

Evolution of Cooperative Behaviour

A Computational Perspective

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Abstract—Several evolutionary theories have been proposed to explain the origin of altruistic and cooperative behaviours. However, these are very broad and complex theories, which also include non-measurable factors. In this project, we tried to empirically prove some of these theories from a computational point of view using genetic algorithms.

Index Terms—GA, Hamilton’s Rule, altruism, cooperation, Green Beard, Selfish Herd.

I. INTRODUCTION

IN this project we decided to investigate the general emergence and selection of social (cooperative and/or altruistic) behaviour from an evolutionary and hereditary point of view simulating several evolutionary dynamics in-silico. Altruism is defined as a behaviour which harms the individual exhibiting it and benefits the recipients. For this reason studying the evolutionary pressure of social traits is not as straightforward as for those traits influencing only the individual fitness. In order to describe the evolutionary dynamics and the impact of the altruistic behaviour a general rule has been devised by W.D. Hamilton¹:

$$rB > C \quad (1)$$

Hamilton’s rule shifts the point of view on natural selection hinting the notion that it favours genetic success rather than reproductive success per se. As a result, the Hamilton’s rule underlies the theory of inclusive fitness in which an organism’s genetic success is generated through cooperation and altruistic behaviour rather than simply from its own genetic heritage. Hamilton’s rule is formulated in very generic terms and, due to this reason, has been target of many criticisms as well as specific contextualization and mathematical derivations [5]. Some of our scenarios were developed using such interpretations and derivations as guidelines. We have implemented simulations considering a generic altruistic action as well as a behaviour specific scenario not strictly explainable using the Hamilton’s rule. In particular we investigated the Selfish Herd theory proposed by Hamilton himself [7].

Moreover, we have to consider and acknowledge that, while our general models support several biological interpretations, they are incapable of capturing the social and environmental components of altruistic behaviour, which exert a huge influence on the latter. In addition, we do not capture complex and still to be fully understood genetic mechanisms as epigenetic regulation in eukaryotes and horizontal gene transfer in bacteria which probably play a very important role [10] [1].

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¹Hamilton’s rule formal definition

II. IMPLEMENTED SCENARIOS

The first natural contextualization of Hamilton’s rule is kinship altruism, which defines relatedness in terms of blood ties. In this formulation the actor exhibits an altruistic behaviour when the recipient of such behaviour is part of the actor’s kin.

Relatedness may also be defined more broadly as any genetic similarity. Many cooperative behaviours may have evolved via common descent or by other mechanisms such as the Green Beard effect [4].

In contrast with the concept of relatedness, cooperative behaviour can also emerge from a selfish action. Specifically, the Selfish Herd theory states that individuals within a population attempt to reduce their predation risk by putting other conspecifics between themselves and predators [7]. Such antipredation behaviour results in aggregations which indeed advantages the whole group.

The source code of all our simulated scenarios can be found at our [GitHub repository](#).

A. Basic kinship

In the beginning we devised a simple simulation to provide a basis for further simulations and to explore the fundamental take home message of the Hamilton’s rule in the kinship domain. For this first simulation, we have encoded the genotype of the agents as a binary number, where 1 codes for altruistic behaviour and 0 for the egoistic one. We then defined a reproductive model which mimics the outcome of sexual reproduction even though we decided to use an haploid set of chromosomes for simplicity. We were able to do so without questioning the applicability of the Hamilton’s rule as the aforementioned mathematical derivations demonstrate that the Hamilton’s rule is not affected by the ploidity and the reproductive model [5]. In our reproductive model two individuals form a couple which will produce three offspring, each of which has a 50% chance of inheriting the genotype of one of the parents. In addition, each offspring has a small chance of being mutated in accordance with biological mutation rates. Our reproductive model is based on complete generational replacement.

