

A theoretical model of coevolution of culture and gene and the effects of mating and learning biases on cultural evolution

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CERTIFICATE

This is to certify that this dissertation entitled "*A theoretical model of gene-culture coevolution and the effects of mating and learning biases on cultural evolution*" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Naven Narayanan Venkatanarayanan at IISER Pune under the supervision of Dr. Sutirth Dey, Associate Professor, Biology Division, IISER Pune during the academic year 2017-2018.



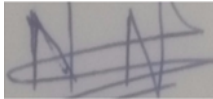
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DECLARATION

I hereby declare that the matter embodied in the report entitled “*Costs and correlates of evolution of increased dispersal in Drosophila melanogaster*” are the results of the work carried out by me at the Department of Biology, IISER Pune, under the supervision of Dr. Sutirth Dey and the same has not been submitted elsewhere for any other degree.



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Abstract

Gene-culture coevolutionary theory examines the effects of cultural traits, in addition to passing on of genetic traits from one generation to the next differentially. I construct a theoretical model that studies, in addition to the contribution of the phenotype of the organism, its interaction with the extended phenotype while determining the fitness of an individual in the population. I study both negative and positive interactions between the organismal phenotype and the extended phenotype. Positive interaction is when the extended phenotype enhances the fecundity of the individual, whereas negative interaction is when the extended phenotype adversely affects the fecundity of the individual. In both cases, the fitness increases as the population evolves with time. Interestingly, however, this increase is faster in the case of negative interaction than in positive interaction. In the second part of my thesis, I extend my model to study the evolution of cultural learning in a sexual system of reproduction. I combine frequency-dependent learning biases namely, conformation bias and novelty bias, and assortative mating (in addition to the usual case of random mating) to examine the evolutionary dynamics of cultural traits. Since the biases modelled are frequency-dependent, I also investigate the cyclical fluctuations in cultural trait values for the two mating systems. My results agree with several results present in literature and also add a few insights to the existing knowledge of cultural evolution.

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INTRODUCTION

The outcomes of evolutionary processes cannot be fully appreciated without understanding how organisms modify the agents of natural selection in their environments, thereby modifying the process of biological evolution itself. This process of organisms modifying their environment is called niche construction (Laland and Brown, 2006). Proponents of the niche construction theory argue for its significance and its inclusion in modern evolutionary theory by claiming that it has several consequences. First, niche construction may contribute and/or modify the flow of energy and matter through ecosystems (Hölldobler and Wilson, 1990). Second, niche construction causes the modification of the environmental selective pressures on the organism by actively altering the environment itself, hence potentially altering the evolutionary trajectories of the concerned organisms (Jones et al., 1994). In addition, these modified selection pressures could be bequeathed to the successive generations, modifying the selection pressures for them as well (Odling-Smee et al., 1996). Another important claim is that niche construction provides a second process in addition to natural selection that would assist the organism's response to the environment it is present in and allow it to adapt (Laland et al., 1999).

Cultural niche construction is a special case of niche construction, where a few cultural traits contribute to forces acting upon on genetic traits (which are evolutionary in nature), which could serve as a powerful tool for explaining evolution and behaviour. Gene-culture and/or culture-culture interactions are a subset of interactions which are included in cultural niche construction.

Gene-culture coevolutionary theory comes under theoretical population genetics and attempts to include in its modelling the effects of cultural traits, in addition to differential transmission of genetic traits from one generation to another (Feldman and Laland, 1996). The importance of including the cultural component while modelling was

demonstrated in a study which showed that the Sickle Cell mutant's frequency in West African populations depends on a cultural trait, namely, yam farming. Populations that cultivated yams and cut trees in those regions create conditions where pools of rainwater remain stagnant, thus allowing mosquitoes to breed there, leading to strong selection of one form of the allele. Hence, in this case, the intensity of selection on a gene depends on the frequency of yam farming- the cultural component here- in the population. A second example of gene-culture coevolution is the evolution of lactose absorption. A significant percentage of human adults cannot break down lactose in their digestive system due to low activity of the lactase enzyme. The cultural practice of dairy farming, however, seems to contribute to a change in the allele frequency of genes that give rise to difference in phenotypes (namely individuals who can/cannot absorb lactose). There were about 90% lactose absorbers in populations with dairy farming traditions, whereas in populations with no dairy farming culture, absorbers accounted for less than 20% of the population. It is therefore quite likely that the cultural practice (dairy farming) had a key role in determining the allele frequencies in these populations (Swallow, 2003; Laland et al., 2001).

In gene-culture models, the methods of transmission of cultural traits need to be defined separately, in addition to the genetic traits. These rules are defined based on the type of transmission being modelled. Vertical transmission occurs when an individual adopts a trait depending on whether its parent (s) has (have) that trait. Horizontal transmission involves the transmission of cultural traits between non-related conspecifics in the same generation, whereas oblique transmission occurs between generations (except from parents). When cultural traits are passed from key individuals in a group, it is termed indirect transmission, whereas frequency-dependent transmission occurs when the cultural trait is learned from the majority in a group (Bonduriansky and Day, 2009). Models detailing the relationship between the genetic aspect of evolution and cultural modifications have become increasingly complex with time (Rendell et al., 2011).

Initial models treated culture similar to any other feature of the phenotype, and while culture affected the individuals in a population, only the genes were passed to the next generation and it was only through the expression of these genes that the population's culture in the subsequent generations could be altered (Tooby and Cosmides, 1990). As the gene-culture coevolutionary theory developed, models allowed for inheritance of cultural traits, which in turn could modify the selection pressures faced by the organisms (Cavalli-Sforza and Feldman, 1981). An extended gene-culture coevolution framework considered the niche construction aspect due to inheritance of genetic as well as cultural traits generating modified selection pressures that affect future generations (Laland et al., 2000).

Despite advances in the field of genomics in recent years, leading to studies ignoring gene-culture coevolutionary theory in the belief that traits are predominantly determined by their underlying genetic basis, it is important to note that several unintuitive results and complex dynamics have resulted from theoretical studies considering culture. In population genetics, where culture is not considered, it is well known that heterozygote advantage would allow for genetic variation to be maintained (Rendell et al., 2011). It has also been shown that cultural trait transmission is not advantageous if the environment is constant or changing very quickly. Rather, it is helpful for the offspring to learn from their parents when the environment is slowly changing (Boyd and Richerson, 1985). These examples show that several potentially unintuitive behaviours are possible in systems when cultural transmission is incorporated.

To understand social learning, formal models to study the interplay between individual learning, social learning, and behavioural responses have been developed. Although these models apply to a wide range of natural systems pertaining to social learning, several general patterns are observed. For instance, it has been observed that social learning is favoured in environments where there is an intermediate level of fluctuation

(Feldman et al., 1996; Bergman and Feldman, 1995). This is because social learning allows quicker response to environmental changes than hard-wired responses, by virtue of the knowledge in the population accumulated over time (Boyd et al., 2011). If the environmental changes are glacial, then there is no significant effect of social learning because selection on the genes of individuals has the same effect. In this case, there would be no benefit in developing a learning machinery, which could be expensive (in terms of resources required). In environments where there are extremely rapid fluctuations, the problem of lack of knowledge arises. Each environment has not been present long enough for the population to develop a knowledge base that would aid in its adaptation. However, at intermediate rates of environmental fluctuation, social learning mechanisms are quicker than genetic adaptation and the individuals in the population also have enough time to gather adaptive knowledge (Winterhalder and Smith, 2000; Boyd and Richerson, 1995). In a given environment, Boyd and Richerson further showed that cultural learning in populations happens only in cases where the individual learning of the trait is relatively simple or when the trait is particularly useful in helping the individual adapt to its environment (Boyd and Richerson, 1995).

A very pertinent idea in the field of cultural inheritance is the costly information hypothesis. The hypothesis pertains to the tradeoff between receiving accurate information at high costs versus acquiring less accurate information at lower costs. Accurate information can be obtained by individuals in the population (in the case that it becomes costly or unavailable) by observing and learning the behavioural patterns of other members of their group (Henrich and McElreath, 2003). Due to the difficulty in learning adaptive behaviours over the course of a lifetime, selection will favour mechanisms that allow extraction of beliefs and practices by individuals from the group they are a part of. Thus, in a certain set of environmental conditions, there exist several heuristic mechanisms and learning biases that may help in the adoption of practices that may prove advantageous to them (Henrich, 2001).

Learning biases, a cultural learning mechanism, can be split into two types: Content bias (also known as Direct bias) and Context bias. Direct bias is a cultural transmission rule characterized by the fact that a few cultural variants of a trait are more attractive than the others and are adopted by the individuals in the population. Directly biased transmission depends on the existence of variability of a cultural trait in the population (Boyd and Richerson, 1985). In contrast with Context biases, Content biases take shape after evaluation of the cultural variant over an extended period of time. This direction of bias need not be the same for all the individuals in the population, as the cultural variant selected by each individual is a decision taken after evaluating which variant is most adaptive in a range of environmental conditions. Direct biases are less valuable when the cost of evaluating each cultural variant in the population is high (Cavalli-Sforza and Feldman, 1981).

Context biases on the other hand are adopted by individuals based on certain metrics which they determine are necessary and desirable. These biases could be based on, for instance, prestige in the group, success in producing offspring, healthy appearance and so on. These biases that arise due to cues taken from individuals who can be imitated - with suitable evolutionary benefits - are termed Model-based biases. There exists another form of context bias termed as Frequency-dependent biases. In this mode of bias, the probability of an offspring obtaining a particular variant of a trait is proportional to the frequency of the variant in the population in the parental generation. Like Model-biased bias, this particular mode of bias requires less time to appropriate a cultural trait using the population's inherent knowledge than direct bias, and hence is much more useful when the process of evaluating trait variants is costly (Henrich and McElreath, 2003).

Cultural learning helps in the acquisition of skills and strategies that affect fitness. The greater the variability in the skill set of the population, the more difficult it becomes to individually learn each variant of a skill and evaluate the optimum choice (immediately demonstrating the cons of Direct biases). The cost associated with attempting to learn each variant in turn increases the pressure to preferentially select a variant from the

existing knowledge in the population. Henrich and Gil-White showed that in cases such as these, individuals will have a greater chance of acquiring an adaptive skill set if they decide to focus on variants which allow them to be relatively more successful and learn the skill in a fashion identical to them (Henrich and Gil-White, 2001). For instance, if the skill under consideration is tool making for hunts, it would be preferential for the learners in the population to look at the hunting return of each individual in the population and imitate the strategy with the highest observed payoff. However, the use of indirect indicators ('hunting returns' in the example above) could be an erroneous indication of the success of the trait variant due to several confounding factors in the environment. Due to this, there have been several instances of humans copying successful individuals across a host of cultural traits but with very few of them actually contributing to the individual's success (Flinn and Alexander, 1982). Hence, this strategy is viable only in cases where information acquisition of the skill is too costly to be individually learnt. The differences in the success of individuals adopting different variants of a skill leads to a demand for successful individuals in the population. In order to learn from them, there is a need to have preferred access to the individual. Learning the skill may also require some assistance from the successful individual. This leads to some form of deference payment by the success-biased learners, which could include deeds such as gifts and offspring care. This deference leads to the creation of a prestige hierarchy, which is thought to be another form of Model-based biases (Boyd and Richerson, 1985).

Another strategy to deal with costly skills is to copy the behaviours, skills, and strategies of the majority. This mechanism of copying a behaviour after considering its frequency in the population over all the individuals is termed as conformity bias. As it depends on the number of individuals displaying a skill, or trait, or behaviour in a social group, it falls under the umbrella of frequency-dependent biases. While the advantage of conformity-biased learning is apparent in information-poor environments, where it is difficult to identify the most successful strategy (sticking to the majority variant of the trait implicitly has the aggregation of all the knowledge and experience of the other members in the community), there are a few disadvantages. First, and most obviously, a high frequency

variant of a trait does not imply that it is successful. Second, if conformity bias is practiced by all the learners, there is no scope for exploration of alternative strategies or behaviours, thus bringing the adaptation and cultural evolution to a halt (Henrich and Boyd, 1998).

Although several theoretical studies in the field of cultural evolution assume that mating of the individuals in a group is completely random, multiple studies have shown that individuals select their partners with similar phenotypes, including education level, height, and eye colour (Domingue et al., 2014; Laeng et al., 2007; Keller et al., 2013). Hence, the phenomenon of assortative mating is a factor that needs to be considered while constructing models related to cultural evolution. Positive assortative mating (homogamy) occurs when individuals of a similar phenotype tend to mate more often than expected by chance, whereas negative assortative mating is the term used when dissimilar phenotypes mate more often than expected by chance (Burley, 1983). This phenomenon has been shown to occur across taxa including birds and fishes in addition to humans (Fernö and Sjölander, 1976; Cooke et al., 1976). Analytical models have shown that assortative mating can increase the genotypic and phenotypic variation in populations (Feldman, 1977; Rice et al., 1978). It has also been shown to influence the dynamics and spread of cultural traits in a population that are generally rare in populations (Creanza et al., 2012; Creanza and Feldman, 2014). In short, these studies indicate the fact that assortative mating is pertinent to building realistic models of cultural transmission and evolution.

In this project, we aim to construct a model that tests certain results from the literature and offer novel insights whilst trying to fill the blanks in gene-coevolutionary theory. We have attempted to incorporate various kinds of interactions between the organism's genotype, its extended phenotype, and the effects it has on the environment, leading to modified selection pressures in the subsequent generations. Our model is fundamentally a modification of the Wright-Fisher model where we consider haploid,

asexual populations of constant population size, which exist in discrete generations. Additionally, I look at the effect of the difference in evolution of systems when the relative contributions of the organism's phenotype and the extended phenotype are changed. This study is done over an extended parameter space of the coefficients that govern the contributions of the phenotype values mentioned above.

In the second part of my thesis, I model individuals with a sexual system of reproduction, in an attempt to combine learning biases and assortative mating to observe the dynamics of evolution of cultural traits. Using this paradigm, I aim to study the adaptive strategies that arise when a population with an array of phenotypes for mate specificity (i.e. how picky an individual is while choosing its mate) and fecundity is coupled with learning biases of different types and intensities. The model concerns itself with a sexual system where all the individuals are polygamous. Further description of the model is given below in the Materials and Methods section.

Methods

All the simulations were done using Python 2.7 programming language and related modules. Graphs have been plotted using SigmaPlot 11.0 and Matplotlib.

Model Description:

The model was constructed in order to study the effects of positive and negative interactions between an individual's inherent phenotype (generated from the underlying genotype) and the extended phenotype, in a population of constant size across generations.

Individual-Based Modelling techniques are used. Every individual in the population is defined by two parameters: an inherent phenotype value (henceforth 'O') and an extended phenotype value (henceforth 'E'). These O and E values represent a gradient of levels that directly contribute to the fecundity of the individual in the following generation. The fecundity of an individual is a linear function of O and E values, scaled by coefficients (c_1 and c_2) that determine the weight of each contributing component. In addition, to make the simulations more realistic, we factor in the contribution of the external environment. This value of the environmental resources (henceforth 'env'), depending on the situation we aim to model, can either remain constant or can vary from generation to generation. The different cases will be detailed in the coming paragraphs. The fecundity function is defined as:

For positive interaction: fecundity =

$$env * \left[(c1 * o) + \left(\frac{c2}{c1+c2} * e \right) \right]$$

a) env = value of the environment, wherein a higher value would imply a richer environment with greater resources hence increasing the fecundity of each individual.

b) c1, c2 = coefficients that determine the contributions of O and E respectively

c) o, e = Values of O and E as defined earlier

For negative interaction: fecundity =

$$env * \left[(c1 * o) - \left(\frac{c2}{c1+c2} * e \right) \right]$$

The resultant fecundity of individual once calculated feeds into the number of offspring with the same genotype, which comprise the next generation. The model assumes a Wright-Fisherian population. Using the fecundity function, the number of offspring for each individual is determined and the relative probabilities of the number of each individual's offspring are calculated. Implicitly, the O and E values determine the relative number of offspring that each individual will have going into the next generation.

