Evolving populations with overlapping generations

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Overlapping Population Models

Abstract

In this paper, we extend a previously published model of an evolving finite population of multi-loci organisms, where the dynamics of the evolving system are described by the cumulants of the population efficacy distribution. We consider the case of overlapping generations and compare it to the previously studied case where generations are discrete. In the weak selection limit, we can solve the dynamics analytically and show that the changes in population genetic variance due to stochastic effects — genetic drift — is twice as great when generations overlap. The comparison of the dynamics of the two models shows many of the features seen in the comparison, performed by Moran, of simple one-locus genetic models with overlapping and non-overlapping generations. Studying the dynamics of the two models gives some insights into these comparisons.

I. Introduction

In models of evolving populations, beginning with the original work of Wright, generations are normally considered to be discrete. That is the entire population dies at once and is replaced by the descendent population. It is interesting to look at a model where population members reproduce individually and the generations overlap. In the case of simple one-locus problems, this comparison has been made extensively by solving the stable end point equilibrium point using diffusion models and Markov chain techniques [Moran, 1958c], [Moran, 1958b], [Moran, 1958a], [Ewens, 1979].

Recently, models of evolving populations with many loci have been considered, where the dynamics of the system are solved in terms of the cumulants or moments of the population efficacy distribution [Woodcock and Higgs, 1996] [Prügel-Bennett, 1997]. These models consider only the case of discrete non-overlapping generations. In this paper we extend the previously published model by Prügel-Bennett, of an evolving finite population of multi-loci haploid organisms, to include the case of overlapping generations. In the weak selection limit, where the stochastic effects of a finite population are significant, we can solve the dynamics analytically. Comparison shows that the effect of genetic drift in the overlapping generation model is twice that of the non-overlapping generation case, due to the extra randomness with which population members die. The rescaling of effective population size seen in one-locus models is seen to apply in this model.

By considering the dynamics of the two models, another scaling regarding the selection strength and mutation rates is observed. This is is not immediately obvious from analysis of the end point distribution.

In section II we present the model of the evolving population. We then describe the calculation briefly in section III and present an example of the results obtained. Analytical results are presented and discussed in section IV. These are compared to the results when generations are discrete. In section V we consider mutation and comment on the results in respect to the work of Moran on simple one locus models.

II. The population model

The model studied is that of asexual reproduction of haploid organisms on a multiplicative fitness landscape. The model and formalism presented here were originally developed to explain the evolution of genetic algorithms and have been solved for a number of problems such as sexual recombination and evolution in a multi-valleyed fitness landscape [Prügel-Bennett and Shapiro, 1994] [Prügel-Bennett and Shapiro, 1997].

We consider a population of N haploid organisms each with L genes that may have either of two possible alleles —

favorable or unfavorable. The efficacy of any population member, E, is simply the sum of the alleles,

$$E = \sum_{i=1}^{L} S_i \qquad \text{where} \qquad \mathrm{S_i} = \{-1, 1\}. \tag{1}$$

In genetic algorithm literature, E is often described as the fitness. However as fitness has a specific meaning in biology, we use the term efficacy in an attempt to avoid confusion. The weighting of population member μ when being selected for inclusion in the next generation and hence its fitness in a biological sense is given by,

$$W_\mu = \frac{\mathrm{e}^{\beta \mathrm{E}_\mu}}{Z} \qquad \text{where} \qquad \mathrm{Z} = \sum_{\mu=1}^{\mathrm{N}} \mathrm{e}^{\beta \mathrm{E}_\mu}, \tag{2}$$

and β is the selection pressure. The exponential of the sum of the alleles makes this a multiplicative model. In terms of s, the selective advantage of a single favourable allele and the selective disadvantage of an unfavourable allele, more commonly used in biology,

$$\beta = \ln\left(1 + \mathrm{s}\right). \tag{3}$$

For small β, $s \approx \beta$. When $\beta = 0$, the weightings are all independent of efficacy and there is no selection, just random sampling of the population. To make selection strength invariant under changes in the number of loci, we can rescale β by $\beta' = \beta/\sqrt{L}$.

At each time step, a population member is selected using the weighting in Eq. (2) and reproduces asexually. Another population member is selected at random to die, making room for the reproduced member and keeping the population size constant.

We introduce bidirectional mutation into the model as,

$$S_i^\mu \to -S_i^\mu \qquad \text{with probability } \gamma. \tag{4}$$

Whenever reproduction occurs, there is a small probability that a favorable allele changes to an unfavorable allele and vice versa.

