

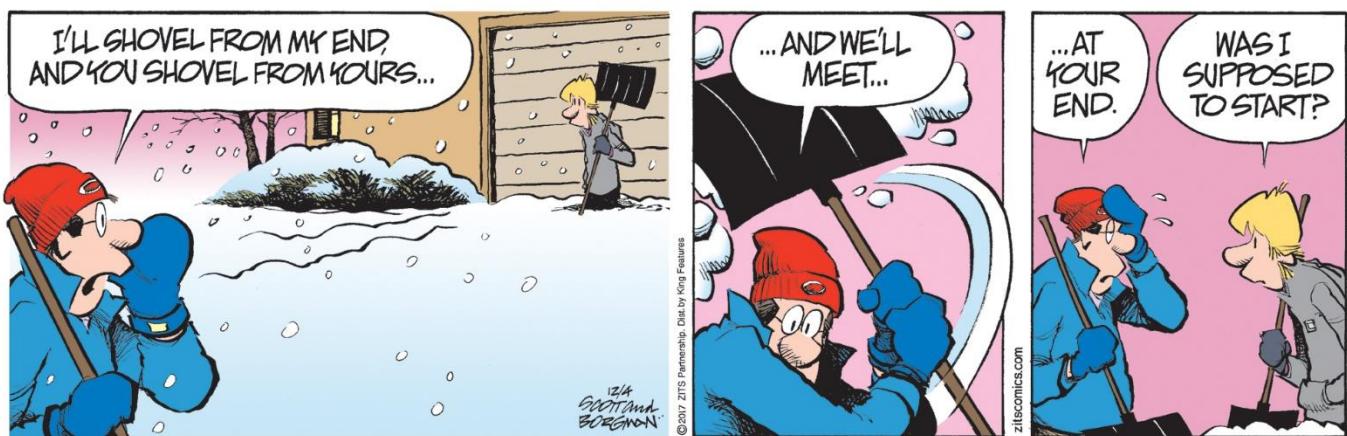
Evolution of cooperative personalities in a cooperation game

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1. Introduction

Many studies on the behaviour of animals searched for the general behaviour of the populations in order to compare it to other populations. Deviations from the mean within the same populations were discarded as random noise due to stochastic processes. Recent empirical data suggest otherwise, where it is seen that within the same population, animals tend to behave the same in different situations. This is seen in birds, chimpanzees, fish, amphibians [1], spiders [2] and insects [3]. This behaviour which is consistent over time (as juvenile and as adult) and context (in interaction with a predator and potential mate) is referred to as personalities [4], much like human personalities. Examples can be found in many character traits like boldness [5], aggression [6] and cooperation [7]. It is remarkable that personalities exist, especially when it is seen from an adaptive perspective. If it is better for individuals to be able to react in any kind of situation the optimal way, then why is this not observed? Why has behaviour evolved toward a more static state instead of an infinite plasticity? In many studies with humans, differences in cooperation would suggest three kinds of cooperative personalities: unconditional cooperators, unconditional defectors and conditional cooperators. [8] In these studies it is seen that a large part of the population chooses for ‘conditional cooperation’: cooperation depending on the environment. The environment could be many different things, such as the person you interact with or other external factors. It could be suggested that the responsiveness of people induces cooperation. [9] To investigate this, responsiveness [10] was introduced in a cooperation game [11], the snowdrift game. Several games come to mind, when thinking of cooperation (snowdrift, prisoner’s dilemma, stag hunt etc), which all show a different side of cooperation. The choice for snowdrift was made because cooperation is inherently intended here and is expected to come up, see 2.1 the snowdrift game. Therefore, the aim for this project is first to look if conditional cooperation can evolve in a snowdrift game and mainly if conditional cooperation can induce the evolution of cooperative personalities.

2. The baseline model

2.1.The snowdrift game

General		Snowdrift		Special case: b=4, c=2	
		C	D	C	D
C	a_{11}	a_{12}	$b - \frac{1}{2}c$	$b - c$	3
D	a_{21}	a_{22}	b	0	4

Table 1. Pay-off matrix of the snowdrift game. C is cooperate, D is defect, b is benefits and c is costs. The vertical C and D is the strategy of the focal individual, the horizontal that of its partner.

Figure 1 shows the fitness graph of the snowdrift game. The benefits ($b=4$) and the costs ($c=2$) are the same as used in the simulations. On the x-axis the population’s mean tendency to cooperate (\bar{P}_0) is given, whereas the y-axis shows the expected fitness (F). When all individuals in the population defect ($\bar{P}_0 = 0$), the best strategy to play is to cooperate ($F_c > F_D$). The mean tendency to cooperate will increase as a result of this. When the tendency to cooperate is 1 for every individual in the population, it would be better to defect ($F_c > F_D$). This would decrease the mean tendency to cooperate. An evolutionarily stable strategy is predicted at around $\frac{2}{3}$ ($P_0^* = 0.67$) of the population.

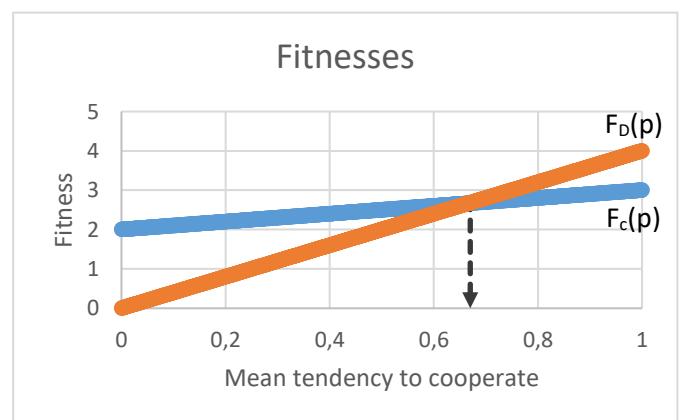


Figure 1. Fitness graph of snowdrift game with benefits = 4 and costs = 2.

2.2. Set-up of the simulation

A population consists of 1000 individuals, which all have a certain intrinsic tendency to cooperate (P_0) between 0 and 1. This trait determines whether the individual cooperates or defects during a given interaction. Each individual has 10 interactions in its lifetime with randomly chosen individuals from the population. The interactions are based on the snowdrift game with benefits = 4 and costs = 2 (the same as in table 1c and figure 1). The pay-offs an individual receives from these 10 interactions are added together. This sum is the individual's fitness. The fitness values of all individuals in the population are used as the weights for a weighted lottery in order to determine which individuals produce how many offspring for the next generation. During the reproduction, there is a chance (μ) of 0.01 that a mutation occurs. This mutation leads to a small change in the P_0 value, taken from a Gaussian distribution with a standard deviation (σ) of 0.01. The model is implemented in C++.

2.3. Evolution in the absence of responsiveness

This model was used as the basis for later developments, but here the aim was mainly to see if the expected equilibrium from the pay-off matrix of the snowdrift game was found.

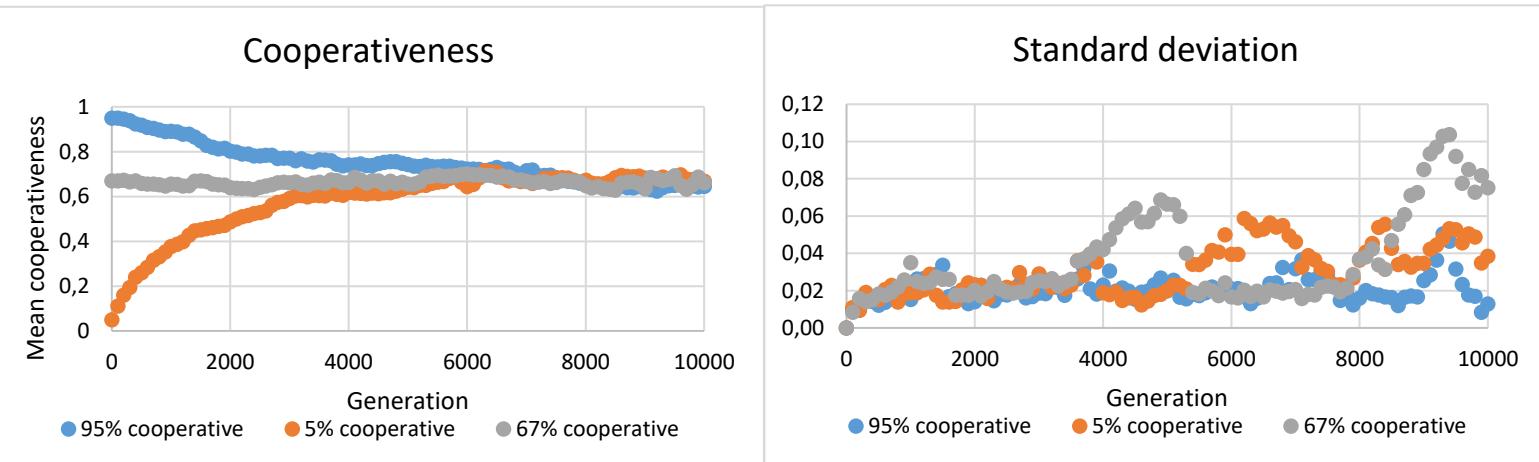


Figure 2a and b. Left: Mean cooperativeness of three populations with different initial values. Right: Standard deviation of mean cooperativeness of three populations.

