study in Conflict and Cooperation*. Ann Arbor paperbacks. University of Michigan Press, 1965.

[5] Graham Kendall, Xin Yao, and Siang Yew Chong. *The Iterated Prisoners' Dilemma*, volume Volume 4. WORLD SCIENTIFIC, 5 2007.

[6] I. Krams, T. Krama, A. Berzins, and M.J. Rantala. The risk of predation favors cooperation among breeding prey. *Communicative and Integrative Biology*, 3(3):243–244, 2010. cited By 8.

[7] G. Manzo. Potentialities and limitations of agent-based simulations: An introduction. *Revue Francaise de Sociologie*, 55(4):653–688, 2014.

[8] Martin A. Nowak. *SPATIAL GAMES*, pages 145–166. Harvard University Press, 2006.

[9] Matjaž Perc, Jesús Gómez-Gardeñes, Attila Szolnoki, Luis M. Floría, and Yamir Moreno. Evolutionary dynamics of group interactions on structured populations: A review, 3 2013.

[10] Paul E. Smaldino. Cooperation in harsh environments and the emergence of spatial patterns, 2013.

[11] Paul E. Smaldino, Jeffrey C. Schank, and Richard McElreath. Increased costs of cooperation help cooperators in the long run. *American Naturalist*, 181(4):451–463, 2013.

[12] Max Souza, Jorge Pacheco, and Francisco Santos. Evolution of cooperation under n-person snowdrift games. *Journal of Theoretical Biology*, 260:581–588, 10 2009.

[13] S.H. Strogatz. *Nonlinear Dynamics and Chaos: With Applications to Physics, Biology, Chemistry, and Engineering*. CRC Press, 2018.

[14] A. Zelezniak, S. Andrejev, O. Ponomarova, D.R. Mende, P. Bork, and K.R. Patil. Metabolic dependencies drive species co-occurrence in diverse microbial communities. *Proceedings of the National Academy of Sciences of the United States of America*, 112(20):6449–6454, 2015. cited By 199.