The coefficient of 'e' in the model is constructed in a more complicated way simply to reduce the speed of evolution of the system. If the rate of fixation is too quick, the interesting dynamics occurring in the intermediate stages of the system's evolution is harder to track. In essence, it can be thought of as a single coefficient, say 'c3' whose range of values is dissimilar to c1.

Additionally, the question of units does not have to arise as coefficients of both 'o' and 'e' can be thought of scaling factors of their relative contributions to fecundity of an individual.

Variations in the model:

1. Tweaking of the environment (env) component:

1. Constant environment: The simplest simulations were run using an environment component that remained constant across generations. Biologically, this means that there was a constant replenishment of resources in the environment and usage of resources by individuals in every generation did not reduce the fecundity of the offspring in the next generation.
2. Temporally changing environment: Comparatively more realistic model, where two other parameters were used to replicate the effects of resource utilization by the population and subsequent reduction in resource amount, leading to lower fecundity among individuals in the later generations. Two parameters called ResAct and ResMax are defined. ResAct is defined as the product of the number of individuals times the sum of the means of the organism phenotype values and extended phenotype values in the population. ResMax is defined as the product of number of individuals and the sum of the maximum values of the organism phenotype and extended phenotype present in the population. The ratio of ResAct to ResMax is termed 'harm' and the value of the 'env' parameter for a generation is simply $1.0 - (\text{harm})$.
 - a) ResMax = Carrying capacity of environment, i.e., if all the O-E pairs were $(\max(o), \max(e))$. Mathematically, $N \cdot \{\max(o) + \max(e)\}$
 - b) ResAct = Actual $\sum_i (o_i + e_i)$ in a given generation where 'o' and 'e' are the organism phenotype and extended phenotype values, respectively

c) $\text{Harm} = \text{ResAct} / \text{ResMax}$

d) $\text{env} = 1 - \text{Harm}$

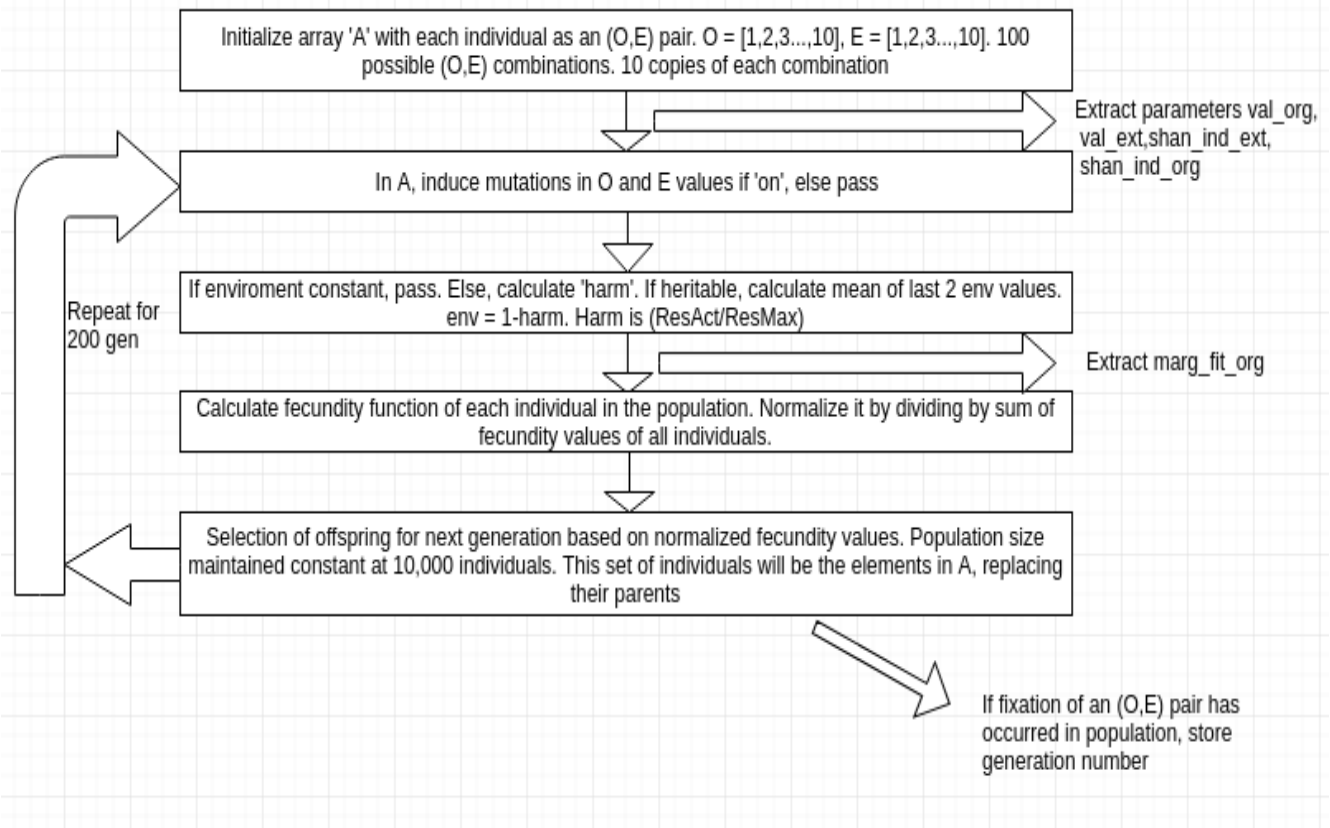
The effect of the individuals in a population is hence taken into consideration using this modification in the value of the environment. Biologically, this means that an individual with higher levels of fitness makes greater use of resources present hence increasing its fecundity, while at the same time reducing the resources present in the environment for other individuals.

3. Persistence and effects of previous generations: In real life, the environment is not unique value for every generation but rather a product of the effects of populations that existed in previous generations as well. To account for such effects the mean of 'env' values of the penultimate and current generations are considered

2. Mutations:

1. Mutation of organism's inherent phenotype and extended phenotype: In this case, there is a mutation in the level of fitness of an individual, both in its extended and inherent phenotype value. There was a 0.5 probability that a mutation could happen to the O or E value, which could change it to one level higher or lower every generation. Currently, we have limited the ability to mutate in only small steps above and below the current value of the individual's phenotype values.
2. Mutation of the organism's phenotype only: Similar to the previous case, except here, the value of the extended phenotype for an individual remains constant with time.

This model can be visualized for simplicity's sake in the form of an algorithm as shown below



As an extension of this study, the effect of the relative contributions of the O and E values on the population-level metrics was observed. In these simulations, the x and y axes are the values of 'c1' and 'c2' which are the coefficients that govern the contributions of the O and E values, which are both variables on which an individual's fecundity function depends, while the z-axis represented the dependent variable under consideration (val_org, val_ext, etc.). The range of c1 (and c2) varied from 1.0 to 10.0 with a step size of 1.0. This meant that the parameter space consisted of a hundred different (c1, c2) combinations, for each of which, there existed a value of the parameter under consideration. Four different cases were considered and comparisons were drawn between them:

1. Positive interaction, non-heritable environment, and absence of mutations
2. Positive interaction, heritable environment, and presence of mutations

3. Negative interaction, non-heritable environment, and absence of mutations
4. Negative interaction, non-heritable environment, and presence of mutations

Cultural evolution and the impact of assortative mating and learning biases

The second part of the simulations examines the impact of mating and biases in the learning of cultural traits. I attempt to compare the difference in evolutionary trajectories whilst comparing populations with random versus assortative mating, both in the presence and absence of biases. As in the previous set of simulations, Individual Based Modelling techniques were used.

Derived from the previous model, every individual in the population is represented by an array of two elements: the first element being the value of the cultural trait is essentially a direct measure of its fecundity, whereas the second element measures the “specificity” of the individual with respect to its mate selection. In other words, a large value of the second element would imply that the individual is willing to mate with individuals who have very dissimilar cultural trait values. The addition of learning biases to this model further complicates the evolutionary dynamics in this model. All simulations are carried out with replicate size of 10.

1. Assortative Mating: An individual ‘I’ is conceptualized as an array [C,V], where ‘C’ stands for the value of the cultural trait, and ‘V’ represents the degree of specificity in mate preference by the individual. Thus, if an individual has values of C as ‘c’ and V as ‘v’, the individual would be willing to mate with all individuals whose C value is within the range from ‘c-v’ to ‘c+v’. Naturally all these values are bounded by the lowest and highest values of C assigned in the simulations. This would mean that individuals with lower V values are pickier about choosing their mates than an individual with a higher V value. This range of V values

creates a variance in mating preferences that can potentially have an impact on the evolutionary trajectories of the cultural trait in the population. In such a model, random mating can be thought of as a special case, in which there is only one V value, which is equal to the value of the maximum C value in the population.

2. Biases: Two important learning biases are incorporated in the model: Conformity bias and Novelty bias. Although they fall under the broader umbrella of frequency dependent biases, they are vastly different from each other. Conformity bias, as defined earlier, is the mechanism of copying a behaviour of the highest frequency in the population. Novelty bias on the other hand is the exact opposite of it. In this case, offspring in the next generation look to learn behaviours that are very limited in number in the population. To model this particular phenomenon, it is essential to introduce an element that captures a cultural trait's frequency in the population. Hence a factor 'd' is introduced to the function that determines the value of the cultural trait of a learner i.e. offspring of the next generation. The product of the factor 'd' and the difference between the most or least present trait in the population (depending on the bias modelled) and the mid-parent value of the trait for 'C'(MPV) is then added/subtracted (depending on the C value of the individual under consideration and its distance from the most or least frequent trait in the population depending on the bias modelled). A larger value of 'd' can be thought of as a greater push/pull towards the most/least frequent trait (depending on the bias) which in turn can potentially alter the rate of adaptation and dynamics of the selection of cultural traits in the population.

Mathematically, for conformity bias:

$$C_{t+1} = MPV \pm d * |C_{MAX \text{ frequency}} - MPV|$$

Whereas, for novelty bias:

$$C_{t+1} = MPV \pm d * |C_{MIN \text{ frequency}} - MPV|$$

Given the two phenomena being modelled, the following combinations of mating and bias that can be studied:

1. Random mating and no bias: The most basic case in which every individual can mate with every other individual and no effects of bias are considered.
2. Random mating with biases: The case where there is a population-level influence on the cultural trait value of an individual, but effects due to mate preference are not visible due to random mating.
3. Assortative mating without biases: In this case, there is no effect of learning biases, thus making the system's evolutionary trajectory a function of purely mate preferences of individuals in the population.
4. Assortative mating with biases: This case considers the effects of both mate preference and learning biases, and any potentially counter-intuitive results that may arise due to the interplay of these two factors.

To study the dynamics of the system in the cases with different mating patterns and learning biases it is essential to define a metric that allows for the quantification of the oscillations observed in the system. The metric that allows us to make this quantification is called Fluctuation Index (FI). A parameter with lower fluctuations in its value over a period of time will have a lower FI whereas a greater fluctuation in a series of values will lead to a higher FI. It is defined as follows:

$$FI = \frac{1}{T * \bar{N}} * \sum_{t=0}^{T-1} |N_{t+1} - N_t|$$

Where,

\bar{N} is the average of all the values of in the set (in this case, the set of C values)

T is the total number of generations

N_t is the t^{th} value in the set of C values.

Parameters for tracking evolution

To the study the evolution of the system, it is vital to have certain well-defined, pertinent parameters whose values indicate the changes in the system with time. The following are the parameters that are tracked in our model which help us analyse how evolution is progressing in our construct:

1. val_org: The population mean of the organism phenotype value in a particular generation. This value is saved in a list every generation for the period of simulation. In the case of the cultural evolution simulations, this parameter also acts as the value of fitness.
2. val_ext: The population mean of the extended phenotype value in a particular generation. This value is saved in a list every generation for the period of simulation.
3. marg_fit_org: This parameter measures the fitness of every individual in the population, which is equal to the non-normalized value of the fecundity function with each individual's corresponding O and E values. The mean over the entire population is taken for each generation and this is plotted against time to act as a measure of evolution.
4. shan_ind_org: This parameter determines the Shannon Index of the population's range of organism phenotype values. Shannon Index is a measure of diversity in a population and is given by the formula $S = \sum(p_i \cdot \ln(p_i))$, where 'i' is a counter starting from 1 and going to 'x', with 'x' being the number of unique values of O in the population and p_i is the probability of occurrence of the i^{th} value in the population. The Shannon Index is calculated every generation and added to a list.
5. shan_ind_ext: This parameter determines the Shannon Index of the population's range of extended phenotype values. Shannon Index is a measure of diversity in a population and is given by the formula $S = \sum(p_i \cdot \ln(p_i))$, where 'i' is a counter starting from 1 and going to 'x', where 'x' is the number of unique

values of O in the population and p_i is the probability of occurrence of the i^{th} value in the population. The Shannon Index is calculated every generation and added to a list.

6. unique combos: This parameter tracks number of unique combinations of organism phenotype and extended phenotype values in the population in a particular generation and adds it to a list which contains the number of unique combinations present in every generation.

RESULTS AND DISCUSSION

All the simulations are run for 200 generations as we have observed that this is more than enough time for the populations to reach fixation and this is displayed in our parameter values obtained over time. Each of the above mentioned parameters have been plotted with respect to time for all different combinations of environment and mutation possibilities mentioned above.

In addition, analysis has been done for the parameter space of c1 and c2 ranging from values 1 to 10 with unitary step size. This means that the parameters have been plotted with respect to two axes each of 10 values i.e. 100 coordinates with their respective parameter value in a particular generation. This is done for all 200 generations simulated.

The results obtained by the simulations can be classified into two different sections

Key for parameters:

1. val_org: The population mean of the organism phenotype value in a particular generation.
2. val_ext: The population mean of the extended phenotype value in a particular generation.
3. marg_fit_org: This parameter measures the fitness of every individual in the population.
4. shan_ind_org: This parameter determines the Shannon Index of the population's range of organism phenotype values.

5. shan_ind_ext: This parameter determines the Shannon Index of the population's range of extended phenotype values.
6. unique_combos: This parameter tracks number of unique combinations of organism phenotype.

Key for graphs:

Each graph has 3 parts determining whether the environment is herited 'h' or non-herited 'nh' followed by whether the environment is changing 'em' or remains constant 'e1' and finally whether there is mutation of O and E values 'm' or no mutation 'nm' or simply mutation of the organism's phenotype value (O) 'om'

For example: nhe1m in the graph would mean that the environment is non-heritable, and there is only single environment and there is mutation in the system.