The simulation begins with a reproduction cycle to form the first families, and then some of these families are randomly selected to go through a “danger phase”. For each of the chosen families, one member is randomly selected to be the actor, while the others will be the recipients. The actor has the choice to either perform the altruistic action bearing a 95% probability of getting killed but allowing the recipients to survive or to do nothing. In this case, the actor escapes the danger phase unharmed, but the recipients die. Whether the

altruistic action is performed or not depends on the genotype of the actor. It is important to note that this simulated scenario is a competitive environment since we select a limited number of individuals for reproduction at each step. In this simulation the fitness function is not explicitly coded and it is just the survival and reproduction of the agents as in natural selection.

B. Extended kinship

In addition to the not so trivial basic kinship model we decided to experiment different and more complex settings.

1) *Multitrait formulation:* One of the aspects that we deemed very important to investigate is the diffusion of the altruistic allele when it is included in more complex genomes. As a result, we designed a variation of the basic kinship scenario in which the genotype of each individual is composed of a second trait in addition to the social one. The second trait is represented as a real number between 0 and 1 and encoded in the genotype with a binary representation. At the moment of reproduction, the selection of individuals will no longer be random but rather a roulette wheel selection with probability proportional to each individual's fitness. The individual fitness is obtained by passing the number encoded by the second trait into an additional fitness function. The secondary fitness function has two maxima to simulate two ecological niches; the two maxima shift every fixed number of steps to mimic a dynamic evolutionary environment. The second trait can have several biological interpretations, for example it can be considered the result of a polygenic interaction where each gene is a single binary digit in the representation of the trait. In this model the overall fitness function can be seen as a composition of collective fitness which is still implicit and individual fitness which is represented by the secondary fitness function.

2) *Ancestry-Based formulation:* Another way to increase complexity of the scenario was changing the settings of the dangerous phase. In this second version of the extended kinship selection we decided to mix the individuals and create random groups that all undergo the dangerous phase. Within these random groups, the actor, if altruist, decides whether to perform the altruistic action based on common ancestry of the recipient. To do so, we decided to store a genealogy tree as a direct acyclic graph. However, due to computational constraints, only the latest three generations (including the current one) are accessible. Considering the distant kinship negligible in terms of benefit, only siblings and first cousins were included in this simulation. Moreover, we explored two slightly different versions of benefit computation. The benefit in the first variant is exclusively tied to the promotion of a specific genotype in future generations. The second one considers a more loose interpretation where the benefit is computed based on the actor perception of relatives regardless of the genotype.

C. Green Beard

A “green-beard” gene has the property of giving rise to a detectable phenotype which leads the carrier to behave

altruistically toward other carriers of the same phenotype [4]. Starting from the basic kinship model, we explored if and when the Green Beard effect occurs. First, we devised a model resembling the Dawkins’ formulation in which a single gene encodes for both altruism and a marker phenotype. Then, we examined the implications of having two genes, one for the visible trait and one for altruistic behaviour, also considering the possibility that these genes are in linkage equilibrium or disequilibrium [4].

All simulations incorporate a reproductive model in which each couple of agents, sampled from the whole population, gives birth to a random number of children drawn from a specified range.

1) *Dawkins’ formulation:* In addition to previous simulations, the altruistic genotype also encodes for the visible phenotype, therefore a single mutation will simultaneously change both [3]. The bearer of the altruistic gene will act altruistically (with a 95% chance of being killed) only in the presence of another agent carrying the green-beard allele.

2) *Multitrait formulation:* Unlike in Dawkins’ earlier simulation, each agent has two genes with two alleles each. Possible combination of traits are shown in Table I of the Appendix, where columns represent the behaviour gene and rows represent the phenotypic marker.

The altruistic action is performed by agents carrying the altruistic allele in the presence of agents carrying the green-beard one. Different allele associations result in the appearance of “impostors” that have the beard but not the altruistic behaviour, gaining a fitness advantage. In addition, one-point crossover mechanism is included into the reproduction process.

