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Computational models for the study of sexual selection dynamics

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"Because the history of evolution is that life escapes all barriers. Life breaks free. Life expands to new territories. Painfully, perhaps even dangerously. But life finds a way." - Michael Crichton, Jurassic Park

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ABSTRACT

Evolutionary dynamics have received extensive speculative treatment, notably by Lamarck and Darwin in the eighteenth and nineteenth century and more recently by Dawkins. Although their developments work primarily in the argumentative realm, sometimes overlooking mathematical formalities, their outcome was nothing short of extraordinary, being capable of tackling millenarian notions about the origin and the meaning of life. The science of evolution, however, has been approached from a myriad of researchers, some of them willing to provide consistent mathematical models fitting our intuitive grasps of biological diversity and natural selection. Two notable examples are Fisher and Hamilton, who, through rigorous mathematical treatment, were able to solve evolutionary problems who puzzled Darwin himself - notably kin selection and the Fisherian runaway. This evidence is suggestive of the fact that wit and reasoning alone are not enough to provide us a clear understanding of evolution: formalisms play a comparable role. Concerning evolution, our belief is that a next step can be taken, beyond mathematical treatment: we believe that computational simulations have the power to grant us a grasp on evolutionary dynamics that enables them to act as a substitute to field research. Because of that, in this work we developed computational models to experiment with hypothesis in evolutionary biology and analysed their results. In particular, we found an equilibrium between kin selection and asexuality, the emergence of fractal behaviour from the reversal of kin selection dynamics, the display of Fisherian runaways in experiments with sexual selection and even the potential for boosting the performance of genetic algorithms for optimization problems through the addition of a new, sexual selection phase.

Modelos computacionais para o estudo de dinâmicas de seleção sexual

RESUMO

Dinâmicas evolucionárias receberam extensivo tratamento especulativo, notavelmente por Lamarck e Darwin nos séculos dezoito e dezenove e mais recentemente por Dawkins. Ainda que suas explorações trabalhem essencialmente na esfera argumentativa, algumas vezes dando pouca importância para formalidades matemáticas, os seus resultados não foram nada menos do que extraordinários, sendo capazes de tombar noções milenares sobre a origem e sobre o sentido da vida. A ciência da evolução, entretanto, tem sido abordada por uma miríade de pesquisadores, alguns deles dispostos a providenciar modelos matemáticos consistentes e representativos da nossa noção intuitiva de diversidade biológica e seleção natural. Dois exemplos notáveis são Fisher e Hamilton, os quais, através de rigoroso tratamento matemático, foram capazes de resolver problemas evolucionários que intrigaram mesmo Darwin - notavelmente *kin selection* e a *Fisherian runaway*. Essa evidência é sugestiva do fato de que intelecto e raciocínio, apenas, não são suficientes para nos prover um entendimento transparente de evolução: formalismos desempenham um papel semelhante. No que diz respeito à evolução, nossa crença é de que um próximo passo pode ser tomado, além do tratamento matemático: acreditamos que simulações de computador têm o poder de nos conceder um vislumbre de dinâmicas evolucionárias que os capacita para agir como substitutos para a pesquisa de campo. Em função disso, nesse trabalho nós desenvolvemos modelos computacionais para experimentar hipóteses de biologia evolucionária e analisar os seus resultados. Em particular, descobrimos um equilíbrio entre *kin selection* e assexualidade, a emergência de comportamento fractal a partir da reversão de dinâmicas de *kin selection*, a revelação de *Fisherian runaways* em experimentos com seleção sexual e até mesmo o potencial para melhorar o desempenho de algoritmos genéticos para problemas de otimização a partir da adição de uma nova fase de seleção sexual.

Palavras-chave: dinâmicas evolucionárias, kin selection, assexualidade, homosexualidade, seleção sexual, algoritmos genéticos, otimização.

1 INTRODUCTION

1.1 Motivation

The mathematical and computational treatment of population dynamics has been studied, at least, since Thomas Malthus MALTHUS (1798). For the economist, the growth of a population should be modelled as an exponential function of time. Another early and significant contribution to population dynamics were the Lotka-Volterra equations LOTKA (1920) VOLTERRA (1926) LOTKA (1910), which modelled predator-prey dynamics as pairs of differential equations concerning the functions of populational growth of each one of the populations (predators and preys).

Ronald Fisher's work was essential to the study of evolutionary and specifically sexual selection dynamics. The concept of *Fisherian runaway* FISHER (1930), for example, is an explanation for the phenomenon in which some species show sexually dimorphic traits - traits exclusive to a single gender - that don't directly enhance individual fitness. A popular example is that of the peacock's tail, a feature that demands generous amounts of energy for its synthesis and additionally impairs the bird's locomotion, making it an easier and more probable prey. This traits, according with fisher, are the result of a process of sexual selection in which a small, pre-existing female preference for the trait (in this particular case, the female preference is for flamboyant tails) has the effect of making it desirable for males to possess that trait. But since flamboyant feathered males are more likely to pass their genes forward, it becomes desirable for females to select them. As a result, female's preferences and male's reproductive success have crossed effects on each other.

The evolutionary process also encompasses the altruism-egoism dichotomy. A gene-centered view of evolution equalizes evolutionary success to the capacity a gene has of maximizing the number of copies of itself in the population. In this sense, a host's gene may benefit similarly from promoting the reproductive success of a close relative comparatively with promoting its own. This line of reasoning yields the concept of *inclusive fitness* and serves as a biological explanation for the phenomenon of altruism between individuals. W.D. Hamilton captured mathematically the conditions on which altruistic behaviour is evolutionarily beneficial in an inequality now known as Hamilton's rule HAMILTON (1964a) HAMILTON (1964b). Richard Dawkins discusses a gene-centered view of evolution and the altruism-egoism dichotomy in his famous work The Selfish Gene DAWKINS (2006).

The computational model of the *genetic algorithm* proposed by HOLLAND (1975) has been used primarily as a search heuristic for solving optimization problems. Even

so, it can be argued that it is useful in investigative approaches to testing evolutionary hypothesis. For example, BECK et al. (2002) developed a virtual environment through genetic algorithms in which the objective function was calculated not by the environment but instead by each female, with each female encoding a particular set of selection criteria in their DNA - thus replacing *natural selection* for *sexual selection*. This environment was used to study implications in the sexual selection process of advanced ages in male populations.

Game theory, although it has not emerged from the study of population dynamics, has proved itself an important tool for understanding the evolutionary theory. The basis for game theory were developed by NEUMANN (1928) NEUMANN; MORGENSTERN (1953), but it was through the work of SMITH (1982a) that was developed the field of evolutionary game theory, in which the concept of *evolutionary stable strategy* is a specialization of the classical game theory concept of *Nash equilibrium* NASH (1950) and can be used to determine in which conditions a small mutation within a population will be able to take over the entire population.

The basis provided by the before mentioned formalisms has been shown to transcend the theoretical realm, enabling the development of a variety of technologies that build upon the concept of natural selection. The tools provided by our formal understanding of how evolution works are particularly valuable to the field of robotics and artificial intelligence, as we can mimic natural evolutionary processes in order to train computer programs to behave cleverly. A notable example is a 2014 study that evolves soft robots through a penalty function that takes under consideration the efficiency of their locomotion CHENEY et al. (2014). The resulting robots exhibit features strikingly analogous to those found in organic creatures, such as teeth, feet and bones. The fact that a theoretical understanding of evolutionary processes is useful to the development of real-world technologies is reason enough to accept the relevance of researching them.

Historically, genetic algorithms have been used successfully and extensively in the resolution of optimization problems. Nevertheless, their potential as a tool for the theoretical study of evolutionary dynamics has been, until now, limited. We can argue that a better understanding of the underlying dynamics of evolutionary meta-heuristics can guide the state of art in genetic algorithms in a positive direction, in addition to advance the field of theoretical evolutionary biology. In short, the computational study of evolutionary dynamics has not only theoretical motivations in biology but also pragmatical motivations in combinatorial optimization. The main advantage of choosing computer models over field research for studying evolutionary dynamics is that we can benefit from the abstraction inherent to computer programs as well as the processing power of a computer to accelerate the simulated evolutionary process in order to capture a far greater window of evolution than we would be able to capture from observation alone.

1.2 Goals

As a fundamental point, we believe that computer models can be used to approach the theoretical study of evolutionary dynamics. This work's primary goal is to verify that belief, but we also intend to investigate a set of selected hypotheses about evolutionary dynamics (to be detailed below) and apply sexual selection dynamics to state-of-art techniques for solving combinatorial optimization problems.

1.2.1   Kin selection, Homosexuality and the gay uncle hypothesis

There is no general consensus about the causes for homosexuality, but it is believed that genetics has at least some influence on the sexual orientation of an individual. According to The American Academy of Pediatrics,

"Sexual orientation probably is not determined by any one factor but by a combination of genetic, hormonal, and environmental influences. In recent decades, biologically based theories have been favored by experts. [...] Although there continues to be controversy and uncertainty as to the genesis of the variety of human sexual orientations, there is no scientific evidence that abnormal parenting, sexual abuse, or other adverse life events influence sexual orientation. Current knowledge suggests that sexual orientation is usually established during early childhood." FRANKOWSKI (2004)

Homosexuality being a characteristic of partial or integral genetic origin, it is natural to ask ourselves how come that the genes responsible for homosexual behaviour were not filtered out by the evolutionary process, given that homosexual individuals are unable to pass their genes forward. Several hypothesis have been proposed to explain this apparent "Darwinian paradox".

One possible explanation is that homosexuality can be at the same time detrimental to a particular gender and beneficial to the other. For example, it has been verified that female relatives of homosexual males have more children than female relatives of heterosexual males. As a consequence, we have the result that male homosexuality, although detrimental to males, can be beneficial to females CAMPERIO CIANI; CERMELLI; ZANZOTTO (2008).

The theories of inclusive fitness and kin selection provide a powerful framework in which the evolutionary benefits of homosexual behaviour can be discussed. The concept of inclusive fitness is that fitness should be measured not only at the individual level but at the level of the set of its close relatives. In this sense, kin selection is the evolutionary strategy of favouring the reproductive success of an individual's relatives, at the cost of the own individual. Following the idea of kin selection, another genetic explanation for homosexuality is that, although detrimental from the individual point of view, homosexuality can be beneficial from a gene-centered view of evolution. An homosexual individual is effectively incapable of passing its genes to the next generation, but that does not mean that homosexual genes cannot be propagated by other individuals, in particular those who are closely related to homosexual ones.

Through the light of kin selection and inclusive fitness, it would be beneficial for an heterosexual organism to have an homosexual one in the family to care for its children, in the absence of children of its own. It could be argued that families with homosexual individuals would have better chances of prospering, given that their children would have better care. As a consequence, heterosexual individuals that are closely related to homosexual ones would spread their genes better in the population than heterosexual individuals without this relationship, and the genetic package associated with homosexuality would be preserved in the population: this hypothesis is known as the "gay uncle hypothesis". And true enough, experimental results have verified that homosexual men are more likely to channel resources to family members than heterosexual men BOBROW; BAILEY (2001). More importantly, studies involving the familiar structure of meerkats have found that dominant individuals enforce the nursing of their offspring by subordinate

ones. Breeding is a luxury granted only to dominant meerkats, and while breeding pairs of dominant meerkats are weakly related, it has been observed that subordinates tend to nurse the offspring of dominants closely related to them GRIFFIN (2003).

We will develop a genetic algorithm environment to test the gay uncle hypothesis through additions to the original model intended to render it possible for children to be nourished by parents and close homosexual relatives. We will track the incidence in the population of alleles related with homosexual behaviour throughout the time and analyse our results through the lens of Hamilton's law HAMILTON (1964a) HAMILTON (1964b). As much as our experimentation with this hypothesis is intended to justify the employment of genetic algorithms in theoretical biology, it has the additional purpose of studying the intricacies of kin selection in evolutionary dynamics. The resulting conclusions may be able to guide forward the state-of-art of typical genetic algorithms.

1.2.2 Sexual selection, Fisherian runaway and the Sexy son hypothesis

It was hypothesized by FISHER (1930) that, when regarding sexual selection, the female's optimal choice is the male who will produce the *male* offspring with the best chance of reproductive success. What this means is that all other characteristics of a male partner, including its caregiver potential, value of its territory or nuptial gifts should be irrelevant in the sexual selection process. This hypothesis is known as the "Sexy son hypothesis".

Another idea proposed by Fisher was that of the *Fisherian runaway*: a cascade of entangled inter-sexual preferences that ultimately has the result of making organisms evolve characteristics of neutral or even detrimental value to those organisms' fitnesses FISHER (1930). The concept of the Fisherian runaway notably solves the puzzle encountered by Darwin when studying the plumage of the male peacock, whose benefits to one's survival are non-existent and whose development costs its carrier a considerable amount of energy that could otherwise be channelled to other concerns.

At first look, the value of sexual selection as an evolutionary tool may seem restricted - after all, the Fisherian runaway has the potential to vastly reduce the fitness of entire populations. But the fact that sexual selection has accompanied evolution on earth for billions of years BUTTERFIELD (2000) is suggestive of the fact that its benefits overcome its harms. And true enough, it is believed that the existence of two separate sexes is a mechanism to encourage sexual selection dynamics: a recent study found that the resilience provided to organisms via sexual selection is great enough to justify nature's efforts to sustain it LUMLEY et al. (2015). Not only that, but a number of studies have found that humans perceive differently the body odour of potential mates according to the discrepancies in their immune systems: they will perceive as most attractive the body odour of mates with immune systems most different to theirs, as this configuration will enforce the development of a particularly resistant offspring, immunity wise SINGH; BRONSTAD (2001) BUTTERFIELD (2000).

Because of the enormous value of sexual selection to natural evolution, we can conjecture that it can provide valuable insights to advance the state-of-art in genetic algorithms for solving optimization problems.

A very important stage for every genetic algorithm is the selection stage, in which agents are selected in accordance with their fitness in a way that ideally should render it

possible for the population to find the global optimum in the search space. The concept of sexual selection, borrowed from biology, can help us design new kinds of selection stages, possibly more efficient than the classical proportional selection, tournament selection and rank-based selection. In fact, GOH; LIM; RODRIGUES (2003) developed a genetic algorithm in which sexual selection is used to avoid premature convergence of the population, by making the selection of females handle the exploration of the search space and the selection of males handle the exploitation of the search space.

We can conjecture that a powerful modelling of sexual selection may be able to render genetic algorithms more efficient, because the evolution of the agents' sexual preference functions may be responsible for accelerating the convergence process: the environment will not only select the fittest agents for reproduction, but the agents themselves will be allowed to select the fittest partners for their own breeding. This way, at the same time that the population will learn which agents are the fittest, the agents themselves will learn how to create the best possible offspring, by mating with the most appropriate partners.

We will develop selection techniques borrowing inspiration from sexual selection and test them on genetic algorithms. Our results will be analysed in comparison with typical genetic algorithms, employing only natural selection.

1.3 Contribution

Our contributions will range from theoretical biology to combinatorial optimization, intersecting the interdisciplinary field of evolutionary dynamics. It is important to note that the contributions to computer science are not restricted to our results concerning optimization: the relevance of every single theoretical biology result we may find is justified by the fact that we successfully employed computer science techniques to develop them. Because none of our conclusions will be the product of field research, we can safely argue that the entirety of this work is intersected by computer science.

From a theoretical standpoint, our contributions will not only provide models and algorithms, but also the tools for analysing the results emergent from them. Because the scientific literature is scarce in this field, our experience and difficulty interpreting the results from our simulations will, we believe, be of fundamental value to the next generation of researchers venturing into works similar to ours.

From a pragmatical standpoint, our contributions will provide new results in combinatorial optimization, particularly with respect to the employment of kin selection and sexual selection to enhance the performance of genetic algorithms. Where we cannot compete with the state-of-art in genetic algorithms, we will point in the directions we think future works should look to in order to develop competitive models, always arguing why we think they have innovative potential.

1.4 Structure of this work

This work is divided in five chapters. The first chapter, in which this section lies, is responsible for detailing the motivation, the goals and the contribution of this work, while also introducing the fundamental concepts necessary to understand it on a superficial basis. The second chapter explains in great detail the underlying concepts behind the

models employed in our research. The goal of the second chapter is to provide the reader with all the necessary basis for understanding our work from the computer science, game theory and biological standpoints. For this reason, it is the longest of all chapters in this monograph. The third chapter is concerned with the methodology behind our models and simulations. Its goal is to summarize the coding of our simulation programs in the richest and most compact fashion, pruning unnecessary implementation techniques and focusing on the core of our models. The fourth chapter details all of our simulations as well as their results, our analysis, hypothesis and explanations. The fifth chapter discusses our conclusions about the models we developed, the results we found, the tools we created for analysing them as well as our successes, failures and planned directions for future works.

2 CONCEPTUAL BASIS

2.1 Evolutionary theory

2.1.1 Natural selection

Although the idea of different species descending from one another dates back to pre-Socratic philosophy, until the 19th century the main view among thinkers was that the organization of species obeyed a predetermined divine order. This view was shared by a variety of philosophers and scientists from Aristotle to Carolus Linnaeus. Although a number of personalities in his time such as Maupertuis, Buffon and his own grandfather Erasmus Darwin were responsible for significant steps in the understanding of evolution, the first extensive and detailed argument in favour of modern evolutionary theory was due to Charles Darwin and his work *On the Origin of Species* DARWIN (1872).

In his famous work, Darwin discusses selective breeding and its potential to create variation within a species by the means of different breeds being generated. He contrasts this idea of *artificial* selection with the idea of *natural* selection, in which not a breeder but the environment itself selects which individuals will thrive and which won't. Although Darwin didn't know about genetics, he acknowledged that some traits were inheritable and thus subject to the evolutionary process: logically, traits that impair the success of an individual will be absent in some generations time because the individuals who carry them will have smaller probability to pass their characteristics to their children compared to the ones who don't. Darwin suggested that natural selection is the fundamental mechanism responsible for the creation of new species, in a similar way that artificial selection is responsible for the creation of new breeds within a species.

2.1.2 Sexual selection

Although satisfied with natural selection as an explanation for the origin of species, Darwin was puzzled by the existence of sexual dimorphism and especially by sexually dimorphic traits that don't necessarily enhance an individual fitness. He proposed the concept of *sexual* selection as an explanation for these traits, arguing that working in parallel with natural selection there is another force of selection that acts from inside the minds of sexually active individuals and is responsible for selecting with which partners these individuals will mate. According to Darwin, these individuals choose their mates using an attractiveness judgement that is aesthetic in appearance but actually an heuristic in its essence, working to select the best partners by looking at hints in their phenotype.

Sexual selection, Darwin noted, worked primarily on the female's side: it was the females who spent most time analysing their potential mates in order to choose a partner, while males usually tried to maximize their reproductive success by mating with various females. A possible explanation for this dichotomy of sexual strategies is that females, being the ones who gestate and bear the children, can't afford the luxury of parallelizing their mates, because the expenditure of each impregnation is theirs. It is thus in a female's best interest to choose the fittest mates in order to maximize their reproductive success without also maximizing their gestational expenditure. This explanation is very similar to the principle known as Bateman's principle BATEMAN (1948).

Examples of unusual traits that are elegantly explained by reasoning about sexual selection are abundant in nature. Giraffes, for instance, are noted for their long necks, which can be up to 2 meters. Paradoxically, even though Giraffes can reach 6 meters in overall height, they typically feed at 2 meters above the ground LEUTHOLD; LEUTHOLD (1972). As a result, the general idea that giraffes evolved long necks in response to the environmental incentive of reaching tall leaves is incapable of explaining the reason behind those extra 4 meters. Sexual selection, on the other hand, offers a valuable hypothesis: as male giraffes typically neck other males to exhibit dominance, long-necked males may have been positively selected by females, giving rise to a process of elongation of the average neck size within the species.

2.1.2.1 Intersexual selection

Bateman's principle suggests that *the gender which invests the most in producing offspring becomes a limiting resource over which the other gender will compete* BATEMAN (1948). Females are typically associated with the gender which invests most in producing offspring, and as a result this competition gives rise to the phenomenon of intersexual selection, in which males compete to be chosen by females. They don't compete directly, though. This competition is established indirectly from the moment in which males develop ornamented features to try and get the attention of females as high quality mates. Examples of sexual ornaments are abundant in nature and particularly in bird species.

2.1.2.2 Intrasexual selection

Intrasexual selection differs from intersexual selection because it prompts a direct competition for females. When we talk about intrasexual selection, we are not talking about ornamented features intended to raise female preference, but about the strategy of fighting to death in order to become the only available mate and thus nullify female's selection criteria.

2.1.3 Fisherian runaway

Ronald Fisher addressed the paradox of ornamented traits that don't directly enhance the fitness of the individuals who possess them. Simple logic gives us the result that no trait that don't enhance the fitness of its carrier should have an incentive to be preserved by the evolutionary process. Nevertheless, nature is abundant with cases of ornaments that not only are not beneficial but impair their carriers, such as the peacock's tail. Fisher suggested that a small pre-existent sexual preference for a particular trait can give rise to a vicious cycle in which both the trait and the preference itself are boosted in a mutual

recurrence process now called *Fisherian runaway* FISHER (1930). Fisher's reasoning was that a small female preference for a particular trait has the tendency of positively selecting males which possess that trait, enhancing their reproductive success and thus their fitness. On the following generations, females which have this preference will have competitive advantage, because they will mate with carriers of the aforementioned trait and thus give birth to an high-fitness offspring.

Fisher suggested that, because the trait and the preference for the trait evolve in correlated fashion, the rate in which they increase is linear with respect to their own size, and thus exponential with respect to time. Richard Dawkins explained this excessive growth by analysing what happens when a female with a preference for a particular trait copulates with a possessor of this trait. According to Dawkins, their offspring will carry both the gene for the preference and the gene for the trait itself, and after that moment they become linked and therefore evolve obligatorily in correlated fashion DAWKINS (1986).

2.2   Game theory

According to Roger Myerson, game theory is "the study of mathematical models of conflict and cooperation between intelligent rational decision-makers" MYERSON (1997). Game theory approaches strategic decision-making scenarios by representing them in the format of *games*. Games, in this sense, are well-defined mathematical objects: each game is defined by its players, the sets of informations and actions available for each player at each decision point and the payoffs for each possible combination of decisions. Game theorists typically study equilibrium scenarios for games - in other words, assignments of strategies for players in which no player can benefit for unilaterally changing its strategy.