Results from simulations with negative interaction between Organism and Extended phenotype (where c1, c2 = 1.0)

Fig 1a

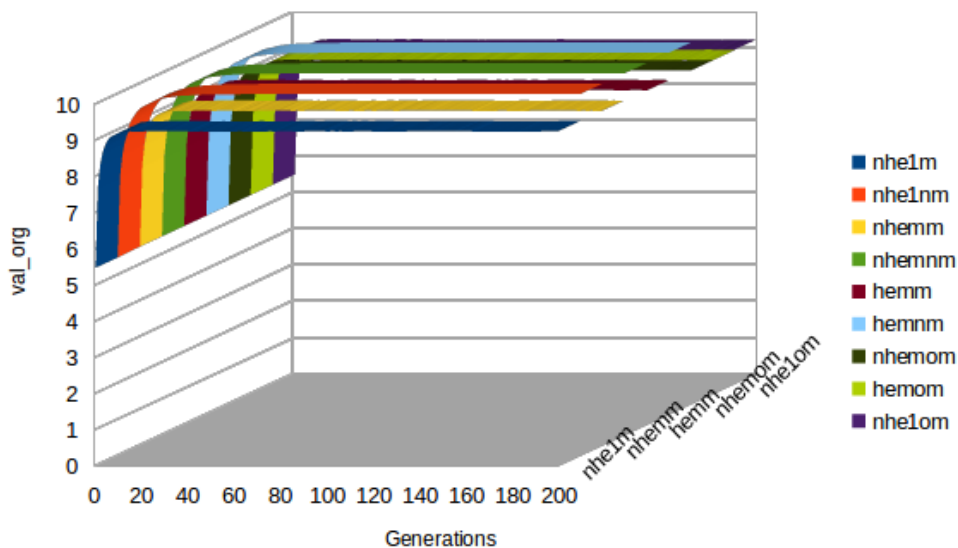


Fig 1b

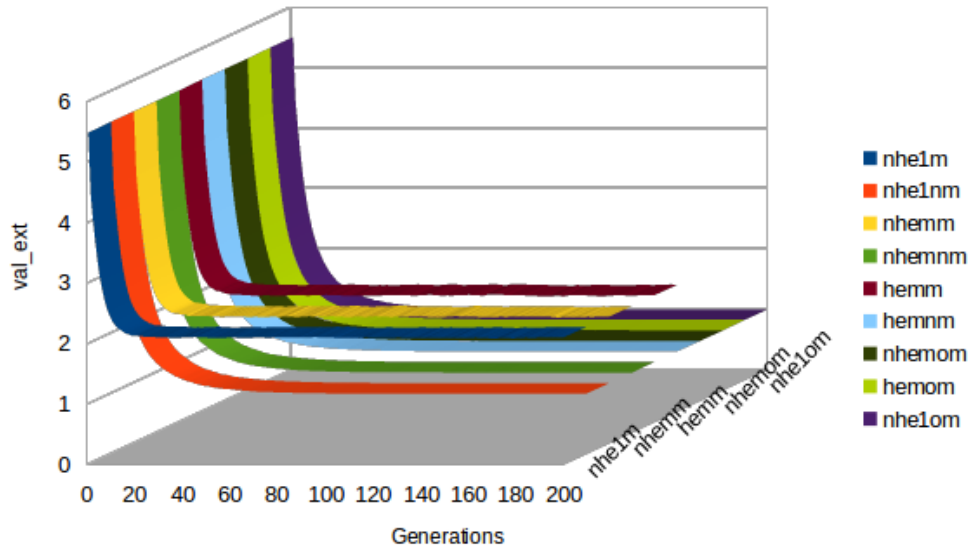


Fig 1c

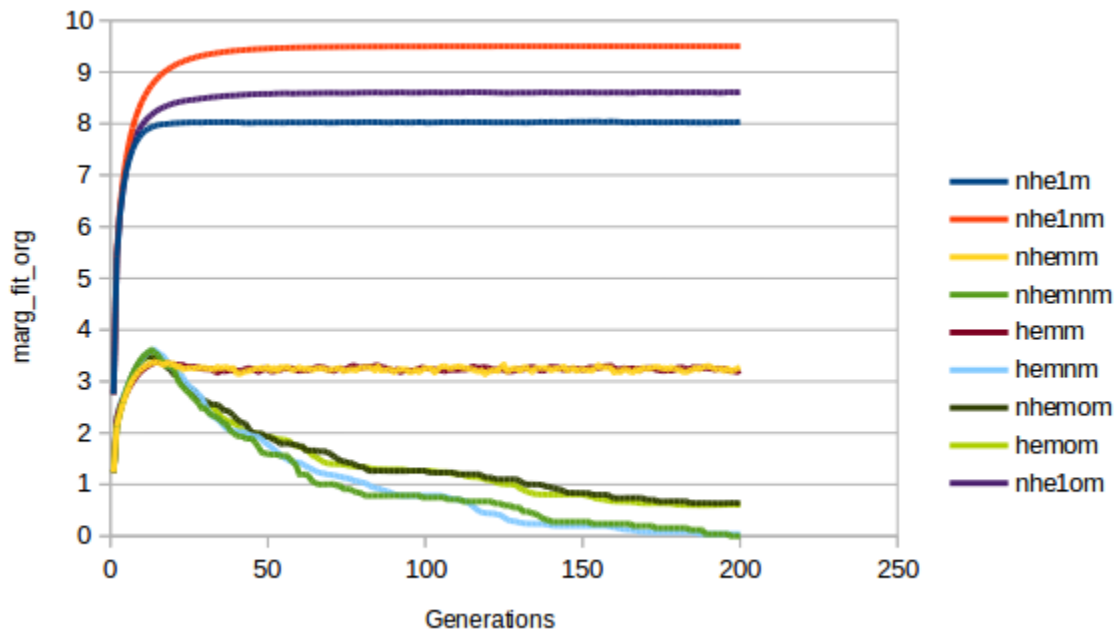


Fig 1d

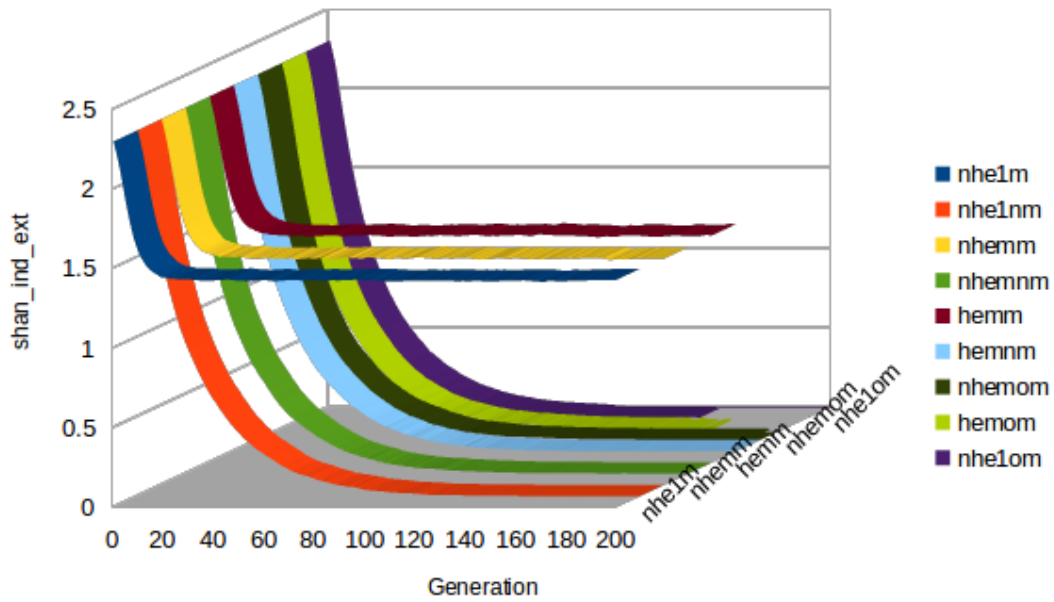


Fig 1e

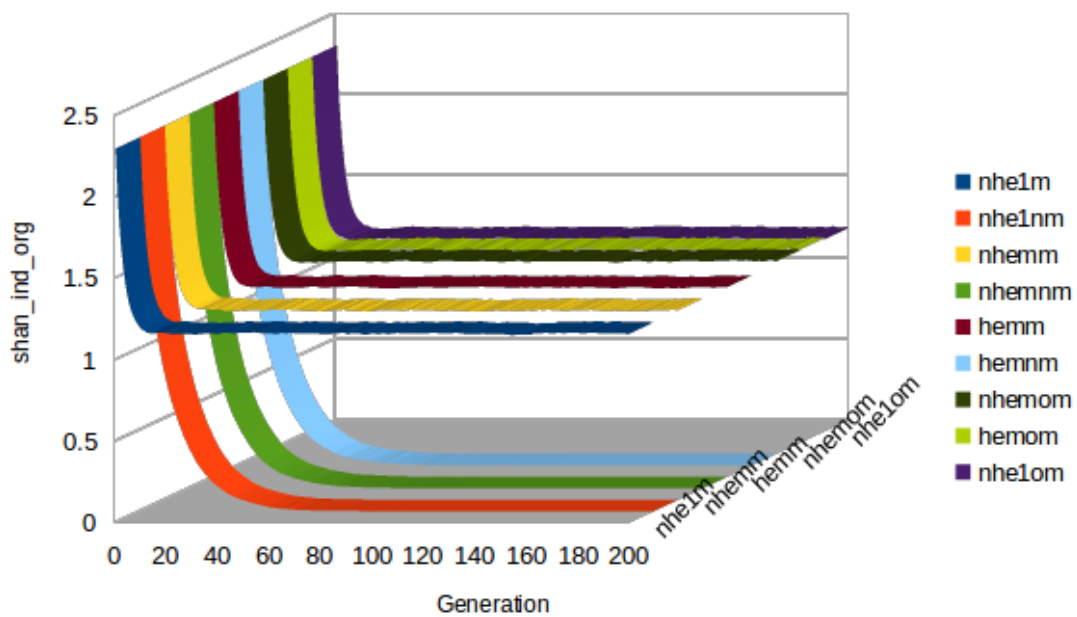
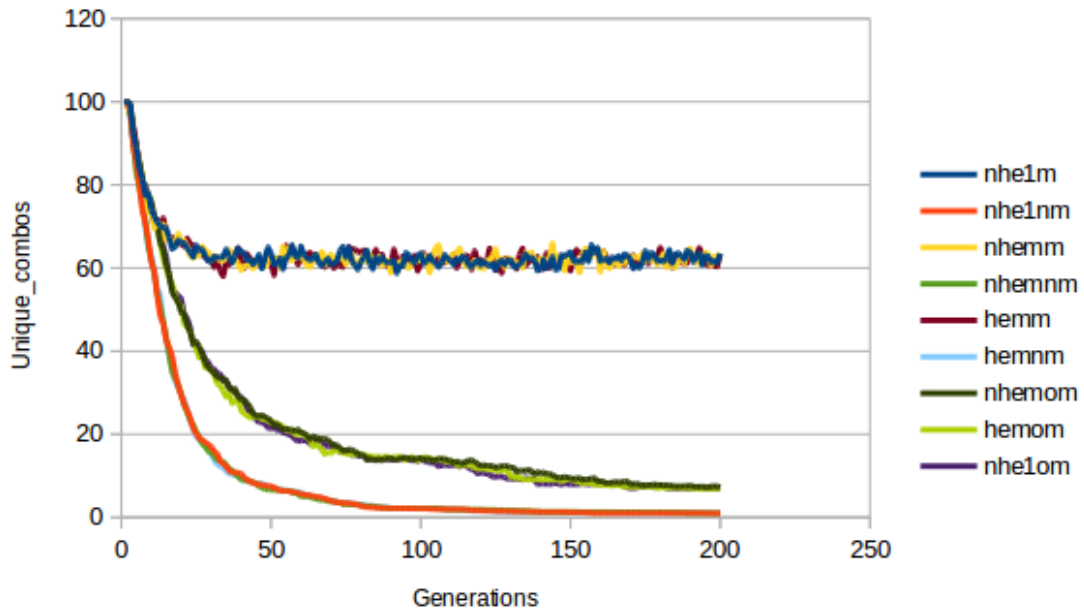


Fig 1f

Fig 1f



When there is mutation of O and E, number of unique combinations does not drop to zero. This means that there is still some diversity after 200 gen. Mutation acts to reduce the strength of selection. This is true in all environments. However the effect of only mutation of O values, although reducing the number of unique combinations, does not allow complete selection of one particular phenotype in the population as seen in the no mutation case.

Mean val_org (level of organism) reaches maximum value of 10 when there is no mutation. However, when there is mutation, this does not happen and mean val_org fixes at a value lower than 10. Mutation of only O values leads to fixation of average value of the parameter at some value between completely mutating individuals (O and E mutation) and no mutation case. There is an opposite trend for val_ext (level of extended phenotype) where with mutations, val_ext mean value is higher. However here, the presence of mutation of O values does not present any difference in parameter values as the results are virtually the same as the no mutation case. This is true for single and changing environment, both heritable and non-heritable.

In the constant environment case, the introduction of mutations seems to reduce the fitness of the individuals in the population. Mutating only the O values also caused reduction in the fitness but the effect was less dramatic than mutating both O and E values. However, in the case of changing environments, mutations do help in increasing the fitness of the individuals regardless of whether the environment was inherited or not. This implies that the presence of mutations injects diversity in the population allowing it to survive in a rapidly degrading environment (env = 1-harm) thus increasing fitness. While only O values were mutated, fitness did increase in changing environments but the effect was not as much as the case where O and E values were both mutated. In the single environment case, the mutations may serve to act in a direction opposite to selection hence slowing it down.