In the first simulation, all genotypes are expressed equally in a linkage equilibrium condition. The alleles in this case are weakly linked in the sense that they can be inherited separately at each reproduction step. Then, under a linkage disequilibrium scenario, only individuals with specified genotypes (beard-altruistic, nonbeard-selfish) are present. The other combinations could only emerge through mutation and cross over.

D. Selfish Herd

In the Selfish Herd theory Hamilton proposed that gregarious behaviour may be considered a form of cover-seeking, in which each individual attempts to reduce its chance of being caught by a predator (selfish behaviour).

We developed a simulation with two kinds of agents: preys and predators. They are both placed on a grid and at each step they can move in neighboring cells. Both agents can see whether there are other individuals within a certain range near them, determined by their sight value. When a predator detects a prey, it will chase it until it is close enough to jump and eat the prey (the jump range is determined by a parameter). Every time a predator catches a prey, it enters the digesting phase, which requires it to remain still for a predetermined amount of steps. The prey’s goal is to survive as long as possible.

Each prey has a real-value genotype in range $[-1, 1]$, corresponding to aggregating or repulsive behaviour, respectively.

Whenever a prey sees other preys in a non-danger situation, it will move towards the herd's center of mass or in the other direction, based on its genotype value. In the presence of a predator, however, all preys will escape, regardless of their genotype.

The number of preys will gradually decrease while the number of predators will remain constant. Once the prey population decreases below a given threshold, they enter the reproduction phase.

III. METHODOLOGIES

Our simulations were built with Mesa [8], a Python agent-based modeling framework. It enables users to build agent-based models with built-in core components, visualize them with a browser-based interface, and evaluate results using Python's data analysis tools. Furthermore, we used two Python graph libraries, Igraph [2] and NetworkX [6], to compute the relatedness of two individuals in the Ancestry Based simulation.

IV. RESULTS AND DISCUSSION

We ran the simulations with the following set of common parameters. N represents the total number of individuals selected as parents at each iteration, r represents the initial ratio of the altruistic allele, mr and dr are mutation rate and death rate respectively.

A. Basic kinship

We ran the basic simulation with the parameters in Table II of Appendix. We set $N = 1000$ to provide a large enough population to partially address the inbreeding problem [5] and small enough to ensure a reasonable computational cost. All the following results were averaged across 20 iterations with the same set of parameters partially ruling out the effect of chance on the outcomes.

We began by running the scenario with $r = 0.5$, in which the altruistic allele took over in the first 300 steps and then reached an equilibrium with the selfish allele (Appendix Fig. 5). The mutation rate, which counteracts the diffusion of the altruistic allele proportional to its frequency in the population, is responsible for this equilibrium; if mutations are not included, the simulation results in the extinction of the selfish allele. Furthermore, we chose to test if, in this favorable circumstance, the competitiveness of the altruistic allele may allow it to take over even if it was not present at all in the original population. With these settings, the altruistic allele can only emerge by mutation simulating the emergence of a new allele through de-novo mutation. It can be seen from Fig. 1 that, in the end, the altruistic allele provides such an advantage that it is still able to reach the same equilibrium as before.

B. Extended kinship

1) *Multitrait*: In the multitrait kinship simulation we used the very same set of parameters of the basic one. We also defined the secondary fitness function, evaluated on the second trait, as:

$$\max \left(e^{-\left(\frac{x-\mu_1}{\sigma}\right)^2}, e^{-\left(\frac{x-\mu_2}{\sigma}\right)^2} \right) \quad (2)$$