Because of its potential for systematising and solving real-world problems of strategic decision-making, game theory has been successfully applied to a wide range of disciplines. Methods involving game theory are abundant in mathematical economics when studying competing economic agents - phenomena ranging from voting systems to oligopolies can be studied by applying game-theoretic solution concepts. Political science makes use of game theory when dealing with the problems, for example, of fair division or war bargaining. More interestingly, game theory in computer science can serve as a theoretical basis to multi-agent systems or work to solve problems in the study of online algorithms and fault tolerance.

Theoretical biology also owes a great deal to game theory: because the measure of *fitness* discussed in evolutionary theory can be thought as a payoff in a game, a generous amount of biological situations can be explained through game-theoretic lenses. The concept of an *evolutionarily stable strategy* SMITH (1982b) is a biological appropriation of the classical concept of Nash equilibrium NASH (1950): while the second studies strategic decision-making between players of a game, the first studies the evolution of populations in which the players of the game are replaced by the genes responsible for biological strategies. Game theory has also been successfully employed to explain the emergence of animal communication, altruism between biological organisms and as a theoretical basis for the concept of kin selection.

2.2.1 Normal-form games

Games are typically represented in *normal form*. Normal-form games consist of what is called a *payoff matrix*: a matrix in which each dimension is associated with a particular player's possible decisions and whose cells contain the payoffs for all players of the combination of decisions they represent.

Consider for example the prisoner's dilemma: two members of a criminal gang are arrested and are given the options of betraying their partner (defect) or remaining silent (cooperate). If both defect, each gets a 2-year prison sentence. If both cooperate, each gets a 1-year prison sentence. If they take different decisions, the one who decided to cooperate gets a 3-year prison sentence while the other is immediately freed. There is no communication between the prisoners.

		Player 2	
		defect	cooperate
Player 1	defect	2,2	0,3
	cooperate	3,0	1,1

Table 2.1: The prisoner's dilemma in normal form

2.2.1.1 *Mathematical formulation*

- There is a finite set P of players p_i, labeled from 1 to m.

- Each player p_k has a finite set S_i of available pure strategies.

- A pure strategy profile is an m-dimensional vector $\vec{s} = (s_1, s_2, ..., s_m)$ where $\forall i \; s_i \in S_i$ representing an association of strategies to players.

- A payoff function is then a function $F \; : \; S_1 \times S_2 \times ... \times S_m \to \mathbb{R}$.

- A normal-form game is finally a 3-uple $G = \langle P, S, F \rangle$.

2.2.2 Types of games

2.2.2.1 Cooperative / Non-cooperative

A cooperative game is a game in which players can make decisions together, possibly forming coalitions consisting of groups of players. This paradigm contrasts with that of non-cooperative games, in which contracts are impossible and each player is forced to make decisions independently of all others.

2.2.2.2 Symmetric / Asymmetric

A symmetric game is one in which the payoffs are not dependent of which players selected which strategies but only on the strategies themselves. For example, in a symmetric game, if the payoff associated with player 1 choosing A and player 2 choosing B is $(3, 2)$, the payoff associated with player 1 choosing B and player 2 choosing A should be $(2, 3)$.

		Player 2	
		A	B
Player 1	A	2,3	0,0
	B	0,0	2,3

Table 2.2: An example of an asymmetric game

2.2.2.3 Zero-sum / Non-zero-sum

In zero-sum games, the overall sum of the payoffs for each player is zero in all cases. This means that the benefit of some players is contrasted with and compensated by the equal expense of the others. Zero-sum games can be thought as totally competitive games, because there is no margin for cooperation towards a better net result and it is each player's best interest to think only about its own gains. Non-zero-sum games are not restricted to payoffs adding up to zero, and thus provide opportunities for players to cooperate towards a common goal - for example, in the prisoner's dilemma, players can cooperate to reach the best outcome for the group (1,1) instead of maximizing their own benefit by trying to reduce their penalty to 0 at the expenses of their competitor (0,3).

2.2.2.4 Simultaneous / Sequential

Simultaneous games are the ones in which each player's decision is taken at the same time. A popular example is that of the "rock-paper-scissors" hand game: no player knows which gesture the other player will choose before he chooses his own. Sequential games, on the other hand, are defined by a number of ordered steps of decision-making. One pop-

		Player 2	
		defect	cooperate
Player 1	defect	4	3
	cooperate	3	2

Table 2.3: The prisoner's dilemma is an example of a non-zero-sum game. In this table we have in each cell the added payoffs of the combination of strategies associated to it, always different from 0.

ular example is the game of chess, in which the white pieces move first and the game is played in turns in which white piece movements are intercalated with black piece movements and vice-and-versa.

2.2.3 Solution concepts for game theory

In game theory, *solving* a game is the same as predicting how that particular game will be played assuming that its players are rational. In this sense, predictions are called *solutions* and the rules for making these predictions are called *solution concepts*.

2.2.3.1 *Rationalizability*

This solution concept is based on the concept of *strategic dominance*. A strategy A is said to *dominate* another strategy B when choosing A always gives an outcome as good as or better than choosing B. This dominance is said to be *strict* when A always gives a better result than B and *weak* when A gives a better result than B at least once and an result as good as B in all other cases.

The *rationalizable* actions are computed through an iterative process. We start with the complete sets of available actions for each player and remove from them all actions who are strictly dominated by other actions. With these updated sets, we re-evaluate strategic dominance given the new possible actions for each player and once again remove all strictly dominated actions. This re-evaluation followed by removal is repeated until

there are no more remaining strictly dominated actions. The resulting sets of actions are the respective rationalizable actions for each player.

2.2.3.2 *Nash equilibrium*

A Nash equilibrium is an assignment of strategies to players such that no player can benefit from changing her or his strategy if the other players keep theirs. It is, in this sense, a player's *best response* to every other strategy played.

In the prisoner's dilemma, the only Nash equilibrium is when all players choose to defect, because no one can benefit from choosing to cooperate giving that the other player will remain defecting. No other equilibria exist in this particular game because whenever at least one player chooses to cooperate, it is in the other player's best interest to defect.

Games with multiple Nash equilibria exist, though. An example is the coordination game called *the driving game*, in which two cars are driving on the same road on opposing directions and have each to choose to swerve on the left or the right of the road. If both choose opposing sides of the road, collisions are prevented (payoff 0,0). If both choose the same side, collisions will happen (payoff -1,-1). See table 2.4 for more details.

		Player 2	
		left	right
Player 1	left	-1,-1	0,0
	right	0,0	-1,-1

Table 2.4: The driving game: an example of a game with multiple Nash equilibria

2.3 Evolutionary game theory

Evolutionary game theory is the field concerned with applying game theory to biological populations subject to evolutionary dynamics. While classical game theory assumes that the players of a game are rational and focused on their own self-interest, evolutionary game theory assumes that the players' decisions are not motivated by their intellect but instead hard-coded in their genotypes. In this sense, because these players are subject to natural selection, the ones whose genotypes encode rational decisions will be positively selected and thus given some time the population will reflect the behaviour of a rational player in game-theoretic fashion.

Evolutionary game theory is rooted in John Maynard Smith and George Price's work about how biological contests can be thought as strategies and which solution concepts

can be used to predict the outcome of these contests in a biological population SMITH; PRICE (1973). This reasoning was developed in an effort to explain the existence of ritualized animal behaviour in conflict situations - in various cases, animals behave as if they were playing a game-theoretic contest, but these scenarios would require perfect animal rationality according with classical game theory. Evolutionary game theory provides instead a means to explain animal strategies in a purely darwinian fashion, without having to ponder about the consciousness or true rationality of each species.

2.3.1 Replicator equation

The replicator equation is a differential equation used to model the dynamics of different types in a biological population. A *type* here means a particular variation within a species. In this equation, each type is represented by an index $i \in \mathbb{N}$ and its proportion in the population by the variable $x_i \in \mathbb{R}$. $\vec{x} = (x_1, ..., x_n) \in \mathbb{R}^n$ is a vector assembled from each proportion $x_i \: \forall i = 1..n$. Given that the fitness of a particular type is dependent of the proportion of every other type, the domain of each fitness function - one for each type i - is $\mathbb{R}^n$ and the fitness function for the type i is denoted by $f_i(x)$. The differential equation is then $\dot{x}_i = x_i(f_i(x) - \phi(x)) \: \forall i = 1..n$, where $\phi(x)$ is the average fitness of the population and is given by $\phi(x) = \sum_{j=1}^{n} x_j f_j(x)$.

A possible generalization of the replicator equation to incorporate mutation is to denote by Q_{ji} the probability of mutation from type j to type i. The differential equation then becomes $\dot{x}_i = \sum_{j=1}^{n} x_j f_j(x) Q_{ji} - \phi(x) x_i$.

The solution to the replicator equation is linked to the concept of an *evolutionarily stable strategy*, discussed in 2.3.2. Because it serves as a basis for the discussion of evolutionarily stable strategies, the replicator equation is one of the primary population dynamics models behind evolutionary game theory.

2.3.2 Evolutionarily stable strategy

Evolutionary game theory models population dynamics making the assumption that, when dealing with competition for sex and resources, each individual within a population behaves adopting a particular *strategy* which is encoded in its genetic code. The concept of an evolutionarily stable strategy is used to define a strategy that, when adopted by a population, cannot be invaded by a small number of mutant individuals adopting an alternative strategy.

This definition is analogous to that of a Nash equilibrium: in the same way that in a Nash equilibrium no player has any incentive to change strategies given that the other players keep theirs intact, in a population with an evolutionarily stable strategy there is no evolutionary pressure in favour of mutations deviating from the status quo. In truth, the conditions responsible for characterizing an strategy as evolutionarily stable are more rigorous than those associated with a Nash equilibrium: we can't accept individuals of the initial population deviating in favour of strategies of equal benefit to that of the one that is evolutionarily stable, because that would render the population heterogeneous - making it "invadable". Thus, for an strategy to be evolutionarily stable, we need not only an absence of evolutionary pressure in favor of deviations but also evolutionary pressure in its contrariety.

Let $E(X, Y)$ denote the payoff of playing strategy X against strategy Y. For a strategy

A to be a Nash equilibrium, we need to guarantee that, for every other strategy $B \neq A$, $E(A, A) \geq E(B, A)$. For a strategy to be evolutionarily stable, we need to guarantee either $E(A, A) > E(B, A)$ or $(E(A, A) = E(B, A)) \wedge (E(A, B) > E(B, B))$.

Because of the similarities in the definitions of a Nash equilibrium and an evolutionarily stable strategy, they often coincide. But because the last definition is stronger than the former, we have the result that every ESS is also a Nash equilibrium, but not all Nash equilibria are ESS. Indeed, it is easy to find examples of games containing Nash equilibria which are not evolutionarily stable. Consider, for instance, the game in Table 2.5. We have Nash equilibria both in (A,A) and (B,B), but (A,A) is not evolutionarily stable because the unilateral deviations (A,B) and (B,A) keep untouched the payoff for the player which deviated.

		Player 2	
		A	B
Player 1	A	2,2	1,2
	B	2,1	2,2

Table 2.5: An example of game in which not all Nash equilibria are evolutionarily stable strategies

2.3.3 Inclusive fitness

It is intuitive to think about the evolutionary process at the individual level. Intuitively, individuals that are able to survive and last long enough to generate fertile offspring have evolutionary advantage and the population's balance will naturally shift towards them. This reasoning often coincides with what happens in nature, but is also misleading in various situations. An individual-centred view of evolution is incapable of explaining, for example, how altruistic and particularly self-sacrificing behaviours originate, as they are nothing but detrimental to the individual.

An examination of the phenomenon of *kin selection* can provide insight about how altruistic, self-sacrificing strategies may have competitive advantage in the evolutionary process. Kin selection refers to the strategy of favouring the survival and reproductive success of close relatives of an individual, even at the cost of this individual's life. The key point is that, at the same time that this strategy impairs the conservation of the individual's lineage, it helps assuring the conservation of lineages of organisms genetically similar to it. This trade-off is of fundamental relevance and the best strategy will shift towards altruism and egoism depending on the balance between the individual's cost and the potential benefit of preserving other lineages, which depends on the size of the made-possible offspring and it's relatedness with the individual. In fact, there is a famous in-

equality describing the factors necessary for altruism to have a competitive advantage in this trade-off, called Hamilton's rule. This rule will be further discussed in 2.3.4.

The example of kin selection argues against an individual-centred view of evolution and in favor of a gene-centred one. From the perspective of a gene, it is irrelevant whether its carrier will thrive or fail as long as the gene itself is copied and efficiently scattered in the population. In this sense, the classical concept of *fitness* for a single organism is not sufficiently sophisticated to deal with how things work in the evolutionary process: the fitness of an individual programmed to sacrifice its own life in order to save a multiplicity of individuals closely related to it will be low - which is paradoxical, as this individual will be successful in scattering its genes in the population. In short, individual fitness does not always correlate with evolutionary success. What is needed is a new concept capable of generalizing individual fitness in order to deal with close relatives: *inclusive fitness*. Inclusive fitness judges an individual not only by its fitness but also by the fitness of its close relatives, its relationship with them and their possibility of generating fertile offspring.

2.3.4   Hamilton's rule

W.D. Hamilton formulated mathematically the conditions upon which altruism should have evolutionary advantage. More specifically, it predicts when an altruistic, self-sacrificing act towards a relative will have evolutionary advantage from the point of view of the actor's genes. This formulation presents itself in the format of an inequality concerning three variables: C, the cost to the actor; r, the genetic relatedness between the actor and the recipient; and B, the benefit to the recipient. The variables C and B are measured in fitness, i.e., in fecundity counts. Hamilton's rule is as it follows: $C < r \times B$. What it means is that the fecundity disadvantage granted to the actor should be surpassed by the fecundity advantage granted to the recipient, modulated by their relationship. If an actor were to assess a genetically identical copy of itself, we would have $r = 1$ and $C = B$. If an actor were to assess a brother, we would have $r = 0.5$ and $C = 0.5 \times B$. If an actor were to assess a cousin, we would have $r = 0.125$ and $C = 0.125 \times B$. This pattern gave rise to a famous quote by J.B.S Haldane in which he states that he would willingly die for three brothers or nine cousins: assuming that the cost of death is identical to the benefit of surviving ($C = B = 1$) and that $r = 0.5$, we need a multiplier of at least $m = 3$ to make the benefit of saving brothers ($3 \times 0.5 = 1.5$) compensate for the cost of dying (1). With $r = 0.25$, we need a multiplier of $m = 9$, as ($9 \times 0.125 = 1.125$).

2.3.5   The handicap principle

In the subsection about the Fisherian runaway (2.1.3) it was discussed how costly and useless features such as the peacock's tail could have evolutionary purpose. The insinuation was that some features are subject to a particular kind of runaway in which male traits and female preferences cross-reference each other, leading to an increase in both the trait and its preference in the population.

That however may not be the only explanation for the emergence of these traits: the handicap principle is an hypothesis that tries to explain costly traits using concepts from the theory of *honest signals*. In biology, signals are traits (*traits* in this case are not restricted to structures, also encompassing behaviours) whose perception by other organ-

isms benefit the signaller. Signals can be honest or dishonest: for example, although false coral snakes are only midly venomous, their patterns resemble those of the highly venomous coral snakes, in a probable case of *Batesian mimicry* (when harmless species evolve to imitate the warning signals of harmful ones). This is an example of a dishonest signal. The handicap principle is concerned with honest signals, arguing that some organisms may develop costly, useless features in the sole purpose of honestly signalling that they have sufficiently high fitness to produce them. This hypothesis provides a new explanation for the peacock's tail: it is possible that male peacock's are selected for their tails because their tails are honest indicators of their overall fitness.

2.4 Evolutionary computation

Broadly, evolutionary computation can be described as the area concerned with the use of Darwinian principles for automated problem solving. Nevertheless, evolutionary computation is not limited by this definition: it can also refer to computer simulations of evolutionary processes, ranging from evolutionary algorithms to artificial life.

2.4.1 Evolutionary algorithms

Evolutionary algorithms can be described as optimization algorithms in which candidate solutions for the optimization problems are analogous to individuals in a biological population, and as such, they are subject to reproduction, mutation, recombination and selection. The quality of the candidate solutions is measured by a *fitness function* applied to the individuals of the artificial population. It is important to note that *optimization problems*, in this sense, are not restricted to real-valued functions, but may also refer to computer programs, neural networks, learning classifiers, etc.

Having the initial population of candidate solutions being created randomly, the simulation of the biological process is done in 3 major steps, that will be repeated until a stop condition is reached: first, we evaluate the fitness for all individuals (in order to be able to compare them); secondly, we select the individuals of top fitness for reproduction; thirdly, we breed these individuals through crossover and mutation to give birth to offspring; and finally, we replace the previous population (or some part of it) with these new offsprings.

2.4.2 Genetic algorithms

A genetic algorithm is a particular type of evolutionary algorithm in which the candidate solutions are represented by strings in some alphabet - generally number strings. Genetic algorithms are the most popular type of evolutionary algorithms, its utilization spanning from bioinformatics to economics and going through chemistry, mathematics, physics and many other areas.

A genetic algorithm is typically an iterative process, ending when a particular terminating condition is met, comprised of two main phases: selection and reproduction. The general framework for a genetic algorithm is presented in Algorithm 1, but the particularities of each phase will be further discussed.

Data: an optimization problem
Result: a (probably but not provably) good solution
create initial population randomly;
while *termination condition not met* **do**
 evaluate the fitness of the population;
 select the best (fitness-wise) individuals for reproduction;
 generate new individuals (offspring) using crossover and mutation;
 replace the worst individuals of the previous population by the best new individuals;
end

Algoritmo 1: General framework for a genetic algorithm

2.4.3 Selection in genetic algorithms

The key point of the selection phase consists on the evaluation of the fitness function. The fitness function is an injection $fitness : S \to \mathbb{R}$ from the set S of candidate solutions to $\mathbb{R}$, and it should be evaluated for every individual in the population in order for it to be possible to compare them.

The fitness being calculated, there is a variety of types of selection that may be employed to collect individuals for the mate pool.

2.4.3.1 Roulette Wheel Selection (RWS)

This type of selection assigns to each individual a probability of being selected that correlates with its fitness.

Each agent i is assigned a probability $p(i) = \frac{f(i)}{\sum_{j=1}^{n} f(j)}$, a fraction that represents the proportion the individual fitness has in the overall sum of all fitnesses. It is easy to see that all probabilities add up to one, as

$$\sum_{i=1}^{n} p(i) = \tag{2.1}$$

$$\sum_{i=1}^{n} \frac{f(i)}{\sum_{j=1}^{n} f(j)} = \tag{2.2}$$

$$\frac{\sum_{i=1}^{n} f(i)}{\sum_{j=1}^{n} f(j)} = 1 \tag{2.3}$$

2.4.3.2 Stochastic Universal Sampling (SUS)

This type of selection attempts to improve the poor performance of selection methods such as the roulette wheel selection, that is impaired by few members of the population having very large fitness comparatively to others.

SUS works by creating the standard roulette wheel of RWS and "spinning" it - choosing a point of the roulette wheel at random. We then proceed to taking a given number (the number of individuals to be selected) of equally spaced steps and selecting the appropriate individual in each step. In short, while RWS works by spinning the roulette N times

and selecting an individual each time, SUS works by spinning the roulette one single time and using this result as a starting point to select N individuals by traversing the wheel and stopping at N evenly spaced points (see Algorithm 2).

Data: a set of candidate solutions representing the newest generation
Result: a selection from the given set representing the next generation's mate pool
calculate $\bar{f} = \sum_{i=1}^{n} f(i)$;
select $\alpha \in [0, \bar{f}]$ at random;
initialize current point in the roulette wheel $cp = \alpha$;
initialize $sum = 0$;
initialize $k = 1$;
calculate the step size $ss = \frac{\bar{f}}{n}$;
while $k < n$ **do**
    if $cp < sum$ **then**
        select the k_{th} individual;
        update the current point $cp = cp + ss$;
    else
        update $k = k + 1$;
        update $sum = sum + f(k)$;
    end
end

    Algoritmo 2: pseudo-code for the Stochastic Universal Selection method

2.4.3.3 Linear Rank Selection (LRS)

This type of selection uses information about the ranking of the individuals instead of their fitness. In order to do that, we rank all individuals in ascending order according to their fitnesses: the first-ranked individual has the lowest fitness while the last-ranked one has the highest. We then assign to each agent i a selection probability $p(i)$ (see equation 2.4).

$$p(i) = \frac{2 \times rank(i)}{n(n+1)} \tag{2.4}$$

We can see that all the probabilities add up to one, as

$$\sum_{i=1}^{n} p(i) = \tag{2.5}$$

$$\sum_{i=1}^{n} \frac{2 \times rank(i)}{n(n+1)} = \tag{2.6}$$

$$\frac{\sum_{i=1}^{n} 2 \times rank(i)}{n(n+1)} = \tag{2.7}$$

$$\frac{\sum_{j=1}^{n} 2j}{n(n+1)} = \tag{2.8}$$

$$\frac{2\sum_{j=1}^{n} j}{n(n+1)} = \tag{2.9}$$

$$\frac{2\frac{n(n+1)}{2}}{n(n+1)} = \tag{2.10}$$

$$\frac{n(n+1)}{n(n+1)} = 1 \tag{2.11}$$

2.4.3.4 Exponential Rank Selection (ERS)

This type of selection is a variation of the LRS that uses exponential - not linear - weighting on the calculation of probabilities. Once again we rank the highest fitness individuals with the last ranks and the lowest fitness individuals with the first ranks. We then assign to each agent i a probability $p(i)$ (see equation 2.12):

$$p(i) = \frac{c^{rank(i)}}{\sum_{j=1}^{n} c^j} \tag{2.12}$$

We can see that all the probabilities add up to one, as

$$\sum_{i=1}^{n} p(i) = \tag{2.13}$$

$$\sum_{i=1}^{n} \frac{c^{rank(i)}}{\sum_{j=1}^{n} c^j} = \tag{2.14}$$

$$\frac{\sum_{i=1}^{n} c^{rank(i)}}{\sum_{j=1}^{n} c^j} = \tag{2.15}$$

$$\frac{\sum_{i=1}^{n} c^i}{\sum_{j=1}^{n} c^{n-j}} = 1 \tag{2.16}$$

While LRS guarantees a probability difference between two agents that linearly correlates with the difference between their ranks, ERS guarantees an exponentially correlated difference in the same case. What this means is that for $c > 1$, we have probabilities that depart from each other way faster than in LRS. The parameter c regulates how fast this departure will be.