Results from simulations with positive interaction between Organism and Extended phenotype (where $c_1, c_2 = 1.0$)

Fig 2a (above) and 2b (below)

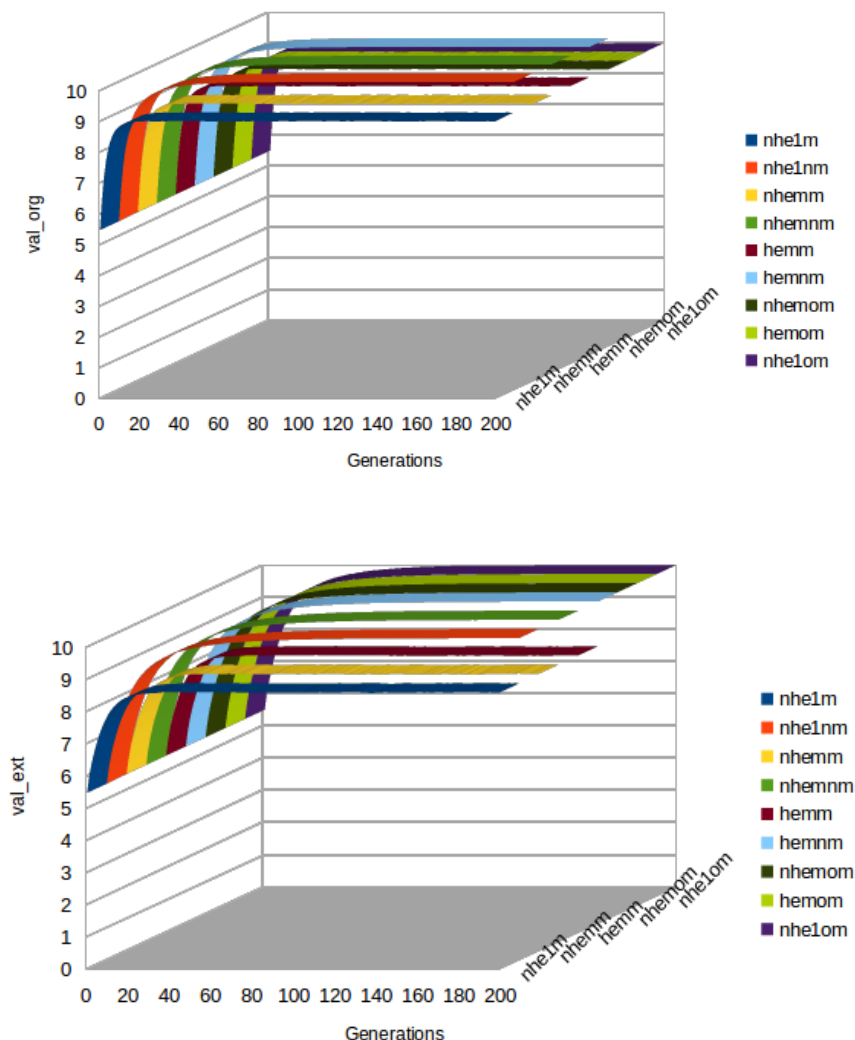


Fig 2c

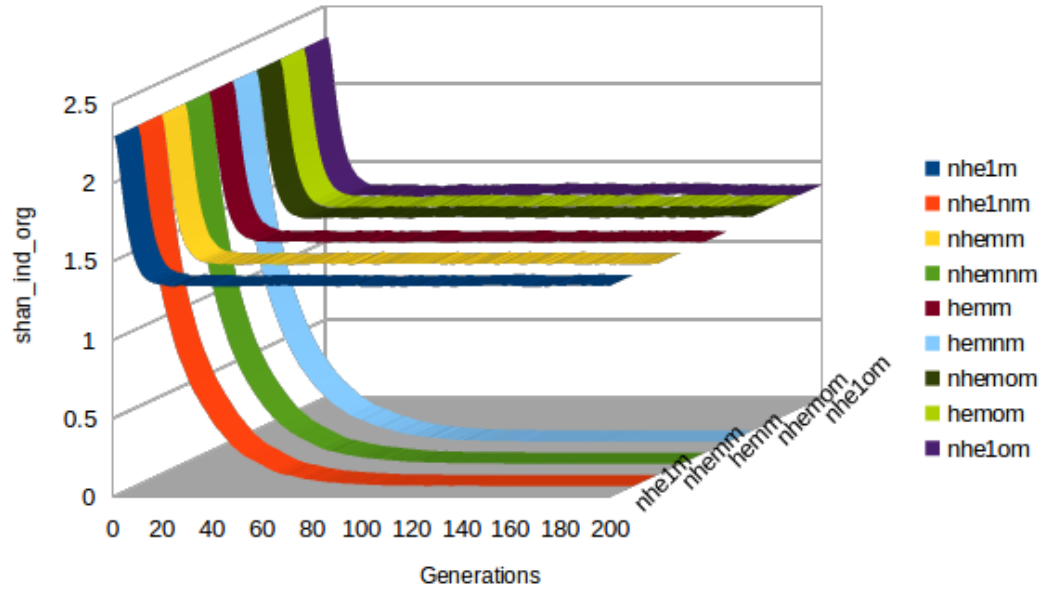


Fig 2d

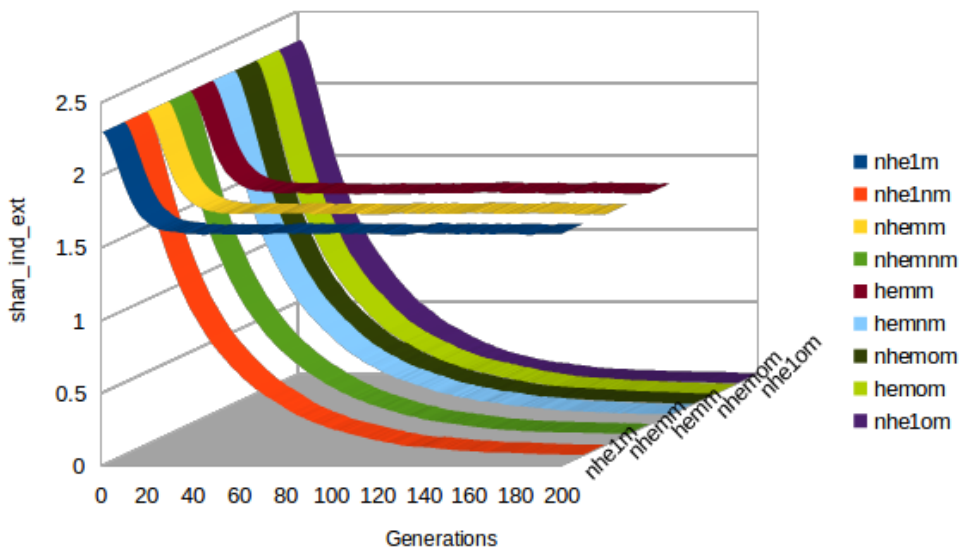


Fig 2e

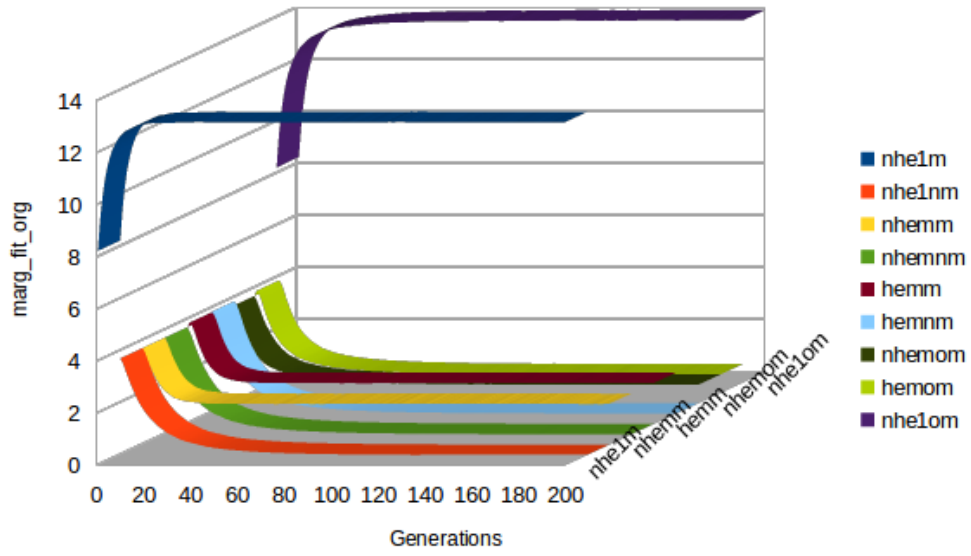
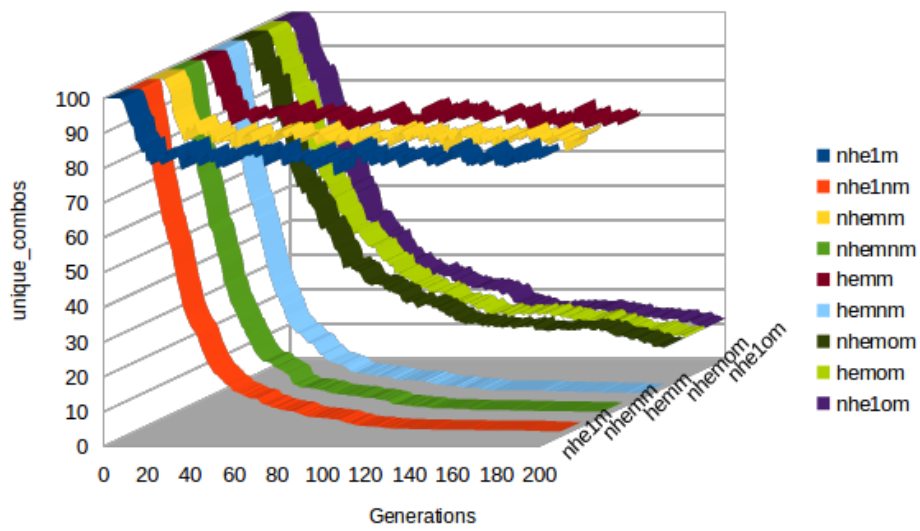


Fig 2f



As expected, val_ext and val_org both increase with time but surprisingly; marg_fit (fitness) reduces even though both the components it is dependent on are selected for higher values. In the single environment case, mutations (both variations i.e. simply O mutations and the O and E mutation case) help increase the fitness values over time. In the single environment case, the only O mutation case does better than mutating both O and E. Even in the changing environment case, mutations help (although the general trend of fitness values is reducing) but in this case, mutation of both parts of the individual's attributes aids in higher fitness values than simply mutating O values. All these are regardless of whether environment is heritable or not. In absence of mutation, fitness reduces the most, regardless of the environment faced.

Fixation does not happen, quite obviously, in the cases where the mutation is switched on. But unlike the Negative Interaction cases, fixation does not happen in the 200 generations observed even when mutation is switched off (although it does get close). The number of unique individuals when only O values are mutated is right in between the number of unique individuals that are present in the presence and complete absence of mutations as is logically expected.

In all the cases (most visible in the single environment case), switching on mutation does tend to reduce the depression of fitness values of the individuals with time with respect to the mutation 'off' case.

Therefore, in a nutshell, the qualitative change of fitness with mutations switching 'on' is the same for both Positive and Negative interactions except in the single environment case where the result is opposite.

When mutations are switched on, the val_ext and val_org means increase with time as expected but do not reach the maximum possible value as is the case when mutations are off. This appears really interesting and can explain the increase in fitness in changing environments (like in the Negative interactions case).

Comparing the rate of reduction of Shannon Index between Positive and Negative interactions, it appears that rate of fixation is faster for both Organism and Extended phenotype values in Negative Interaction cases for all cases (mutation and non-mutation cases). Also, interestingly, while in the Negative Interaction case, mutation of simply 0 values still allows for fixation over time, but in the Positive Interaction cases, the Shannon Index value fixates to a non-zero value even after 200 generations.

The above model was used to study the effect of the contributions of the organism phenotype and extended phenotype (c_1 , c_2) to the fecundity of an individual in the population and on the other parameters we have constructed to study the evolution of the system under consideration. In addition, we have extended our study to look at an extended parameter space of (c_1, c_2) ordered pairs on the metrics used for quantifying evolution. In simpler terms, this means that we are tracking the previously described parameters for different values of (c_1, c_2) pairings to see if there are any general or unique trends that are observable using our simulations. As mentioned in the Methods section, there are four different cases that are being considered and the results garnered are summarized below. I have varied the values of c_1 and c_2 from 1.0 to 10.0 with a step size of 1.0 which gives a total of 100 unique combinations of (c_1, c_2) pairings.

Results:

1. Positive interaction, non-heritable environment, and absence of mutations:
 - `Marg_fit_org`: Simply due to the way the fecundity function is defined in the model, the populations with higher values of c_1 and lower values of c_2 have a higher starting value of the parameter under consideration i.e. `marg_fit_org`. However, at the end of 200 generations, it is observed that the value of the parameter goes to nearly 0 in the cases where c_1 is at its lowest ($c_1 = 1.0$) and

where c_2 is at its highest ($c_2 = 10.0$). The general trend seen is that the marg_fit_org of the population, regardless of the (c_1, c_2) combination seems to be going down over time. The highest value of the parameter after 200 generations as expected is when $(c_1, c_2) = (10.0, 1.0)$. This reduction in the parameter is due to both the 'val_org' and 'val_ext' values nearing the optimum value which increases the resource used by the population every generation which decreases the 'env' which is part of the fecundity function.

- **Shan_ind_ext:** The highest value of Shannon Index (SI) of the set of values of the extended phenotype after 200 generations (implying greatest diversity in population) was for $(c_1, c_2) = (10.0, 1.0)$. This result can be attributed to the minimal contribution (or impact) of c_2 to the value of the fecundity function hence reducing the strength of selection on the val_ext parameter. This would lead to greater variation existing in the population and this is observed in the values resulting from the simulation. Using similar arguments we can explain the result that the (c_1, c_2) combination with the lowest SI was $(1.0, 10.0)$. Qualitative decreasing trend observed over time is similar to the way in which the 'marg_fit_org' parameter reduced.
- **Shan_ind_org:** The highest value of Shannon Index (SI) of the set of values of the extended phenotype after 200 generations (implying greatest diversity in population) was for $(c_1, c_2) = (1.0, 10.0)$. The lowest value of SI was observed to be $(c_1, c_2) = (10.0, 1.0)$. This result can be attributed to the high differential in selection coefficient exacerbated by the extremely high value of c_1 (for instance 10.0) which increases the strength of selection causing a reduction in variation. This is observable in this case as the mutations in this simulation are turned off. Qualitative decreasing trend observed over time is similar to the way in which the 'marg_fit_org' parameter reduced. A pertinent point to note is that the contribution of the organism's phenotype to fecundity is always going to be significantly greater than the extended phenotype's contribution regardless of the value of c_1 and c_2 . This means there is always going to be selection of some significant strength. This is apparent as the difference in SI detailed in the earlier

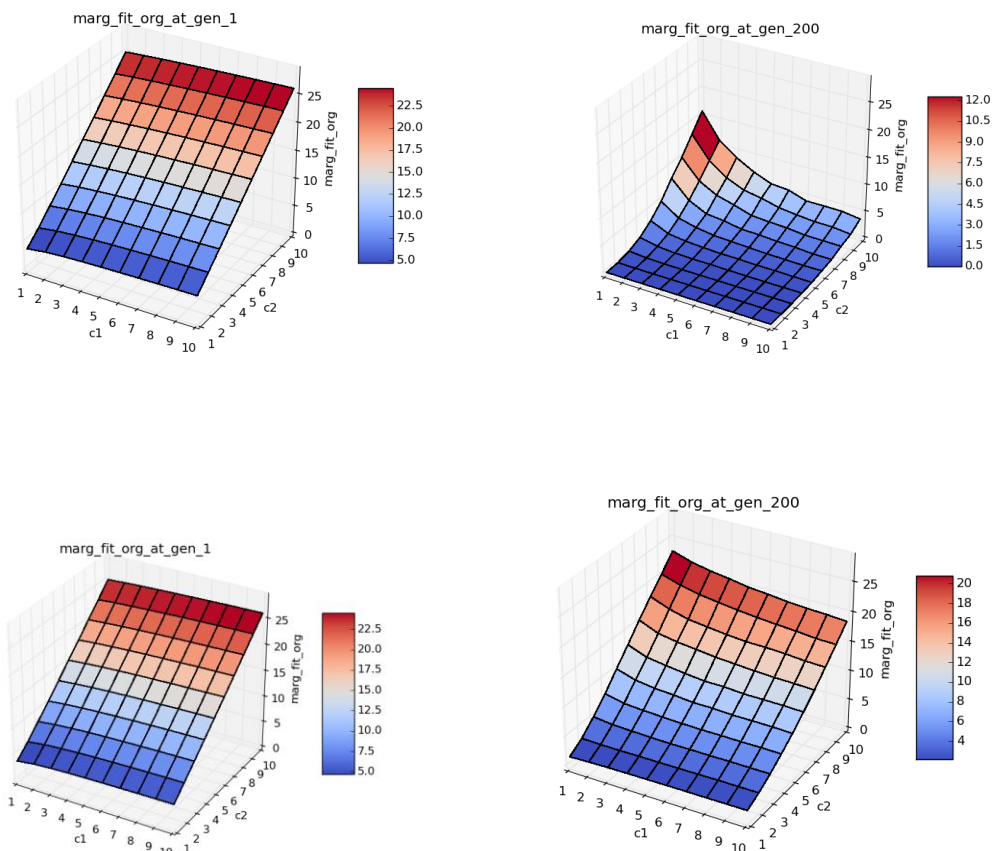
part of this paragraph occurs during the early part of the simulation (~30-50 generation) and tends to 0 for all combinations of c_1 and c_2 . This is especially important to explain the behaviour of the 'unique_combos' parameter.