III. Calculating the dynamics

Rather than follow the exact composition of the evolving population, we follow some macroscopic variables which describe the population. The variables used are the cumulants of the population efficacy distribution. The first and second cumulants are familiar as the mean and variance of the distribution. The third and fourth cumulants describe the skewness and kurtosis of the distribution. To describe the distribution fully, there are an infinite number of cumulants but we find that the first four are sufficient in most cases for our theory predictions to match simulation results. Indeed just considering the first two cumulants analytically gives considerable insight into the dynamics of the system. In previous papers, where non-overlapping generations are considered [Prügel-Bennett and Shapiro, 1997], a cumulant generating function has been derived and used to calculate the cumulants after selection. In the case of overlapping generations, we find the expected efficacy of the population member which reproduces and calculate the small perturbation to the cumulants which this causes. As we wish to model the average case, we take a technique from statistical physics and consider an average over an ensemble of an infinite number of finite populations.

The complete calculation process is detailed in Appendices A-C. In this paper we consider the case of weak selection. Appendix D is a discussion of what weak selection means in this sense.

Figure 1 shows an example of the theoretical model and simulation results plotted together. The simulation data is produced by simulating the population and recording the efficacy cumulants at each generation after selection and mutation. The results are averaged over 1,000 runs of the simulation and the error bars are approximately the size of the symbols on the plot. Here we use just four cumulants and numerically calculate the change in cumulants after each reproductive event. The errors here are due to the limited number of cumulants considered. Considering further cumulants and their fluctuations gives greater accuracy but with just four cumulants we capture the full dynamics of the system. The example is for a population size of 100 organisms each with 96 genes. The starting point has randomly assigned alleles which naturally gives a population variance of L and the population evolves to a final equilibrium point where selection is balanced against the disruptive effect of bidirectional mutation.

In addition to performing the calculations numerically we can derive analytical solutions in the weak selection limit. Much of the analysis in this paper comes from a comparison of the analytically derived results for the first four cumulants. Details of the derivation are given in the Appendices.

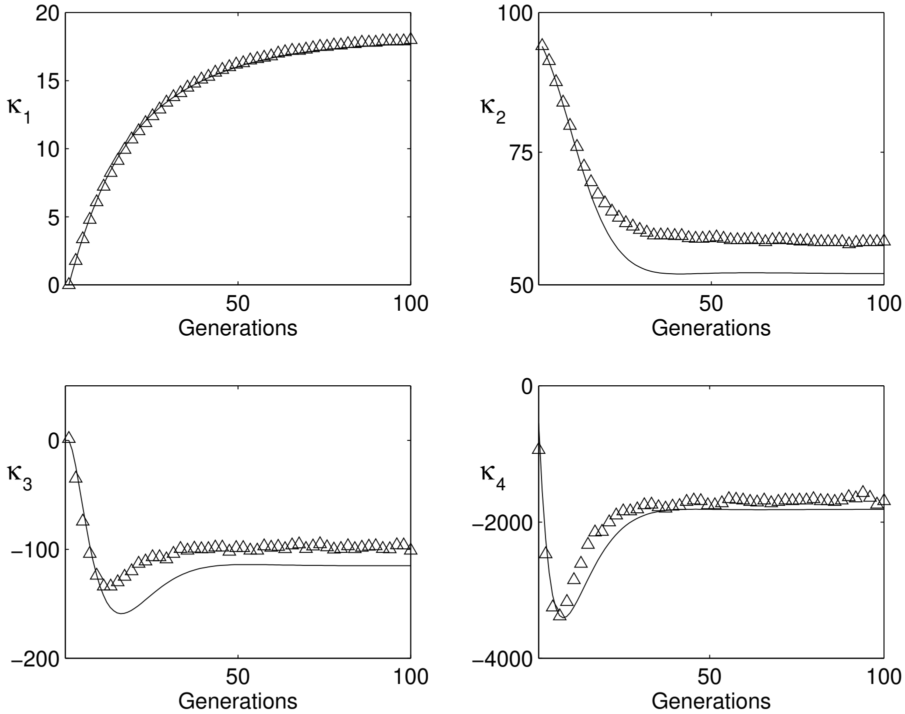

Fig. 1. Comparison of theory predictions and simulation results of the first four cumulants of an evolving population with overlapping generations. Simulations are averaged over 1,000 runs. Population size is 100. Each member consists of a 96 loci string, selection pressure $\beta = 0.1/\sqrt{96}$ and the mutation rate is 2/96.