Figure 2a shows the mean cooperativeness of three different populations to see if the value of 0.67 that is predicted for our version of the snowdrift game, is reached. The standard deviations show that the variation is quite low, with some larger outbursts, which is due to stochasticity. With so little variation (more than 95% of the data is between 0.67 ± 0.04), it is fair to say that no personalities emerged. The expected cooperativeness equilibrium is indeed found at approximately 0.67.

3. Introducing responsiveness

3.1. Including responsiveness in the model

Responsiveness is introduced as another trait value (P_i) which is either 0 or 1. An individual with a P_i of 0 is unresponsive and one with a P_i of 1 is responsive. A responsive individual can observe which strategy its partner used in a previous interaction (see appendix B for more detailed description) and respond to that by adapting its own strategy. The responsive individual does have to pay a fitness price¹ for this, however. Responsiveness is also affected by mutation; during the reproductive phase, there is a 0.01 chance of mutation (μ) which turns a responsive individual into an unresponsive individual and vice versa.

¹ Since this price is subtracted from an individual's fitness, it is possible an individual ends up with a negative fitness. To prevent this from happening, every individual receives a baseline fitness of 11 times the price.

3.2.Evolution of responsiveness

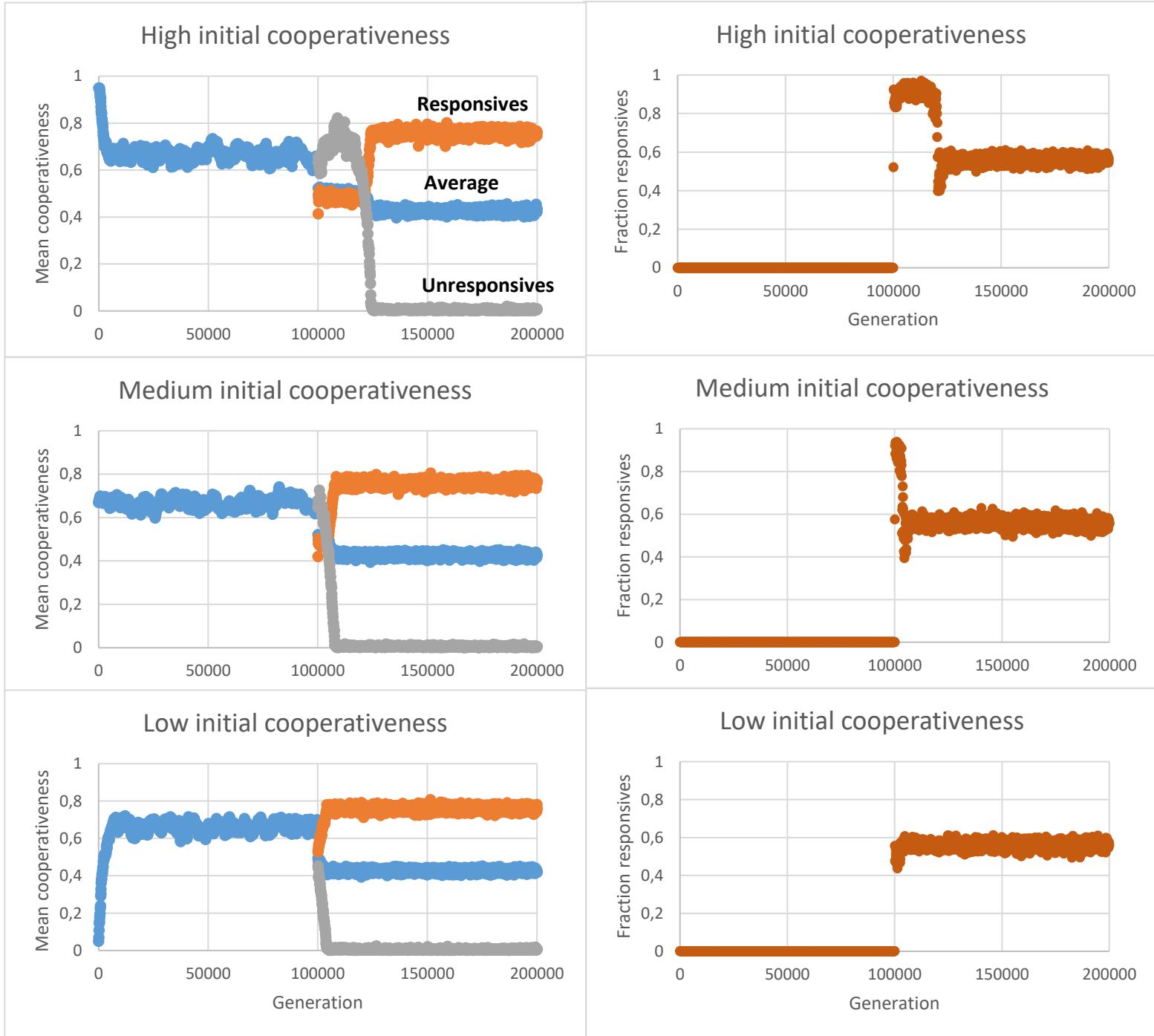


Figure 3. Left: Mean cooperativeness for unresponsive and responsive individuals and the population mean for three different populations. Right: Fraction responsive individuals in three different populations. Responsiveness could not occur for the first 100,000 generations.

In this simulation, the price for being responsive was 0.0. This was done in order to observe the dynamics of the system when responsiveness can evolve. The mean cooperativeness goes to the equilibrium at $\frac{2}{3}$ cooperativeness in all three populations before the responsiveness can occur. Then, responsiveness emerges very quickly in all three cases; in the one with low initial cooperativeness, the fraction responsive individuals go to an equilibrium immediately, but the ones with high and medium initial cooperativeness first reach a high fraction of responsive individuals, before reaching the same equilibrium of around 55% responsive individuals. At the moment the responsiveness emerges the unresponsive individuals reach an equilibrium where they always defect, while the

responsive ones have a high cooperativeness. The high initial cooperativeness case shows an intermediate state, where unresponsive individuals keep a high responsiveness for a bit longer before going to almost no cooperation. All the cases show a fall in the average of the population as responsiveness emerges.

Thus, responsiveness is able to emerge from a totally unresponsive population. Unresponsive individuals always seem to choose defect over cooperation.

3.3. Effect of price of the evolution of responsiveness

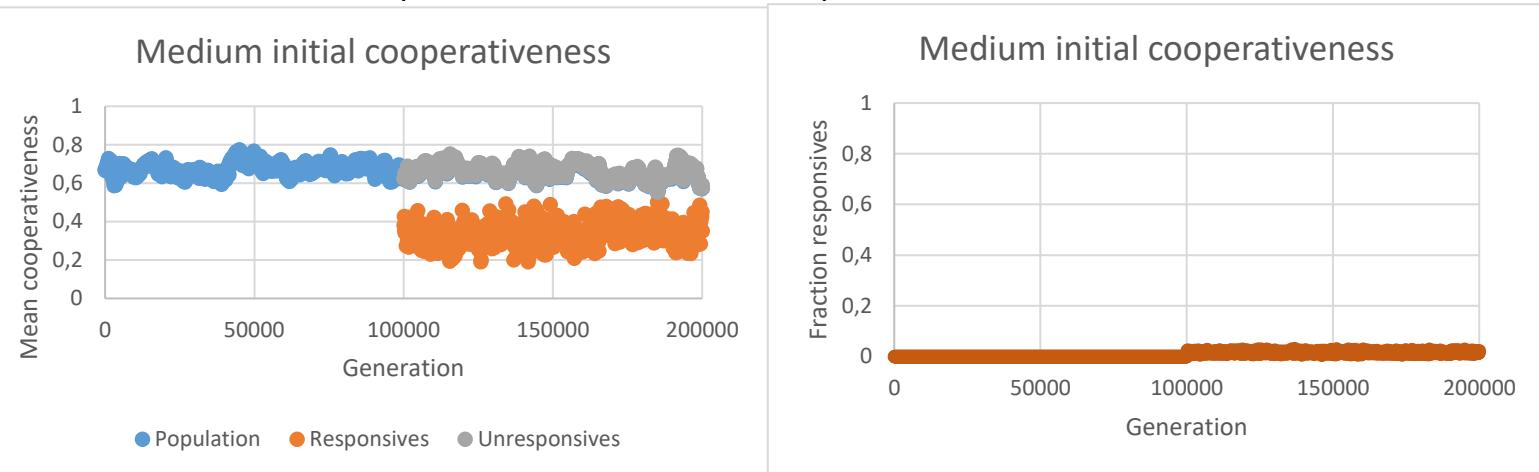


Figure 4. Left: Mean cooperativeness of responsive and unresponsive individuals and the population average for a population with medium initial cooperativeness. Right: Fraction responsive individuals in a population with medium initial cooperativeness.