2.4.3.5 Tournament Selection (TOS)

Tournament Selection works by randomly selecting a set of k individuals and selecting the fittest individual from then, which will be added to the mate pool. This process is repeated n times, where n is the size of the mate pool (see Algorithm 3).

Data: a set of candidate solutions representing the newest generation
Result: a selection from the given set representing the next generation's mate pool
for $i = 1..n$ **do**
> randomly select a set S of k individuals;
> add the fittest individual $\in S$ to the mate pool;

end

Algoritmo 3: pseudo-code for the Torunament Selection method

2.4.3.6 Truncation Selection

Truncation selection works by selecting an arbitrary proportion $p \in [0, 1]$ of the population. This selection is made by selecting the $n \times p$ fittest individuals in the population, where n is the size of the mate pool.

2.4.4 Crossover in genetic algorithms

2.4.4.1 One-point crossover

This crossover operator works by receiving two parents with chromosomes of length L and randomly selecting a point $0 < p < L$. The resulting offspring will display chromosome segments from both parents, one of them in each segment determined by the bipartition of the chromosome length at point p (see Equations 2.17 and 2.18).

$$\text{offspring}_1 : \text{parent}_1[1, p - 1] \,||\, \text{parent}_2[p, L] \tag{2.17}$$

$$\text{offspring}_2 : \text{parent}_2[1, p - 1] \,||\, \text{parent}_1[p, L] \tag{2.18}$$

2.4.4.2 Two-point crossover

Two-point crossover works in a similar manner to one-point crossover, the difference being in the number of partition points being selected (two). This time we select two points $0 < p_1 < L - 1$ and $p_1 < p_2 < L$. the resulting offspring will be as it follows (see Equations 2.19 and 2.20).

$$\text{offspring}_1 : \text{parent}_1[1, p_1 - 1] \,||\, \text{parent}_2[p_1, p_2 - 1] \,||\, \text{parent}_1[p_2, L] \tag{2.19}$$

$$\text{offspring}_2 : \text{parent}_2[1, p_1 - 1] \,||\, \text{parent}_1[p_1, p_2 - 1] \,||\, \text{parent}_2[p_2, L] \tag{2.20}$$

2.4.4.3 "Cut and splice" crossover

"Cut and splice" crossover works in a similar manner to one-point crossover, the difference being that instead of selecting one bipartition point p for both parents, we select $0 < p_1 < L$ for parent$_1$ and $0 < p_2 < L$ for parent$_2$. The result is an absence of guarantee about the length of the offspring chromosomes (see Equations 2.21 and 2.22).

$$\text{offspring}_1 : \text{parent}_1[1, p_1 - 1] \,||\, \text{parent}_2[p_2, L] \qquad (2.21)$$

$$\text{offspring}_2 : \text{parent}_2[1, p_2 - 1] \,||\, \text{parent}_1[p_1, L] \qquad (2.22)$$

2.4.4.4 Uniform crossover

This crossover operator works at the gene - and not segment - level. This means that each parent's chromosome is partitioned before and after each individual gene, and this partitions are the ones interchanged in order to create the offspring. This operator also works with a parameter known as the *mixing ratio*, which determines the probability that each gene has of receiving load from parent$_1$ (a mixing ratio of 0.5 determines equal probabilities for both parents). The process of creation of each member of the offspring is given by the following algorithm (Algorithm 4):

Data: two chromosomes: parent$_1$ and parent$_2$
Result: a member of their offspring
initialize $offspring$ as a L-dimensional vector;
for *i=1..L* **do**
 if *random $\alpha \in [0, 1] \leq$ mixing-ratio* **then**
  offspring$[i] = $ parent$_1[i]$;
 else
  offspring$[i] = $ parent$_2[i]$;
 end
end
return offspring;

Algoritmo 4: pseudo-code for the generation of an individual member of the offspring under the uniform crossover operator

2.4.4.5 Arithmetic crossover

This crossover operator works by linearly combining the two parent vectors in order to generate offspring. The value α is a randomly chosen weighting factor (see Equations 2.23 and 2.24).

$$\text{offspring}_1 : \alpha \times \text{parent}_1 + (1 - \alpha) \times \text{parent}_2 \qquad (2.23)$$

$$\text{offspring}_2 : \alpha \times \text{parent}_2 + (1 - \alpha) \times \text{parent}_1 \qquad (2.24)$$

2.4.4.6 Heuristic crossover

This crossover operator uses an heuristic to guide the direction of the search, by analysing the fitness of both parents and assuming that the vector difference between the best and worst parent will give an estimate of the best search direction. r is a randomly selected weighting factor to be applied in this difference vector. (see Equations 2.25 and 2.26).

$$\text{offspring}_1 : \text{best-parent} + r \times (\text{best-parent} - \text{worst-parent}) \tag{2.25}$$

$$\text{offspring}_2 : \text{best-parent} \tag{2.26}$$

2.4.5 Mutation in genetic algorithms

2.4.5.1 Bit string mutation

This mutation operator is suitable for bit string chromosomes, and works by inverting the bit of each position with a probability of $\frac{1}{L}$ (L being the chromosome length). The expected value of mutations per mutated individual is then $L \times \frac{1}{L} = 1$ (See Algorithm 5

Data: a chromosome c
Result: c's mutation under bit string mutation
initialize $mutated$ as a L-dimensional vector;
for *i=1..L* **do**
    if *random $\alpha \in \{false, true\}$* **then**
        mutated[i] = ¬mutated[i];
    end
end
return mutated;

Algoritmo 5: pseudo-code for the mutation of an individual under bit string mutation

2.4.5.2 Flip bit

This mutation operator is suitable for bit string chromosomes, and works by simply inverting all the bits in the chromosome (See Algorithm 6).

Data: a chromosome c
Result: c's mutation under flip bit mutation
initialize $mutated$ as a L-dimensional vector;
for *i=1..L* **do**
    mutated[i] = ¬mutated[i];
end
return mutated;

Algoritmo 6: pseudo-code for the mutation of an individual under flip bit mutation

2.4.5.3 Boundary

This mutation operator is suitable for integer and float-valued chromosomes, and works by randomly choosing a position of the chromosome and replacing that position's value with the lower or upper bound for an allele's value (See Algorithms 7 and 8).

Data: a chromosome c
Result: c's mutation under lower-bound boundary mutation
initialize $mutated$ as a L-dimensional vector;
randomly choose an integer $i \in [1, L]$;
mutated$[i]$ = lower-bound;
return mutated;

Algoritmo 7: pseudo-code for the mutation of an individual under lower-bound boundary mutation

Data: a chromosome c
Result: c's mutation under upper-bound boundary mutation
initialize $mutated$ as a L-dimensional vector;
randomly choose an integer $i \in [1, L]$;
mutated$[i]$ = upper-bound;
return mutated;

Algoritmo 8: pseudo-code for the mutation of an individual under upper-bound boundary mutation

2.4.5.4 Non-uniform

2.4.5.5 Uniform

This mutation operator is suitable for integer and float-valued chromosomes, and works by randomly choosing a position of the chromosome and replacing that position's value with an uniform random value selected between given lower and upper bounds (See Algorithm 10).

Data: a chromosome c
Result: c's mutation under uniform mutation
initialize $mutated$ as a L-dimensional vector;
randomly choose an integer $i \in [1, L]$;
mutated$[i]$ = random $\alpha \in$ [lower-bound, upper-bound];
return mutated;

Algoritmo 9: pseudo-code for the mutation of an individual under uniform mutation

2.4.5.6 Gaussian

This mutation operator is suitable for integer and float-valued chromosomes, and works by randomly choosing a position of the chromosome and incrementing that position's value with an Gaussian distributed random value selected between given lower and upper bounds. If the resulting value happens to exceed the bounds, it is clipped. (See Algorithm 10).

Data: a chromosome c
Result: c's mutation under Gaussian mutation
initialize $mutated$ as a L-dimensional vector;
randomly choose an integer $i \in [1, L]$;
$mutated[i] = mutated[i] + random\ \alpha \in [\text{lower-bound}, \text{upper-bound}]$;
$mutated[i] = \min(mutated[i], \text{upper-bound})$;
$mutated[i] = \max(mutated[i], \text{lower-bound})$;
return mutated;

Algoritmo 10: pseudo-code for the mutation of an individual under Gaussian mutation

2.4.6 Terminating condition in genetic algorithms

Because genetic algorithms are meta-heuristics, they have no analytical way of determining when the process should be terminated. And although their aspiration is to find the optimal solution to an optimization problem, they rarely are able to find *the* perfect solution in feasible time - bumping instead in worse solutions of comparable fitness -, so it would not be practical to wait for the optimal solution to terminate the process, as it would take more time we are willing to spare: it should be terminated way sooner. As a result, there is a variety of heuristics typically employed as terminating conditions in genetic algorithms. A simple heuristic is to predetermine a limit for the number of generations and stop the process upon reaching this number, but the number of generations in itself does not tell us much about the resources spent, as the time and space complexity of the inner steps of an iteration can vary largely from GA to GA. A more pragmatical heuristic would be to allocate a budget of some resource (time, space or even money) and terminate the process when this budget is reached. Alternative heuristics would be to wait until successive generations fail to generate better results (the search has reached a plateau) or even manual inspection.

3 METHODOLOGY

3.1 Homosexuality and the gay uncle hypothesis

In order to test the gay uncle hypothesis (discussed briefly in 1.2.1), we need to develop a genetic algorithm environment in which (i) homosexual behaviour can be accurately modelled (ii) homosexuality is a genetic trait (iii) heterosexual and homosexual organisms alike can carry the homosexual allele and (iv) homosexual organisms care for their close relatives.

For the purposes of simple experiments, homosexual behaviour can be modelled as asexuality - in truth, homosexual behaviour involves sex, but this can be abstracted from our model as it does not generate offspring.

It is fundamental that homosexuality is modelled as a genetic trait, but it is also important that heterosexual organisms can carry the homosexual allele, as the basis for the gay uncle hypothesis is that homosexual behaviour persists due to the effort of heterosexual organisms. In order to model a trait to be inexpressive even in the event of its genetic code being present in the genotype of its carrier, we can resort to emulating a genetic predisposition to homosexuality: each chromosome should carry a gene responsible for encoding its carrier's probability of developing homosexual behaviour. This way, two sibling organisms would be expected (in a statistical viewpoint) to have similar predispositions to homosexuality, although they could have distinct sexual orientations. This modelling is coherent with our current understanding of homosexuality, as it was observed that identical twins can feel attracted to different genders BAILEY (1991). This modelling would also allow for the gay uncle phenomenon to happen, as heterosexual organisms would be able to pass down the genetic predisposition accounting for their siblings' homosexuality. One important concern however remains: modelling the homosexual trait as a clean spectrum consisting of a single gene may be responsible for leaving it too susceptible to mutations and thus undesirably resistant to natural selection. A better alternative would be to emulate the ruggedness of real-life genetic landscapes by making the sexual orientation section of chromosomes n-dimensional and interpreting it as coordinates in a n-dimensional landscape. This way, evolutionary processes guided towards or away from homosexuality would surface clearer, as it would be possible for us to clearly see the population trying to optimize the homosexual landscape.

A second key aspect of this modelling concerns requirement (iv) of paragraph 1: we need to account for homosexual organisms taking care of their close relatives. This behaviour could be emulated by forcing homosexual agents to nurture a particular subset of its relatives, such as the set of its nephews and nieces, but this decision raises two

concerns: not only our computer program would need to maintain genealogical records (which would lead to an increase in space and time complexity), but we would be responsible for introducing a bias due to our arbitrary selection of nurture-worthy relatives. If we otherwise force homosexual agents to employ a kin selection strategy, we would guarantee that they are caring for their close relatives and at the same time ease our program's burden.

It might be interesting not to force kin selection upon homosexual agents, but rather to implement it as a genetic trait: all chromosomes could carry a gene responsible for encoding its carrier's degree of predisposition to kin selection strategies. This decision may have interesting results: we could predict, according to the gay uncle hypothesis, that because homosexuality is dependant of kin selection, the genes for homosexuality and kin selection should increase or decrease in a correlated fashion.

As always, it is important that organisms are subject to natural selection, and thus every organism should be subject to a fitness function that is independent of its sexual orientation. This fitness measure is an abstraction meant to be indicative of the individual's ability to collect and process resources, win territorial disputes, resist diseases - in short, indicative of its survival potential, unrelated to sexual dynamics. To keep the details of the fitness measure as abstract and general as possible, a portion of each organism's genotype will encode coordinates in a n-dimensional space, and the fitness function will be defined as a real-valued function $f : \mathbb{R}^n \to \mathbb{R}$. This decision enables us to study the gay uncle hypothesis under varied types of search spaces, which can be easily generated via mathematical properties of real-valued functions.

3.1.1 Genotype structure

Our genotype will be composed by two sections of variable lengths, both defined by real-valued vectors. The first, called p_1, will be connected to natural selection, with its structure being an abstraction of the biological fitness of an individual and thus taken under consideration in the selection (see Section 3.1.2) phase of our algorithm. The second, called p_2, will be connected to the determination of the organism's sexual orientation (see Section 3.1.5).

3.1.2 Selection

The selection phase, as always, will rely on the computation of the fitness function. In this particular experiment, however, the fitness function is not applied to the entirety of the individual's genotype, but rather to the first section of each genotype. This first section consists of a n_1-dimensional vector $p_1 : (v_1, v_2, ..., v_{n-1}, v_n)$ that works as the input for the fitness function $f : \mathbb{R}^n \to \mathbb{R}$, which is arbitrarily-defined.

3.1.3 Reproduction

For organization purposes, because the genotype structure is divided in two logical sections, the crossover operator will work differently in each section. Both sections consist of real-valued multidimensional vectors - their dimensionality being n_1 and n_2 respectively. For this reason, they can be subject to the same crossover types, which are: one-point crossover, two-point crossover, uniform crossover, arithmetic crossover and

heuristic crossover.

3.1.4 Mutation

As did the crossover operator, the mutation operator will work separately in each section of the genotype.

3.1.5 Sexual orientation determination

In our model, sex orientation will be determined stochastically. More precisely, the p_2 section of the genotype will be interpreted as coordinates in a multidimensional, real-valued landscape, in which the value in each coordinate is representative of a particular probability of the agent being born homosexual. At the moment of birth of each agent, our algorithm will use the p_2 section of its genotype as coordinates in a predefined landscape and the value of the landscape in that point will modulate the probability of the agent having its homosexual field marked as *true*.

3.1.6 Nurture dynamics

Our model will work with a augmented fitness system in which each agent's fitness will be determined not only by a function applied to its genotype but also by the amount of nurture that agent has accumulated. This nurture counter will be added to the evaluation of the fitness function and the resulting value will be used for selection purposes. This decision allows us to make kin selection relevant, because the nurture added by a close relative in the kin selection phase will have a positive effect for the agent in the selection phase.

3.1.7 Kin selection dynamics

In our model, kin selection dynamics will correspond to a process in which each homosexual agent will increment the nurture counter of each individual in the population by a value that is modulated by both the kin selection parameter K and the genetic similarity $d(h, c)^{-1}$ between the donor and the receiver, where $d(h, c)$ is the average of the absolute differences between matching alleles on the genotypes of h and c (see Algorithm 11).

> **for** *each new child c* **do**
> > **for** *each homosexual agent h in population* **do**
> > > $c.nurture = c.nurture + K \times d(h, c)^{-1}$;
> >
> > **end**
>
> **end**

Algoritmo 11: Pseudo-code for kin selection dynamics

3.2 Sexual selection, Fisherian runaway and the Sexy son hypothesis

In order to test any hypothesis concerning sexual selection, we need to develop a genetic algorithm environment in which (i) sexual preference can be accurately modelled and (ii) sexual preference is a genetic trait.

In order to address the first requirement, it is necessary for us to formalize the mechanics of sexual selection. In the natural world, sexual preference takes under consideration the phenotype of organisms, but if we were to try and define the emergence of phenotypes from genotypes, our model would most certainly be subject to unhealthy doses of biases, and we want to avoid arbitrary modelling decisions at all costs. A better alternative would be for us to make sexual preference directly dependant on the genotype, defining it as a function whose domain is the set of all possible genotypes and the image is the set of all possible sexual gradings potential mate organisms could receive.

This way, if we, without loss of generality, take the genotype to be defined as an N-dimensional vector of elements of the arbitrary set Γ, we can define the structure of a *sexual preference function* ϕ as $\phi : \Gamma^N \to \mathbb{R}$. We can use the set of the real numbers to represent the sexual grading spectrum, smaller numbers representing weaker preferences and greater numbers representing stronger ones.

Our models will deal primarily with the Sexy son hypothesis, which states that, for a female organism, all characteristics of male partners other than the potential to produce male offspring with the best chance of reproductive success are comparatively irrelevant. In order to experiment with this hypothesis, we will analyse the relationship between female preference for sexy sons and a number of parameters such as the size of each offspring and the reproductive frequency of male and female agents.

3.2.1 Genotype structure

Our genotype will be composed by two sections of variable lengths, both defined by real-valued vectors. The first, called p_1, will be connected to natural selection, with its structure being an abstraction of the biological fitness of an individual and thus taken under consideration in the selection (see Section 3.1.2) phase of our algorithm. The second, called p_2, will be connected to the definition of the sexual preference function (See 3.2.4).

3.2.2 Selection

As with the previous experiment, here the selection phase will rely on computation of the fitness function, which will not be applied to the entirety of the individual's genotype, but rather to the first section of each genotype. This first section consists of a n_1-dimensional vector $p_1 : (v_1, v_2, ..., v_{n-1}, v_n)$ that works as the input for the fitness function $f : \mathbb{R}^n \to \mathbb{R}$, which is arbitrarily-defined.

3.2.3 Mutation

As did the crossover operator, the mutation operator will work separately in each section of the genotype.

3.2.4 Definition of the sexual selection function

The sexual preference function is a function $\phi : \Gamma^N \to \mathbb{R}$. We will experiment with Gaussian and polynomial sexual preference models, each one of them detailed below. In both models, v_i represents the i-th component of the agents' genotypes.

The Gaussian model works with multidimensional Gaussian functions

$\phi(v_1, v_2, .., v_{n_1}) = A \cdot e^{-\sum \frac{(v_i - \mu_i)^2}{\sigma_i{}^2}}$, where A, μ_i and σ_i are the parameters codified in the agents' genotypes and thus subject to evolution.

The polynomial model works with a multidimensional polynomial function $\phi(v_1, v_2, .., v_{n_1}) = \sum_{i=1}^{n_1} \sum_{j=0}^{k} c_{ij} \cdot v_i^j$, where c_{ij} is the j degree polynomial coefficient in the i-th dimension. The coefficients $c_{ij} \mid i \in \{1, 2, .., n_1\}, j \in \{0, 1, .., k\}$ will be codified in the p_2 section of the genotype in lexicographic order and thus subject to evolution.

4 EXPERIMENTAL EVALUATION

## 4.1 Kin selection, Homosexuality and the Gay uncle hypothesis

In order to understand how evolutionary dynamics works in rugged, real-life landscapes, we must first understand it on a simpler level. Because of this, our first experiments will take place on a landscape defined by a simple bi-dimensional Gaussian function ($f(x, y) = 1000\, e^{-\frac{x^2+y^2}{100^2}}$). Working with such a smooth function gives us the advantage of being able to measure the speed and the *straightness* of the evolutionary path on the landscape, whereas a complex function would frustrate us because it would be responsible for trapping the evolutionary process in local optima.