- Unique_combos: Although the initial loss of variation in all populations is uniform, after the simulations have run for 200 generations, it is observed that there are a greater number of unique combinations for parameter values where c_1 is high and c_2 is low i.e. in the most extreme scenario $(c_1, c_2) = (10.0, 1.0)$. This can be explained by invoking arguments already presented to explain the trends of Shannon Indices of both, the organism and extended phenotype values. The reasons are twofold: a) The coefficient of 'O' values is always going to be high causing strong selection to take place as far as organism phenotype values are considered which immediately reduces variation along that axis. b) The 'E' values, however, face weaker selection due to lower coefficient values hence providing variation in the population. This explains why the most number of unique combinations exist for low c_1 values and high c_2 values.
- Val_ext: In general, the trend is one in which the parameter value is increasing. The maximum value of this parameter occurs for $(c_1, c_2) = (1.0, 10.0)$. This agrees with our prediction as in this particular case i.e. a high c_2 value, the contribution of 'E' value to the fecundity is high and hence there is strong selection for that particular trait. This justification is lent further credence as it is observed that the 'val_ext' parameter increases slowly with increasing c_1 values as this means that the relative impact of the coefficient of the extended phenotype is reduced hence reducing the strength of selection on that trait.
- Val_org: As expected, val_org fixates at the end of 200 generations regardless of the (c_1, c_2) pair. However, faster fixation happens with increasing values of c_1 peaking at $c_1 = 10.0$. There is also a slight dip in rate of fixation with increasing c_2 values which is to be expected given the fact that the contribution of the coefficient of 'E' values increases with regards to the fecundity function.

2. Positive interaction, heritable environment, and presence of mutations

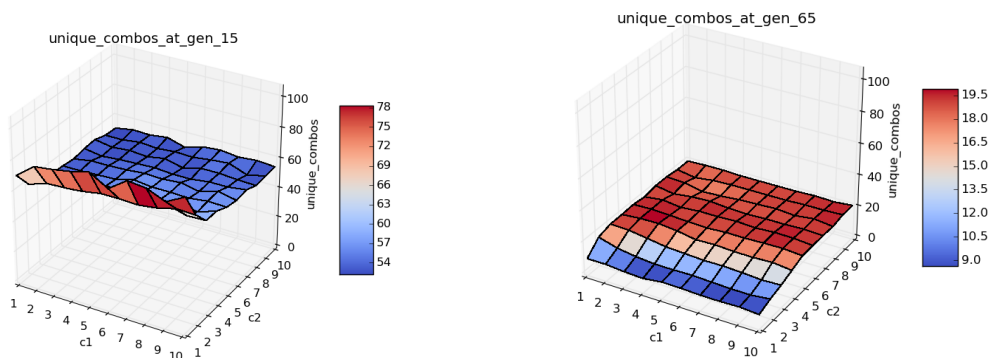
- Marg_fit_org: The qualitative trend of parameter values over time resembles the case where no environment is inherited and there is no mutation in that it reduces over all combinations of (c1,c2). However, the degree to which it reduces is slightly different. The rate of reduction of the parameter is much lesser in this case. After 200 generations, the value of the parameter across all combinations of c1 and c2 is higher than its counterpart in the case where there is no environment inherited and there are no mutations. (Upper row: No mutation, no heritable environment at generations 1 and 200 from left to right. Lower row: With mutation and inherited environment at generations 1 and 200 from left to right)

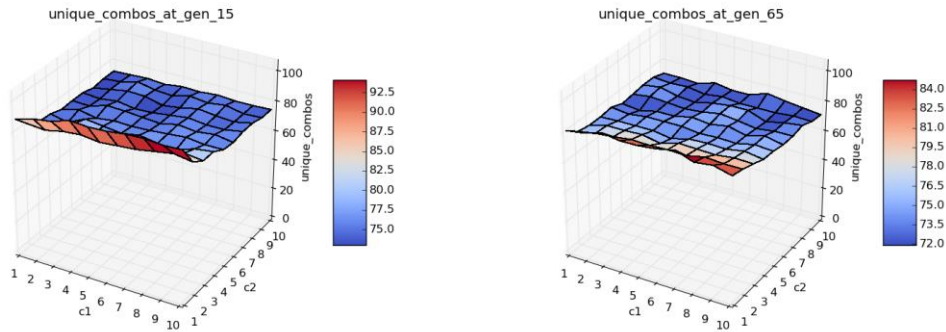
Fig 3a (i – ii above, iii – iv below)



- **Shan_ind_ext:** There is a general reduction in the value of Shannon Index (SI) in the population of the extended phenotype over time just as expected due to selection. It is observed that SI remains high in cases where the range of c_2 values are on the lower side and c_1 values are on the higher side (the most revealing example naturally being $(c_1, c_2) = (10.0, 1.0)$). However, unlike the previous case, the presence of mutations in this scenario prevents the value of SI from ever going to 0 by injecting variation in every generation.
- **Shan_ind_org:** The highest value of Shannon Index (SI) of the set of values of the extended phenotype after 200 generations (implying greatest diversity in population) was for $(c_1, c_2) = (1.0, 10.0)$. The lowest value of SI was observed to be $(c_1, c_2) = (10.0, 1.0)$. The value of the parameter does not go to 0 as in the earlier case due to the presence of mutations which maintains variation in the population. Over 200 generations there is some reduction in SI but its effect is counteracted by the presence of mutations.
- **Unique_combos:** This pattern observed over time is markedly different from the previous case. There is a uniform decrease in unique individuals over the parameter space but as evidenced by the Shannon Indices of the organism and extended phenotype, variation continues to exist due to the presence of mutations in the system. (For 15 and 65 gens) (Upper row: No mutation, no heritable environment, Lower row: Mutation and inherited environment)

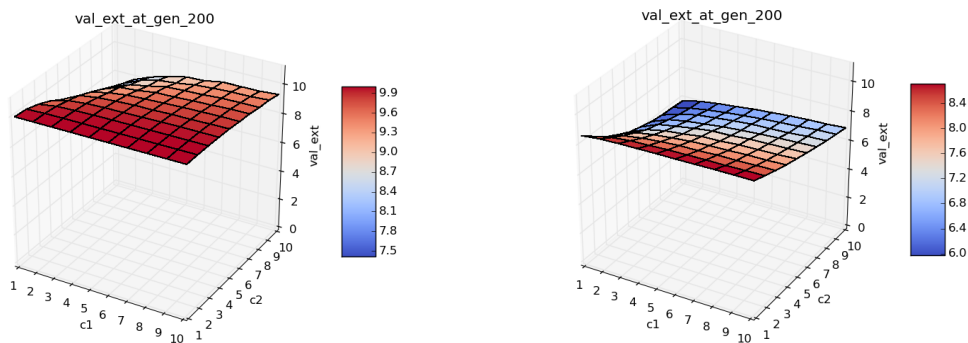
Fig 3b (i – ii above, iii – iv below)





- Val_ext: At the end of the run, the parameter is highest for low values of c1 and fairly consistent across the range of c2 values. This is expected given in scenarios where c1 is low, the coefficient of 'E' values in the simulation have a greater contribution to the fecundity of an individual. The value of the parameter does not fix to the maximum possible value unlike the case where there is no mutation and no herited environment. Hence, the maximum value of the parameter is lesser than the maximum possible attainable as the selection and mutation act as opposing forces counterbalancing each other. This is further visible when the Shannon Indices of the populations are observed. (Left : No mutation, no heritable environment, Right: With mutation and inherited environment)

Fig 3c (i – ii, from left to right)



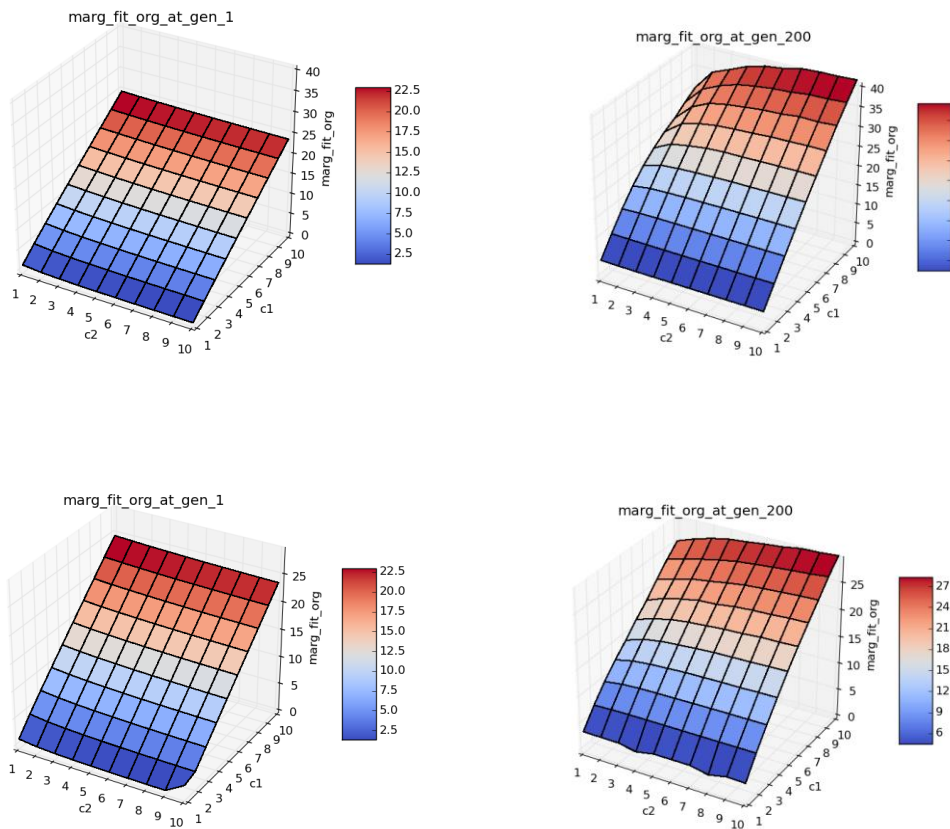
- Val_org: The trajectory is similar to that of 'val_ext' in that there is no fixation of the parameter over time. Also, as expected, the rate of reaching the maximal possible value of the parameter is fastest in the case where $(c1,c2) = (10.0,1.0)$. Here as well, the strength of selection is counteracted by the introduction of mutations which maintains variation in the population that selection looks to reduce.
3. Negative interaction, non-heritable environment, and absence of mutations
- Marg_fit_org: Unlike observed in the cases of positive interaction, Marg_fit_org increases with time. This implies that the average fitness in the population is actually increasing. This difference is observed because 'val_ext' fixates to a lower value over time. This reduces the 'harm' parameter which increases value of 'env' (defined as $1-harm$) and directly impacts the value of the parameter under consideration. The maximum value of the parameter as expected is present for higher values of $c1$ as it contributes significantly to the fecundity function. The values of 'marg_fit_org' is also higher for higher values of $c2$ as it is observed that 'val_org' fixates to lower values for higher values of $c2$.
 - Shan_ind_ext: The highest value of Shannon Index (SI) of the set of values of the extended phenotype after 200 generations (implying greatest diversity in population) was for $(c1,c2) = (10.0,1.0)$. This result can attributed to the minimal contribution (or impact) of $c2$ to the value of the fecundity function hence reducing the strength of selection on the val_ext parameter. This would lead to greater variation existing in the population and this is observed in the values resulting from the simulation. Using similar arguments we can explain the result that the $(c1,c2)$ combination with the lowest SI was $(1.0, 10.0)$. Qualitative decreasing trend observed over time is similar to the way in which the 'marg_fit_org' parameter reduced.
 - Shan_ind_org: Due to the strength of selection on 'O' values due to the way the model is set up, fixation of the optimal value of 'val_org' happens very quickly

and across all (c1,c2) combinations. Hence this particular parameter goes to 0 overall (c1,c2) values with the first 150 generations.

- **Unique_combos:** The general trend over the parameter space is that the variation reduces due to selection over generations. As the reduction in variation in 'O' values is uniform, the reduction in unique combinations of 'O' and 'E' value individuals depends on the rate of reduction of variation of 'E' values in the population which is indicated by the 'shan_ind_ext' parameter. The highest value of Shannon Index (SI) of the set of values of the extended phenotype was for (c1,c2) = (10.0,1.0) and this pattern is mirrored in the general trend observed in the 'unique_combos' parameter.
 - **Val_ext:** Unlike the positive interaction scenario, the 'val_ext' parameter is selected for lower values. This is due to the fact that smaller values of 'E' for individuals, in negative interaction cases, increases their fecundity value allowing them to have greater fitness. In fact, the maximum 'marg_fit_org' for negative interactions is higher than it is for positive interactions which is a very counterintuitive result which stems from this difference in selection of optimal 'val_ext' values between the two types of interactions.
 - **Val_org:** In contrast to 'val_ext' values, 'val_org' values fixate to the maximum possible value regardless of the (c1,c2) pair similar to the positive interaction case of no mutation. The rate of fixation of values is uniform across all (c1,c2) pairs.
4. Negative interaction, heritable environment, and presence of mutations
- **Marg_fit_org:** Unlike observed in the cases of positive interaction, Marg_fit_org increases with time. This implies that the average fitness in the population is actually increasing. This difference is observed because 'val_ext' fixates to a lower value over time. This reduces the 'harm' parameter which increases value of 'env' (defined as 1-harm) and directly impacts the value of the parameter under consideration. The maximum value of the parameter as expected is present for higher values of c1 as it contributes significantly to the fecundity

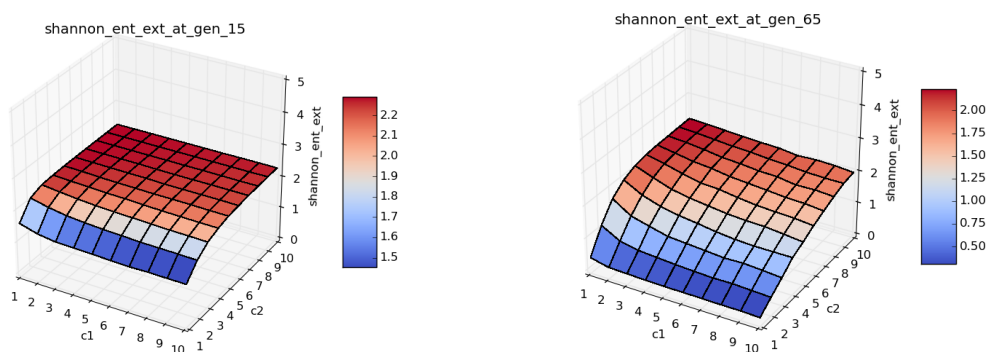
function. The values of 'marg_fit_org' is also higher for higher values of c2 as it is observed that 'val_org' fixates to lower values for higher values of c2. However, the increase in fitness is not as much as it is in the case of negative interaction in the absence of mutations. This is because mutations reduce the efficacy of selection and hence 'val_ext' parameter does not go to lower values. This in turn reduces the fecundity of the individuals in the population. Another reason for the reduced value of the parameter is the fact that the 'val_org' reaches a lower maximum due to mutation weakening the effects of selection. (Upper row: No mutation, no heritable environment at generations 1 and 200 from left to right. Lower row: With mutation and inherited environment at generations 1 and 200 from left to right)