In this simulation, the price was set to 5.0. This is very high, and as a result of this, responsiveness was not a viable strategy. Figure 4a shows the average cooperativeness, which is almost the same as the cooperativeness of the unresponsive individuals, because almost no responsive individuals are present. This is seen in the graph on the right. The price is too high for responsiveness to maintain a substantial part of the population. Now, only due to stochasticity very low numbers of responsive individuals are present in the population.

Calculating the threshold price

According to Wolf et al. [12], the fitness price an individual pays for obtaining information has to be sufficiently low in order for responsiveness to emerge in the population. The exact value can be calculated by the following formula.

$$\text{price} < ((a_{12} - a_{22}) + (a_{21} - a_{11})) * \text{sd}(P_0)^2$$

The different α values are the values from the payoff matrix, see table 1. This simplifies the formula to the following.

$$\text{price} < \left(b - \frac{1}{2}c \right) * \text{sd}(P_0)^2$$

In the simulation with a price of 0.0, we found that the standard deviation was approximately 0.02. This leads to the assumption that the price can be no larger than 0.0012 if responsiveness is to emerge.

First, a price of 0.001 was tested to see if responsiveness could occur.

Price for responsiveness: 0.001

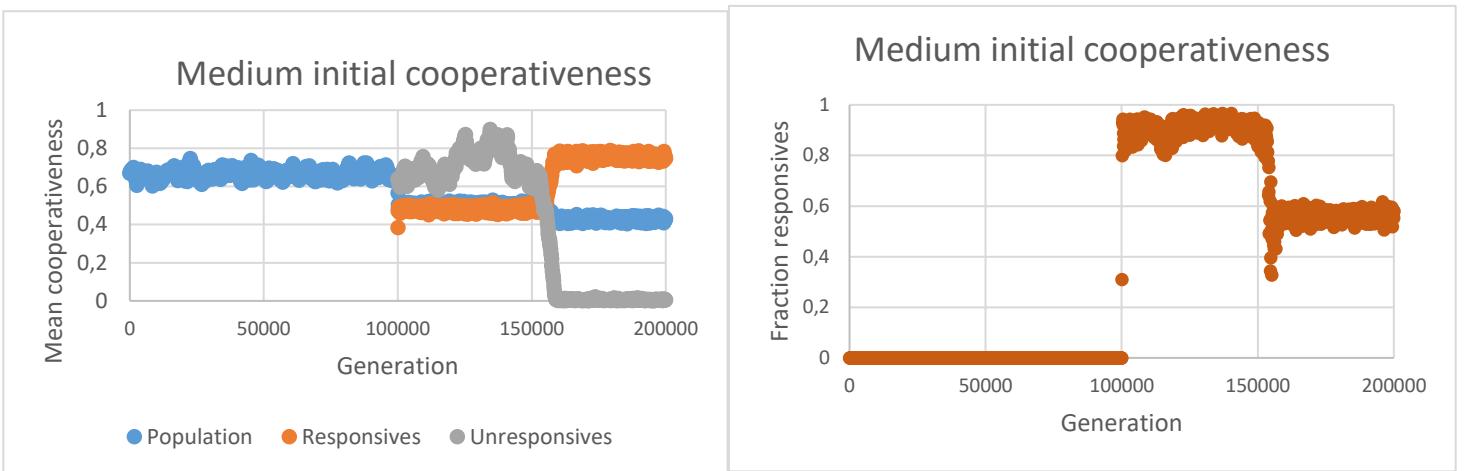


Figure 5. Left: Mean cooperativeness of responsive and unresponsive individuals and the population average for a population with medium initial cooperativeness. Right: Fraction responsive individuals in a population with medium initial cooperativeness.

Responsiveness emerges very quickly, within 100 generations. Therefore, several other simulations with different prices were investigated, ranging from 0.005 till 0.5.

Price for responsiveness: 0.5

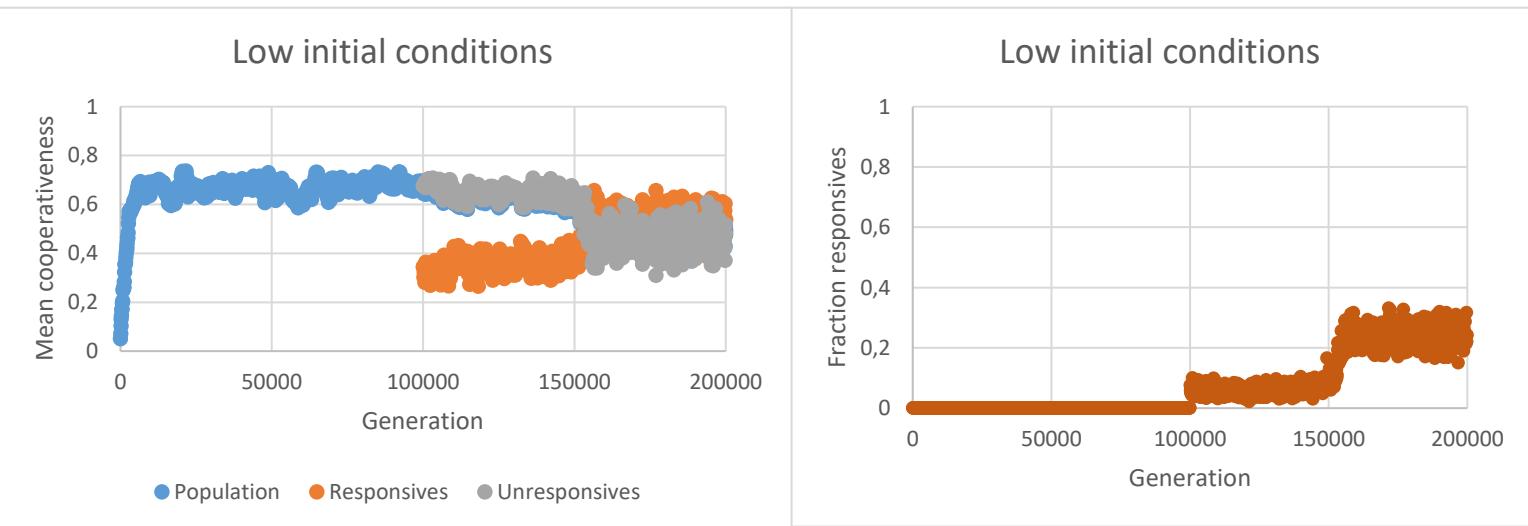


Figure 6. Left: Mean cooperativeness of responsive and unresponsive individuals and the population average for a population with low initial cooperativeness. Right: Fraction responsive individuals in a population with low initial cooperativeness.

Standard deviation P0

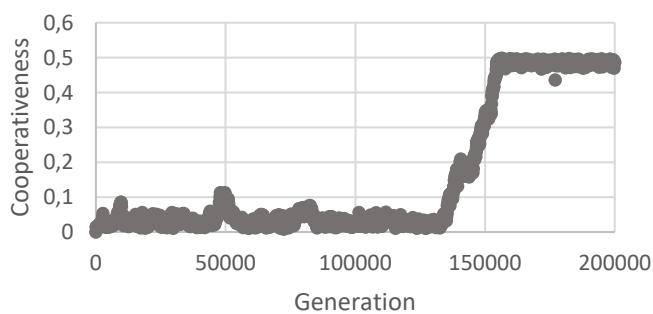


Figure 7. Standard deviation of the P_0 values of the unresponsive individuals.

One of the three populations (different initial cooperativeness) which were tested at first, showed an emergence of responsiveness. Upon these findings, ten additional simulations were performed under the same circumstances (see extended data E). Out of the ten simulations, eight showed an emergence of responsiveness. The right shows a responsiveness fraction of 20 – 25%. These findings seem to go directly against the previously shown equations of the maximum price for responsiveness.

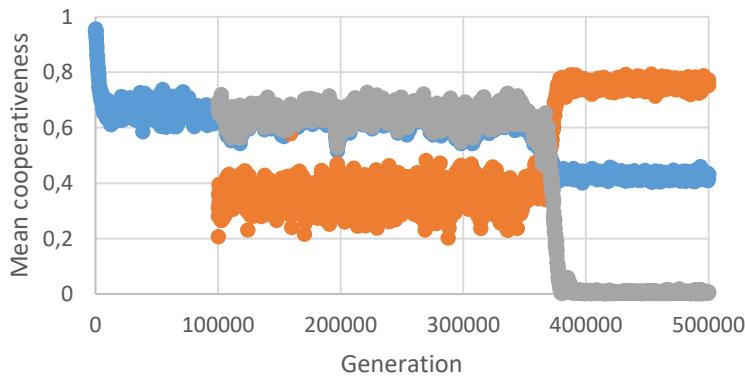
Therefore, we looked into the standard deviation of the P_0 values, see figure 7. Here it can be seen that the variation reaches very high level (0.5!) just before the responsiveness is introduced in the population. When looking back into the equation suggested by Wolf et al., this price is not too high for responsiveness to emerge with this variation. Interestingly, the variation stays very high, which suggests very high differences in strategy of the unresponsive individuals.