IV. Comparison of overlapping and non-overlapping generations

We first consider the case without mutation. Solving the dynamics of the evolving population analytically in terms of a cumulant expansion yields a truncated set of coupled equations. These describe the cumulants after one reproductive event in terms of the initial cumulants and the selection pressure. For the first four cumulants in the case of overlapping generations we have the result,

$$\begin{aligned}
\kappa_1' &\approx \kappa_1 + \frac{\kappa_2}{N}\beta \\
\kappa_2' &\approx \kappa_2 - \frac{2\kappa_2}{N^2} + \frac{\kappa_3}{N}\beta \\
\kappa_3' &\approx \kappa_3 - \frac{6\kappa_3}{N^2} + \frac{\kappa_4}{N}\beta \\
\kappa_4' &\approx \kappa_4 - \frac{14\kappa_4}{N^2} - \frac{12\kappa_2^2}{N^2}.
\end{aligned} \tag{5}$$

where κ_n are the cumulants of the finite population. High order cumulant terms and small terms have been truncated in these expressions, as detailed in the Appendices.

The case of non-overlapping generations has already been published [Prügel-Bennett and Shapiro, 1997] and yields the results.

$$\begin{aligned}
\kappa_1' &\approx \kappa_1 + \kappa_2\beta \\
\kappa_2' &\approx \kappa_2 - \frac{\kappa_2}{N} + \kappa_3\beta \\
\kappa_3' &\approx \kappa_3 - \frac{3\kappa_3}{N} + \kappa_4\beta \\
\kappa_4' &\approx \kappa_4 - \frac{7\kappa_4}{N} - \frac{6\kappa_2^2}{N}.
\end{aligned} \tag{6}$$

These expressions are very similar to those in Eq. (5) but the overlapping case has an extra factor of N as it describes only one reproductive event. The non-overlapping case describes one generation — N reproductive events. When selection is weak, the change over one generation is small and we can compare the two sets of expressions directly.

The significant difference between these expressions is the factor of two in the term independent of selection strength. These describe the changes in cumulants due to stochastic sampling effects — genetic drift.

This difference is well known in terms of the fixation rate of one-locus models and was first shown in a comparison by Moran [Moran, 1958c]. The factor for the loss of variance of the population efficacy distribution (κ_2), due to genetic drift presented here, is identical to the decreasing probability of having a heterogenous population in a simple one-locus genetic model when subject to random sampling and no mutation. In the absence of selection pressure, the distribution variance of the non-overlapping model decreases each generation by the factor, $\left(1-\frac{1}{N}\right)$. With overlapping generations, the decrease in variance after N reproductive events is $\left(1-\frac{2}{N^2}\right)^N$. For reasonable size N it is clear that the rate of decrease in variance and hence the rate of genetic drift in the overlapping generation model is approximately twice that of the non-overlapping case. This doubling stems from the extra variance in the model through the randomness with which population members die.

Moran's comparison was originally between the standard Wright model of the time of N diploid organisms with non-overlapping generations and a model of 2N haploid organisms with overlapping generations and thus also involves a rescaling of population size [Ewens, 1979]. In this comparison we consider in both cases a population of N haploid organisms and thus any differences in the expressions are due to the effect of overlapping generations without this need to rescale the population size.

Figure 2 shows a comparison of the dynamics of a population with overlapping and non-overlapping generations, subject to the same selection pressure and no mutation. The population gradually converges to N copies of one of the original population members and thus the variance decreases to zero. The faster genetic drift in the overlapping model results in the variance decreasing faster and the population evolves to a lower final efficacy.