4.1.1 No kin selection

Our first step towards understanding the evolutionary dynamics of homosexuality should be to measure exactly how fast a population without the benefit of kin selection will drive homosexuals to extinction. This speed should be analysed comparatively with the speed with which natural selection works - that is, the speed at which the population moves towards the fitness global optimum. Figure 4.1 shows that (i) the evolutionary paths of both natural selection and homosexuality converge to the origin of the landscape and (ii) the convergence speed of natural selection is vastly superior to that of homosexuality.
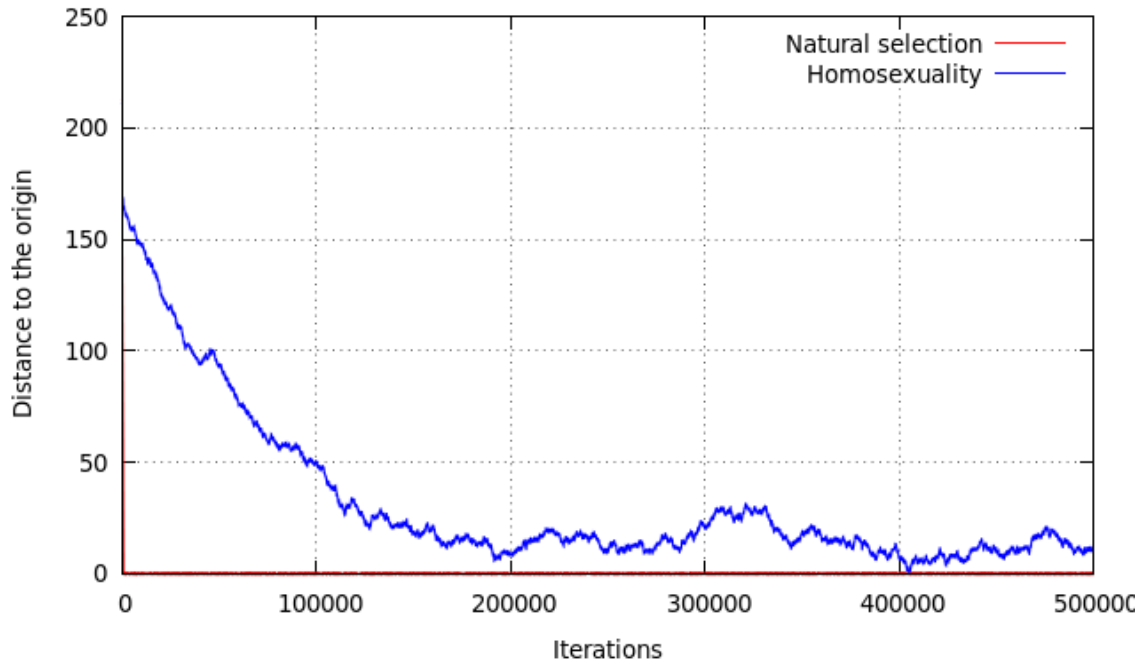
(a) Average distance per iteration from the agents' coordinates to the origin of the landscape for both natural selection and homosexuality
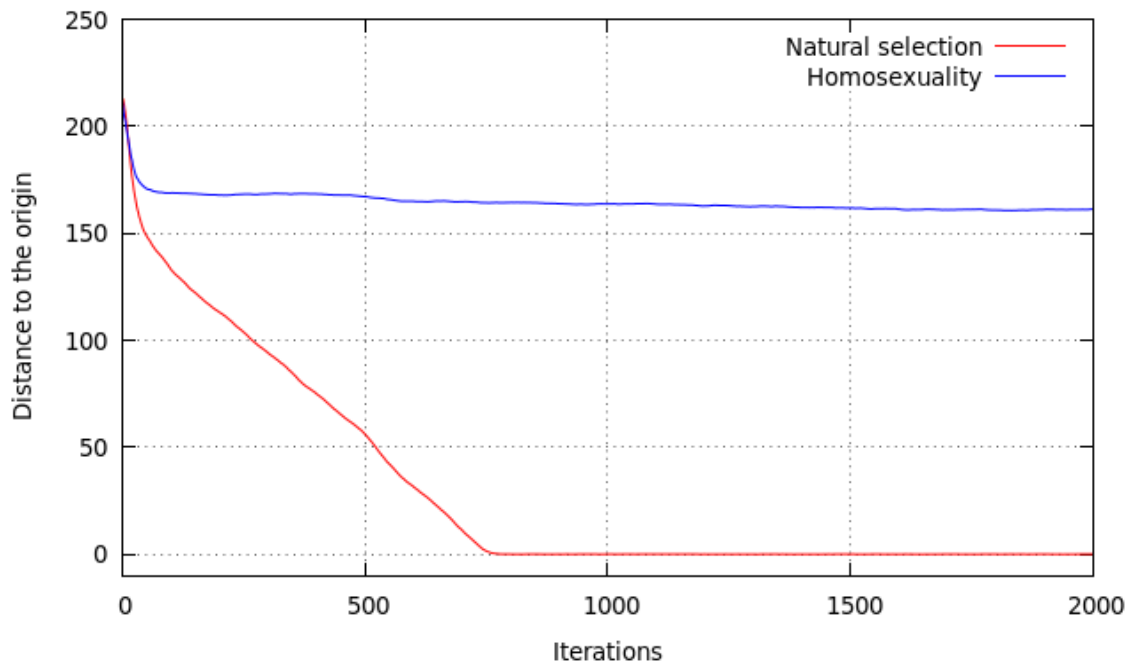

(b) Average distance per iteration from the agents' coordinates to the origin of the landscape for both natural selection and homosexuality. The range of iterations is clipped to picture the extremely fast evolution of natural selection.

Figure 4.1: Pop. size: 1000; Mate pool size: 100; $K = 0.0$

The natural selection curve has an approximately linear pattern ranging from iteration 0 to iteration 800. We ran linear regression analysis on the data within this range with a linear hypothesis $D(t) \approx a + b\, t$ (t is the number of iterations) and found $a = 160.493$ and $b = 0.213$, resulting in the model $D(i) \approx 160.493 - 0.213\, t$. The homosexuality curve

has an approximately hyperbolic pattern throughout the whole simulation. We ran linear regression analysis on the data with a polynomial hypothesis $D(t) \approx C\ t^n$ and found $C = 147266.625$ and $n = -0.7312$, resulting in the model $D(t) \approx 147266.625\ t^{-0.7312}$. A comparison between the data points and the fitted functions can be seen in Figure 4.2.
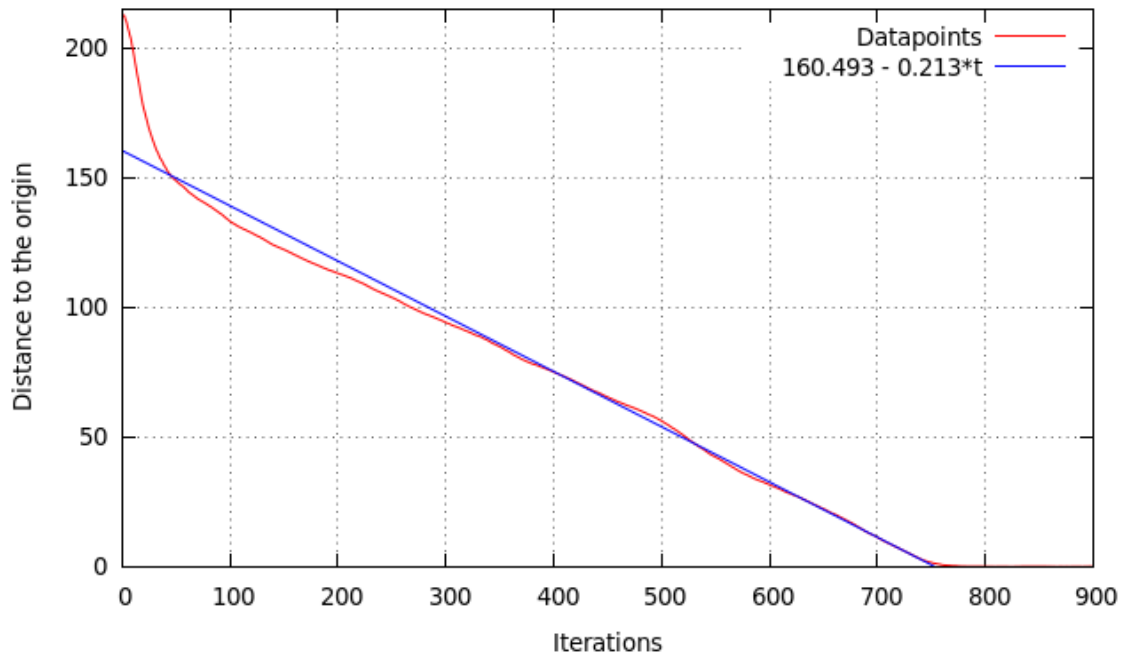
(a) Evolutionary curve for natural selection fitted with $D(t) \approx 160.493 - 0.213\ t$.
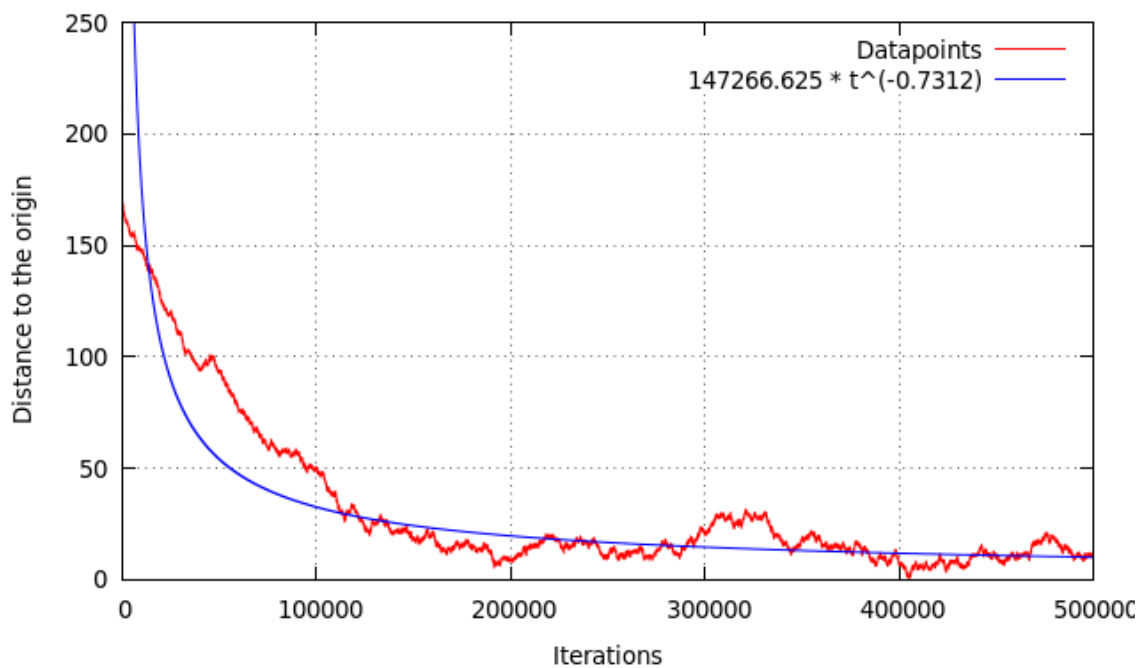
(b) Evolutionary curve for homosexuality fitted with $D(t) \approx 147266.625\ t^{-0.7312}$.

Figure 4.2: Pop. size: 1000; Mate pool size: 100; $K = 0.0$

4.1.1.1 Convergence speed

The convergence speed of natural selection is approximately constant between iterations 0 and 800 and can be calculated as the derivative of the fitted function $D(t) \approx 160.493 - 0.213\,t$: $(160.493 - 0.213\,t)' = -0.213$. After iteration 800, natural selection reaches an equilibrium at $D(t) = 0$ and the convergence speed becomes 0.

The convergence speed of homosexuality can be calculated as the derivative of the fitted function $D(t) \approx 147266.625\,t^{-0.7312}$: $(147266.625\,t^{-0.7312})' = 147266.625 \times (-0.7312)\,t^{-1.7312} = -107681.356\,t^{-1.7312}$

4.1.2 Kin selection

Adding kin selection to our model corresponds to making each homosexual agent increment the *nurture* value of every other agent in the population. The amount of incremented nurture is modulated by the genetic similarity between the donator and the receiver - which accounts for homosexual agents prioritizing their close relatives - and by a parameter K - which represents the degree of kin selection.

4.1.2.1 Convergence speed

As with our experiments without it, in our experiments with kin selection homosexuality evolved significantly slower than natural selection [how much?] and their speed ratio also decreased significantly compared to our experiments without kin selection [how much?], meaning that the evolution of homosexuality is (i) slower than that of natural selection and (ii) slower with kin selection than without it.

4.1.2.2 Global optima

The analysis of the evolutionary paths clearly shows us that whereas the path for natural selection aims for the origin of the landscape, the path for homosexuality stabilizes way sooner, being contained within the contour lines $\sqrt{x^2 + y^2} = 174$ and $\sqrt{x^2 + y^2} = 176$ in the last 7541 iterations (or $\frac{7541}{27541} = 27.38\%$ of the total execution time). These contour lines correspond to $z \approx 0.780$ and $z \approx 0.787$, resulting in the homosexuality predisposition being contained in a range of size 0.007 or 0.7% of the whole spectrum. (see Figure 4.3).
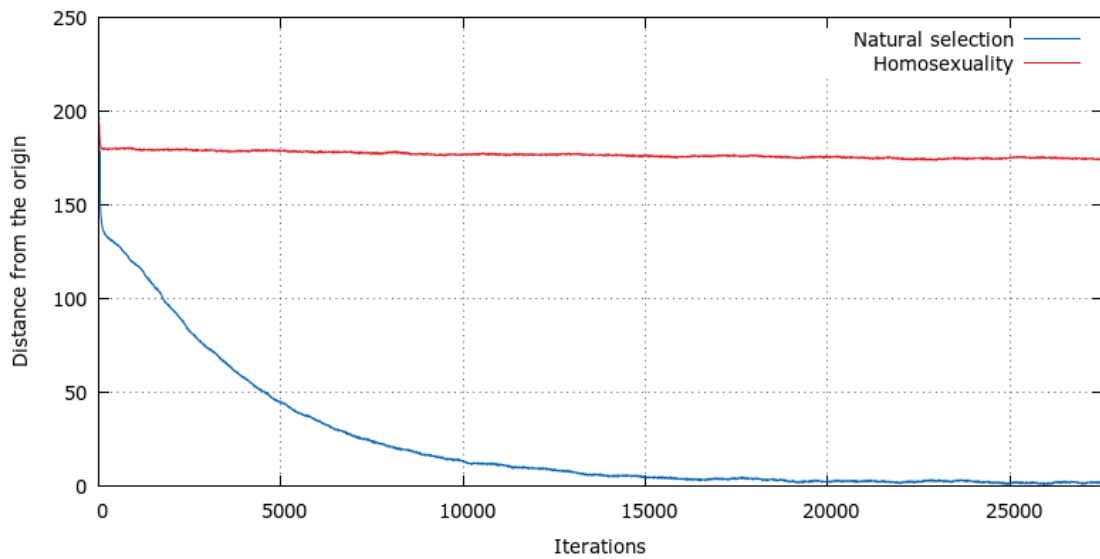
(a) Average distance per iteration from the agents' coordinates to the origin of the landscape for both natural selection and homosexuality
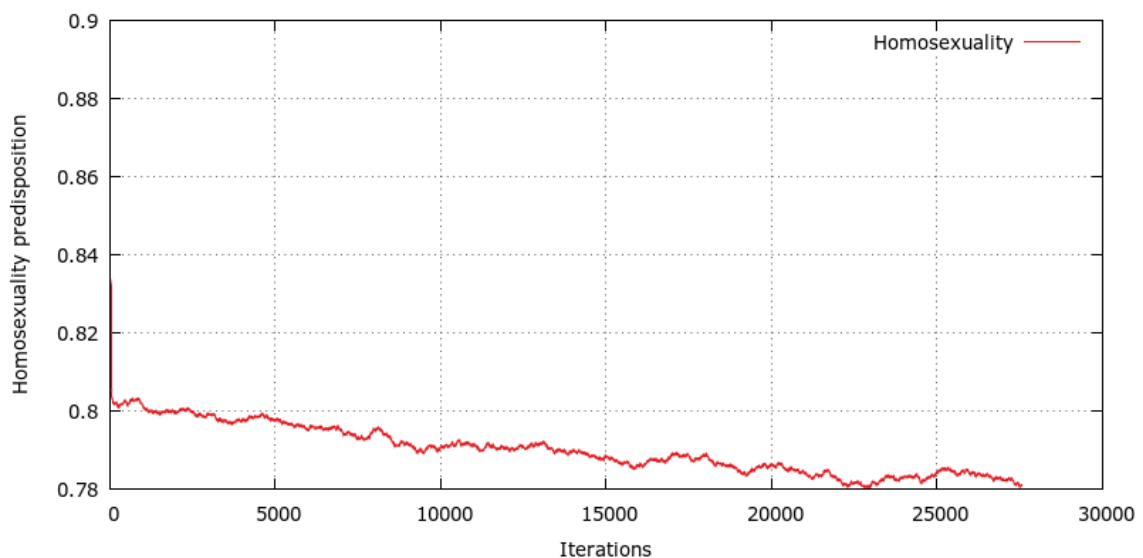


(b) Homosexuality predisposition per iteration

Figure 4.3: Pop. size: 1000; Mate pool size: 100; $K = 0.1$

### 4.1.2.3   *Role of the kin selection parameter*

Simulations with no kin selection are modelled with a kin selection parameter $K = 0$. The fact that their population behaves in a different fashion than those of simulations with positive kin selection suggests that the parameter K has an important role in the evolutionary dynamics of homosexuality, perhaps being responsible for determining the proportion between heterosexual and homosexual agents in a population.

We ran multiple simulations with varying K values and observed that, for our set of parameters, the amount of kin selection has negligible effect on the proportion of heterosexuals to homosexuals, but significant effect on the natural selection convergence speed. This result suggests that there is an equilibrium proportion of homosexuals in a popula-

tion that is independent from the kin selection parameter for sufficiently large values of K.
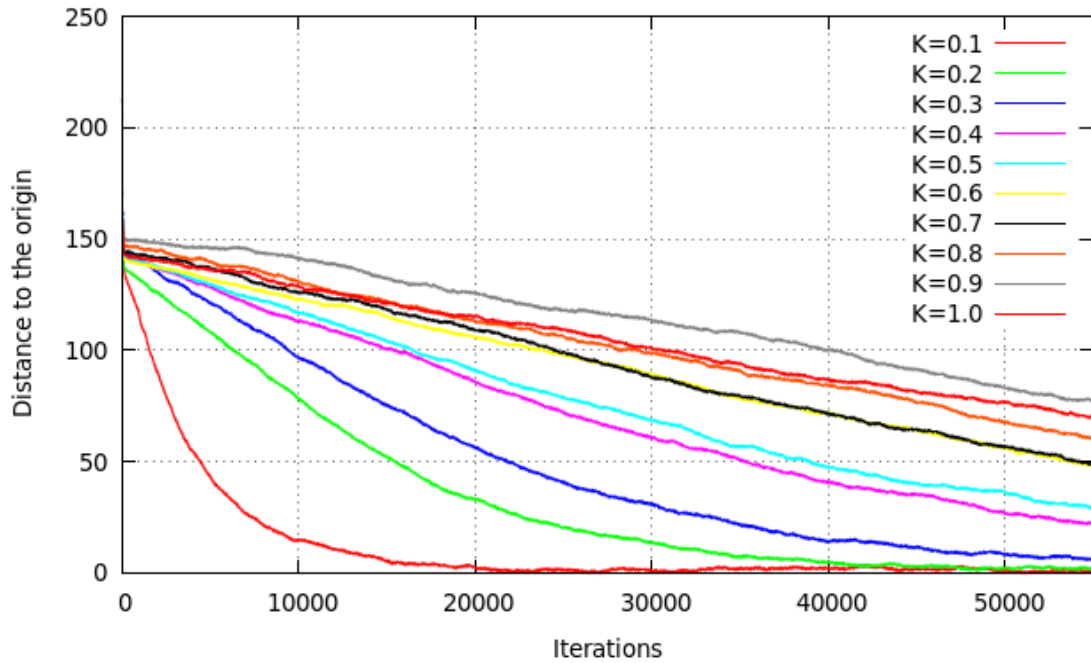
(a) Average distance per iteration from the agents' coordinates to the origin of the landscape for natural selection
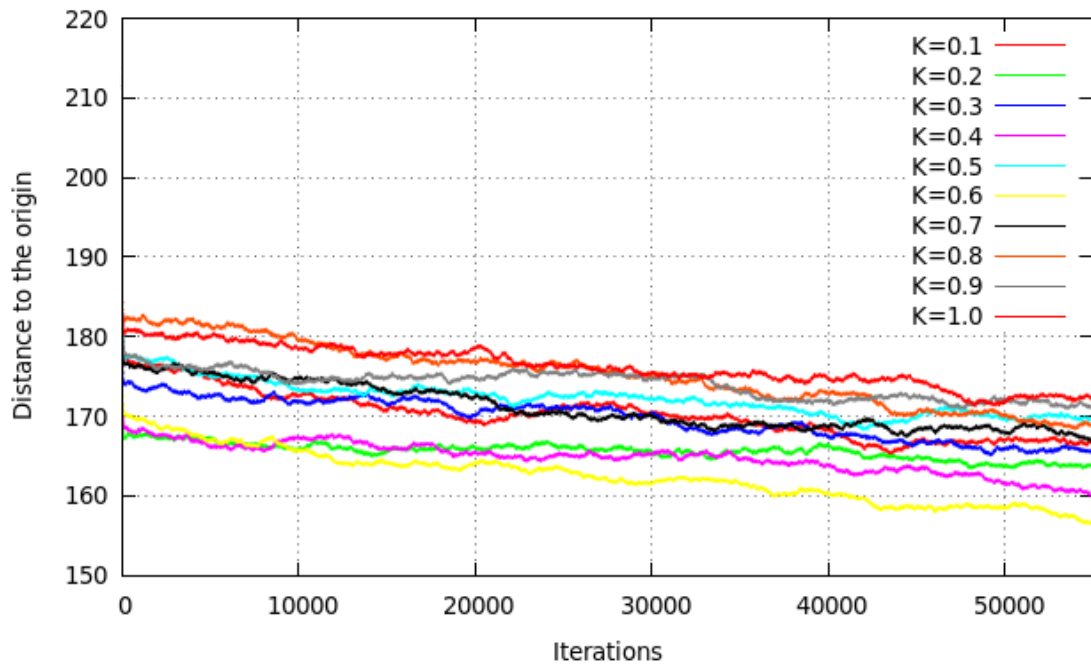
(b) Average distance per iteration from the agents' coordinates to the origin of the landscape for homosexuality

Figure 4.4: All curves start at $x = 0$, $y = 250$. Pop. size: 1000; Mate pool size: 100; $K \in \left[\frac{x}{10} \mid x \in \mathbb{N}, 1 \leq x \leq 10 \right]$

Figure 4.4 shows the natural selection and homosexuality evolutionary curves for dif-

ferent values of K. Their convergence speed is clearly not constant, and the evolutionary motion appears to be determined by a function in the format $C\,t^n$ with $n < 0$, as evidenced by the asymptotes $t = 0$ and $D(t) = 0$. We ran linear regression analysis on the natural selection data with a polynomial hypothesis $D(t) \approx C\,t^n$ and compiled the results in Table 4.1. The exponent n appears to grow logarithmically with respect to K, and a linear regression analysis with hypothesis $n(K) \approx a + b \log K$ gives us $a = -0.085$ and $b = 0.583$, resulting in the growth model $n(K) \approx -0.085 + 0.583 \log K$ (See Figure 4.5).