4. Responsiveness as a continuous trait

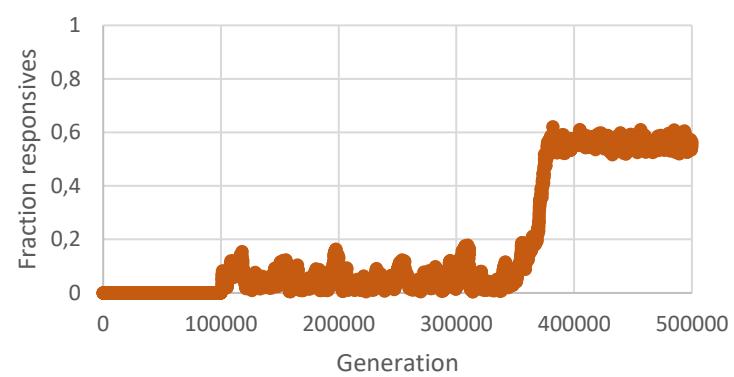
Instead of individuals always being responsive or always being unresponsive, the tendency to be responsive was changed to be anything between 0 and 1. This way the model would become more realistic, because responsiveness is sort of like a spectrum: some individuals respond more than others, but don't always respond. From the personality's perspective, a more static behaviour is expected, but this can also be slightly plastic. Therefore, it is more logical to have a slight change in the responsiveness instead of a choice between responsive and unresponsive.

Price for responsiveness: 0.0

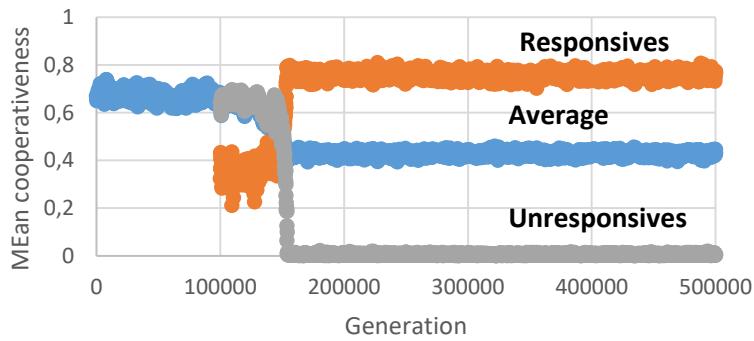
High initial cooperativeness



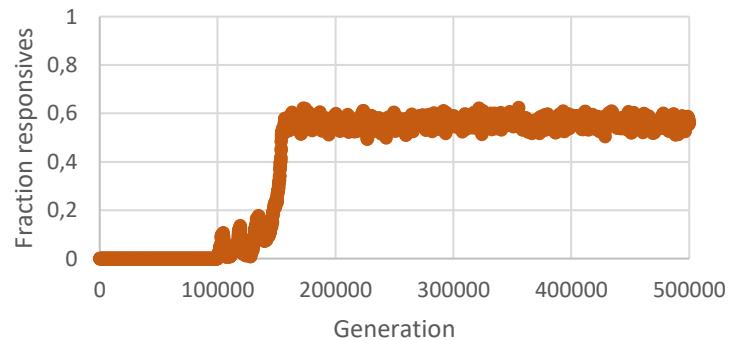
High initial cooperativeness



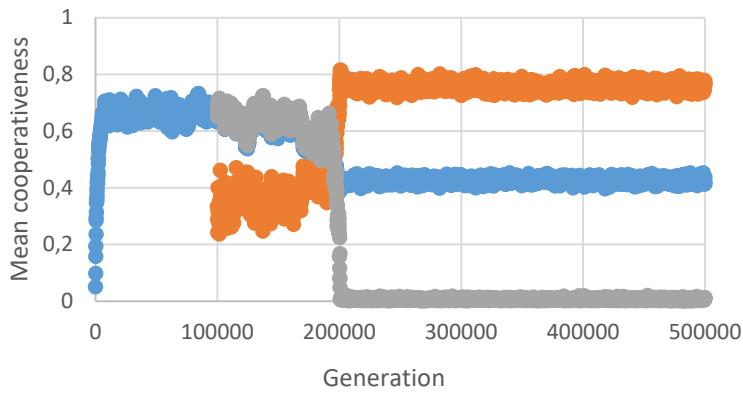
Medium initial cooperativeness



Medium initial cooperativeness



Low initial cooperativeness



Low initial cooperativeness

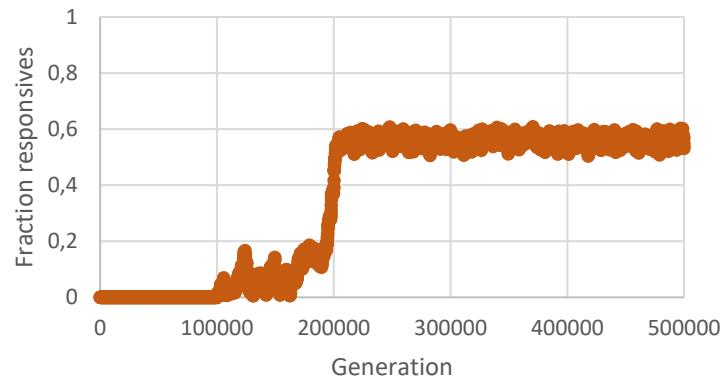
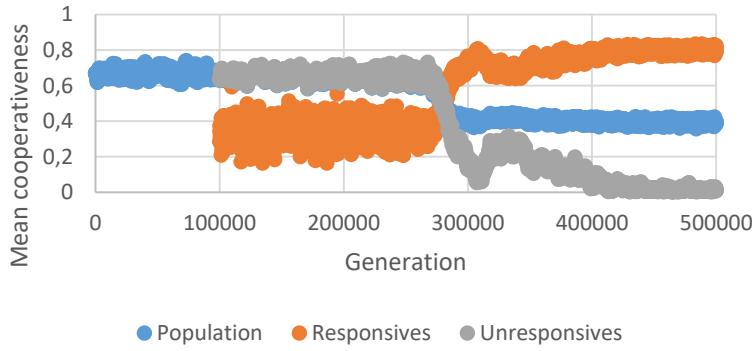


Figure 8. Left: Mean cooperativeness for unresponsive and responsive individuals and the population mean for three different populations. Right: Fraction responsive individuals in three different populations. Responsiveness could not occur for the first 100,000 generations.

Responsiveness emerges and reaches the same equilibrium as with the Boolean responsiveness. This can be seen in the right graphs. Thus, responsiveness emerges when it is a continuous trait, however it takes longer to reach this equilibrium. The unresponsive individuals choose defect over cooperation in the end, as seen before, while the responsive ones go to high cooperation levels.

Price for responsiveness: 0.3

Medium initial cooperativeness



Medium initial cooperativeness

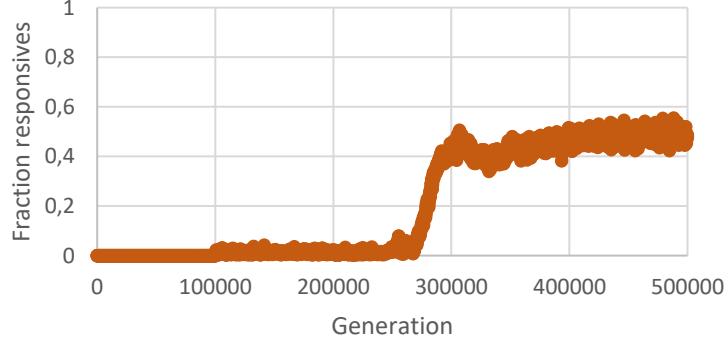


Figure 9. Left: Mean cooperativeness of responsive and unresponsive individuals and the population average for a population with medium initial cooperativeness. Right: Fraction responsive individuals in a population with medium initial cooperativeness.

Standard deviation P0

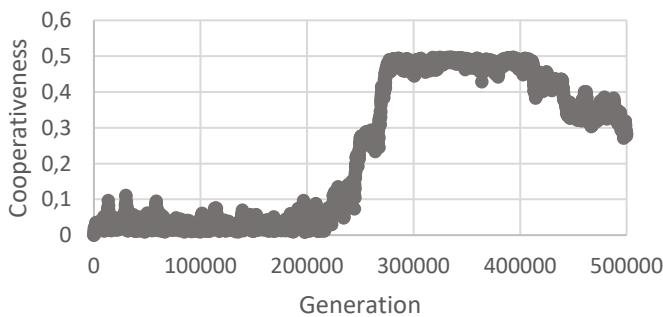


Figure 10. Standard deviation of the P_0 of the unresponsive individuals.

Introducing a higher price shows that the expected value of a maximum price also doesn't seem to apply for continuous responsiveness. The right graph shows that after about 250,000 generations responsiveness occurs in the population. The variation before responsiveness occurs, seems lower than in the case with no price, see figure 8 high initial conditions. Figure 10, the standard deviation does reach a high level of 0.5 upon the responsiveness can occur. Here the standard deviation seems to decrease and with that it seems personalities disappear from the population again.