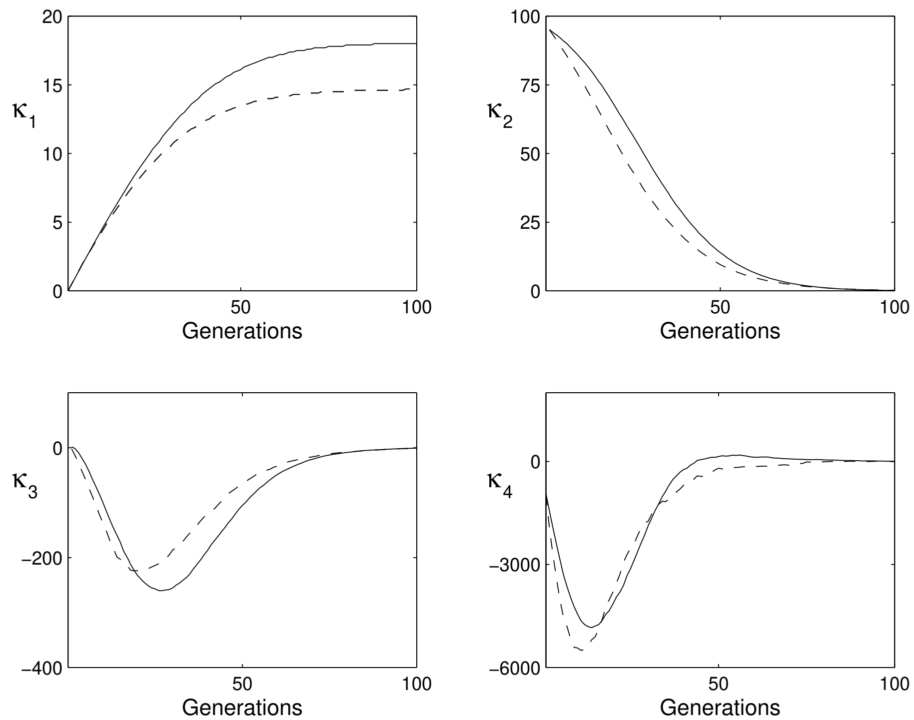

Fig. 2. Comparison of evolving populations with overlapping (dashed line) and non-overlapping (solid line) generations. Results are simulations averaged over 10,000 runs and error bars are approximately the thickness of the lines. Population size is 100. Each member consists of a 96 loci string and selection pressure $\beta = 0.05/\sqrt{96}$. There is no mutation.

There are two scalings in these comparisons which are of interest. If we rescale the overlapping generation case population size to $2N$ and apply $2N$ reproductions, the change in cumulants are equivalent to one generation of the non-overlapping case. This is well known in comparisons of one-locus models as the rescaling due to effective population size [Ewens, 1979]. The factor of two scaling being the result of extra randomness with which population members die and thus the variance in the lifetime of each population member [Hill, 1972].

It is also interesting to note that we can double the selection pressure in the overlapping generation model and the dynamics of the two models will match but with the overlapping population model evolving at twice the rate. This dynamic behaviour is not apparent in comparisons when only the end point distribution is considered. This has been the case in previous comparisons of one-locus models.

V. Mutation

When bidirectional mutation is included, the population will no longer converge to a single member of the initial population but will evolve to a stable distribution. Mutation will act to push the population to its maximum entropy state of zero mean efficacy and variance of L. Selection acts to increase the mean efficacy and decrease the population variance. These two competing forces reach an equilibrium point dependent on the parameters of the model.

The scaling relationship we observed for selection still holds when mutation is included in the model. Whilst the probability of mutation is small, doubling the mutation rate has the same effect, to first order, as applying the mutation operator twice. By doubling the mutation rate and selection pressure of the overlapping case, the dynamics will match that of the non-overlapping case. The same equilibrium distribution will be reached but in half the number of reproductive events. Figure 4 shows the dynamics of the overlapping and non-overlapping cases overlayed. The time axis of the overlapping generation curve are rescaled so that $N/2$ reproductive events are equivalent to one generation.