K	C	n
0.1	1610411.026	-1.327
0.2	4299460.037	-1.271
0.3	145132.152	-0.8493
0.4	7487.573	-0.485
0.5	3512.910	-0.3953
0.6	1497.122	-0.2878
0.7	1540.558	-0.2884
0.8	913.698	-0.2246
0.9	610.330	-0.1707
1.0	598.783	-0.1778

Table 4.1: Fitting of the curves for natural selection (See Figure 4.4) with hypothesis $D(t) \approx Ct^n$ where t is the number of iterations and $D(t)$ the distance to the origin on iteration t.
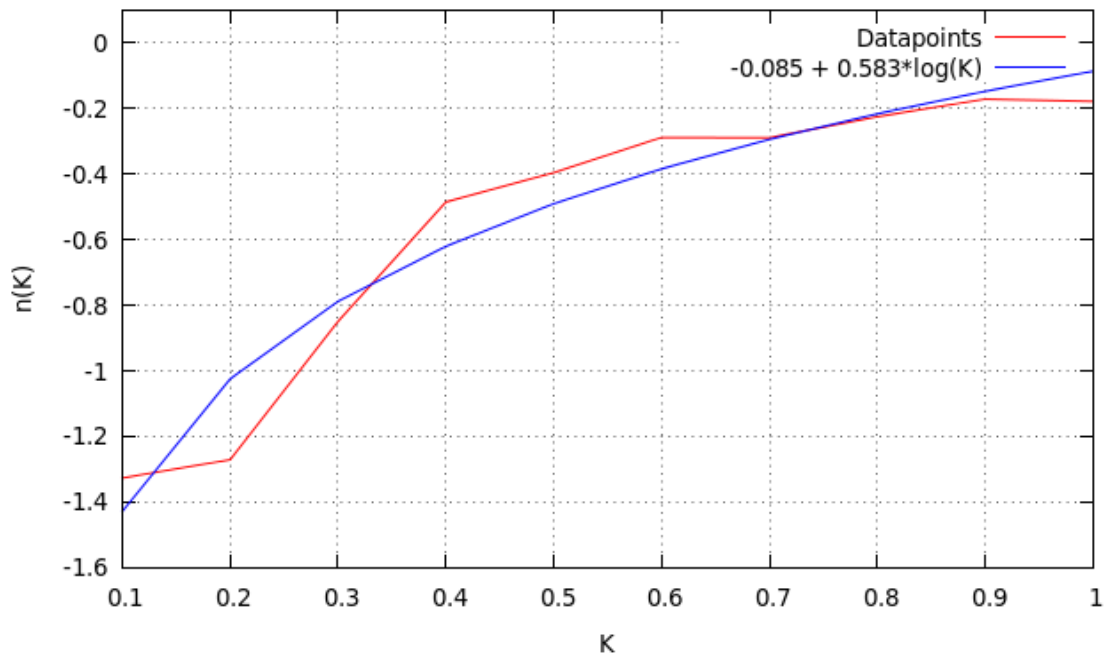

Figure 4.5: Fitting of the data points of the curve $n(K)$ as $n(K) \approx -0.085 + 0.583 \log K$.

4.2 Unalike selection

In the previous section we verified that kin selection is beneficial to homosexuality and has a pivotal role in assuring its survival in biological populations simulated by our model. It is natural for us to ask ourselves what are the limitations of kin selection with respect to homosexuality: how necessary it is that the homosexual donor and its recipient are genetically related? Could homosexuality be maintained even if we revert the direction of kin selection? In order to address these questions, we ran simulations in which homosexual agents engage in a dynamic we call *unalike selection*: rather than nurturing their closest relatives, homosexual agents nurture their most distant ones. This decision, of course, forces homosexual agents to give advantage to their strongest rivals in the evolutionary process, so the outcomes of unalike dynamics have a paradoxical nature that makes them difficult to predict.

Recall Algorithm 11 for kin selection dynamics. It uses the inverse of the measure of genetic difference to modulate the amount of donated nurture. Our algorithm for unalike selection will do the opposite and use the very measure of genetic difference to play the same role (See Algorithm 12). This way, the amount of nurture donated will be linearly and not inversely proportional to the difference between the donor and the receiver's genotypes.

for *each new child c* **do**
    for *each homosexual agent h in population* **do**
        $c.nurture = c.nurture + K \times d(h,c)$;
    end
end

Algoritmo 12: Pseudo-code for unalike selection dynamics

4.2.0.4 *Structure of the evolutionary path*

The exchange of kin selection for unalike selection alters the evolutionary path of homosexuality significantly. Whereas in the previous model the evolution of homosexuality followed an approximately rectilinear path towards the origin, this time it follows an extremely rugged path which folds itself perpendicularly to the average direction of movement. This ruggedness accounts for a fractal-like shape for the curve, its length extending considerably when stretched (see Figure 4.6).

(a) Iteration 24901

(b) Iteration 44901

(c) Iteration 74901

(d) Iteration 99901

(e) Iteration 124901

(f) Iteration 149901

(g) Iteration 174901
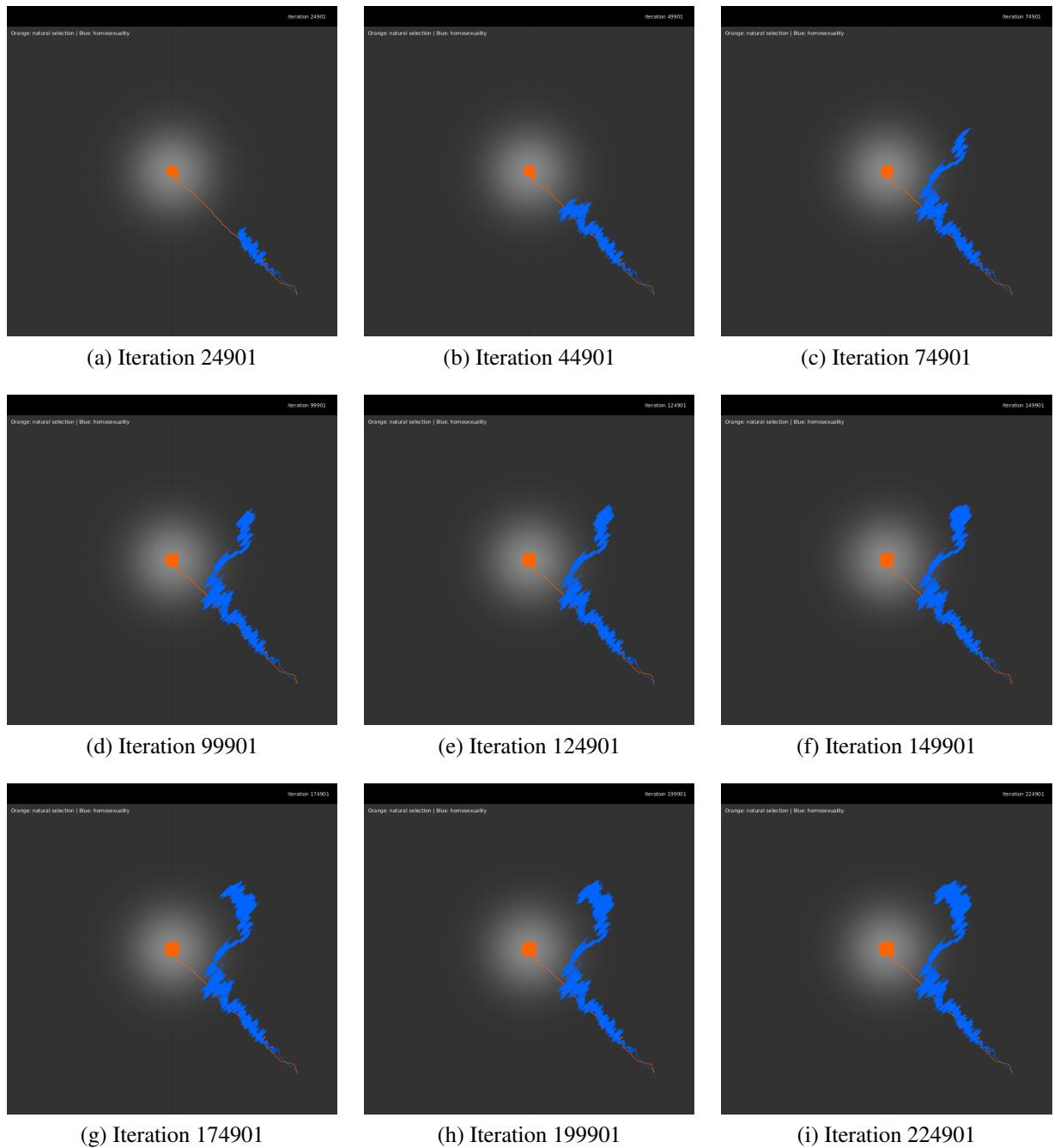
(h) Iteration 199901

(i) Iteration 224901

Figure 4.6: Evolution of natural selection (orange) vs homosexuality (blue): the average genotypes for both natural selection and homosexuality are plotted in a bi-dimensional grid. Pop. size: 1000; Mate pool size: 100; $K = 0.01$

In order to measure this ruggedness, we must resort to the study of fractal dimensions. Measuring the length of structures with statistical self-similarity - that is, shapes whose small portions can be considered reduced-scale images of the whole -, is not particularly useful, because their length is determined by the scale in which they are measured. For example, the length of the coastline of Britain - as is the general case for coastlines - is known to increase exponentially with the reduction of the length of the ruler used to measure it RICHARDSON; ASHFORD (1993). For this reason, we will measure our curves using a measure D of self similarity discussed by Mandelbrot in MANDELBROT

(1967) (for more information about fractals, see .1).

Figure 4.7 shows the relationship between the measured length N and the ruler size $\frac{1}{r}$ for the evolutionary paths of both natural selection and homosexuality at $K = 0.01$. The graph for natural selection is almost perfectly rectilinear for $-1.517 < \log \frac{1}{r} < 6.023$ and its slope can be easily calculated as $D = \frac{0.000 - 6.865}{6.023 - 0.000} \approx -1.140$, which means that the natural selection evolutionary path has dimensionality only slightly superior to 1 and can be thought as an almost straight line.

Theory of fractal dimensions predicts that plotting these quantities with a logarithmic scale applied to both axis should result in a straight line with a slope coinciding with the similarity exponent D. Our graph for the evolutionary path of homosexuality does not follow this pattern, but for reasons explained in Appendix .1, we will approximate it as a straight line and calculate its slope as $\frac{0.000 - 12.380}{6.211 - 0.000} \approx -1.993$, which leads to the conclusion that the similarity exponent of this path is almost that of a bi-dimensional object ($D = 2$).
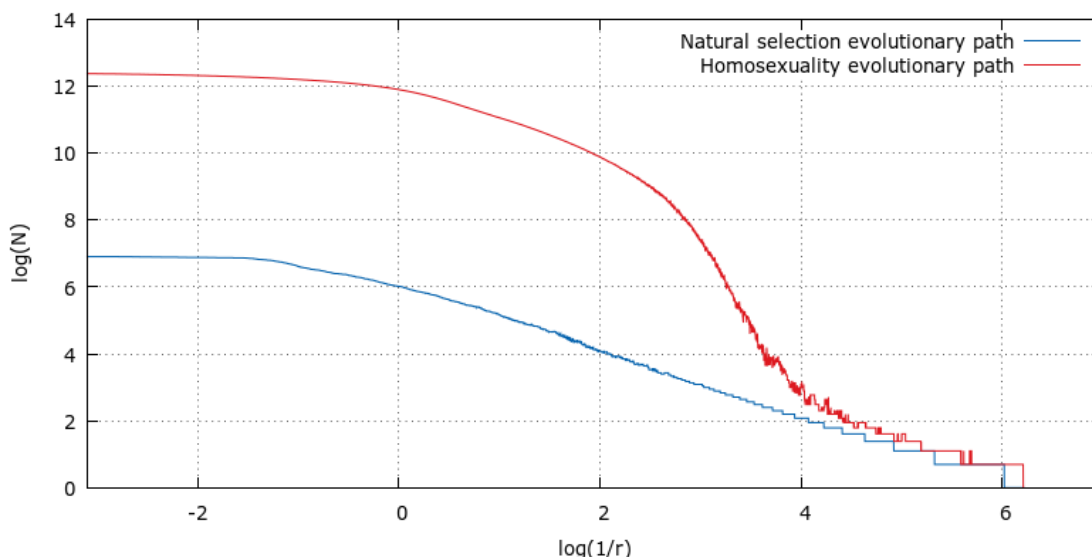

Figure 4.7: Measurement of the evolutionary path length N with respect to the ruler size $\frac{1}{r}$. Pop. size: 1000; Mate pool size: 100; $K = 0.01$

Even if we can calculate the dimensionality of evolutionary paths, our analysis of their structure would be incomplete without an explanation for their fractal shape. We believe this phenomenon can be explained from the indirect consequences of unalike selection: by giving advantage to their least close relatives (agents with very low homosexuality predispositions), homosexual agents give rise to an evolutionary pressure that works in the direction of their extinction. Intuitive reasoning therefore suggests that unalike selection should speed up the extinction of homosexuality, but that line of reasoning ignores the fact that homosexual agents are most beneficial to those that are most different from them. This benefit creates an evolutionary pressure in the opposite direction, making homosexuality advantageous for agents with low homosexuality predispositions. This clash of evolutionary pressures creates a paradoxical situation in which groups of agents with high homosexuality predispositions have advantage in lowering their overall homosexuality predisposition (because they are impaired by the advantage they concede to their rivals) and groups of agents with low homosexuality predispositions have advantage in increasing theirs (because they are benefited by the advantage they rivals concede them). In short,

the farther an agent is from the middle of the homosexuality predisposition spectrum, the higher will be his advantage to approach that middle. This creates an environment in which neither homogeneous heterosexual nor homogeneous homosexual populations can be stable - the equilibrium must be some place in between. This equilibrium, however, exists only at a very broad scale: if you look closely at the evolutionary path, you will be able to see the population oscillate violently, slave to one evolutionary pressure at each moment, and this oscillation gives the curve its fractal shape. You can see the evolutionary path for homosexuality at different scales in Figure 4.8.
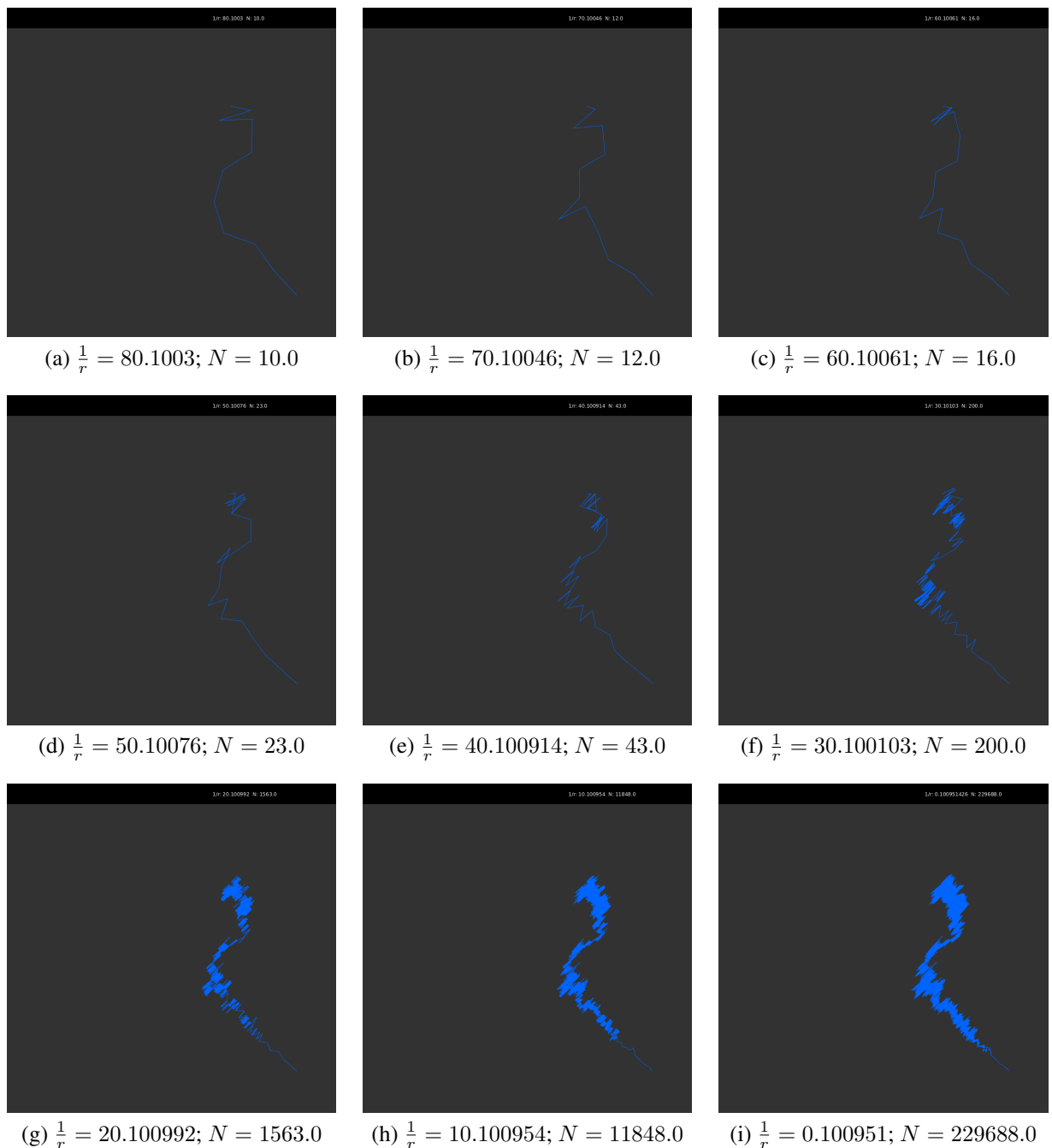

(a) $\frac{1}{r} = 80.1003$; $N = 10.0$

(b) $\frac{1}{r} = 70.10046$; $N = 12.0$

(c) $\frac{1}{r} = 60.10061$; $N = 16.0$

(d) $\frac{1}{r} = 50.10076$; $N = 23.0$

(e) $\frac{1}{r} = 40.100914$; $N = 43.0$

(f) $\frac{1}{r} = 30.100103$; $N = 200.0$

(g) $\frac{1}{r} = 20.100992$; $N = 1563.0$

(h) $\frac{1}{r} = 10.100954$; $N = 11848.0$

(i) $\frac{1}{r} = 0.100951$; $N = 229688.0$

Figure 4.8: Evolution of the measurement of the homosexuality evolutionary path length N for varying scales r. Pop. size: 1000; Mate pool size: 100; $K = 0.01$

4.2.0.5 *Global optima*

The evolutionary path of homosexuality clearly shows that the curve has a certain adversity to the origin, avoiding at all costs to cross a particular contour line of the Gaussian landscape. The Z value of this contour line determines the optimal amount of homosexuality predisposition, from which we can deduce the optimal proportion between heterosexual and homosexual agents in the population for a given value of the parameter K. Although determining this optimal amount from bi-dimensional paths is possible, we can get a clearer shot of the evolution of homosexuality predisposition by plotting the average distance per iteration from the agents' coordinates to the origin for both natural selection and homosexuality (see Figure 4.9). We can deduce from the graphs that the optimal homosexuality predisposition lies within the range $[0.3, 0.5]$ and consequently that the optimal proportion between heterosexuals and homosexuals is between $10 : 3$ and $10 : 5$.
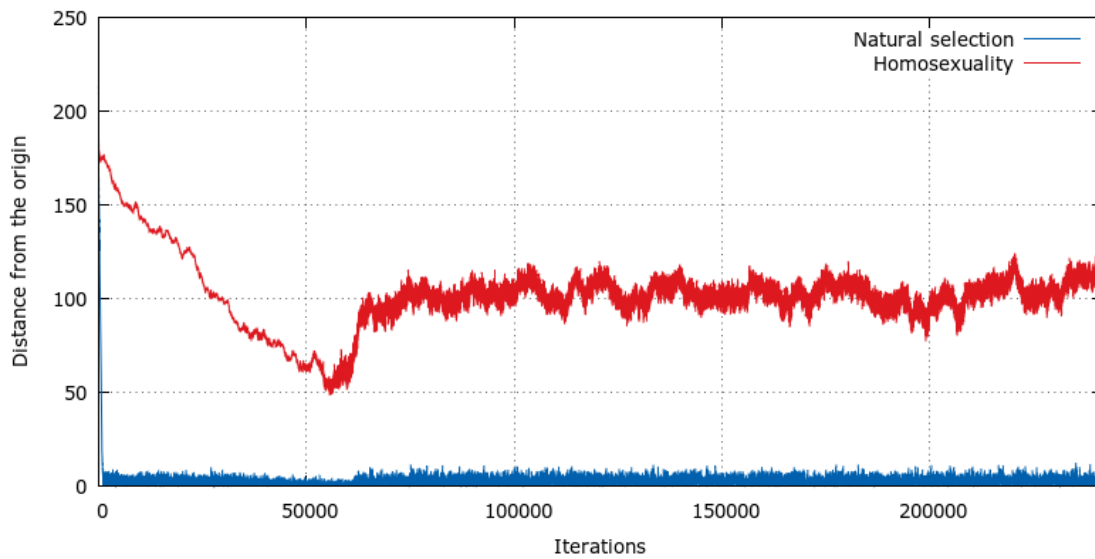
(a) Average distance per iteration from the agents' coordinates to the origin of the landscape for both natural selection and homosexuality
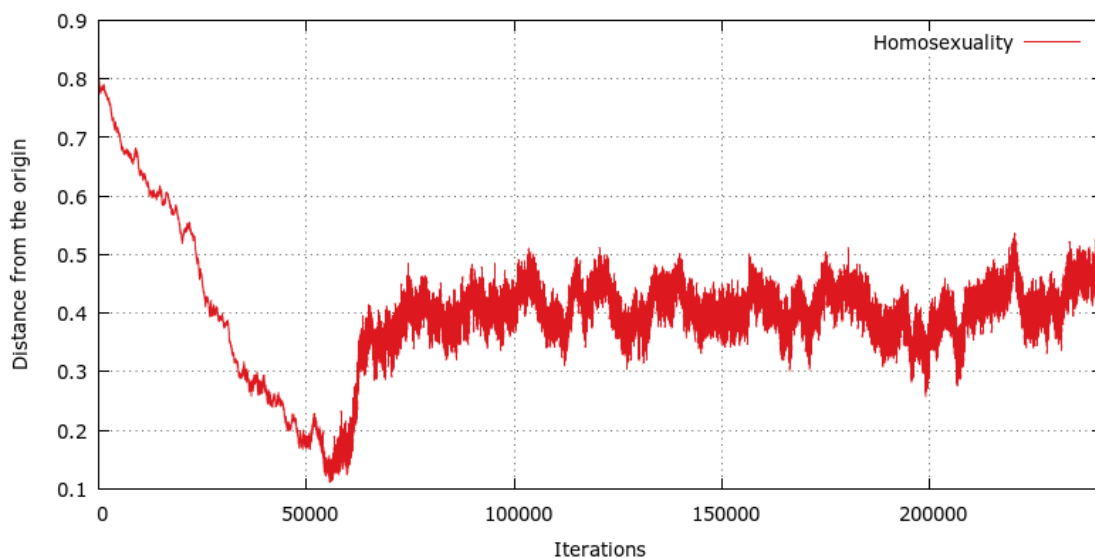
(b) Homosexuality predisposition per iteration

Figure 4.9: Pop. size: 1000; Mate pool size: 100; $K = 0.01$

4.3   Sexual selection, Fisherian runaway and the Sexy son hypothesis

On the following experiments, we will work with *raw* sexual selection, that is, a model in which nothing besides individual fitness and sexual selection are modelled. In this simplified model, we can expect to observe the precise mechanics of how sexual selection aids the evolutionary process, guiding the population to local and global optima in a complementary fashion to natural selection. We can also expect to observe contexts in which sexual selection not only does not guide the population to optima but also inhibits the natural selection process, as predicted by the *fisherian runaway*. The reasoning behind our choice of raw sexual selection is that it gives us the power to observe evolutionary dynamics phenomena (such as the Sexy son hypothesis and Fisherian runaways) as well

as the effects of sexual selection in combinatorial optimization problems.