Price for responsiveness: 0.5

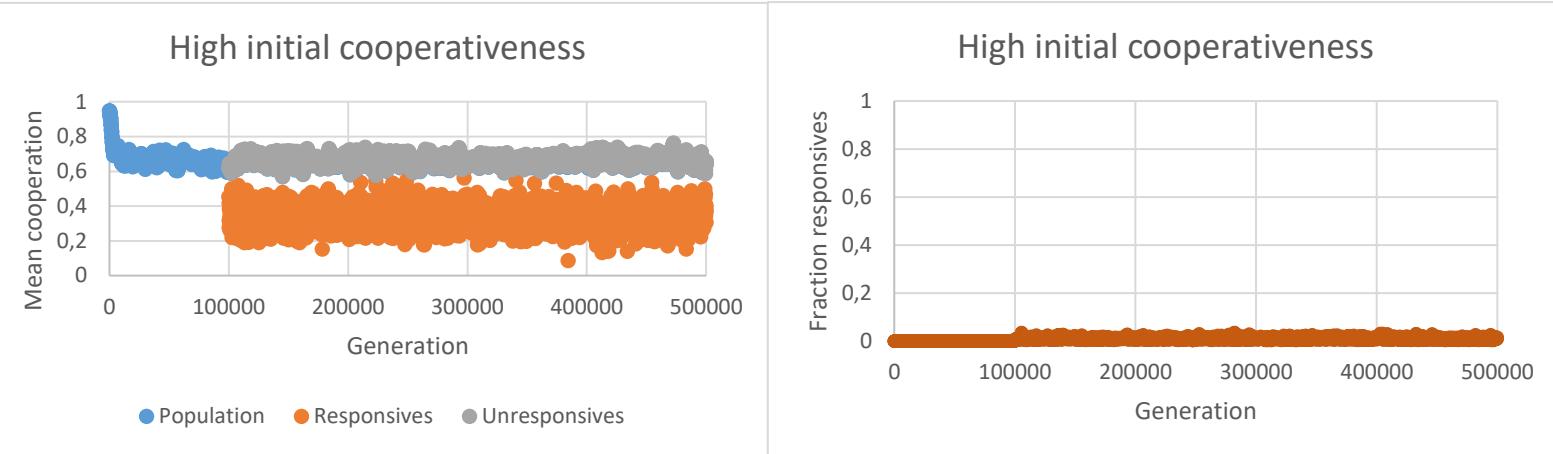


Figure 6. Left: Mean cooperativeness of responsive and unresponsive individuals and the population average for a population with high initial cooperativeness. Right: Fraction responsive individuals in a population with high initial cooperativeness.

This simulation was performed with three different initial conditions, where none showed an emergence of responsiveness. Above shows only the high initial conditions, in which case the mean cooperativeness goes to an expected $\frac{2}{3}$ cooperation in absence of a high number of responsive individuals.

5. Conclusion and discussion

In our project we want to tackle the question “Can responsiveness evolve and does this induce the emergence of personalities?”. As seen in the results above, we see that responsiveness can evolve in populations and in fact we found that it could even spread when the price for being responsive was a factor 50 higher than suggested by the paper of Wolf et al. In the first responsiveness model, we found that there is a clear difference in strategy of responsive and unresponsive individuals. When introducing the responsiveness as a tendency, the same equilibria were found. In short, both questions have a positive answer.

It seems that by introducing responsiveness to a population, a clear difference in strategy is sparked as two obvious personalities emerge. Responsive individuals tend to go for cooperation, while the unresponsive individuals end up defecting most of the time. This is probably due to a discrepancy in the pay-off matrix of the game dynamics of the snowdrift game. Between $\alpha_{12}(b - c)$ and $\alpha_{21}(b)$ for an unresponsive individual interacting with a responsive individual, α_{21} gives a higher fitness than α_{12} , and therefore defecting is the strategy which will be more successful. As a result of this, unresponsive individuals in a highly responsive population tend to defect after reaching equilibrium (see figure 3, high initial responsiveness). Due to the emergence of responsiveness, the average cooperativeness of the population decreases and the number of unresponsive individuals becomes very low. Only after the unresponsive individuals change their strategy to defect more often, will they regain a substantial part of the population.

Wolf et al. suggested a maximum price for responsiveness to emerge in an unresponsive population. This is based on the variation of the population, but, as can be seen in figure 1, the standard deviation fluctuates a lot in the population. The maximum price that was calculated was based on

the standard deviation being 0.02, but in the higher peaks the standard deviation could reach 0.1 and higher. Could this explain the responsiveness still emerging at a price of 0.5? If we took the standard deviation of 0.1, the max price would be 0.03, which is still a factor of at least 15 lower than what we found.

Interestingly, we see in figure 7 that the standard deviation reaches a high level in which the price is not too high to let responsiveness emerge. The standard deviation of the cooperativeness among unresponsive individuals stays very high and therefore a clear difference in personalities is very likely. When introducing the responsiveness as a continuous trait, the standard deviation did also reach a high level after which responsiveness emerged. Although, it did not stay high, but decreased. This suggests that no personalities emerged. Overall, some interesting findings have been observed, which definitely need more research to clarify the continuous responsiveness scenario. One suggestion would be to let the strategy chosen by the individuals evolve over time, so that responsive individuals do not immediately choose the opposite of the partner.

The emergence of personalities was observed in the first responsive model, but introducing this as continuous responsiveness showed little variation. Something to look into for the future would be adding a slight change in price for every individual, so that some individuals pay less fitness price for being responsive than others. In this way, it could be that personalities even with a continuous responsiveness could emerge from an unresponsive population.

Another suggestion for future research is the introduction of signalling. Individuals can show different behaviour than the behaviour they would exhibit in an interaction. This could influence the emergence of responsiveness in a population. Finally, studying meta-populations could perhaps be interesting. Due to smaller population sizes in these meta-populations, variation would be larger. Therefore, responsiveness would be able to emerge more easily.

6. Literature list

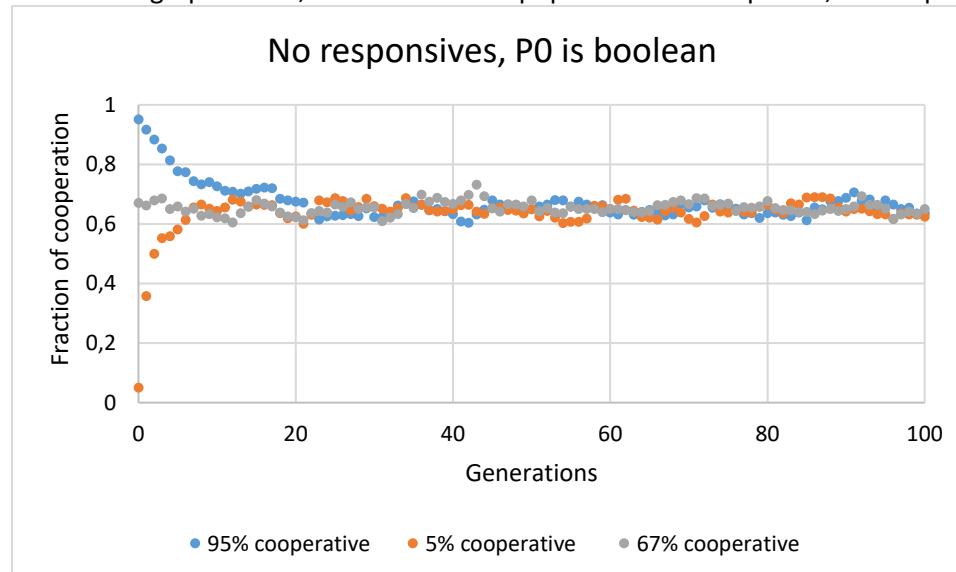
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Appendix

A. Model in the absence of responsiveness

Data of the model in which an individual's strategy is either always cooperate or always defect. As seen in the graph below, two thirds of the population will cooperate, as is expected.



Above shows the development of the mean fraction of cooperatives in a population of three population with different initial conditions. The blue points represent the population with 95% cooperatives, grey the one with 67% and orange the one with 5%.

B. Detailed depiction of the implementation of responsiveness

Partner →	Responsive	Unresponsive
Focal ↓		
Responsive	$C_f = 1 - P_{\text{mean}}$ $D_f = P_{\text{mean}}$ $C_p = 1 - P_{\text{mean}}$ $D_p = P_{\text{mean}}$	$C_f = 1 - P_0(p)$ $D_f = P_0(p)$ $C_p = P_0(p)$ $D_p = 1 - P_0(p)$
Unresponsive	$C_f = P_0(f)$ $D_f = 1 - P_0(f)$ $C_p = 1 - P_0(f)$ $D_p = P_0(f)$	$C_f = P_0(f)$ $D_f = 1 - P_0(f)$ $C_p = P_0(p)$ $D_p = 1 - P_0(p)$

Table 3. Chances a focal individual and its partner receive a certain fitness based on the different strategies played in different scenario's. The f means focal, p means partner, D is to defect and C is to cooperate.