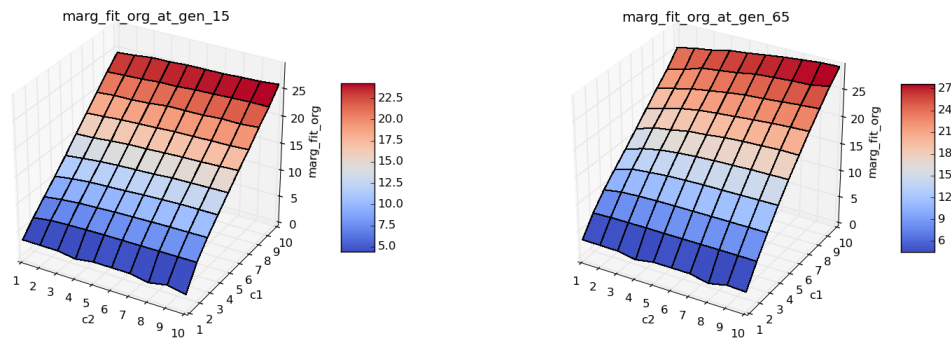
Fig 4a (i – ii above, iii – iv below)



- Shan_ind_ext: The highest value of Shannon Index (SI) of the set of values of the extended phenotype after 200 generations (implying greatest diversity in population) was for $(c1,c2) = (10.0,1.0)$. This result can be attributed to the minimal contribution (or impact) of $c2$ to the value of the fecundity function hence reducing the strength of selection on the val_ext parameter. This would lead to greater variation existing in the population and this is observed in the values resulting from the simulation. Using similar arguments we can explain the result that the $(c1,c2)$ combination with the lowest SI would be the ones where $c1$ values are extremely low and $c2$ values are extremely high. Qualitative decreasing trend observed over time is similar to the way in which the 'marg_fit_org' parameter reduced. These values do not go to 0 for any $(c1,c2)$ combination due to the introduction of mutations every generation which is the cause for variation in the population.
- Shan_ind_org: Due to the strength of selection on 'O' values due to the way the model is set up, fixation of the optimal value of 'val_org' happens very quickly and across all $(c1,c2)$ combinations. Unlike the 'no mutation' case, this particular parameter does not go to 0 due to mutations being turned 'on' injecting variation into the population. (Upper row: No mutation, no heritable environment after 15 and 65 generations from left to right, Lower row: Mutation and inherited environment after 15 and 65 generations from left to right)

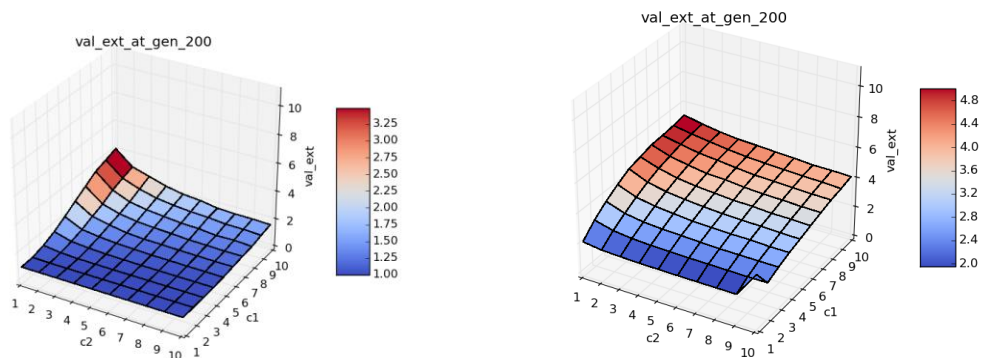
Fig 4b (i – ii above, iii – iv below)





- Unique_combos: The general trend over the parameter space is that the variation reduces due to selection over generations. This effect is not seen as much in this particular case as mutations are 'on'. As the reduction in variation in 'O' values is uniform, the reduction in unique combinations of 'O' and 'E' value individuals depends on the rate of reduction of variation of 'E' values in the population which is indicated by the 'shan_ind_ext' parameter. The highest value of Shannon Index (SI) of the set of values of the extended phenotype was for $(c1, c2) = (10.0, 1.0)$ and this pattern is mirrored in the general trend observed in the 'unique_combos' parameter. The parameter value also never goes to 0 in any combination of $c1$ and $c2$ values due mutations providing variation every generation.
- Val_ext: Lower values are selected in this case much like the case where there were no mutations. In negative interaction cases, the smaller values of the extended phenotype component increases the individuals' fecundity value allowing them to have greater fitness. The presence of mutations counteracts the effect of selection and hence this parameter's values do not go as low as they did in the 'no mutation' case. This in turn reduced the 'marg_fit_org' parameter of the population for the entire set of $(c1, c2)$ values as a higher average 'val_ext' value in the population reduced the fecundity of the individuals. (Left : No mutation, no heritable environment, Right: With mutation and inherited environment. After 200 generations)

Fig 4c (i – ii, left to right)



- Val_org: This parameter increases but fixes at a lower value than that of the 'no mutation' case. As expected the effect of mutations counters the effect of selection. The increase of the parameter is uniform over the entire parameter space.

Part 2

The second part of the simulation work involved the study of the effects of two different types of mating (random and assortative) coupled with two types of frequency dependent biases (conformity and novelty).

The results obtained will be considered by looking at the effect of the factor 'd' which can be biologically thought of as the strength of adoption of a particular cultural trait from the population. A higher value of 'd' would imply a greater push or pull in the direction of the required most/least common trait (depending on the type of bias) hence implying a greater magnitude of change in the individual's cultural trait value every generation as compared to a case with a smaller 'd' value when all other parameters are considered equal.

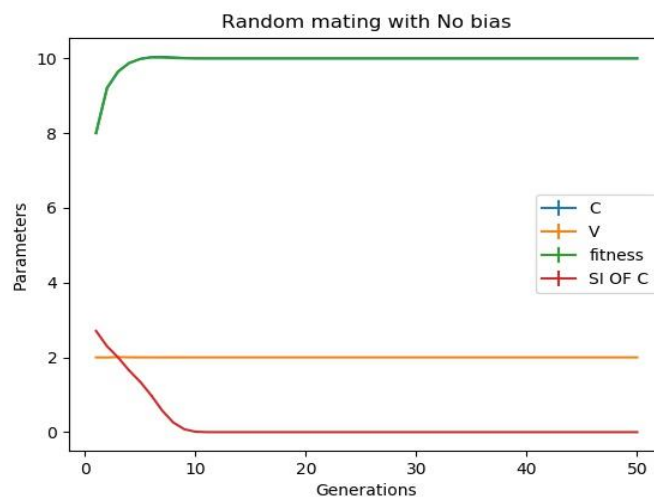
Following this will be an analysis of the results from the Bias axis. For a randomly mating population, the individual effects of biases will be compared to each other highlighting the difference in their qualitative and quantitative impact on the evolution of a cultural trait.

The third part of the results includes the layer of complexity that is assortative mating. To look at the impact of assortative mating, it is compared to the results obtained by random mating in cases where there is also either type of bias present.

The initial trivial case considered was where purely random mating without any biases was simulated. As expected, there is fixation of a particular cultural trait value. In addition, the assortative mating case was considered without the impact of any biases.

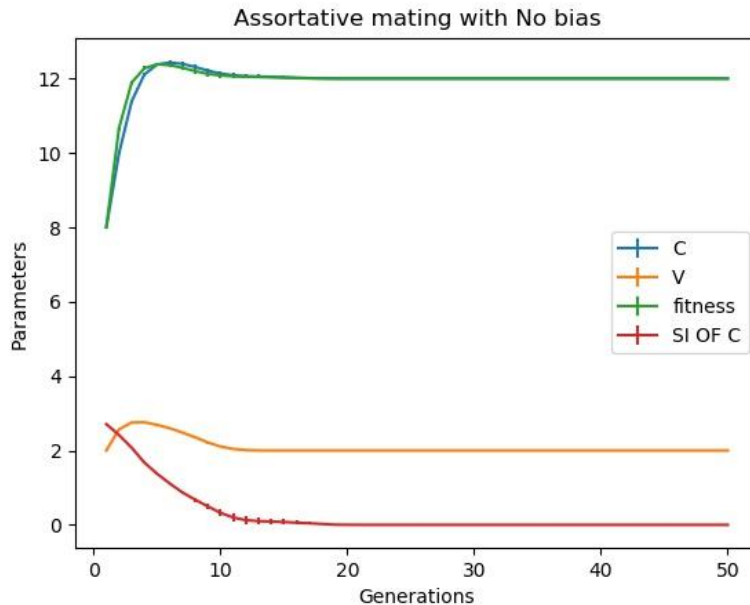
(Note: All error bars in black and white graphs are Standard Deviations and all error bars in colour graphs are Standard error)

Fig 5



As it is already apparent, the C values end up fixing at one particular value and the absence of mutations due not induce variation of any sort. The V values also do not face any selection unlike the C values (which is the only parameter under selection) and hence remain constant through the course of the run.

Fig 6



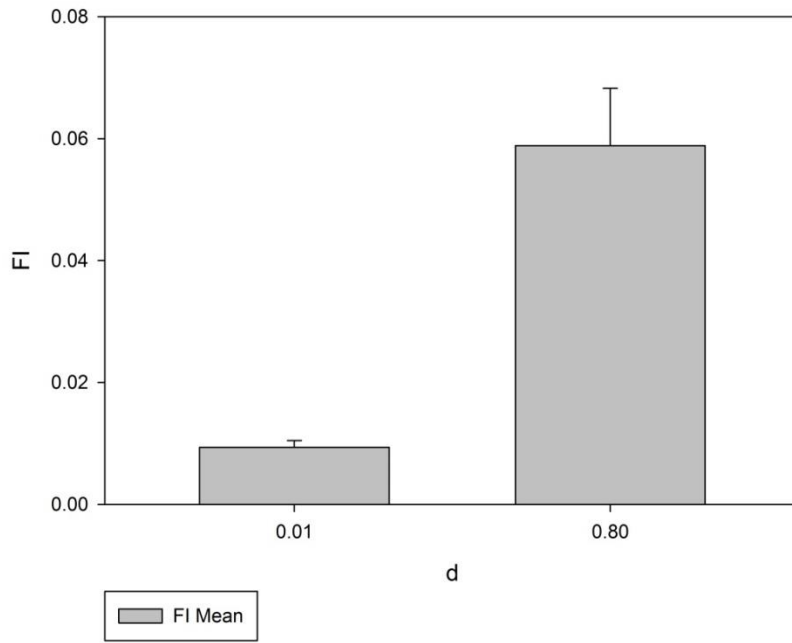
In the case of assortative mating, selection happens here with the populations reaching a slightly higher fitness value than that of the random mating case. In addition, there is a very characteristic hump that appears at the very beginning of selection. There is also a concomitant increase in the mean value of V initially before it settles down. This settling down of the V value happens at a time similar to the fixation of the C value (and therefore fitness) of the population. This hump can be attributed to the effect of initial presence of a greater variety of individuals and hence greater ease of partner finding for individuals with low V values. The reduction of this variation in time could have led to reduction in frequency of individuals with higher C values and lower V values. The rate of fixation of the cultural trait takes at least twice as long to fixate in the case of assortative mating (13 generations) as compared to the random mating case (7 generations) in part due to the initial increase of the phenotypic variance as depicted in

the graph (the hump). Rice et al. and Feldman et al. have, using analytical models, reached the same conclusion and stated that due to the increased correlation between mates in the assortative mating case for cultural traits, there is an increase in the phenotypic variance in the population (Feldman, 1977; Rice et al., 1978). Several large scale experimental studies show a similar result with positive assortment being claimed to increase inclusive fitness without additional effort required during reproduction. Although the model constructed by me does not consider these factors, hence not having a similar hypothesis, the fact that fitness of individuals in the population increases due to assortative mating is agreed to in this study (Thiessen and Gregg, 1980).

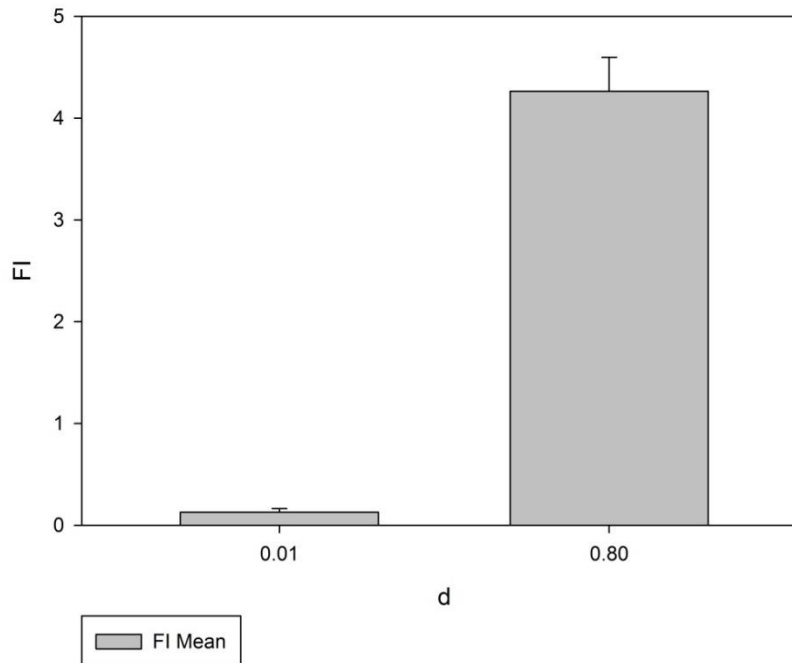
1. Impact of the 'd' parameter: The initial trivial cases do not consider the impact of the parameter 'd' on the dynamics of the system. The values of the parameter are as follows: 0.01, 0.05, 0.08, 0.1, 0.5, and 0.8. Following the introduction of the 'd' parameter in the system the use of the Fluctuation Index metric allowed us to quantify the degree of amplitude of fluctuations and further allowed us to look at the impact it had on altering the usual evolutionary trajectory which occurred in the absence of this parameter.

