

MSc Computational Methods in Ecology and Evolution

Evolutionary Modelling

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Question 1 Time to fixation

In the lectures we derived that the time to fixation for pure random genetic drift (no selection, no mutation), was proportional to the population size $\tau_{fix} \sim N$.

- a) A calculation for the time to fixation, or loss, using the diffusion approximation that accounts also for the initial frequency x_0 gives

$$\tau = -2N(x_0 \ln x_0 + (1 - x_0) \ln(1 - x_0))$$

i) plot $\tau/2N$, ii) what value of x_0^* maximises the time? iii) explain intuitively (e.g. by symmetry) why there is a maximum at this value x_0^* .

- b) Plot τ now as a function of N for $x_0 = 0.01, 0.1, 0.5$ and $100 \leq N \leq 10^8$. Use this plot to argue that changes in population size have a much greater effect on τ than changing the initial frequency.

- c) If the initial frequency arises as a de novo mutation $x_0 = 1/N$. Show, for $N \gg 1$, that in this case

$$\tau \approx 2 \ln N.$$

What has happened to the linear dependence on N above?

- d) If now the mutant is under selection, we showed in the lectures that the establishment time was approximately, $\tau_{est} \approx \frac{1}{2s}$. At establishment, what will be the frequency of the mutant?

- e) Using this result, show a rough estimate of the time to fixation, once the mutant has established is

$$\tau_{fix} \approx \frac{1}{s} \ln(2Ns)$$

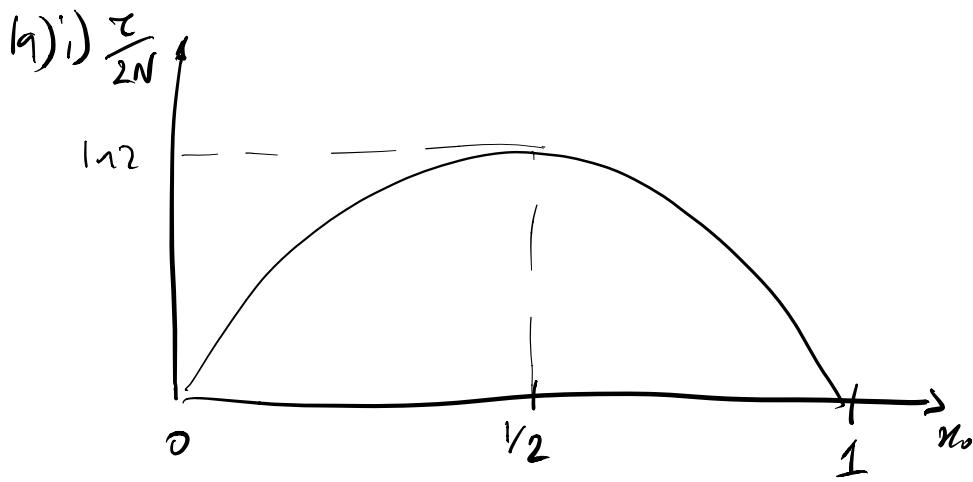
assuming the deterministic approximation $t^* = \frac{1}{s} \ln \left(\frac{1}{x_0} - 1 \right)$, where t^* is the time for a mutant to reach frequency $\frac{1}{2}$, assuming a deterministic model of selection. Is this an underestimate or overestimate of the time to fixation?

- f) Putting this together with the time to establishment show that including establishment the time to fixation of a new mutant is approximately