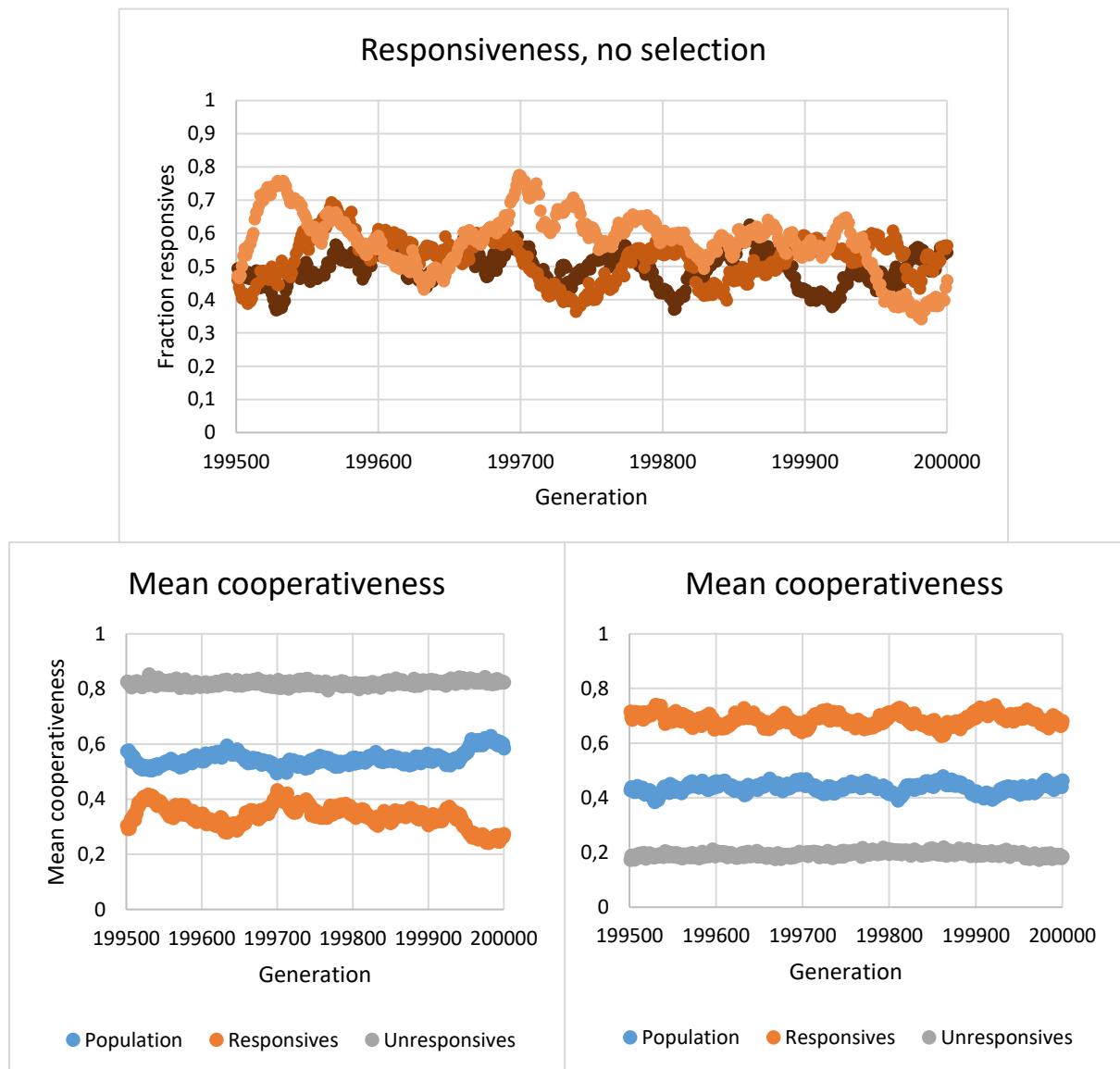
Above, four scenarios in model 1.1 are laid out an individual can be responsive and unresponsive and can interact with a responsive and unresponsive individual. It shows the chances an individual which is either responsive or not responsive will cooperate or defect when interacting with a responsive or not responsive individual. C_f = chance focal individuals cooperate, D_f = chance focal individual defects, C_p and D_p are the same but than for the partner. P_{mean} is the average cooperativeness in the last generation, where P_0 is an individual's intrinsic cooperativeness.

C. Quantifying the effects of genetic drift and mutation

This is a control model to see if an equilibrium is found in the responsiveness. Therefore, no selection is made for the next generation based upon fitness. Instead of a weighted lottery, a uniform distribution is used for determining the next generation.

Three replica populations are run in a simulation over 200,000 generations. The last part is the most useful, due to the absence of initialisation effects (which come about when there is not much variation just yet), therefore only the last 500 generations are shown.

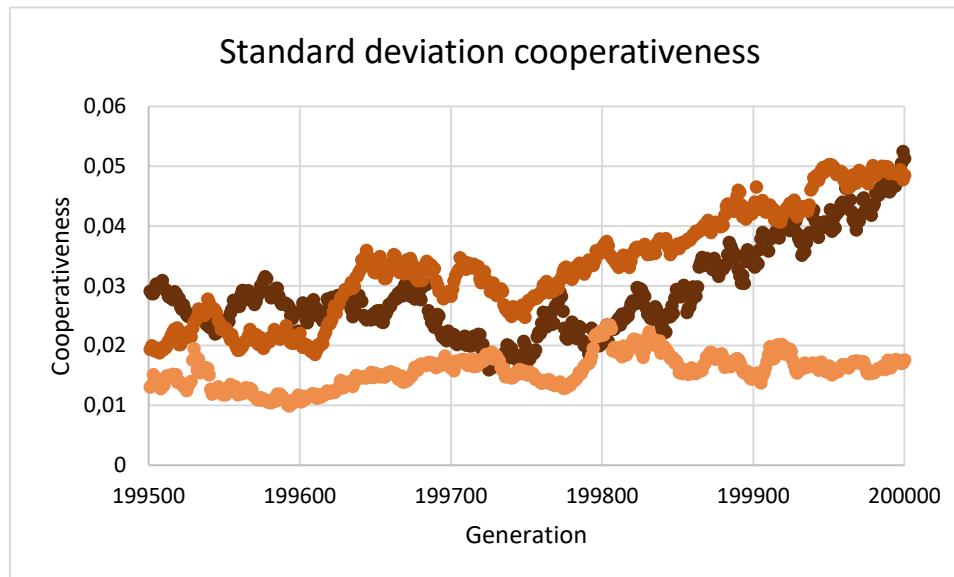
As no selection is acting on the populations, the fraction responsive individuals in the population goes to random oscillations around 0.5 as is expected.



Above shows the fraction of the populations which is responsive. The mean cooperativeness of two of the three replicas is also shown. Blue is the average of the population, grey shows the average of the unresponsive individuals and orange that of the responsive individuals.

Two different outcomes of drift are shown in the graphs above, where drift pushes the two different population to different average cooperativeness. Interestingly, the unresponsive individuals always seem to have little variation, at least less than the responsive individuals. This makes sense when

responsive individuals randomly encounter unresponsive and responsive individuals and are therefore more influenced by chance, while unresponsive stick to their intrinsic cooperativeness.



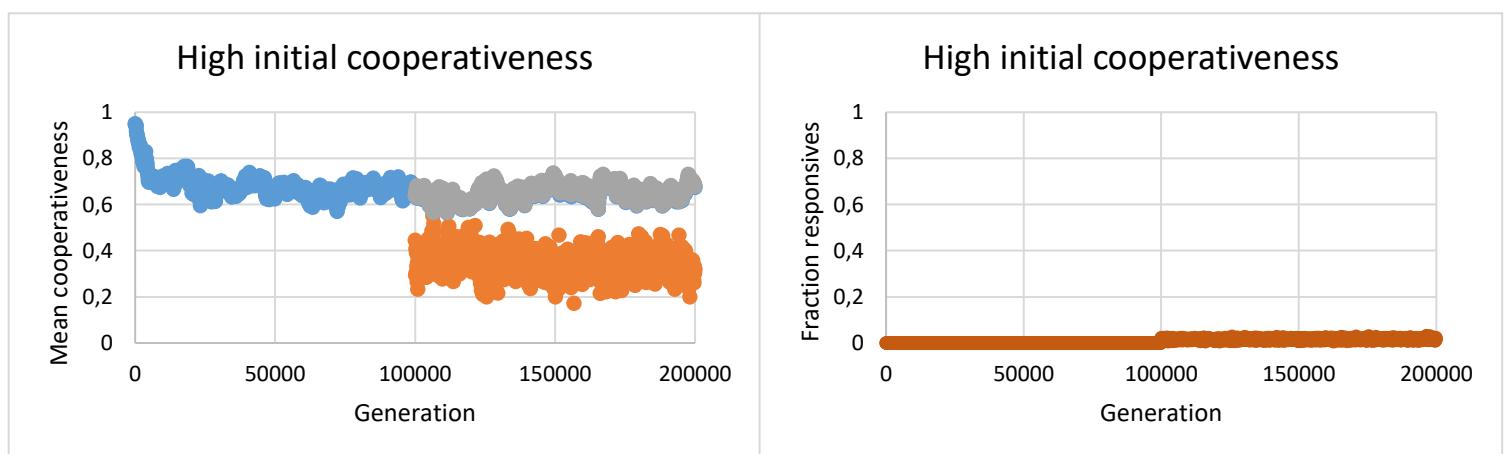
Above shows the standard deviation of the unresponsive individuals of three populations.