4.3.1 Fitness landscapes

By the same line of reasoning we adopted when experimenting with the gay uncle hypothesis, we decided to work with a simple bi-dimensional Gaussian function

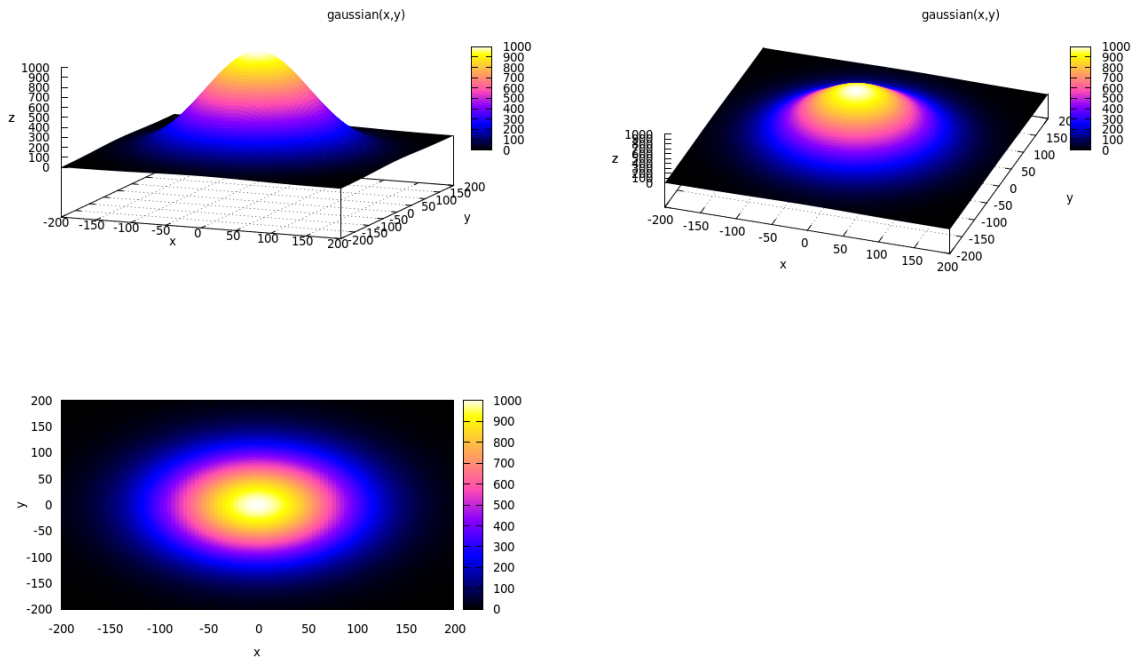$$\text{Gaussian}(x, y) = e^{-\frac{x^2 + y^2}{100^2}} \tag{4.1}$$

Figure 4.10: Bi-dimensional Gaussian function seen from different angles

However, because we want to evaluate the potential of sexual selection for solving optimization problems, we will also work with a variation of the Ackley's function, a popular benchmark for testing genetic algorithms.

The original version of the Ackley's function is the following:

$$\text{Ackley}(v) = -a \cdot \exp(-b \cdot \sqrt{\sum_{i=1}^{n_1} v_i{}^2}) - \exp(\sum_{i=1}^{n_1} \cos(c \cdot v_i)) + a + \exp(1) \tag{4.2}$$
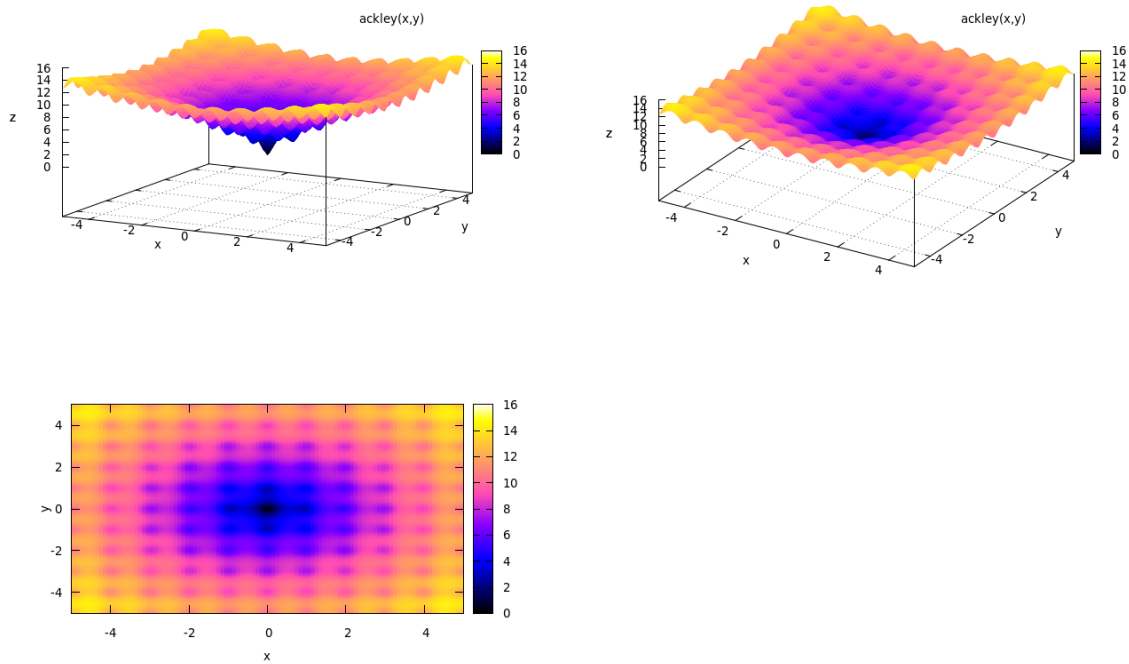
Figure 4.11: Bi-dimensional Ackley's function seen from different angles

We applied a small modification to it in order to render it compatible with the roulette wheel selection. As this selection method works with a non-negative domain of fitness values, we composed the original Ackley's function with the $\exp$ function:

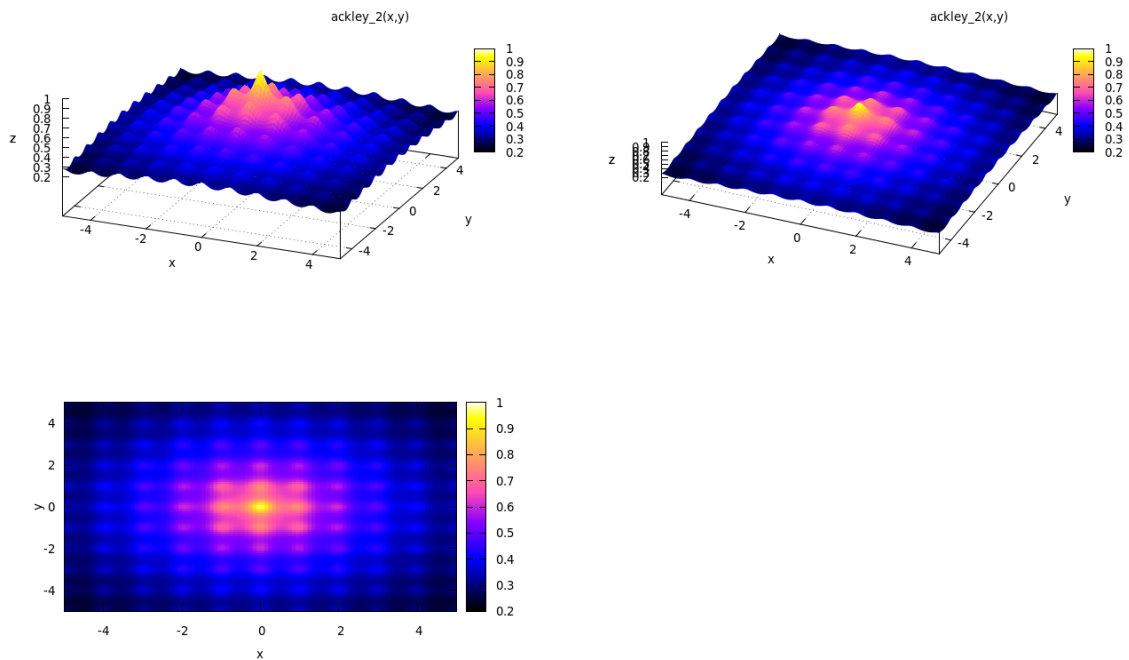$$\text{Ackley}_2(v) = \exp(0.1 \cdot \text{Ackley}(v)) \tag{4.3}$$

Figure 4.12: Bi-dimensional, modified Ackley's function seen from different angles
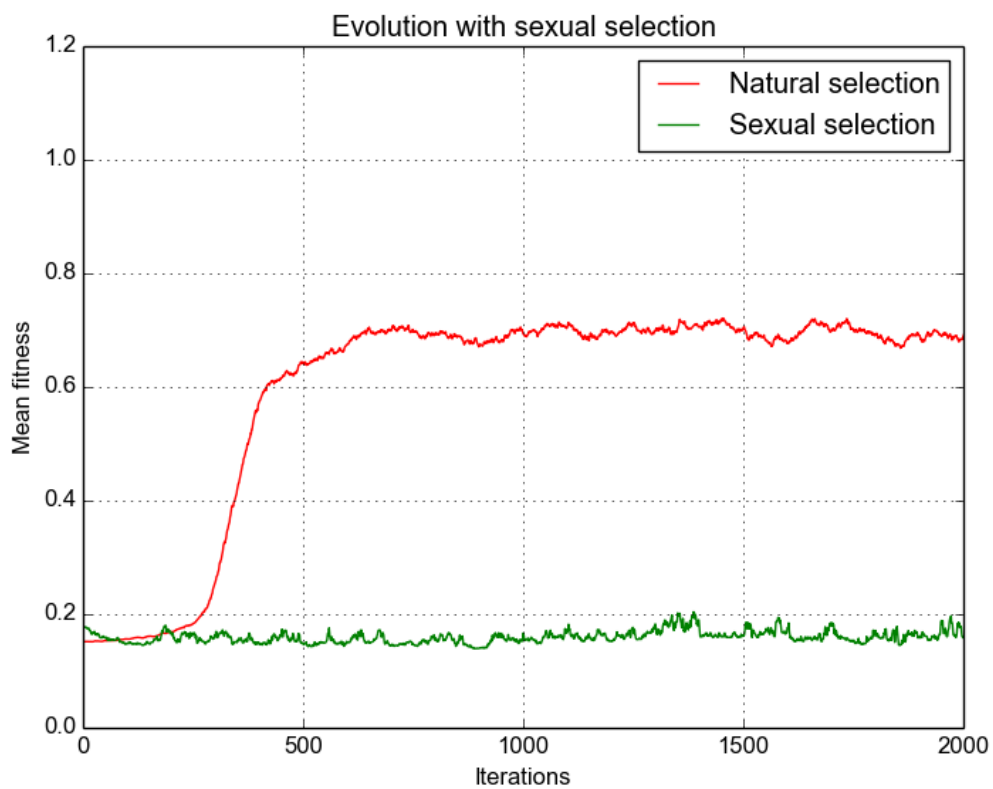
4.3.2 Plain natural selection

As we did in the previous section, our first step will be to experiment with a decremented model in order to be able to compare it with our regular model and point out the peculiarities of each one of them. Thus our first simulations will experiment on natural selection alone, with the sexual selection section of the genotype being repressed (it will not have any effect on evolutionary processes).

As was the case with our "no kin selection" model in Section 4.1, the evolutionary path of natural selection is approximately rectilinear throughout the whole process, being subject to random walks only in the closest proximity to the global maximum, due to the effects of the mutation rate (See Figure 4.14). The sexual selection evolutionary path, not surprisingly, does not show a preferred direction, exhibiting characteristics of a random walk consistently throughout the whole process. This of course happens because the sexual selection section of the genotype does not have any effect on evolutionary processes, and is consequently subject only to mutation. In our experiments with the Gaussian landscape, the population converges to a configuration of mean fitness approximately 9.5 by the 500th iteration, while in our experiments with the modified Ackley's landscape, the population converges to a configuration of mean fitness approximately 0.7 by the same time (See Figure 4.13). The discrepancy in these plateaus reflects the more difficult nature of the Ackley's landscape in comparison to the Gaussian landscape.
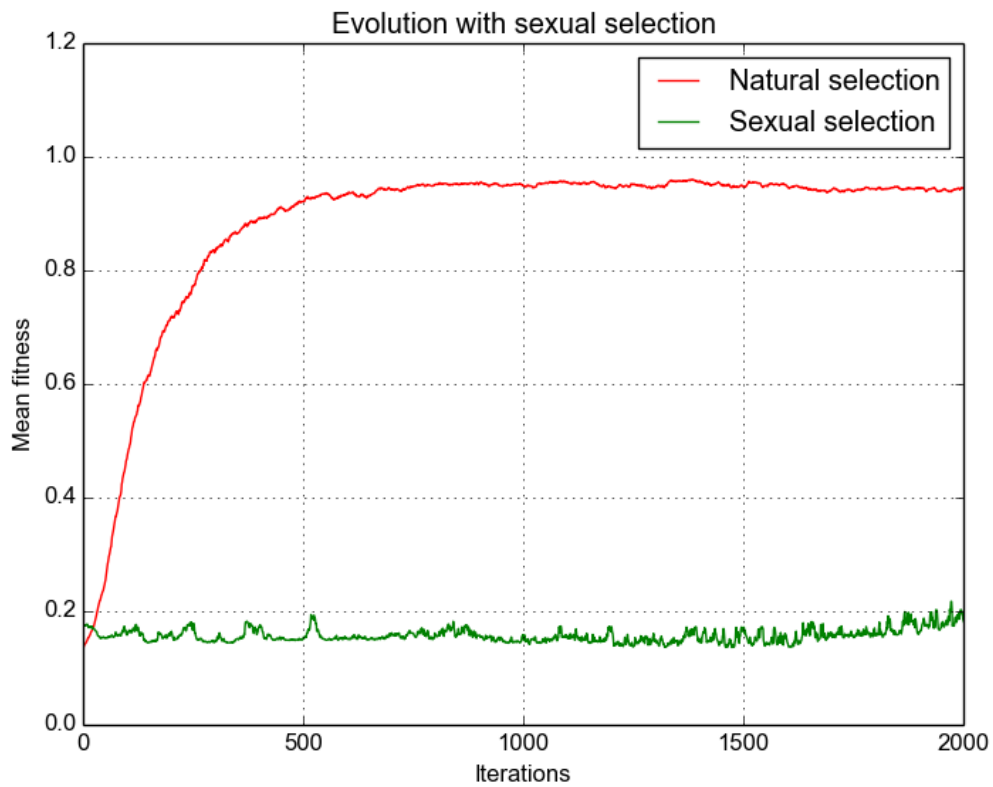
(a) Gaussian landscape

(b) Modified Ackley's landscape

Figure 4.13: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; Without sexual selection.

(a) Iteration 109

(b) Iteration 219

(c) Iteration 329

(d) Iteration 439

(e) Iteration 549

(f) Iteration 659

(g) Iteration 769

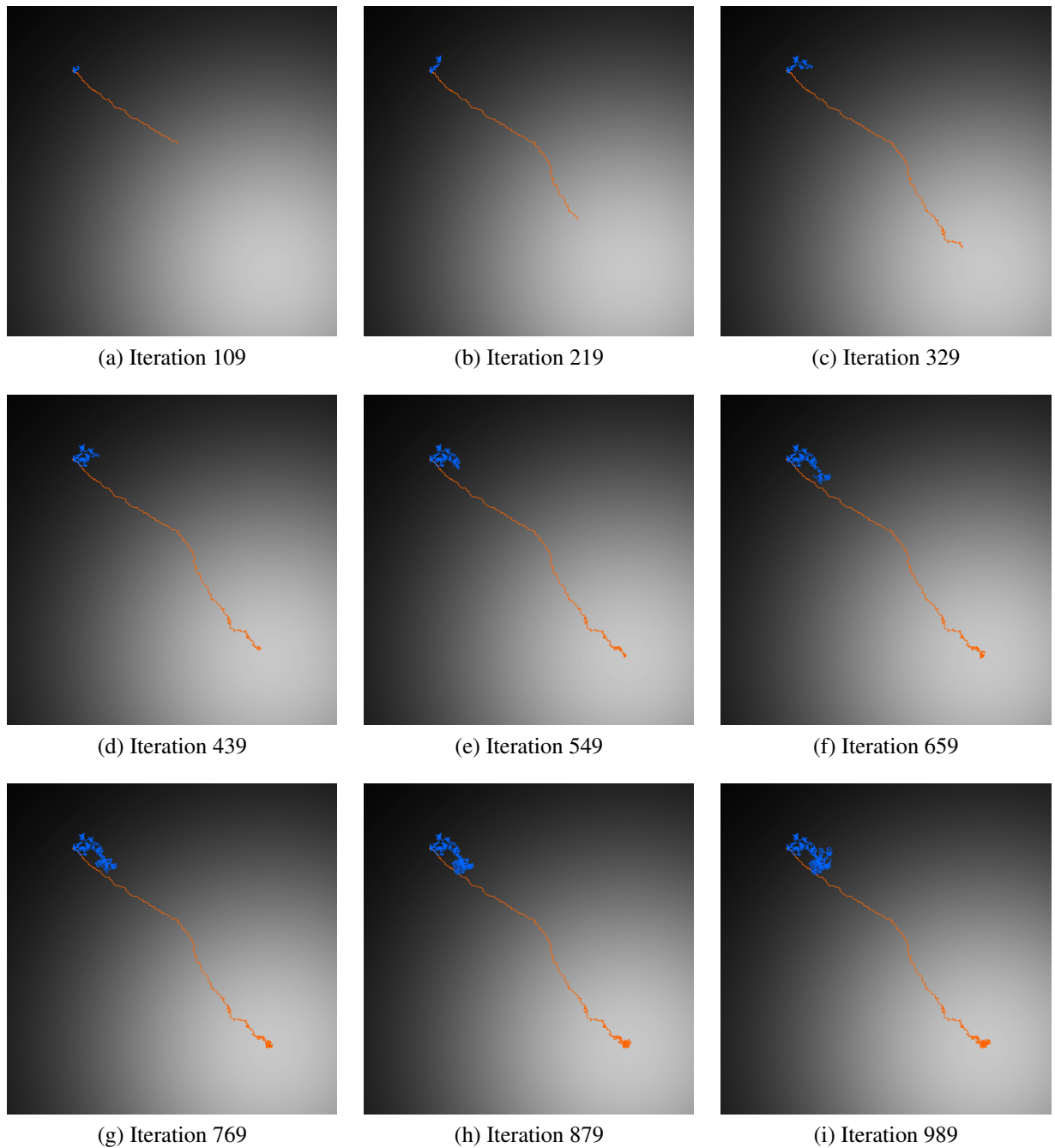(h) Iteration 879

(i) Iteration 989

Figure 4.14: Evolution of natural selection (orange) vs sexual selection (blue): the average genotypes for both natural selection and sexual selection are plotted in a bi-dimensional grid. Pop. size: 1000; Mate pool size: 100; Gaussian landscape; Without sexual selection.

4.3.3 Gaussian sexual selection with fixed standard deviation

We experimented with fixed standard deviation values ($\sigma \in \{0.125, 0.25, 0.5, 1.0, 2.0, 4.0\}$) for the Gaussian sexual selection model in order to analyse the evolutionary dynamics emergent from the subtraction of one degree of freedom from the sexual preference function.

The results we obtained are remarkable in the sense that they expose a fundamental

benefit of the sexual selection approach to genetic algorithms: in most cases, the sexual preference function outperforms natural selection itself in optimizing the fitness landscape. Figures 4.15 (Gaussian landscape) and 4.16 (modified Ackley's landscape) plot the population's mean fitness (natural selection curve) versus the fitness of the maximum of the mean sexual preference function (sexual selection curve) through time for varied values of standard deviation. With respect to the Gaussian landscape, we see that the general pattern is that the natural selection curve rises above the sexual selection curve for a short amount of time, and after that the sexual selection curve increases to values very close to the landscape's global maximum, approaching the asymptote *mean fitness* $= 1$ and surpassing the population's mean fitness. The same is true for the modified Ackley's landscape with $\sigma \in \{0.125, 0.25\}$. What this means is that, after sufficient time, sexual selection becomes a better estimator of the landscape's maxima than the genetic algorithm itself.

Because of the power of sexual selection, the performance of this model not only rivals that of the original genetic algorithm model (with the population's mean fitness converging only a hundred iterations after the plain natural selection model), but also surpasses it if we look to the fitness of the maximum of the mean sexual preference function. The sexual preference function is able to estimate the global maximum of the Gaussian landscape for $\sigma \in \{0.25, 0.5\}$ and surpass the performance of the plain natural selection model, which converges to a mean fitness of only 0.95. For the modified Ackley's landscape, the sexual preference function also estimates better solutions than the plain natural selection model, outperforming it in three cases $\sigma = 0.125, \sigma = 0.25, \sigma = 0.5$ and even accomplishing the impressive feat of estimating solutions with fitness values of 0.95 (for $\sigma = 0.125$) and 1.0 (for $\sigma = 0.25$). For comparison, the plain natural selection model is able, at its best moment, to produce solutions with fitness 0.7.