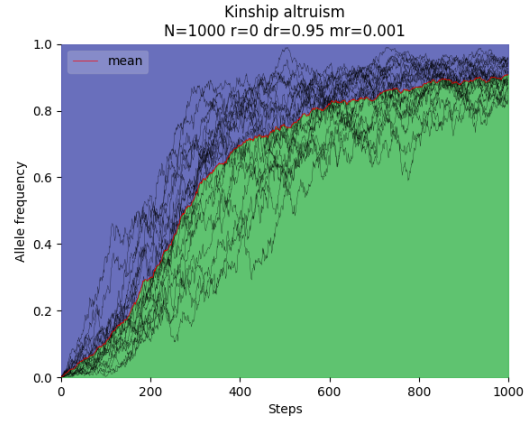


Fig. 1: Results of the basic scenario where altruists can only emerge due to mutation ($r = 0$).

where μ_1 and μ_2 represent the best values for the second trait (x) and indeed correspond to the two peaks in the fitness landscape. σ represents the standard deviation of the modes in the fitness landscape. As mentioned before every 100 steps μ_1 and μ_2 change in order to simulate a dynamic evolutionary environment. We also impose the two means to maintain a minimum distance in order to preserve two distinct niches. The inclusion of the individual component in overall fitness does not interfere with the diffusion of the altruistic allele, as shown in Fig.2. We plotted the mean, maximum, and lowest fitness values at each step to ensure that the individual component actually exerted some evolutionary pressure on the population. As seen in Appendix Fig.6, following the initial drop caused by the shift in the fitness landscape, the population's mean fitness increases, showing that there is evolutionary pressure.

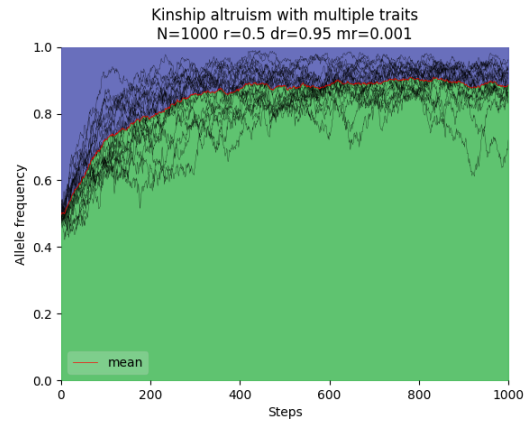


Fig. 2: Results of the kinship scenario with selection over multiple traits.

2) *Ancestry-Based formulation*: We ran the Ancestry-Based scenario with several sets of parameters, including the number of generated offspring and recipients. However, we discovered that such a configuration may result in the altruistic benefit only under certain unrealistic conditions. Let us assume a infinitely large population and just first order relationships.

In this case the average benefit of the altruistic actor would be

$$avg(B) = 0.5 \times n_{recipients} \times \frac{1}{n_{families}} \quad (3)$$

which is the probability of two individuals sharing the same genotype, given the fact that they are siblings (0.5), times the chance of having a sibling among the recipients ($n_{recipients} \times \frac{1}{n_{families}}$).

It can be clearly seen that $avg(B) > 1$ can be obtained only when the number families is lower than the number of recipients. Having a small number of families results in a very small scale simulation where inbreeding is a major issue. Moreover, increasing the number of recipients results in more unrelated individuals benefiting from the sacrifice of the actor, “washing away” the advantage of the relatives. In our simulation the population is finite, further shrinking the recipients’ probability of belonging to the actor’s family.

Furthermore, the contribution of longer-term relatives to B decreases proportionally to the relatedness between the recipient and the actor, hence plays no major role in this context. To summarize, even if it is mathematically possible to find a set of parameters that results in an advantage for altruists, the simulation would lose all the biological significance. We hypothesize that the “missing brick” in this scenario is the social behaviour of the individuals which should tend to aggregate relatives and thus play a major role in the success of the allele.

C. Green Beard

We evaluated Dawkins’ formulation using the same parameters previously outlined in the kinship model. We observed how the altruism allele frequency emerges over the selfish allele (Appendix Fig. 7). Identical outcomes are obtained by either setting the mutation to zero or allowing the altruistic behaviour to emerge solely through de-novo mutations.