Although, more variation is perhaps expected in the three populations shown above, the small standard deviation is due to the small mutation rate ($= 0.01$). On top of that, these graphs show only the last 500 generation, more variation could be possible over the whole course.

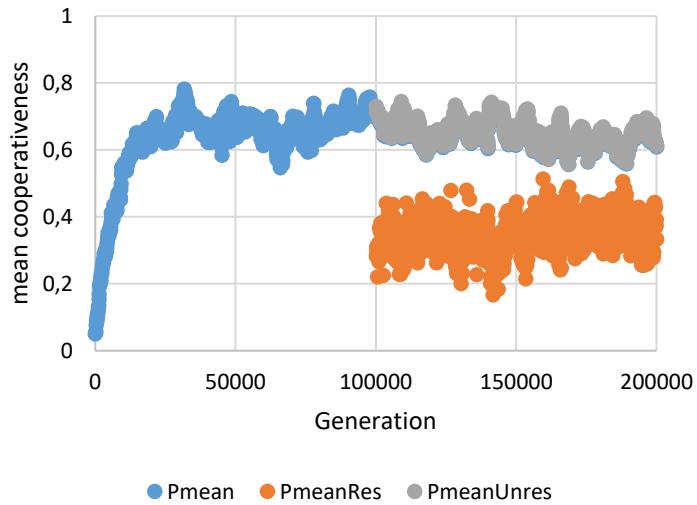
The null model of model 1.1 shows that without selection on responsiveness an equilibrium of 0.5 is reached with high fluctuations. Generic drift takes over the main strategies for the populations. This shows the robustness of the model 1.1.

D. Effect of a high price on the evolution of responsiveness

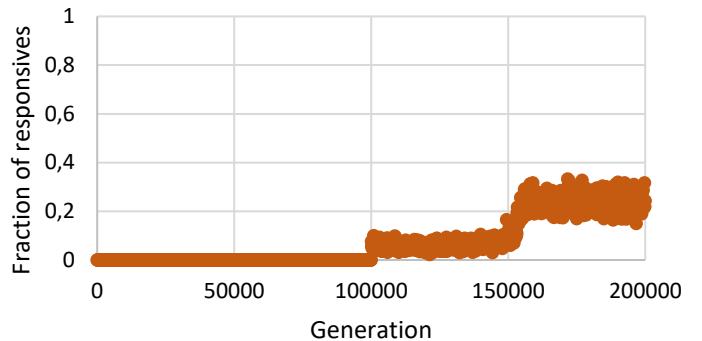
Below the data for the high price for responsiveness is shown for high and low initial conditions.



Low initial cooperativeness



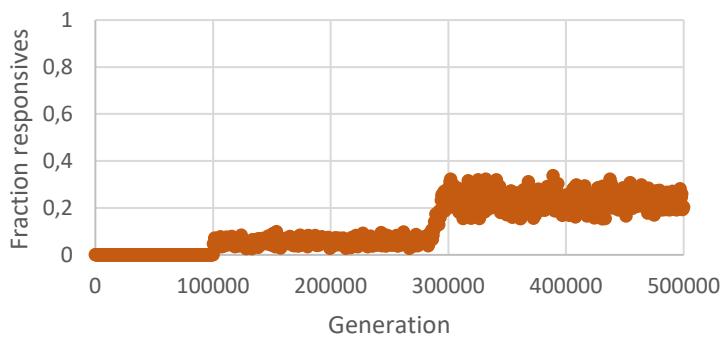
Low initial cooperativeness



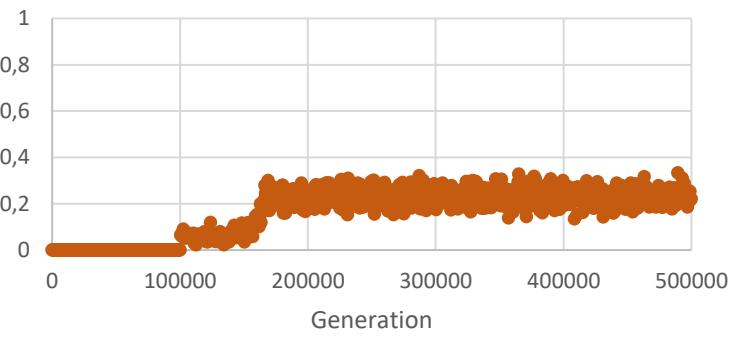
Both the graphs for high initial cooperativeness and the graphs for low initial cooperativeness show extremely low responsiveness and therefore a similar average to no responsiveness (first 100,000 generations).

E. Responsiveness with a price of 0.5 extra data

Initial cooperativeness 0.35



Initial cooperativeness 0.85

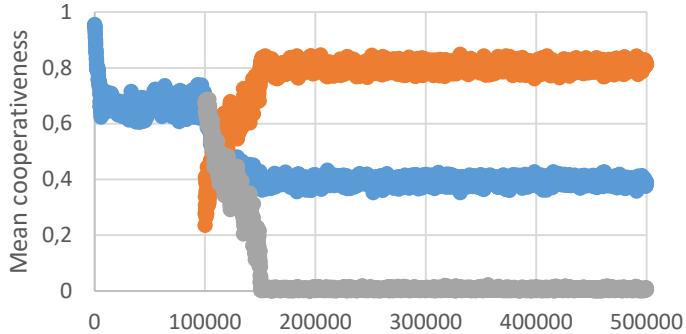


Two of the 10 extra simulations run for responsiveness price of 0.5 with several different initial conditions. The simulations first run 100,000 generation to get to equilibrium as seen before. Then responsiveness is introduced by mutations. In 8 of the 10 simulations, responsiveness came up. The lower fraction of responsive individuals is in line with the higher price for responsiveness.

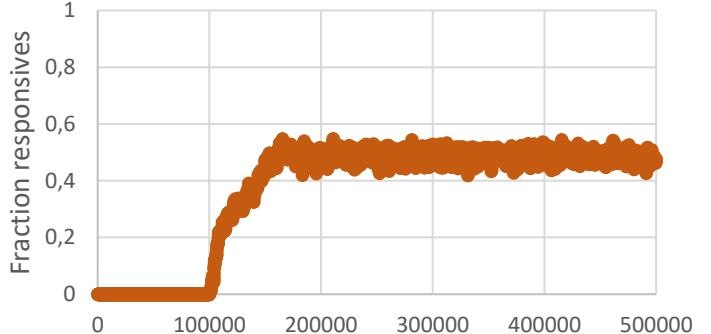
F. Responsiveness as continuous trait extra data