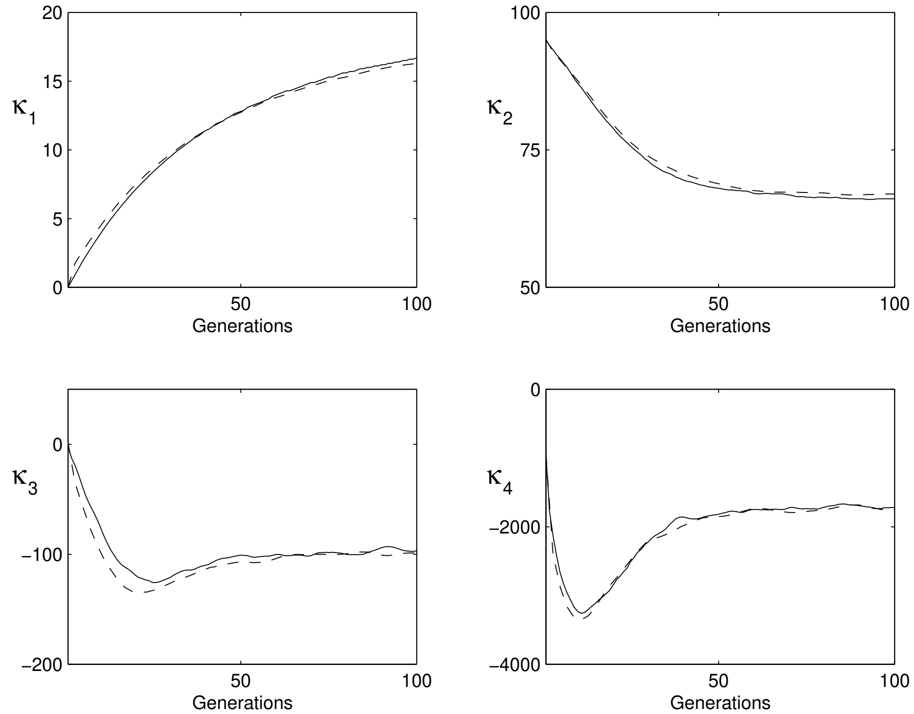

Fig. 3. Comparison of overlapping and non-overlapping generation models with mutation. Overlapping generation results are rescaled with $N/2$ reproductive events equivalent to one generation to show how it is evolving at twice the rate. Population size is 100. Each member consists of a 96 loci string. For the non-overlapping model mutation rate, γ, is $1/96$ and selection pressure $\beta = 0.05/\sqrt{96}$. For the overlapping model, parameters are rescaled with $\gamma = 2/96$ and $\beta = 0.1/\sqrt{96}$.

Moran extended the simple single locus model to include the effect of bidirectional mutation and selection [Moran, 1958b] [Moran, 1958a]. Again overlapping and non-overlapping generations were compared using a diffusion equation method and an approximate solution for the stable end point distribution was derived. Moran showed that the solution of the two models have the same form but differ by a factor of two in the mutation probability and selection pressure terms. In Moran's model, both these terms are normalised by population size and thus by rescaling population size, both models evolve to the same end point distribution.

We can also understand this result in terms of the second scaling we observe, as doubling these factors offset the increased genetic drift produced through overlapping generations. Thus the equations of motion of the systems will be identical except for a factor of two in the overlapping case. From our dynamical analysis, it is clear that we evolve to the same end point distribution but at twice the rate.

VI. Discussion

The model shown here has been extensively studied when populations are considered to be discrete. We have shown by solving the dynamics analytically, that when overlapping populations are considered, the rate of genetic drift in the system is doubled.

The rescaling of effective population size, well known in comparisons of one-locus models with overlapping and non-overlapping generations, is seen to apply to these models. By modelling the dynamics however, we observe another scaling relationship, whereby doubling mutation rate and selection pressure cause the same end point to be reached at twice the rate.

VII. Appendix

A. Calculating the dynamics

The cumulants can be calculated from the moments of the distribution.

$$\begin{aligned}
\kappa_1 &= \langle E\rangle \\
\kappa_2 &= \left\langle E^2\right\rangle - \langle E\rangle^2 \\
\kappa_3 &= \left\langle (E-\langle E\rangle)^3\right\rangle \\
\kappa_4 &= \left\langle (E-\langle E\rangle)^4\right\rangle - 3\left(\kappa_2\right)^2,
\end{aligned} \tag{7}$$

where $\langle\ldots\rangle$ represents the expected values averaged over the population. We can calculate the change in cumulants after one reproduction event, by considering the change in the moments of the distribution, due to reproduction of population member μ and death of population member ν.

$$\begin{aligned}
\kappa_1 &= \left(\langle E\rangle + \frac{E_\mu}{N} - \frac{E_\nu}{N}\right) \\
\kappa_2 &= \left(\langle E^2\rangle + \frac{E_\mu^2}{N} - \frac{E_\nu^2}{N}\right) - \left(\langle E\rangle + \frac{E_\mu}{N} - \frac{E_\nu}{N}\right)^2
\end{aligned} \tag{8}$$

Expanding these terms and then averaging over all ways of selecting population member μ and assuming population member ν is chosen at random gives,

$$\begin{aligned}
\langle\kappa_1\rangle_s &= \kappa_1 + \frac{\langle E_\mu\rangle_s}{N} - \frac{\langle E\rangle}{N} \\
\langle\kappa_2\rangle_s &= \kappa_2 + \frac{\langle E_\mu^2\rangle_s}{N} - \frac{\langle E^2\rangle}{N} - 2\langle E\rangle\frac{\langle E_\mu\rangle_s}{N} + 2\frac{\langle E\rangle^2}{N} - \frac{\langle E_\mu^2\rangle_s}{N^2} + 2\frac{\langle E_\mu\rangle_s\langle E\rangle}{N^2} - \frac{\langle E^2\rangle}{N^2},
\end{aligned} \tag{9}$$

where $\langle\ldots\rangle_s$ represents the average over all ways of performing selection. Only the first two cumulants are quoted here as the expressions become very large and unwieldy. The higher cumulants are however calculated in exactly the same fashion.