(Fig 7 & 8 are present in the next page; above and below respectively)

Random Mating with Conformation Bias



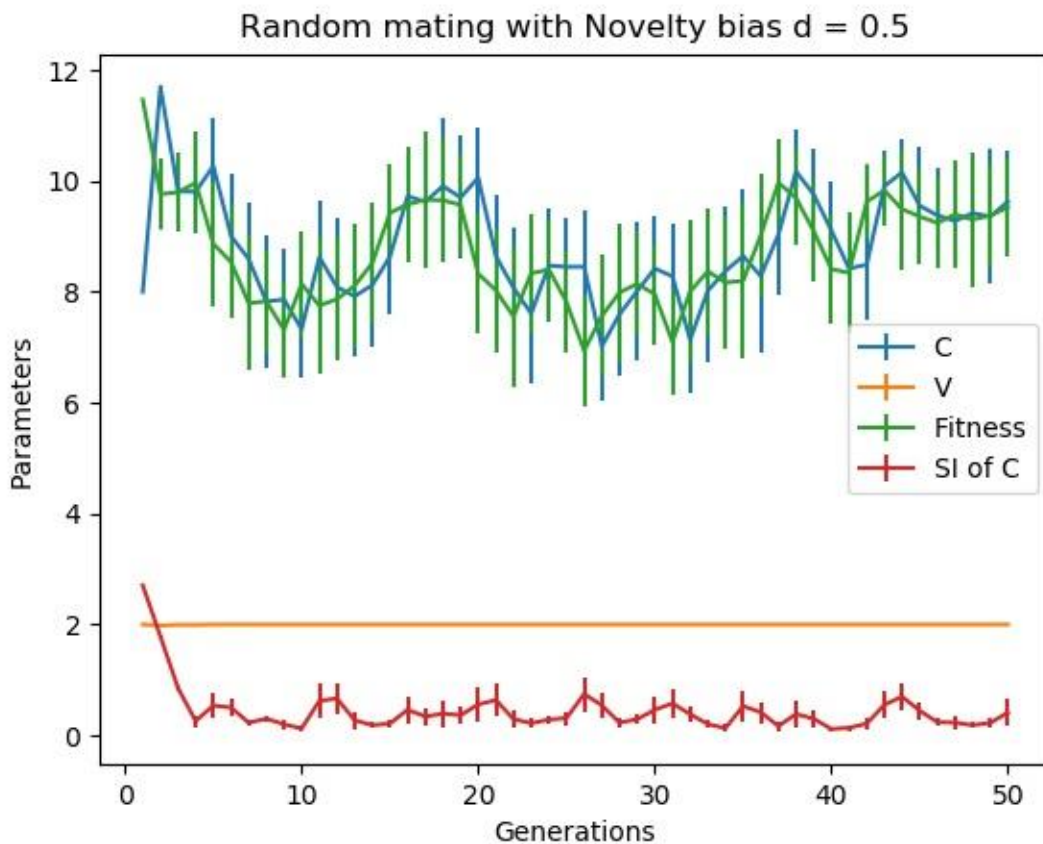
Random Mating with Novelty Bias



It is apparent that in both types of biases i.e. confirmation and novelty, the increasing value of 'd' increases the amplitude of fluctuations in the system. The 'd' values

compared here are 0.01 (the lowest) and 0.8 (the apogee) which are the extremal values in the simulations. All the FI values for the intermediate values of 'd' were below the FI of the 'd' = 0.8 scenario. To drive home the impact of 'd' on the deviation from the initial trivial case, a pertinent case where 'd' = 0.5 (novelty bias) is shown below

Fig 9



In all my simulations regarding cultural learning biases, I have assumed the simplest case as far the external environment case i.e. 'env' = 1 which implies that the resources are constant and replenished every generation. This environment is therefore stable over time with all the cultural traits having the same spectrum of impact on the fitness of the individual. Previous studies have done studies with varying environments temporally and drew the conclusion that more stable environments favour the alleles for strong conformist transmission. In our case, as the work is done on a phenotypic level, the allele refers to a trait (Henrich and Boyd, 1998). Kendal et al. took it a step further and

showed that novelty biases have higher mean fitness in a population when the environmental variation is extremely low (in our case, it is zero) (Kendal et al., 2009). Additional studies have also confirmed the negative relationship between impact on fitness of frequency-dependent biases and environment stability (Nakahashi, 2007; Wakano and Aoki, 2007). Given below are figures from my model that agree with these results

Fig 10

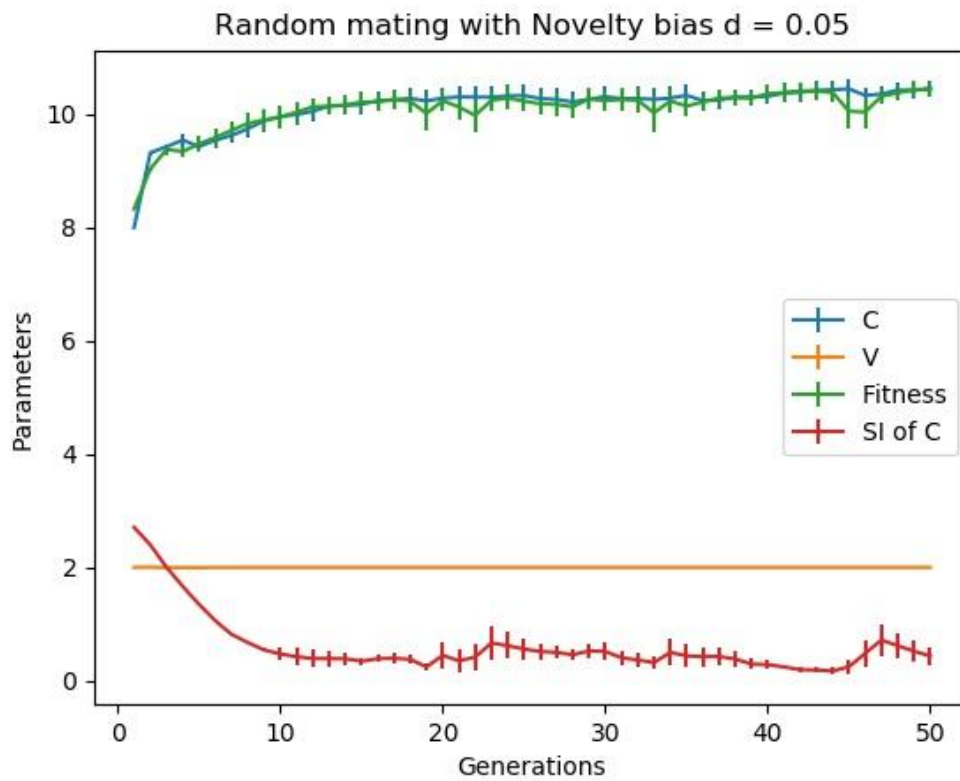
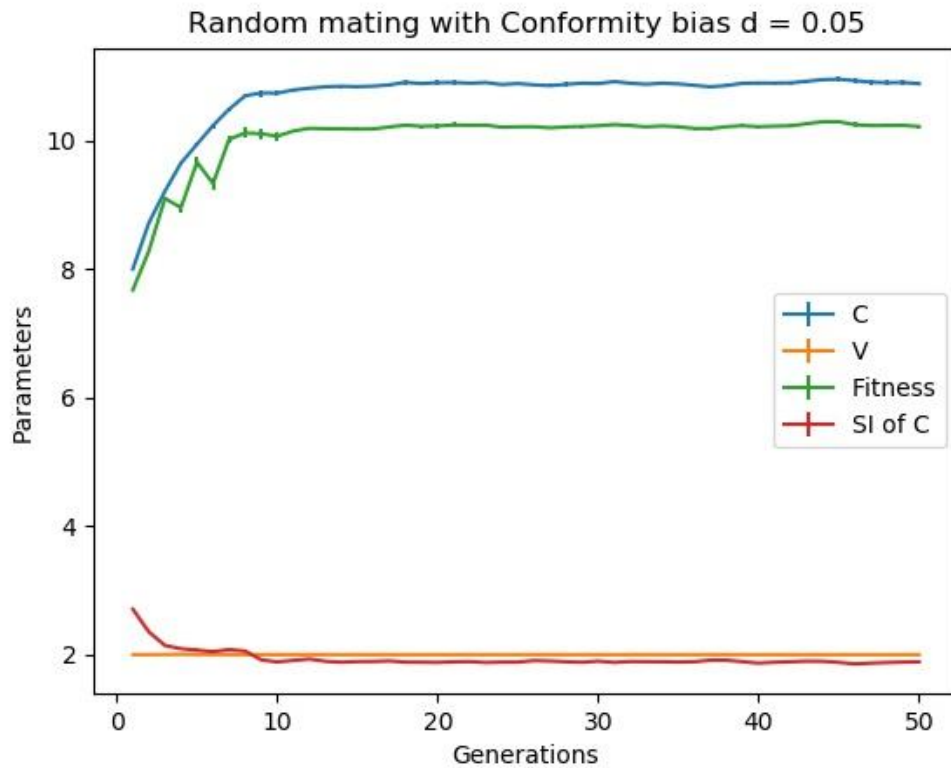


Fig 11



There is a slight increase in values of fitness which agrees with other studies. However, I further add that these results are only true for low values of 'd' in the case of novelty bias. Higher values of 'd' on the other hand create large amplitude fluctuations that not only prevent fixation of one particular cultural trait but also reduces the mean fitness of the population due to degree of contribution towards the push/pull of the individual's phenotype towards the most/least frequent trait regardless of its fitness. This phenomenon is shown for high values of 'd' in the case of novelty bias below.

Fig 12

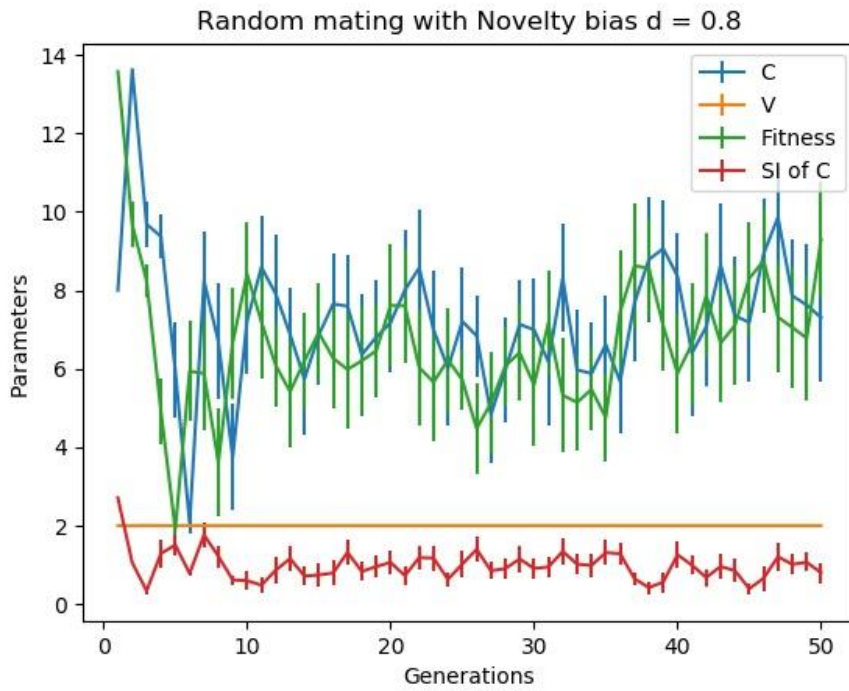
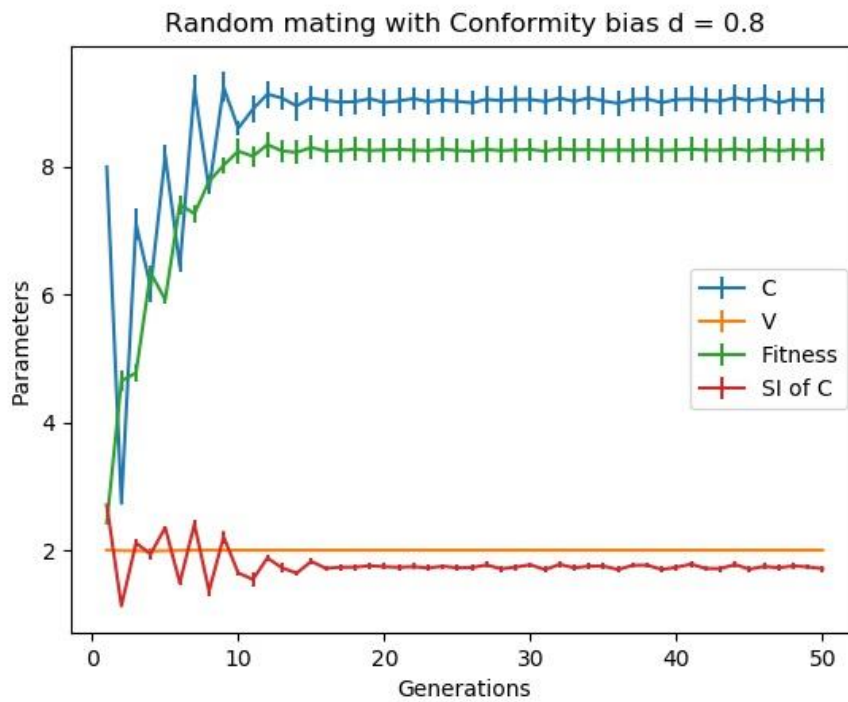


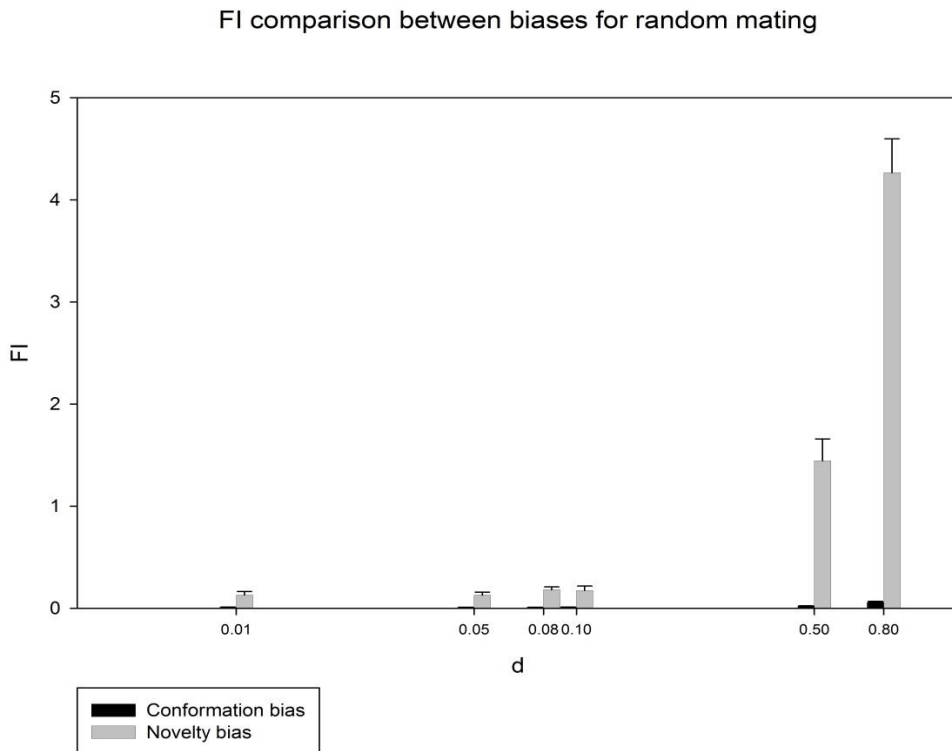
Fig 13



This phenomenon of oscillations is not seen in the case of conformity bias for the entire range of 'd' values. A previous study by Efferson et al claims the same result as they observed that this particular bias can result in homogeneity of behaviour as induces adoption of behaviours most frequent in population and this drives it to fixation. They further showed that strong novelty bias can result in oscillatory behaviour as the trait in minority is driven to majority, after which it is rejected and hence reduces in frequency. Both these predictions made were in the case of a constant environment very much like the simulations performed here (Efferson et al., 2008). Shown above is a figure that is agreement of the previously mentioned predictions.