These results strongly suggest that studying sexual selection may be useful not only from the theoretical but also from the practical standpoint.
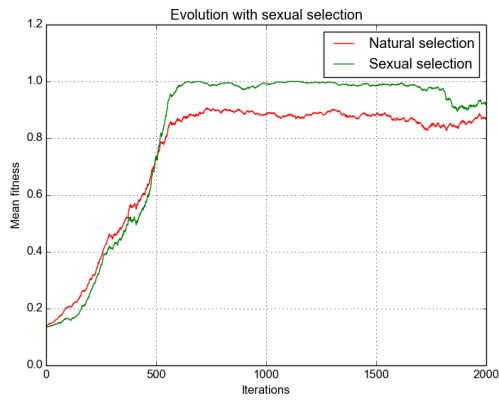
(a) $\sigma = 0.25$

(b) $\sigma = 0.5$

(c) $\sigma = 1.0$
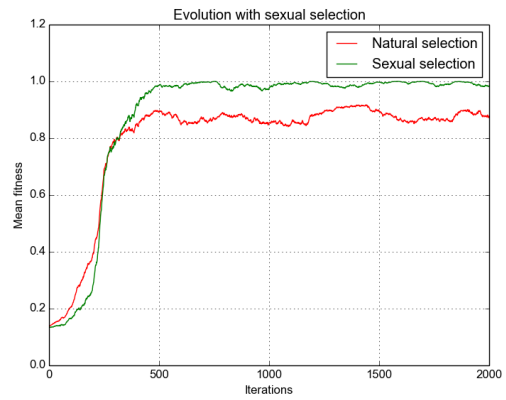
(d) $\sigma = 2.0$
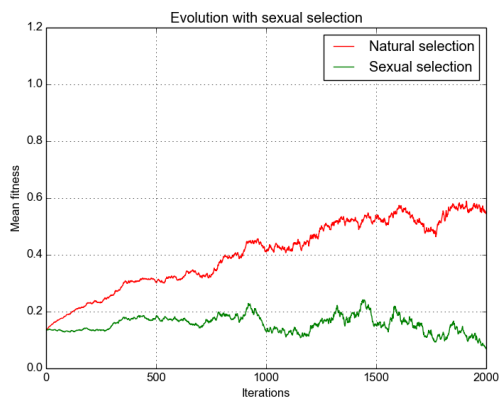
(e) $\sigma = 4.0$

Figure 4.15: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; Gaussian landscape; Gaussian sexual selection with fixed standard deviation.
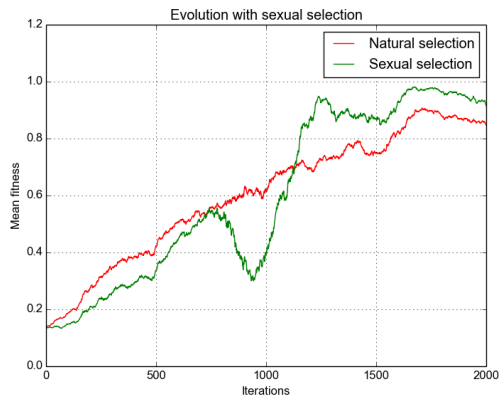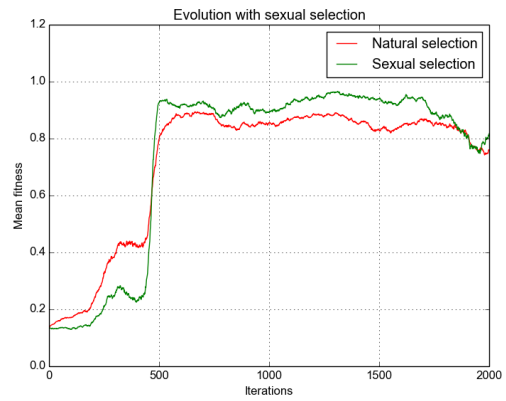
(a) $\sigma = 0.125$

(b) $\sigma = 0.25$

(c) $\sigma = 0.5$

(d) $\sigma = 1.0$

(e) $\sigma = 2.0$

(f) $\sigma = 4.0$

Figure 4.16: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; modified Ackley landscape; Gaussian sexual selection with fixed standard deviation.

4.3.4 Gaussian sexual selection with variable standard deviation

As soon as we allow the standard deviation of the sexual selection Gaussian function to vary, the population suddenly becomes increasingly sensitive to small mutations. It is reasonable to suggest that this is due to the fact that by granting more freedom to

sexual selection (in this case, the additional freedom of one parameter), we are making the population a greater victim to *fisherian runaways*.

It is important to note, however, that as though randomness becomes an important factor when variable standard deviation is introduced, the paths of both natural and sexual selection are consistently intertwined. This phenomenon can most easily be observed by comparing the behaviour of both paths from iterations 662 to 1104 (See Figure 4.17): the appearance of a "random walk blob" in the sexual selection path prompts the appearance of a similar blob in the natural selection path just a few iterations after. This effect is observable throughout the whole process: small perturbations in the sexual selection path typically prompt analogous perturbations in the natural selection path. Not only that, but we can observe how the main direction of natural selection path is shifted towards the left side of the landscape (see Figure 4.13 for comparison), arguably following the sexual selection path. This phenomenon gives us an interesting look on the *fisherian runaway* as it happens: a small perturbation in the initial conditions shifts the sexual selection path to the left; this is followed by the natural selection path shifting towards the left in order to keep up with sexual selection; from this moment on, both paths are intertwined in an endless race towards the same direction. However, they do not end up always going left because the evolutionary pressure always points in the direction of the landscape's global maximum (remember; our landscape is unimodal), which happens to be in the proximity of the right end of the landscape.

The emergence of Fisherian runaways in our results are able to explain why the performance of this particular model is significantly surpassed by those of the experiments with fixed standard deviation values, as this phenomenon is responsible for deviating the direction of natural selection.

Figure 4.17: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; Gaussian landscape; Gaussian sexual selection with variable standard deviation.
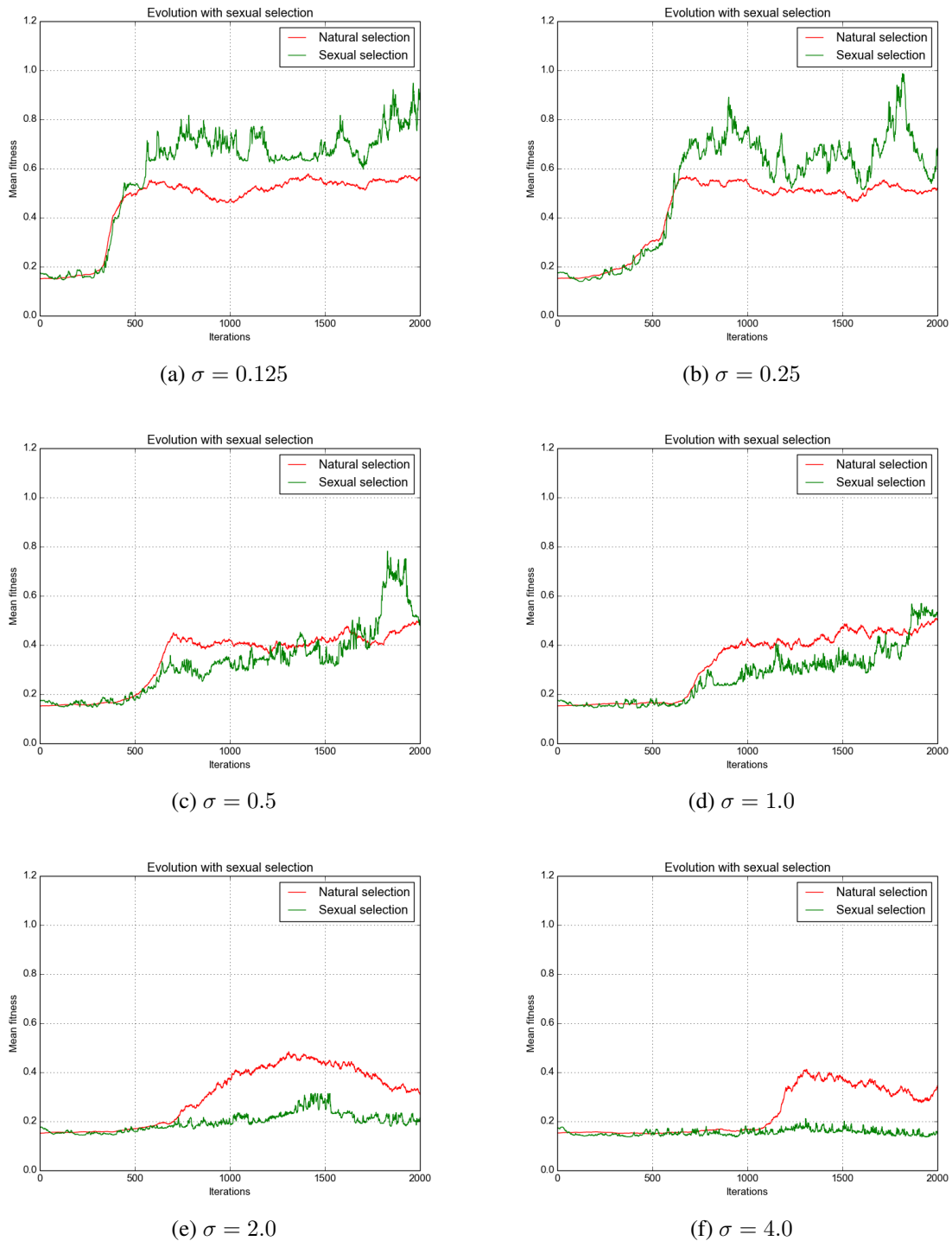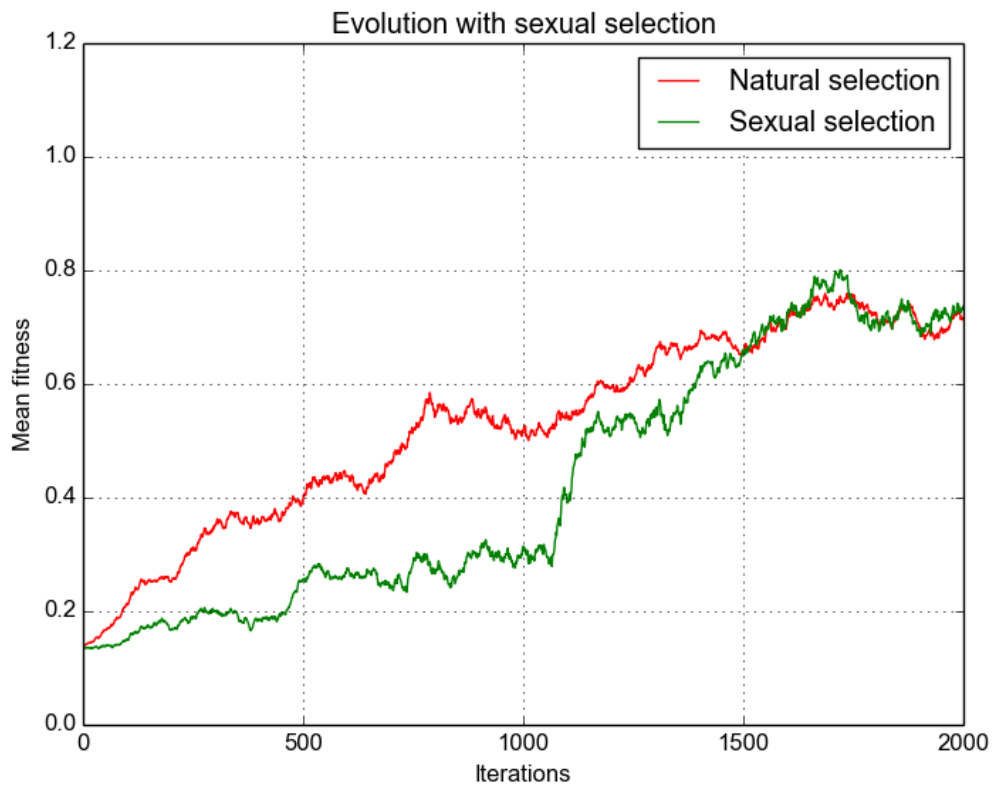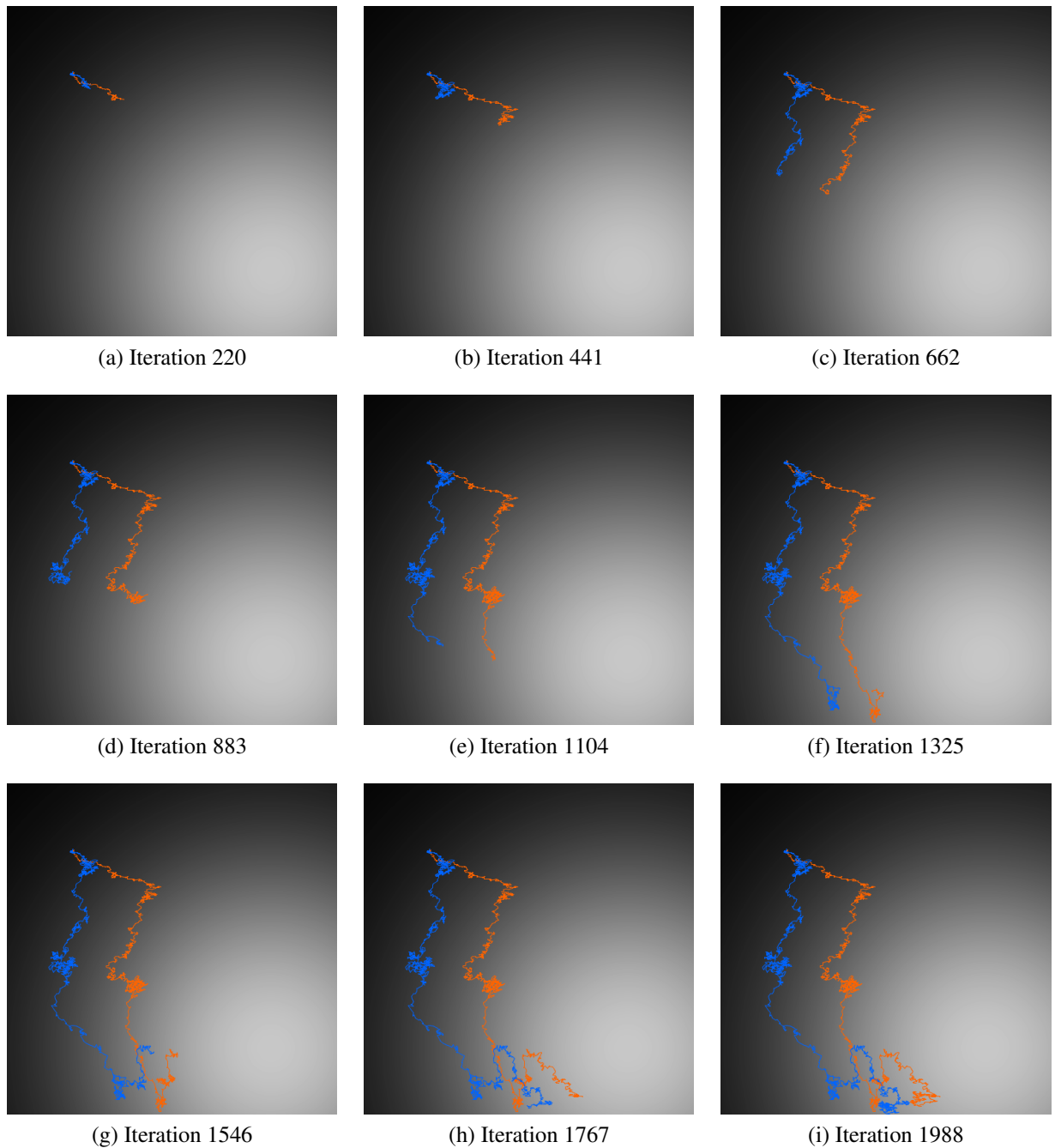
Figure 4.18: Evolution of natural selection (orange) vs sexual selection (blue): the average genotypes for both natural selection and sexual selection are plotted in a bi-dimensional grid. Pop. size: 1000; Mate pool size: 100; Gaussian landscape; Gaussian sexual selection with variable standard deviation.

4.3.5 Polynomial sexual selection

We experimented with the polynomial sexual preference model using varied polynomial degrees and two different fitness landscapes. With respect to Gaussian landscapes, we observed a convergence speed comparable to that of the Gaussian sexual preference model, with the population generally approaching the mean fitness of 0.8 near the 500th iteration. However, this model appears to be more reliable, as even its worst performances

are able to surpass the middle of the fitness spectrum by the 1000th iteration. For comparison, the worst performance of the Gaussian sexual preference model ($\sigma = 4.0$) takes 2000 iterations to linearly climb the fitness spectrum to the point of a mean fitness of 0.6, which gives us a slope of $\frac{0.6}{2000} = 3 \cdot 10^{-4}$ iterations per fitness unit. At the same time, the worst performance of the polynomial sexual preference model gives us a slightly better slope of $\frac{0.8}{2000} = 4 \cdot 10^{-4}$ while additionally reaching a mean fitness of 0.6 by the 700th iteration (slope: $\frac{0.6}{700} \approx 8.57 \cdot 10^{-4}$). These better results can be conjectured to be due to the hypothesis that this sexual preference model is less subject to the negative effects of Fisherian runaways than the former.

It is fundamental to note, however, that we are comparing these two sexual selection models with respect to the population's mean fitness, as we did not plot the fitness of the solutions estimated by the sexual preference function.

(a) polynomial degree: 1

(b) polynomial degree: 2
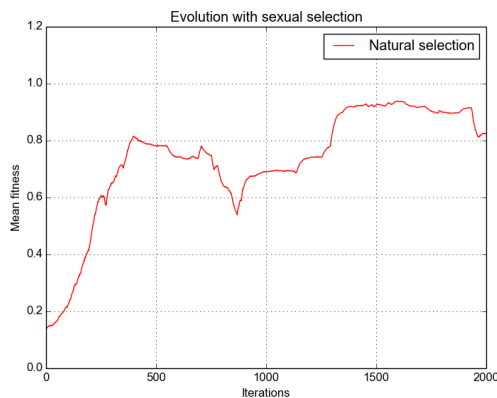
(c) polynomial degree: 3
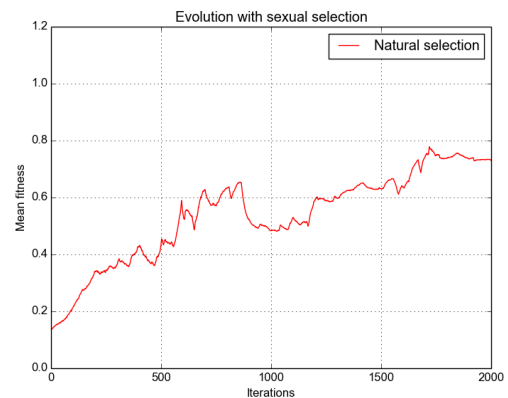
(d) polynomial degree: 4

Figure 4.19: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; Gaussian landscape; Polynomial sexual selection with varying degrees.

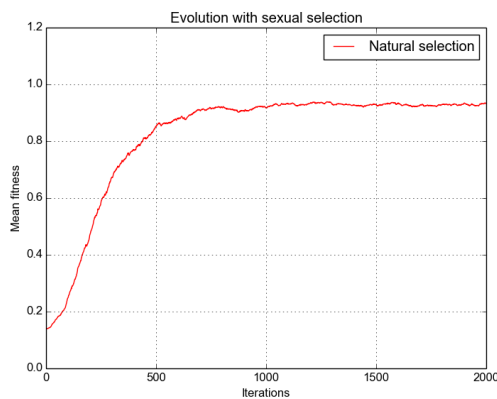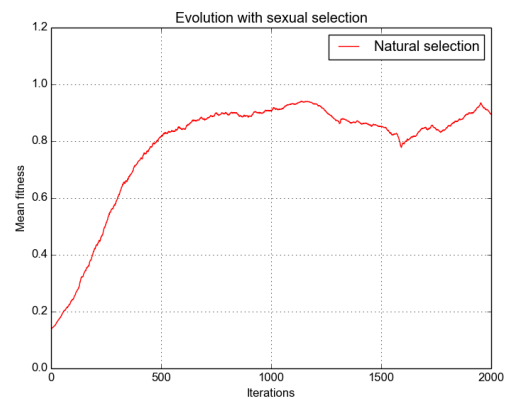(a) polynomial degree: 1

(b) polynomial degree: 2

(c) polynomial degree: 3

(d) polynomial degree: 4
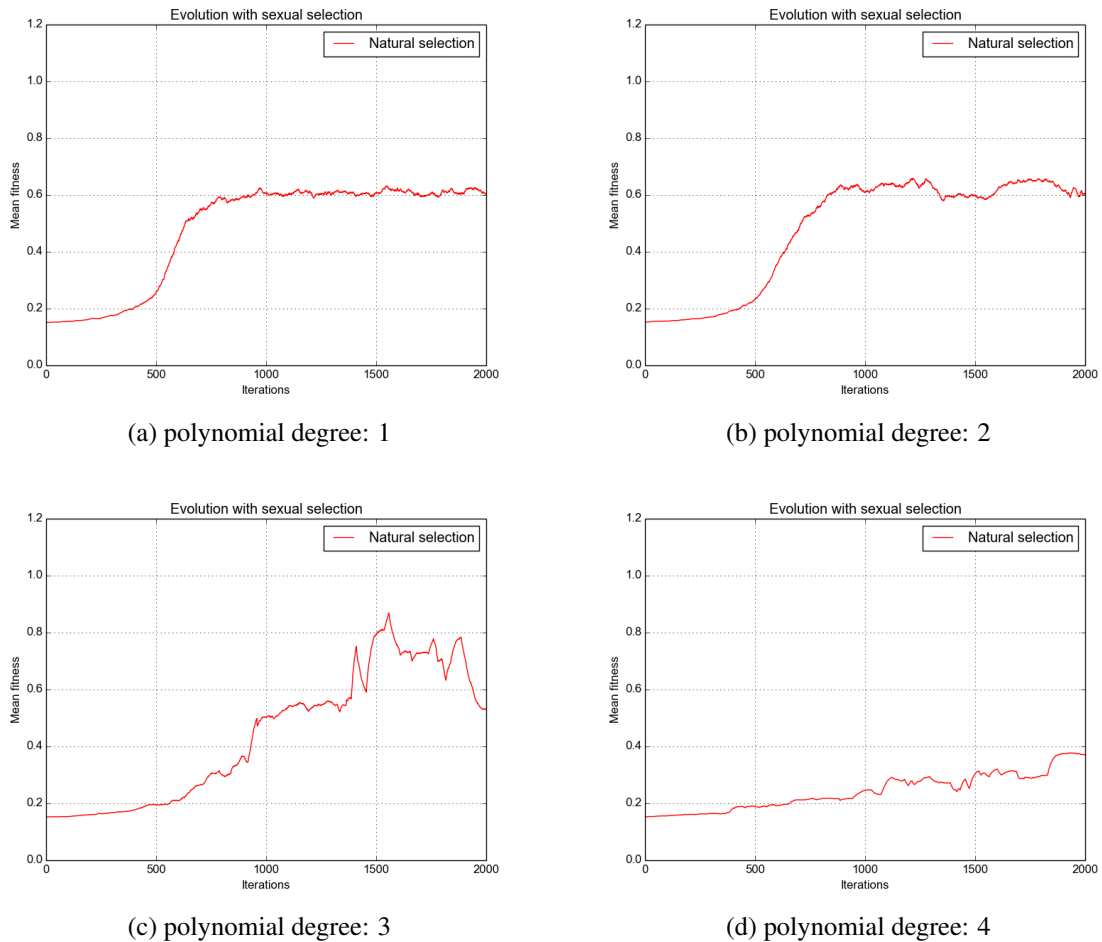
Figure 4.20: Fitness evolution of natural selection (red) vs sexual selection (green). Pop. size: 1000; Mate pool size: 100; Modified Ackley's landscape; Polynomial sexual selection with varying degrees.