For a finite population, the expected efficacy of the selected member is simply the weighted sum over the population,

$$\left\langle E_\mu^n\right\rangle_s = \sum_{\mu=1}^{N} W_\mu E_\mu^n, \tag{10}$$

where E_μ^n is E_μ raised to the power n. We model the average dynamics of the system by considering the average over an infinite number of finite populations — an ensemble — and describe this ensemble as a continuous distribution, $\rho\,(E)$. If selection is sufficiently weak that we are not selecting from the extremes of the distribution, (see Appendix D for a discussion of this effect) the summation can be rewritten as an integral over $\rho\,(E)$,

$$\left\langle E_\mu^n\right\rangle_s \approx \frac{\int_{-\infty}^{\infty}\rho\,(E)\,\mathrm{e}^{\beta\mathrm{E}}\mathrm{E}^{\mathrm{n}}\mathrm{dE}}{\int_{-\infty}^{\infty}\rho\,(E')\,\mathrm{e}^{\beta\mathrm{E}'}\mathrm{dE}'}. \tag{11}$$

As $\rho\,(E)$ is typically close to a Gaussian, a convenient way to describe the ensemble distribution in terms of its cumulants is the Gram-Charlier expansion. This allows the distribution to be described to any degree of accuracy by the number of cumulants used. When only two cumulants are considered this has exactly the form of a Gaussian.

To derive the first four moments accurately, we must use the first four cumulants in the expansion.

$$\rho\,(E) = \frac{1}{\sqrt{2\pi K_2}}\exp\left(\frac{-\left(E-K_1\right)^2}{2K_2}\right)\left[1+\sum_{n=3}^{N}\frac{K_n}{n!K_2^{n/2}}H_n\left(\frac{E-K_1}{\sqrt{K_2}}\right)\right]$$

where $H_n\,(x)$ are Hermite polynomials,

$$H_3\,(x) = x^3 - 3x \qquad H_4\,(x) = x^4 - 6x^2 + 3. \tag{12}$$

This expansion form has the advantage that we can perform the integration in Eq. (11) analytically and assuming β is small, truncate to terms in single powers of β, to give,

$$\begin{aligned}
\left\langle E_\mu \right\rangle_s &= K_1 + K_2\beta \\
\left\langle E_\mu^2 \right\rangle_s &= K_2 + K_1^2 + (2K_1K_2 + K_3)\,\beta \\
\left\langle E_\mu^3 \right\rangle_s &= K_3 + 3K_1K_2 + K_1^3 + \left(3K_1K_3 + 3K_2^2 + 3K_1^2K_2 + K_4\right)\beta \\
\left\langle E_\mu^4 \right\rangle_s &= K_4 + 3K_2^2 + K_1^4 + 6K_1^2K_2 + 4K_3K_1 \\
&\quad + \left(4K_2K_1^3 + 4K_1K_4 + 12K_2^2K_1 + 10K_3K_2 + 6K_3K_1^2\right)\beta. \qquad (13)
\end{aligned}$$

where the terms K_n is the nth cumulant of the ensemble distribution.

Using these expressions in the terms changing cumulants in Eq. (9) gives,

$$\begin{aligned}
\kappa_1' &\approx \kappa_1 + \frac{K_2}{N}\beta \\
\kappa_2' &\approx \kappa_2 - \frac{2K_2}{N^2} + \frac{K_3}{N}\beta \\
\kappa_3' &\approx \kappa_3 - \frac{6K_3}{N^2} + \frac{K_4}{N}\beta \\
\kappa_4' &\approx \kappa_4 - \frac{14K_4}{N^2} - \frac{12K_2^2}{N^2}. \qquad (14)
\end{aligned}$$

As an alternative to deriving analytical results we can simply perform a numerical integration of Eq. (11) using the Gram-Charlier expansion and substitute numerically into the terms in Eq. (9).