Despite the fact that green-beard genes have been reported [9], the Green Beard effect has been widely criticized since it is unlikely that one gene can code for both altruism and a detectable phenotypic tag. To make our model more biologically plausible, we investigated multitrait theories. We found that if the effect is caused by separate alleles in linkage equilibrium, the impostor genotype overruns the population, while the true-beard decreases in frequency and is eventually lost (Fig. 3a). In contrast, in a linkage disequilibrium condition, true-beard is facilitated through (Fig. 3b).

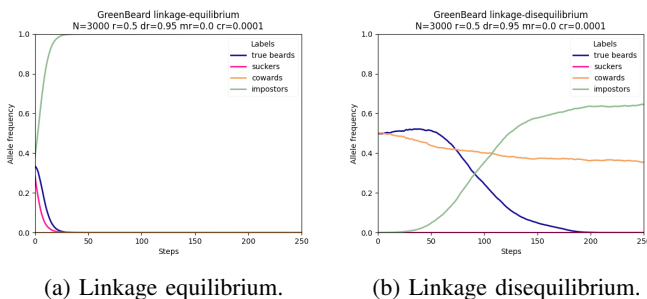


Fig. 3: Results of the Green Beard scenario

We have shown that in some circumstances, a green-beard gene is favoured even when the carriers share no other genes. This might imply that genetic relatedness at the altruism locus, rather than across the entire genome (kinship relatedness), is the most important prerequisite for altruism.

D. Selfish Herd

We attempted to validate the Selfish Herd theory by simulating several scenarios using a grid of 100x100 cells with 200 preys and 15 predators. The simulations were all founded on the premise that predation risk is a fundamental element influencing the agent behaviour. Predation risk is conditioned by the number of predators, the jump range of the predators and the position of the prey with respect to the predator and the other preys. The position of each prey is dependent on its genetically regulated behaviour. Different combinations of parameters (i.e., jump range and number of predators) and therefore different predation risk, result in the selfish gene usually taking over the population. As it can be seen from Fig. 4, the selfish allele frequency within the population increases proportionally to the jump range and the number of predators. As we can see from Appendix Fig 8a, with an high predation risk (high number of predators and high jump range), the diffusion of the selfish allele is around 100%. Differently, we can see in Appendix Fig. 8b that with less predators and smaller jump range, and hence smaller predation risk, the selfish allele diffusion is around 50%.

This demonstrates how preys, located distant from their nearest neighbors, are more vulnerable in dangerous situations than those who are surrounded by neighbors. We have shown how a selfish action can also bring benefit to other preys and therefore results in a form of cooperation.

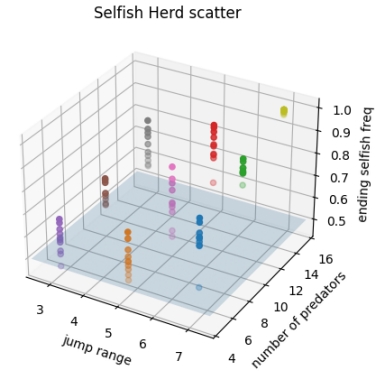


Fig. 4: Results of the Selfish Herd with different combinations of number of predators and jump range.

V. CONCLUSION

In this work, we investigated several evolutionary theories concerning the emergence of cooperative behaviour and their plausibility using biologically meaningful simulations. The most difficult aspect of devising these simulations lies in balancing the scale, detail level and the biological relevance

against computational complexity. We had to make several assumptions which decreased the level of significance but actually made the simulations feasible. Furthermore, it should be noted that we simulated biological theories on which there is no universal consensus in the biology field and are object of debate, highlighting some of the critical points as we did with the Green Beard and Ancestry-Based simulations.

VI. CONTRIBUTIONS

The whole code for this project was developed from scratch by the authors of this report. To be more specific, the workload was split into two parts. The first part, carried out by M.V. Cavicchioli and P. Demurtas, included all the simulations and plots regarding the *Kinship domain* while the second part, carried out by E. Barba and R. Cervesato, dealt with *Green Beard* and *Selfish Herd*. On the other hand, the theoretical work and the analysis behind every simulation were carried out by all the four authors equally.