Price for responsiveness: 0.3

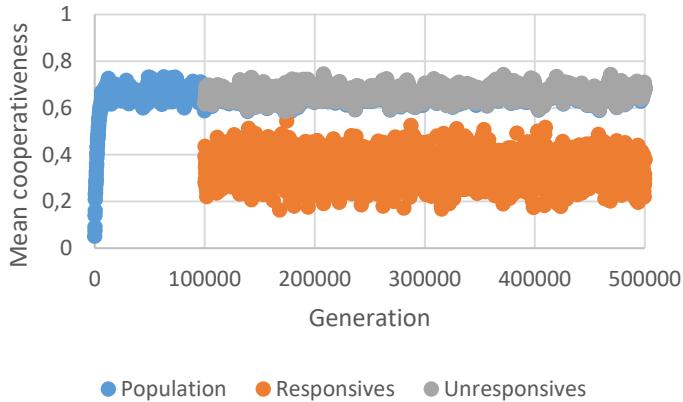
High initial cooperativeness



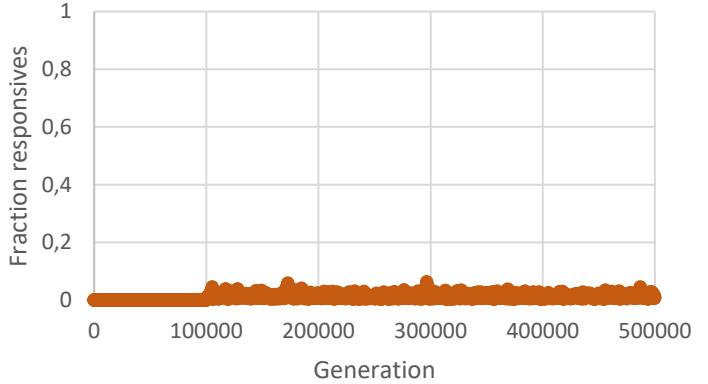
High initial cooperativeness



Low initial cooperativeness



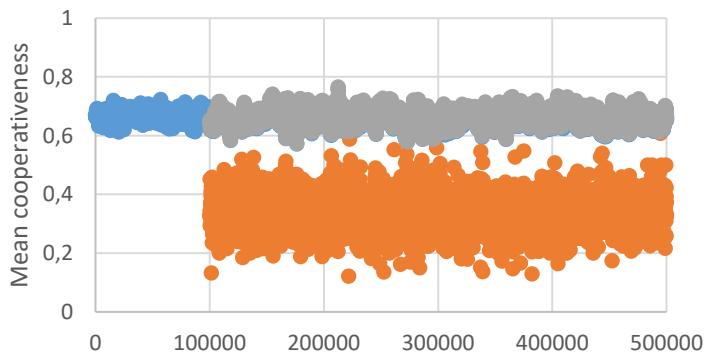
Low initial cooperativeness



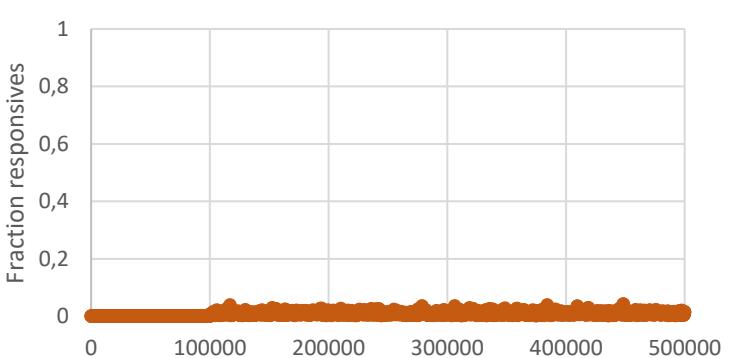
Above shows in high initial cooperativeness an emergence of responsiveness, while in the low initial cooperativeness no responsiveness could occur.

Price for responsiveness: 0.5

Medium initial cooperativeness

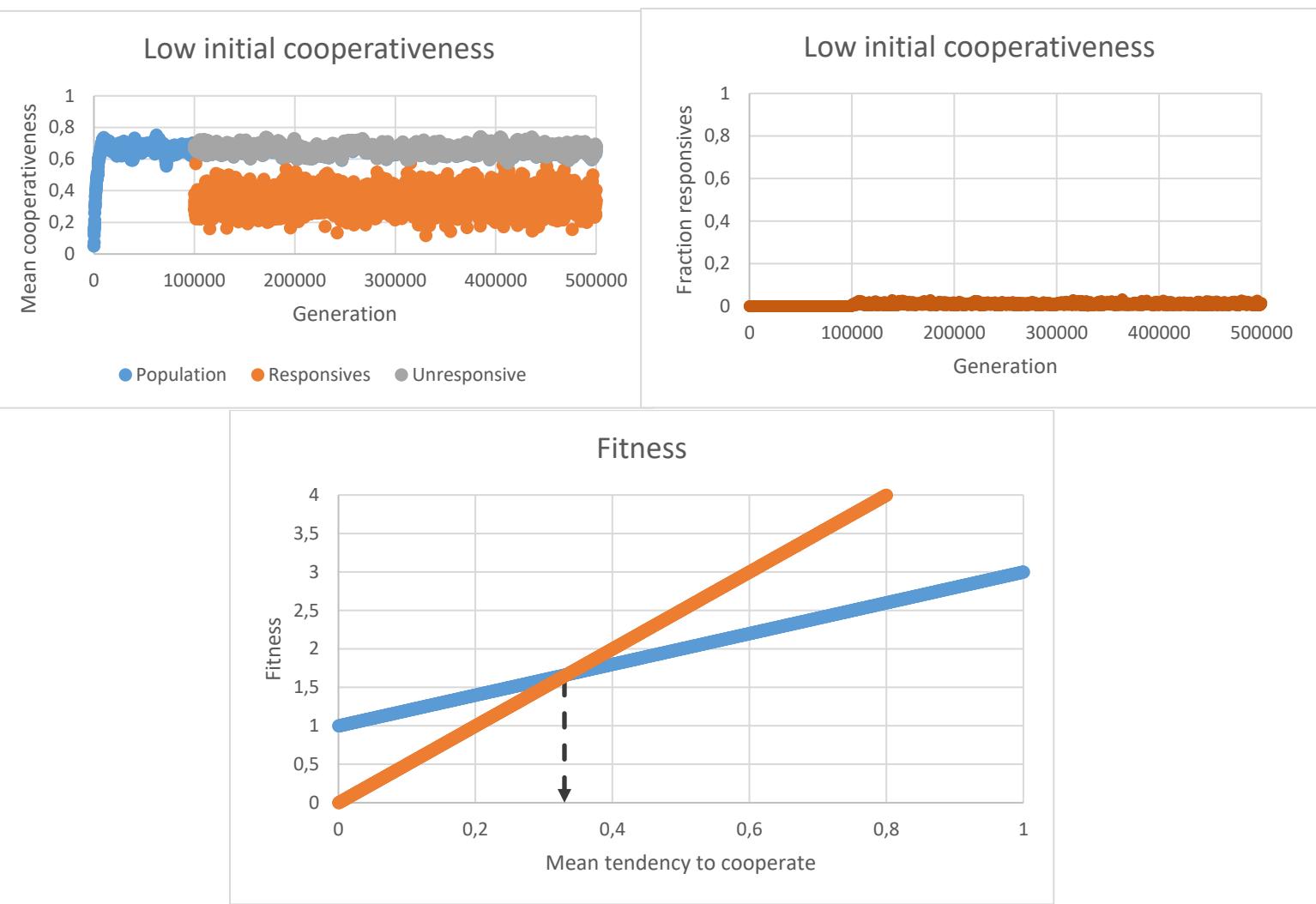


Medium initial cooperativeness



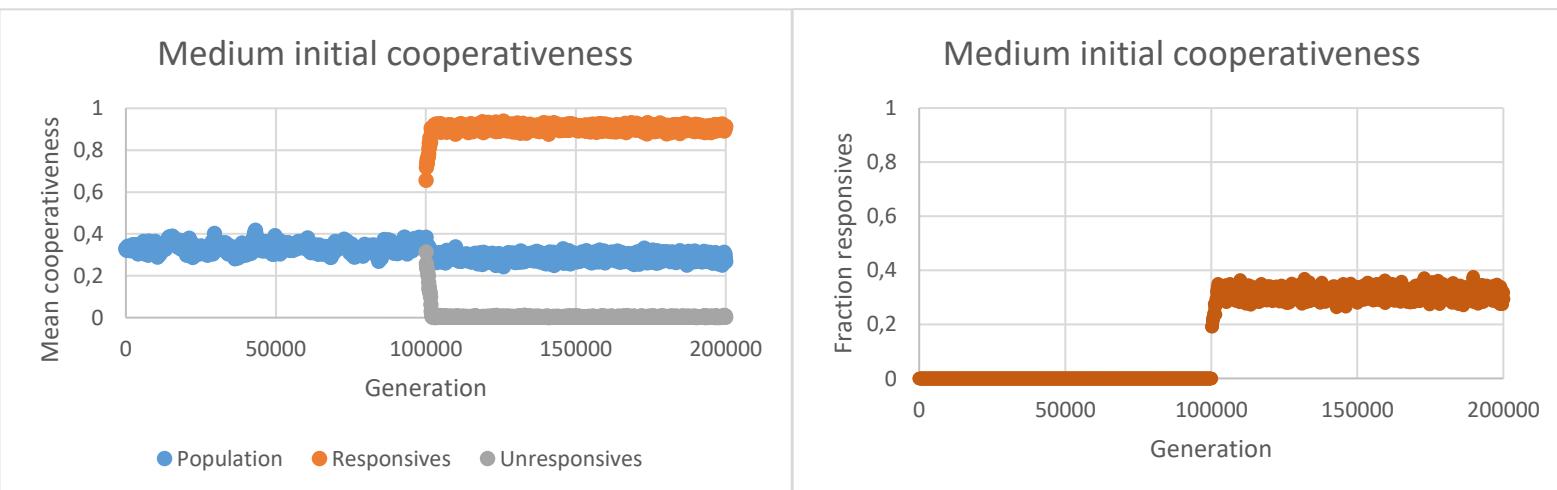
The above graphs show no emerge of responsiveness.

G. Different benefits and costs in snowdrift game



Fitness graph of snowdrift game with benefits = 5, costs = 4.

To see if the dynamics of a snowdrift game change when benefits and costs are different, the equilibrium was changed to 1/3. This was done by calculating the new benefits and costs, 5 and 4 respectively.



The left shows the mean cooperativeness for the average of the population, responsive individuals and unresponsive individuals. The right is the fraction of responsive individuals in the population.

It can be seen that the equilibrium is lower than expected, but that the dynamics qualitatively don't change. Still the unresponsive individuals defect resulting in the fact that the responsive individuals cooperate more. Therefore, changing the benefits and costs doesn't change the game dynamics qualitatively.