2. Impact of the biases: Although it has been shown that the impact of 'd' exists for both biases, the extent of impact on the fluctuations for both the biases is vastly different. In fact, the type of fluctuation is characteristic of the bias.

Fig 14



The FI values for confirmation vs novelty bias are compared for the entire range of 'd' values (X-axis which is in log scale). It is quite obvious that the impact of the same 'd' value on a population of individuals that learns via novelty bias is much more (in terms of variation of C values from generation to generation) than a population that learns its cultural traits via a confirmation bias. The difference, as can be observed, is several magnitudes larger, especially as the value of 'd' continues to increase. Once again, to show to the difference in oscillations between the two types of biases a comparison of two graphs is given for the 'd' = 0.8 case

Fig 15

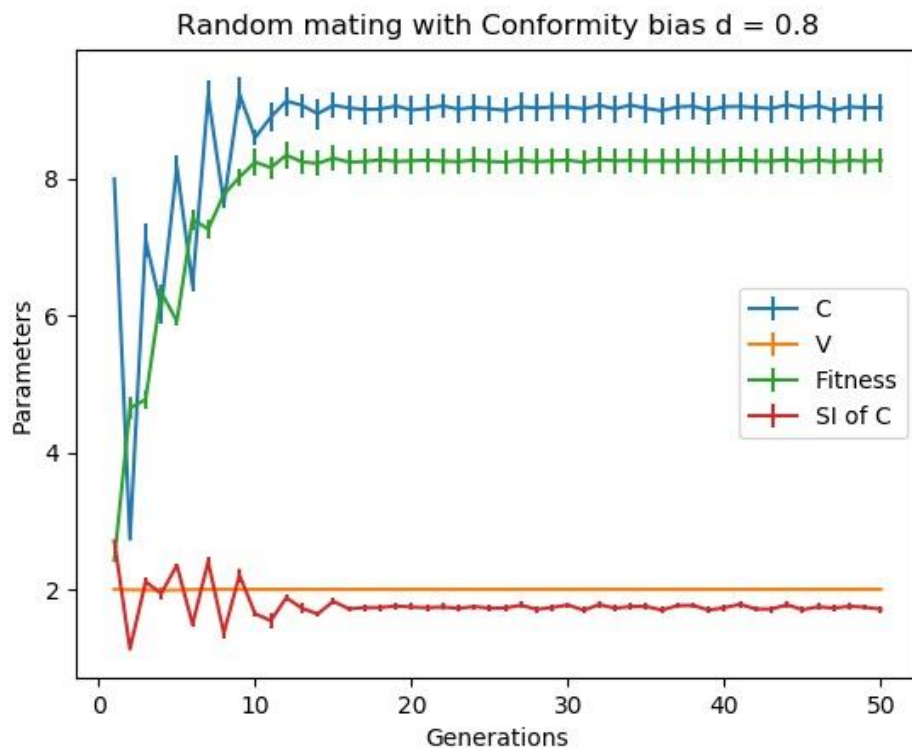
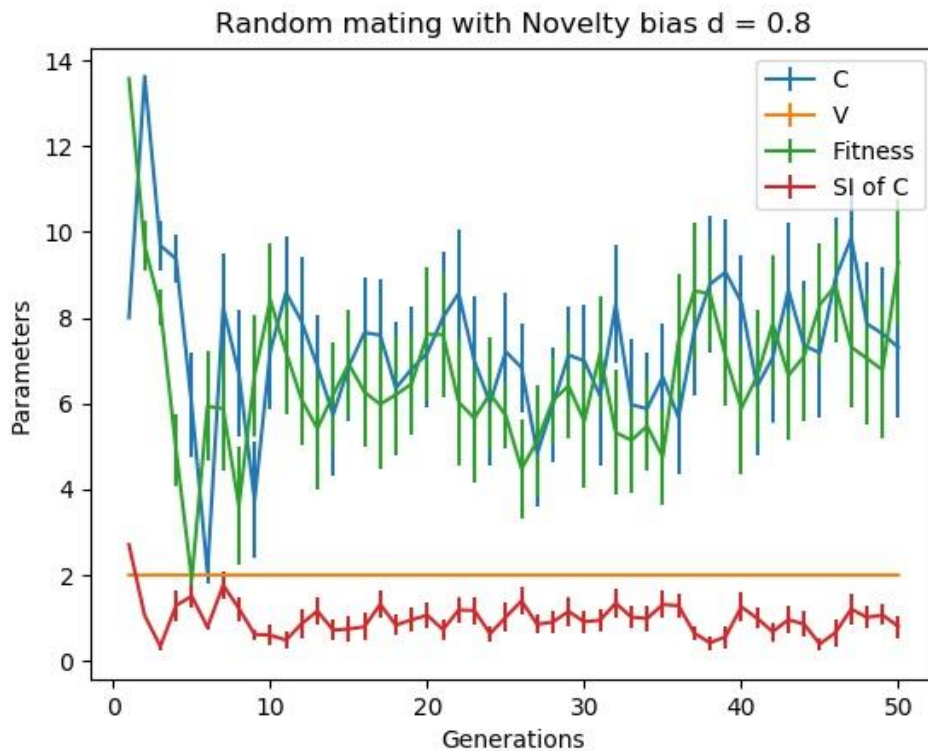


Fig 16

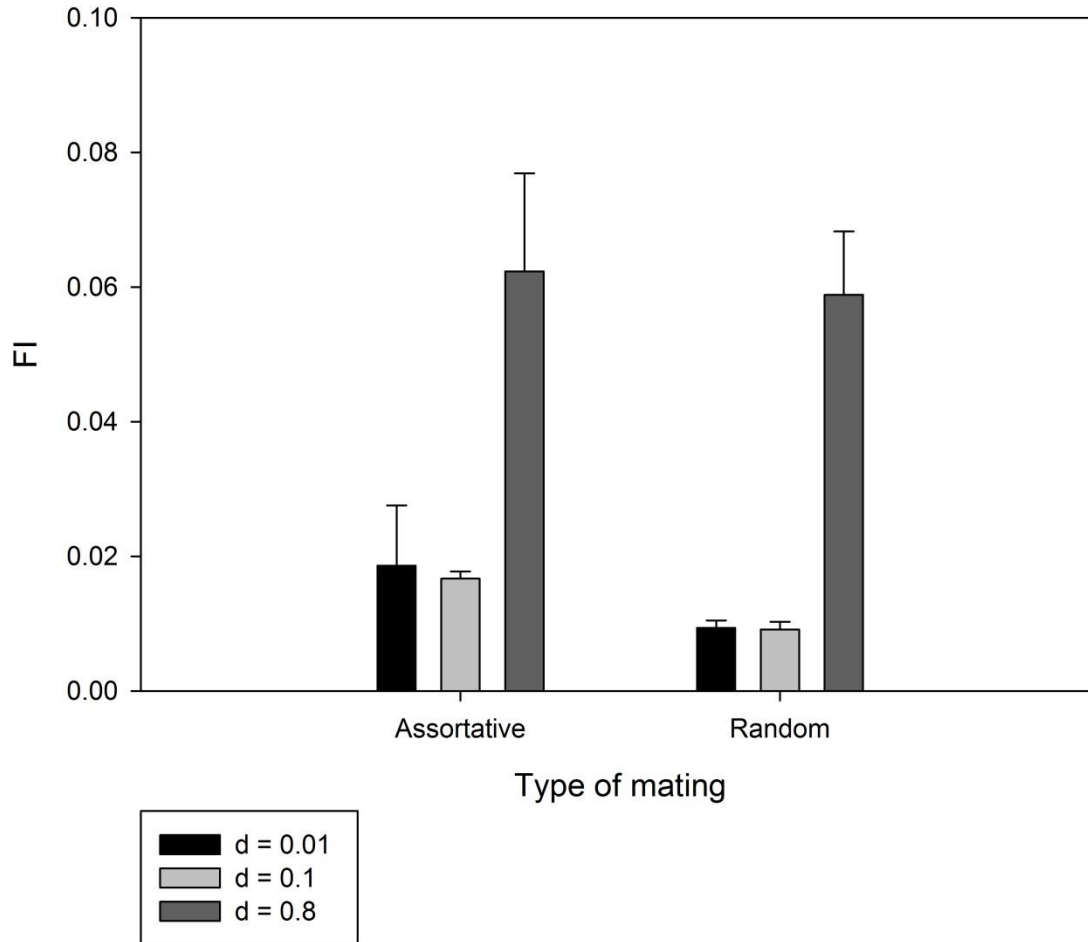


As it can be observed, the fluctuations are much more in the novelty bias case. What is also noticeable is the drop-off in the maximum C value that is fixing which in turn directly impacts the fitness of the population simply due to the way the system is modelled. This drop-off is more prominent in the case of the novelty bias scenario.

3. Impact of the mating type: Another layer of complexity can be added by considering different mating strategies in addition to the biases.

Fig 17

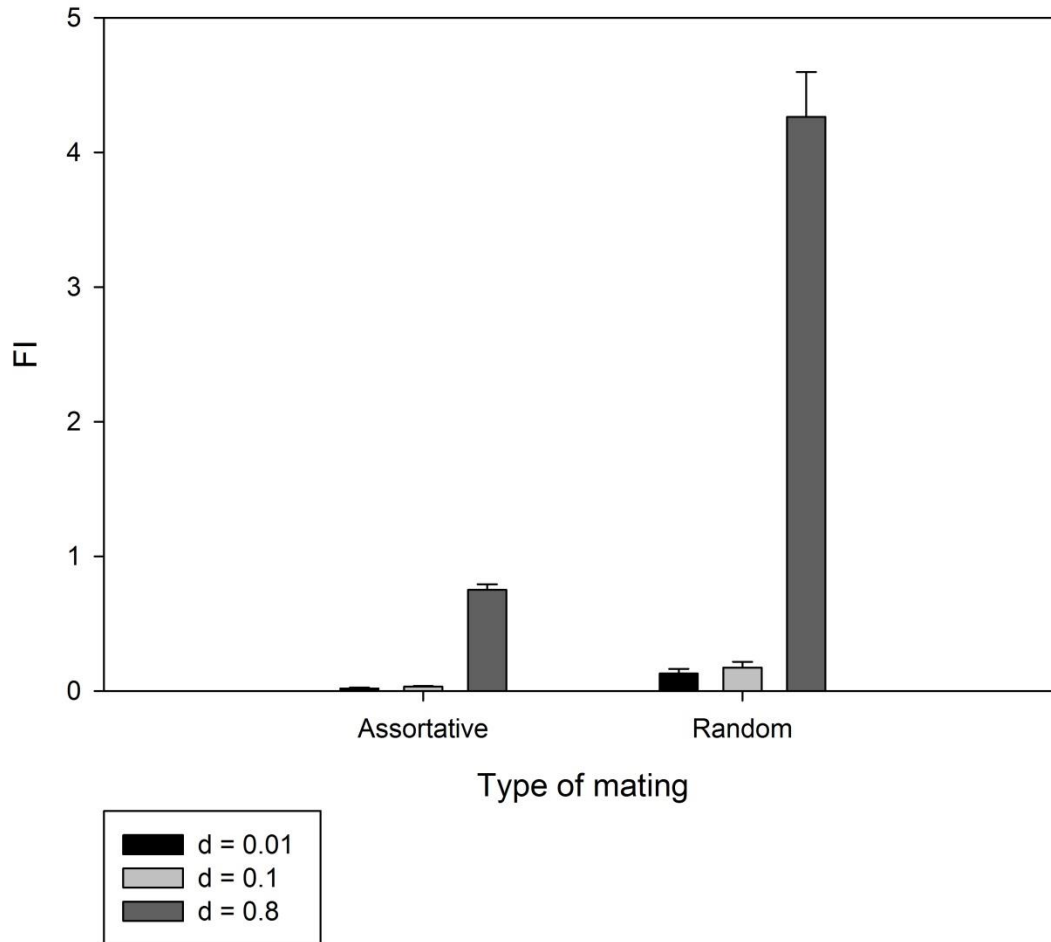
Effect of type of mating on fluctuation in conformation bias



In the above graph, comparisons have been made across 3 different types of 'd' values. In the case of confirmation bias, the type of mating does not have a very significance difference as far as FI values go indicating the fluctuations are not too different. However, the FI is slightly higher for the assortative mating for lower 'd' values and higher FI values for d = '0.8'.

Fig 18

Effect of type of mating on Novelty bias



In the above graph, across all 3 values of 'd' the FIs for random mating is higher than the FIs of assortative mating. This result is expected however. In the case of the confirmation bias, the value of 'd' helps push/pull the cultural trait value of every individual towards the mode in the population. This push/pull occurs in the direction of selection as it is the fittest individual trait that will eventually occur in greater frequency in the population. The higher values of FI in the novelty bias scenarios are also to be expected as the 'd' value pushes/pulls the cultural trait values of individuals in the population towards the cultural trait value of the lowest frequency in the population

which is in a direction opposite to regular selection as selection drives the population to fixation of one particular cultural trait by increasing its frequency with time.

Conclusions

The importance of considering the effect of cultural traits on evolution has been argued for in order to explain several experimental results (Feldman and Laland, 1996; Swallow, 2003). This has led to several models hypothesised with various degrees of contribution from the cultural part of the system (Cavalli-Sforza and Feldman, 1981; Laland et al., 2000; Tooby and Cosmides, 1990). There exist a few theoretical models of cultural evolution in literature which are either analytical in nature and or at times use ideas from population genetics to simulate outcomes. In my project I have used techniques of Individual Based Modelling (IBM) to tackle this pertinent issue of incorporating culture into classical theories of evolution. Although simplistic, my model seems to agree with several expected predictions relating to the effects of mutations, fluctuating and constant environments, and impact of evolution due to differentially weighted contributions of organism and extended phenotype components to fitness of individuals. In addition to this, the model provides an interesting result wherein, for a given set of conditions, antagonistic interactions between organism phenotype and extended phenotype have higher fitness than interactions that add on to each other. Although the basal model is simplistic with a linear polynomial in two variables defining the fitness function, more complicated dynamics can be obtained with the help of more complicated forms to define fitness functions.

A few modifications to the above constructed model allowed me to study the impact of mating types, and types of learning biases on evolution. Several studies have looked at assortative mating and its impact on evolution whereas others have looked purely at cultural learning biases. However, in nature these phenomena are not as mutually exclusive as these models assume them to be. This leads to the significance of my model which studies their effects independently and in conjunction with each other. Several results obtained agree with predictions from previous studies. In addition, the

analysis of Fluctuation Index (FI) provided novel insights into the dynamics of the mean of the cultural traits in the population. My results show that increasing the strength of push/pull towards the cultural trait value of maximal/minimal frequency (depending on the bias) increases the amplitude of fluctuations high enough to impact the mean fitness of the population. In addition, the amplitudes of fluctuations are very characteristic of the type of learning bias observed in the population. All these results have been obtained for very trivial fitness functions dependent only on the value of the cultural trait. It would be interesting to study the implications of mating types crossed with learning biases for complicated fitness functions as well as fluctuating environments and cases where mutations exist. The above sets of results further indicate the importance of cultural transmission and further work needs to be done along this interesting avenue of research.

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