B. Finite Sampling Effects

The cumulants of the ensemble will vary slightly from the cumulants of the finite population due to the well known sampling effect when a finite population is drawn from a continuous distribution. We have used κ_n for the cumulants of the finite distribution and K_n for the continuous ensemble distribution. We move between the two using the relationships,

$$\begin{aligned}
\kappa_1 &= K_1 \\
\kappa_2 &= N_2K_2 \\
\kappa_3 &= N_3K_3 \\
\kappa_4 &= N_4K_4 - 6N_2\left(K_2\right)^2/N \qquad (15)
\end{aligned}$$

where $N_2 = \left(1 - \frac{1}{N}\right)$, $N_3 = N_2\left(1 - \frac{2}{N}\right)$ and $N_4 = N_2\left(1 - \frac{6}{N} + \frac{6}{N^2}\right)$. These effects become significant when accurately comparing theory predictions with simulation results when a large number of cumulants are calculated. However for an empirical comparison, we can assume $\kappa_n \approx K_n$.

C. Mutation

By considering the expected change in efficacy due to each change of allele we can show that the efficacy of population member, μ, after mutation is given by,

$$\left\langle E_\mu \right\rangle_m = \Gamma E_\mu \qquad \text{where} \qquad \Gamma = (1 - 2\gamma)\,,$$

and $\langle \ldots \rangle_m$ represents the average of all ways of performing mutation. Extending this to the other exponents is an exercise in combinatorics,

$$\begin{aligned}
\left\langle E_\mu^2 \right\rangle_m &= \Gamma^2E_\mu^2 + L\left(1 - \Gamma^2\right) \\
\left\langle E_\mu^3 \right\rangle_m &= \Gamma^3E_\mu^3 + \Gamma E_\mu\left(1 - \Gamma^2\right)(3L - 2) \\
\left\langle E_\mu^4 \right\rangle_m &= \Gamma^4\left(E_\mu^4 + 2E_\mu^2(4 - 3L) + 3L(L - 2)\right) \\
&\quad + 2\Gamma^2\left(E_\mu^2 - L\right)(3L - 4) + L(3L - 2)\,. \qquad (16)
\end{aligned}$$

Deriving analytical expressions for the cumulants by including these terms is unwieldy. In practice, the efficacy of the selected population member is calculated from Eq. (11) and the above expressions used to correct for mutation, before the value is substituted numerically into the terms in Eq. (9).

D. *Weak Selection*

We have assumed in this calculation that weak selection is used and have used the approximation in two places. What we mean by weak selection can be seen considering these approximations.

We describe the finite population as a continuous ensemble average. When using strong selection, population members are drawn from the extreme of this distribution. It is in this extreme where the difference between the ensemble and any particular finite population will be greatest and the change from a summation in Eq. (10) to a continuous integral in Eq. (11) will break down.

Figure 4 shows this error in $\langle E_\mu \rangle_s$ and $\langle E_\mu^2 \rangle_s$ when a population member is drawn with changing selection strength. The original population consists of 100 members with efficacy randomly assigned from a unit Gaussian. The error bars are simulation results averaged over 10,000 selections. As selection strength increases, the efficacy of the selected member gradually tends to a limit — that of the fittest member of the finite population. The solid line deviating from the simulation results is a numerical integration of Eq. (11) and it is clear that it is a good approximation for $\beta < 1$. To make selection strength invariant under changing variance, β can be rescaled as $\beta' = \beta/\sqrt{K_2}$. For an initially random population $K_2 \approx L$, and thus $\beta = 1/\sqrt{L}$ is a good estimate of the upper limit of selection strength for selection to be considered weak. As population size increases this limit increases as the highest efficacy in the finite population increases. This effect is slow however as $E_{max} \approx \sqrt{\ln(\mathrm{N})}$.