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APPENDIX A

ADDITIONAL GRAPHS

TABLE I: Possible genotypic combinations for green beard multitrait formulation

	selfish (0)	altruist (1)
beardless (0)	coward	sucker
green-beard (1)	impostor	true-beard

TABLE II: Basic parameters of kinship altruism

N	r	mr	dr
1000	0.5	0.001	0.95

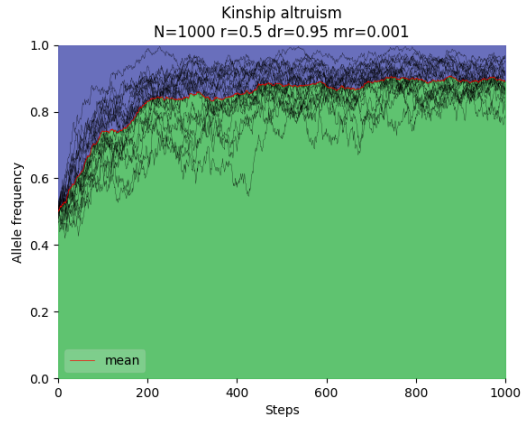


Fig. 5: Results of the basic scenario with equal starting allele frequencies.

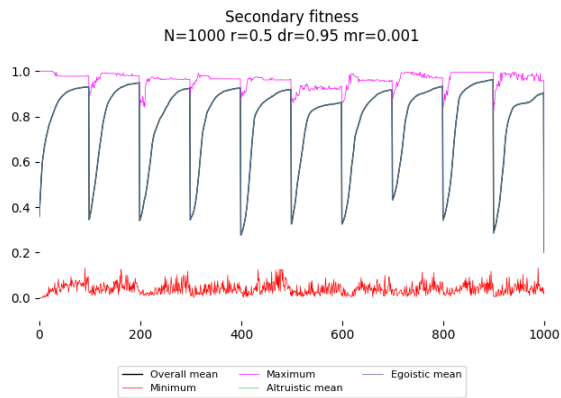


Fig. 6: Second trait fitness value in a dynamic landscape.

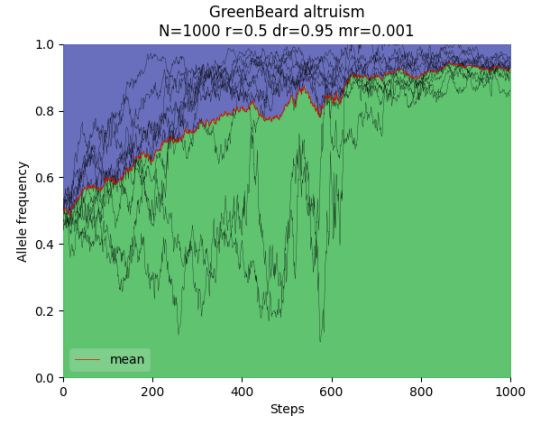
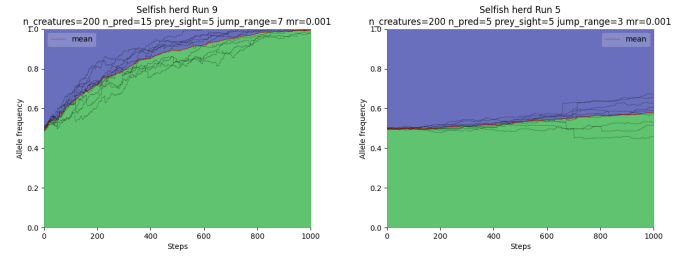


Fig. 7: Results of the Green Beard basic scenario with equal starting allele frequencies.



(a) High predation risk. (b) Low predation risk.

Fig. 8: Results of the Selfish Herd scenario