A notable feature of the before mentioned results is the fact that the polynomial sexual preference model becomes highly subject to the effects of mutation with high polynomial degrees. This phenomenon can be observed from the graphs in Figure 4.19, in which polynomial degrees 1 and 2 generate smooth fitness curves while polynomial degrees 3 and 4 generate rugged ones. This is probably due to the fact that the genes encoding the polynomial coefficients of the sexual preference function are all subject to the same amount of mutation, but coefficients associated with high degrees are far more decisive in the general behaviour of a polynomial than the ones associated with small degrees. Because of that, a probably effective solution for this shortcoming is to modulate the mutation rate of genes encoding polynomial coefficients proportionally to the inverse of power function of the degree - for example, the mutation rate of the gene responsible for the coefficient of degree 1 could be two times greater than the one responsible for the coefficient of degree 2, four times greater than the one responsible for the coefficient of degree 3, eight times greater than the one responsible for the coefficient of degree 4, etc.

4.4 Final remarks

4.4.1 Kin selection, Homosexuality and the Gay uncle hypothesis

Our first and more basic result concerns the convergence speeds of both natural selection and homosexuality. We found that, while natural selection behaves linearly in the observed interval, homosexuality exhibits an hyperbolic pattern, fitting into an power function with exponent ≈ -0.7.

Adding kin selection to the model enabled us to uncover very interesting results. Notably, the presence of kin selection has the effect of stabilizing the average homosexuality predisposition at values suitable for the coexistence of heterosexual and homosexual organisms. This result is suggestive of the fact that kin selection is the tool that enables homosexuality to be evolutionarily feasible, as the gay uncle hypothesis predicts. Not only that, but our results also demonstrate the enormous power of kin selection, as they clearly show how the most insignificant amount of the parameter K can lead to paradigmatic shifts in the evolutionary history.

4.4.2 Unalike selection

The experimentation with the novel model of unalike selection provided us with very interesting results about how evolutionary dynamics shape the structure of the evolutionary path. By reversing the direction of kin selection, our expectations were that homosexuality would simply be selected out more vigorously than with no kin selection at all. Much to our surprise, we discovered that unalike selection has a similar role to kin selection in sustaining homosexuality, because it enforces homosexuals and heterosexuals to care for one another, creating dynamics comparable to those of predator and preys.

The most interesting aspect of these experiments was the formats of the evolutionary paths resulting from them. Because unalike selection enforces agents to care for their most distant relatives, it overlaps an existing evolutionary pressure with another one of comparable strength and opposite direction. This phenomenon makes the evolutionary path curve a self-similar structure, because the same pressures exist at all scales. By zooming into the curve and measuring its length at varied scales, we were able to calculate its fractal dimension as ≈ 2.

4.4.3 Sexual selection, Fisherian runaway and the Sexy son hypothesis

Our experimentation with sexual selection was not only able to uncover clear displays of Fisherian runaways and Sexy son dynamics in action, but also to provide us with information about how much effect sexual selection can have on natural selection, which can be used to develop clever ways to enhance the performance of state-of-art genetic algorithms for optimization problems. Particularly, we have observed the monumental potential of sexual selection as an estimator of the landscape's maxima, as some of our results indicated that the solutions found by the sexual preference function were of better quality than those found by natural selection itself.

With respect to combinatorial optimization purposes, we were able to observe the shortcomings of our sexual selection model, an important result because it enables us to know where to look for in order to enhance its performance in further studies. We conjec-

tured that Fisherian runaways are the main factor contributing to performance issues in our algorithm, as it deviates the climb in the fitness landscape. We were also able to observe that some varieties of our model are less subject to the effects of Fisherian runaways: the polynomial sexual preference model, for instance, seems to outperform the Gaussian sexual preference model in this aspect. Although our time was insufficient to test all of our hypothesis, we also conjectured that the performance of the polynomial sexual preference model could be enhanced through decreasing the mutation rate of genes associated with high-degree polynomial coefficients. This hypothesis, along with experimenting with a myriad of potentially (and probably) more efficient sexual preference models, is reserved for further studies.

5   CONCLUSIONS AND FUTURE WORK

The work we set out to do was to provide evidence that computer models are a valid, successful approach to investigating evolutionary dynamics. It was our belief that, in the same way that mathematical models expanded upon the intuitive reasoning of an older fashion of evolutionary biology, computer simulations could provide a next step in the progression of thinking about evolution. This belief was justified by the fact that field research is usually expensive and often powerless to record all the minutiae of the evolutionary history, while computer simulations, if carefully programmed, can give us a full grasp on the information about the evolution of artificial creatures.

In order to prove our point, we developed a series of three simulations, trying to address evolutionary puzzles demanding perhaps more information than field research could possibly give us. The first one elaborated about kin selection and the Gay uncle hypothesis, and our results were able to find and measure the equilibrium between kin selection and homosexuality. This analysis was only possible because we had access to all instants of the evolutionary process and also because the abstract encoding of our genotypes allowed us to track the path of the population in the fitness landscape. The second simulation concerned a variation of kin selection we named *unalike selection*. This variation reverses the direction in which kin selection works, and we were able to identify and measure its results in the evolutionary path of our artificial population. Notably, we found that this modification was responsible for self-similar curves with multi-fractal behaviour. This result relied heavily on the plasticity with which our program's code allowed us to shape the fitness landscape, making it a bi-dimensional Gaussian function: on the real world, our analysis would be impossible or extremely difficult because of the complexity of typical biological landscapes. The third simulation concerned sexual selection, and through it we were able to clearly observe the display of Fisherian runaways and Sexy son dynamics, as well as obtain information about the directions one should take in order to make sexual selection a viable addition to genetic algorithms for optimization problems. We developed two flavours of sexual selection for genetic algorithms, each one relying on a particular function encoding. One of these flavours proved itself to be extremely powerful, outperforming the original genetic algorithm model, while the other one exhibited signs suggesting that its performance can be improved by a subtle modification in the mutation mechanism.

The fact that we worked with experiments in-between the realms of mathematics and field research enabled us to uncover results hidden from both perspectives. We were able to draw conclusions inaccessible from the mathematical sense by reporting behaviours not yet tackled by mathematical models while we were also able to draw conclusions inacces-

sible from the biological sense by abstracting complex details about real-life reproduction and observing the behaviours emergent from the distilled evolutionary system we created.

5.1 Future Work

For all the three simulations we set out to do, the combinatorial explosion of parameter configurations forbids us from exhaustively testing all of them. Because of that, there are obvious gaps in our experiments, and they should be addressed in future works. A particularly important one is that of the fitness landscape benchmarks, from whose we tested only a small portion. With respect to the Gay uncle hypothesis, we are left to wonder about the implications of adopting very large or very small kin selection parameters (K), as we were able to test only a limited spectrum. With respect to unalike selection, future works should address the relationship between the kin selection parameter and the measured fractal dimension of the evolutionary path curve, as we tested this model exclusively with $K = 0.01$. The simulation with the greater potential for expansion, however, is the third, concerning sexual selection. Because its implications for combinatorial optimization have great potential, future works should test sexual selection over a series of benchmarks for genetic algorithms and propose modifications to render them general and efficient. The fine tuning of the parameters of the Gaussian sexual selection model is left to future research, as well as experimentations with the hypothesis that modulating the mutation rate in the polynomial sexual selection model could render it more efficient. Not only that, but future works should expand our model proposing new varieties of sexual selection beyond Gaussian and polynomial sexual selection. The potential for innovation is unlimited, as the encoding of the sexual preference function can draw inspiration from any class of functions (polynomials, power functions, logarithms, etc.). A model with particular potential is employing artificial neural networks **?** or finite state machines to compute the sexual preference function, which would further expand the limits of what the sexual preference function can estimate.

REFERENCES

BAILEY, J. M. A Genetic Study of Male Sexual Orientation. **Arch Gen Psychiatry**, [S.l.], v.48, n.12, p.1089, 1991.

BATEMAN, A. J. Intra-sexual selection in Drosophila. **Heredity**, [S.l.], v.2, n.3, p.349–368, Dec. 1948.

BECK, C. W. et al. A Genetic Algorithm Approach to Study the Evolution of Female Preference Based on Male Age. **Evolutionary Ecology Research**, [S.l.], v.4, p.275–292, 2002.

BOBROW, D.; BAILEY, J. Is male homosexuality maintained via kin selection? **Evolution and Human Behavior**, [S.l.], v.22, n.5, p.361 – 368, 2001.

BUTTERFIELD, N. J. Bangiomorpha pubescens n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the mesoproterozoic/neoproterozoic radiation of eukaryotes. **Paleobiology**, [S.l.], v.26, n.3, p.386–404, 2000.

CAMPERIO CIANI, A.; CERMELLI, P.; ZANZOTTO, G. Sexually Antagonistic Selection in Human Male Homosexuality. **PLoS ONE**, [S.l.], v.3, n.6, p.e2282+, June 2008.

CHENEY, N. et al. Unshackling evolution. **SIGEVOlution**, [S.l.], v.7, n.1, p.11–23, 2014.

CLARKE, D. A.; MINSKY, M. L. Computation: finite and infinite machines. **The American Mathematical Monthly**, [S.l.], v.75, n.4, p.428, 1968.

DARWIN, C. **On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life**. sixth.ed. [S.l.]: J. Murray, 1872.

DAWKINS, R. **The Blind Watchmaker**. [S.l.]: Longman Scientific and Technical, 1986.

DAWKINS, R. **The selfish gene**. [S.l.]: Oxford University Press, 2006.

FISHER, R. **The genetical theory of natural selection**. Oxford: Clarendon Press, 1930.

FRANKOWSKI, B. L. Sexual Orientation and Adolescents. **Pediatrics**, [S.l.], v.113, n.6, p.1827–1832, 2004.

GOH, K. S.; LIM, A.; RODRIGUES, B. Sexual Selection for Genetic Algorithms. **Artif. Intell. Rev.**, Norwell, MA, USA, v.19, n.2, p.123–152, Apr. 2003.

GRIFFIN, A. S. A genetic analysis of breeding success in the cooperative meerkat (Suricata suricatta). **Behavioral Ecology**, [S.l.], v.14, n.4, p.472–480, 2003.

HAMILTON, W. D. The genetical evolution of social behaviour. I. **Journal of Theoretical Biology**, [S.l.], v.7, n.1, p.1–16, July 1964.

HAMILTON, W. D. The genetical evolution of social behaviour. II. **Journal of theoretical biology**, [S.l.], v.7, n.1, p.17–52, July 1964.

HARTE, D. **Multifractals**. [S.l.]: Chapman |& Hall/CRC, 2001.

HEISENBERG, W. Kausalgesetz und Quantenmechanik. **Erkenntnis**, [S.l.], v.2, n.1, p.172–182, 1931.

HOLLAND, J. **Adaptation in Natural and Artificial Systems**. Ann Arbor, Michigan: University of Michigan Press, 1975.

LEUTHOLD, B. M.; LEUTHOLD, W. Food habits of giraffe in Tsavo National Park, Kenya. **African Journal of Ecology**, [S.l.], v.10, n.2, p.129–141, 1972.

LOTKA, A. J. Contribution to the Theory of Periodic Reactions. **The Journal of Physical Chemistry**, [S.l.], v.14, n.3, p.271–274, Jan. 1910.

LOTKA, A. J. **Elements of Physical Biology**. [S.l.]: Williams and Wilkins, Baltimore, 1920.

LUMLEY, A. J. et al. Sexual selection protects against extinction. **Nature**, [S.l.], 2015.

MALTHUS, T. **An Essay on the Principle of Population**. London: J. Johnson, 1798.

MANDELBROT, B. How Long Is the Coast of Britain? Statistical Self-Similarity and Fractional Dimension. **Science**, [S.l.], v.156, n.3775, p.636–638, 1967.

MCCULLOCH, W.; PITTS, W. A logical calculus of the ideas immanent in nervous activity. **Bulletin of Mathematical Biology**, [S.l.], v.52, n.1-2, p.99–115, 1990.

MYERSON, R. B. **Game theory - Analysis of Conflict**. [S.l.]: Harvard University Press, 1997.

NASH, J. F. Equilibrium points in n-person games. **Proceedings of the National Academy of Sciences**, [S.l.], v.36, n.1, p.48–49, 1950.

NEUMANN, J.; MORGENSTERN, O. **Theory of games and economic behavior**. 3. ed..ed. Princeton, NJ: Princeton Univ. Press, 1953.

NEUMANN, J. von. Zur Theorie der Gesellschaftsspiele. **Mathematische Annalen**, [S.l.], v.100, n.1, p.295–320, Dec. 1928.

RICHARDSON, L. F.; ASHFORD, O. M. **Collected papers of Lewis Fry Richardson**. [S.l.]: Cambridge University Press, 1993.

SINGH, D.; BRONSTAD, P. M. Female body odour is a potential cue to ovulation. **Proceedings of the Royal Society B: Biological Sciences**, [S.l.], v.268, n.1469, p.797–801, 2001.

SMITH, J. M. **Evolution and the Theory of Games**. Cambridge, UK: Cambridge University Press, 1982.

SMITH, J. M. **Evolution and the Theory of Games**. [S.l.]: Cambridge university press, 1982.

SMITH, J. M.; PRICE, G. R. The Logic of Animal Conflict. **Nature**, [S.l.], v.246, n.5427, p.15–18, 1973.

VOLTERRA, V. Variation and fluctuations of the number of individuals of animal species living together. In: **Animal Ecology**. [S.l.]: McGraw-Hill, 1926.

WOLFRAM, S. **A new kind of science**. [S.l.]: Wolfram Media, 2002.

.1 Fractals, multifractals and fractal dimensions

Measuring the length of structures with statistical self-similarity - that is, shapes whose small portions can be considered reduced-scale images of the whole -, is not particularly useful, because their length is determined by the scale in which they are measured. For example, the length of the coastline of Britain - as is the general case for coastlines - is known to increase exponentially with the reduction of the length of the ruler used to measure it RICHARDSON; ASHFORD (1993). For this reason, it is more useful to catalogue the relationship between ruler size and measured length than to catalogue a particular length measured with a particular ruler - this way, we have the means to extrapolate our data and calculate the length of a curve for any ruler length we can imagine. Mathematician Benoit Mandelbrot discusses a measure of the exponent of similarity of a self-similar curve (called D) in his famous paper "How long is the coastline of Britain?" MANDELBROT (1967). This exponent of similarity is closely related to the idea of dimensionality, and can in fact be thought as an extension of our everyday concept of dimensions. When we say that a square is a bi-dimensional object, we really are saying that it is quadratically self similar: a $10\times$ scaling applied on a 1×1 square will result in an object composed of $10^2 = 100$ self-similar 1×1 squares. This is the reason why 1-dimensional objects scale linearly, 2-dimensional objects scale quadratically and 3-dimensional objects scale cubically with respect to an increase in side length. However, although our naive definition of dimensionality deals with positive, integer-based exponents, there are some examples of objects that scale with exponents in between these integer values. For instance, a $2\times$ scaling applied on the Sierpinski gasket WOLFRAM (2002) will result in an object composed of 3 self-similar gaskets, which gives us an exponent of self similarity $\frac{\log 3}{\log 2} \approx 1.5849$. By the same measure, the coastline of Britain was calculated by Richardson as approximately 1.25 RICHARDSON; ASHFORD (1993).

Theory of fractal dimensions predicts that plotting $\log N$ as a function of $\log \frac{1}{r}$ should result in a straight line with a slope coinciding with the similarity exponent D. This happens because typical fractals have exponential rates of self-similarity, their scaling being determined by some equation in the format $N(r) = Cr^D$. Because the exponent D is constant for all possible ruler sizes, the rate between $\log N(r) = \log Cr^D$ and $\log \frac{1}{r}$ is given by:

$$\frac{\log Cr^D}{\log \frac{1}{r}} =$$

$$\frac{\log C + \log r^D}{\log 1 - \log r} =$$

$$\frac{\log C + D \log r}{0 - \log r} =$$

$$\frac{\log C + D \log r}{- \log r} =$$

$$\frac{\log C}{- \log r} + \frac{D \log r}{- \log r} =$$

$$-\frac{\log C}{\log r} - D$$

For sufficiently large values of r, the term $-\frac{\log C}{\log r}$ approaches zero, and because the

measure of dimensionality is concerned with $r \to 0$, we have $\lim_{r \to 0}(-\frac{\log C}{\log r} - D) = -D$. However, whereas typical fractals have constant slopes, our graph (see **??**) has a drastically different shape, its derivative varying along the x axis. Structures with this property are called *multifractal systems* - a generalization of a fractal whose similarity exponent varies with the length of the ruler HARTE (2001). This phenomenon is easily explained: our path behaves as a multifractal because its fractal nature is contained within a particular range of ruler sizes. For very large ruler sizes, an increase in ruler size is irrelevant: our calculation will always measure the distance between the path's two endpoints. Likewise, for very small ruler sizes, a decrease in ruler size is irrelevant: our calculation will always measure the path's total length, accurate to pixel level. Because of this, the slope of our graph approaches zero towards both $-\infty$ and ∞. This phenomenon is not restricted to our results, though - it is inherent to any physical object. Think for example of the west coast of Britain: for any ruler size larger than the distance between its two endpoints, we will always measure that exact same distance, whereas for any ruler size shorter than a Planck length HEISENBERG (1931), we will always measure the same length, accurate to quantum levels. This is due to the fact that the coast of Britain is limited by the distance between its endpoints - it does not extend forever for zoom factors < 1 - and because the ruler size is limited by the uncertainty principle, which states that the Planck length is the smallest measurable length HEISENBERG (1931). The physical world is, after all, limited by physics in a fashion deeply similar to the way the digital world is limited by pixel size and memory limits. In short, if we want to accurately measure the dimensionality of our path, we must select a range of ruler sizes for which the slopes in our graph are significantly larger than zero. Making this decision is necessary even when measuring the dimensionality of a clearly typical fractal as the evolutionary path of natural selection: Figure 1 shows us that if we extend our range of ruler sizes to very large values of r, we break the rectilinear structure of the graph even for natural selection.
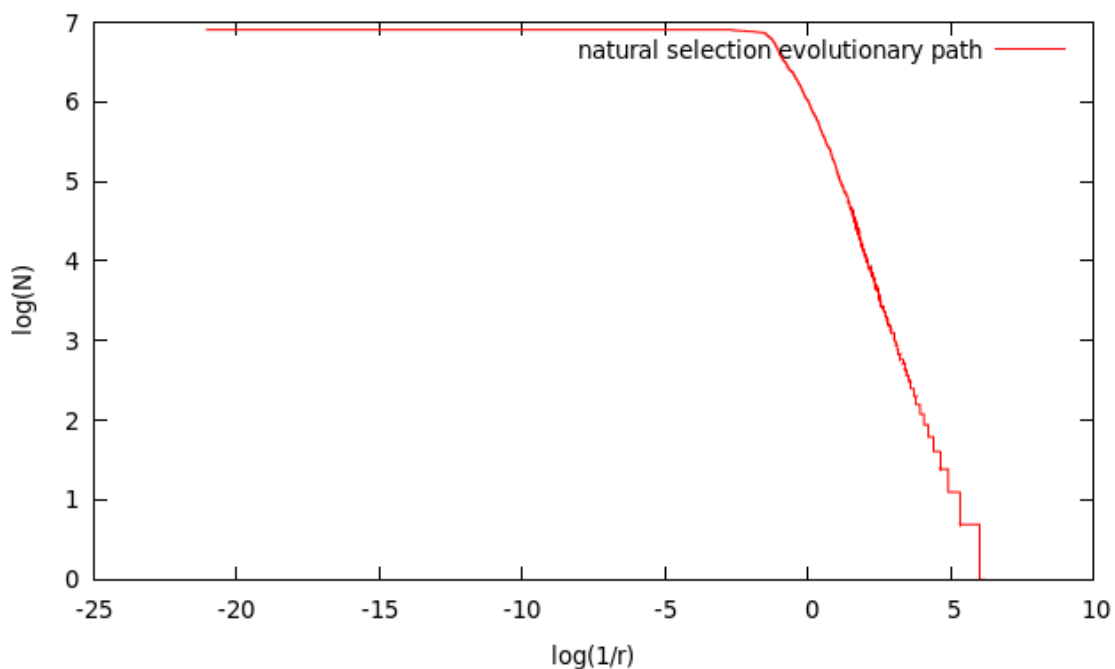

Figure 1: Measurement of the natural selection evolutionary path length N with respect to the ruler size $\frac{1}{r}$. Pop. size: 1000; Mate pool size: 100; $K = 0.01$