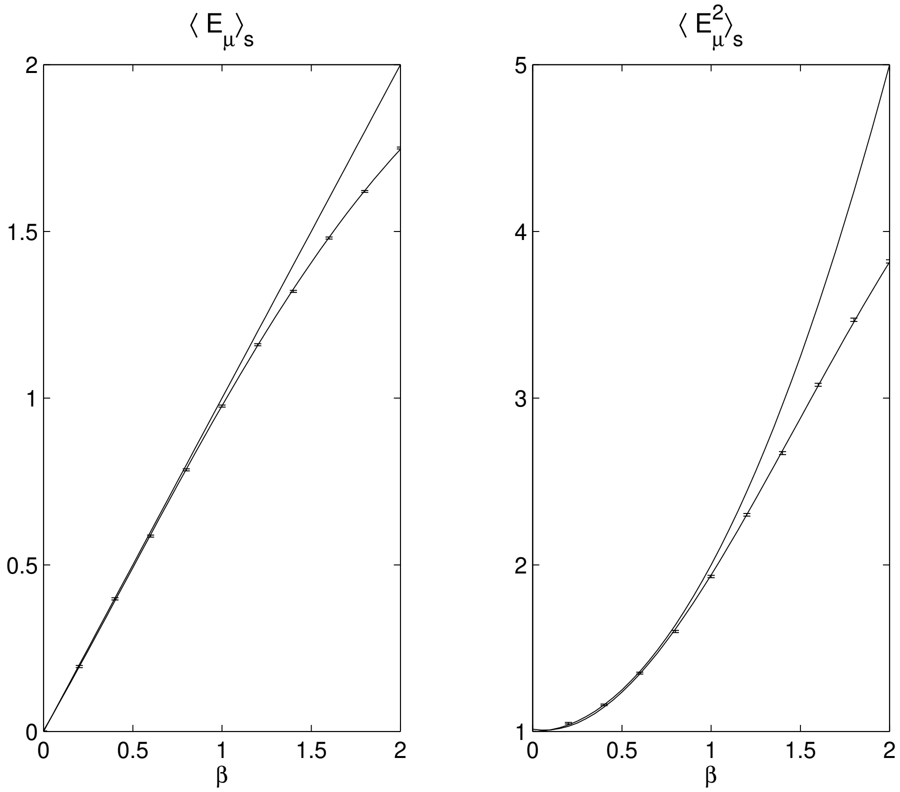

Fig. 4. Comparison of simulation results and numerical integration when selecting with varying selection strength. Simulations are for a population of 100 drawn from a unit Gaussian and are averaged over 10,000 selections.

Rather than naively performing the transform to give Eq. (11) we can make use of the identity,

$$\frac{1}{A} = \int_0^\infty \mathrm{e}^{-\mathrm{sA}} \mathrm{ds}. \tag{17}$$

to bring up the normalisation factor in Eq. (10). We can then average it over the ensemble to give,

$$\langle E_\mu^n \rangle_s = N \int_0^\infty \int_{-\infty}^\infty E^n \mathrm{e}^{\beta \mathrm{E} - \mathrm{s}\mathrm{e}^{\beta \mathrm{E}}} \rho(\mathrm{E}) \left[\int_{-\infty}^\infty \rho(\mathrm{E}') \, \mathrm{dE}' \right]^{\mathrm{N}-1} \mathrm{dEds}. \tag{18}$$

The resulting integral allows for the finite population effect and is the solid line plotted through the error bars in Figure 4. It allows any selection strength to be modelled but analytical expressions can not be derived and it must be calculated numerically.

Having made this first approximation, we truncate the analytical expressions by assuming β^2 is small. Clearly from the expected range of β allowed, this is a fair approximation.

References

[Ewens, 1979] Ewens, W. J. (1979). *Mathematical Population Genetics*. Springer-Verlag.

[Hill, 1972] Hill, W. (1972). Effective Size of Populations with Overlapping Generations. *Theoretical Population Biology*, 3:278–289.

[Moran, 1958a] Moran, P. A. P. (1958a). A general theory of the distribution of gene frequencies I. Non-overlapping generations. *Proceedings of Royal Society B*, 149:113–116.

[Moran, 1958b] Moran, P. A. P. (1958b). A general theory of the distribution of gene frequencies I. Overlapping generations. *Proceedings of Royal Society B*, 149:102–112.

[Moran, 1958c] Moran, P. A. P. (1958c). Random Processes in Genetics. *Proceedings of the Cambridge Philosophical Society*, 54:60–71.

[Prügel-Bennett, 1997] Prügel-Bennett, A. (1997). Modelling Evolving Populations. *J. Theor. Biol.*, 185:81–95.

[Prügel-Bennett and Shapiro, 1994] Prügel-Bennett, A. and Shapiro, J. L. (1994). An Analysis of Genetic Algorithms Using Statistical Mechanics. *Phys. Rev. Lett.*, 72(9):1305–1309.

[Prügel-Bennett and Shapiro, 1997] Prügel-Bennett, A. and Shapiro, J. L. (1997). The Dynamics of a Genetic Algorithm for Simple Random Ising Systems. *Physica D*, 104:75–114.

[Woodcock and Higgs, 1996] Woodcock, G. and Higgs, P. G. (1996). Population Evolution on a Multiplicative Single-Peak Fitness Landscape. *Journal of Theoretical Biology*, 179:61–73.