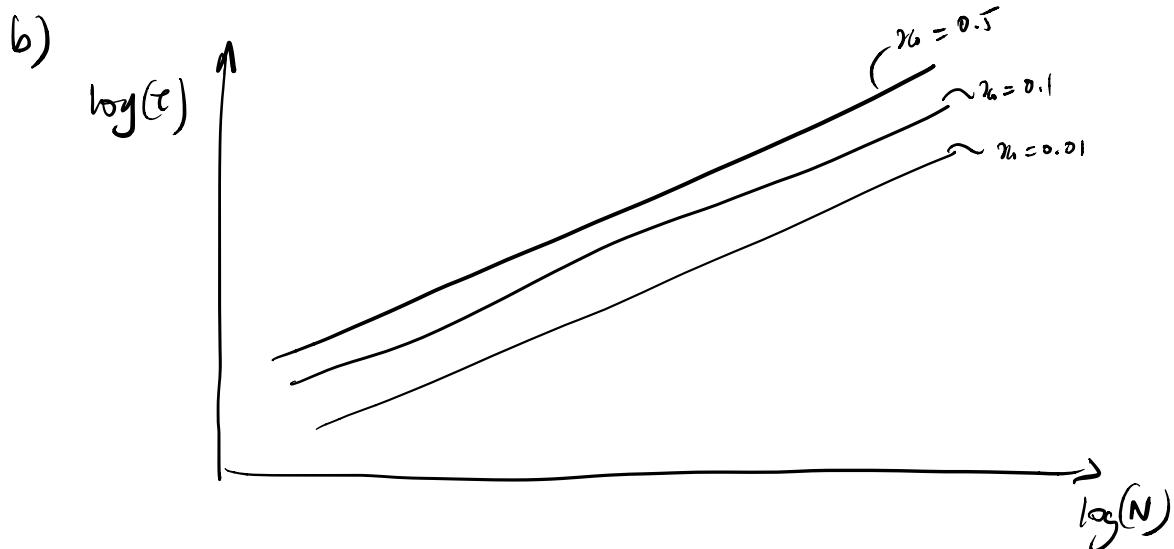
$$\tau_{fix} \approx \frac{1}{s} \left(\frac{1}{2} + \ln(2Ns) \right)$$

- g) i) Which factor, selection or drift is dominant in determining the time to fixation and explain your reasoning? ii) What else is this calculation ignoring?

Plot on
log-log
scale.



- ii) There is a maximum at $n_0 = 1/2$, since at this initial frequency we would expect by symmetry that there would be an equal probability of fixation or loss, and for any value $n_0 \neq 1/2$ the time should decrease as we are closer to either fixation or loss.



We see for typical changes in initial freq. the change in τ is small relative to orders of magnitude change in τ , due to orders of magnitude change in N .

$$\begin{aligned}
 c) \quad \tau &= -2N (\pi_0 \ln \pi_0 + (1-\pi_0) \ln (1-\pi_0)) \\
 \tau(\pi_0=\frac{1}{N}) &= -2N \left(\frac{1}{N} \ln \frac{1}{N} + \left(1 - \frac{1}{N}\right) \ln \left(1 - \frac{1}{N}\right) \right) \\
 &\approx -2N \left(\frac{1}{N} \ln \frac{1}{N} + 1 \times \ln 1 \right) \\
 &= -2 \ln \left(\frac{1}{N} \right) = 2 \ln N
 \end{aligned}$$

a) The frequency of the mutant at establishment is $\frac{1}{2Ns}$

c) If $t^* = \frac{1}{s} \ln \left(\frac{1}{\pi_0} - 1 \right)$ is the time for the mutant to reach a frequency of $1/2$, we can use this as a rough order of magnitude estimate of the time to fixation.

\Rightarrow with $\pi_0 = \frac{1}{2Ns}$ the establishment freq (assuming $2Ns > 1$)

$$\tau = \frac{1}{s} \ln \left(\frac{1}{2Ns} - 1 \right) \approx \frac{1}{s} \ln (2Ns).$$

This would be an underestimate since it would take longer to reach a frequency of $n=1$.

f) The time to establishment is $\frac{1}{2s}$ from $\pi_0 = \frac{1}{N}$

$$\begin{aligned}
 \Rightarrow \tau_{fix} &= \frac{1}{2s} + \frac{1}{s} \ln (2Ns) \\
 &= \frac{1}{s} \left(\frac{1}{2} + \ln (2Ns) \right)
 \end{aligned}$$

g) i) the size of the first term in the bracket compared to the second term determines the relative importance of establishment vs deterministic growth.

1) This whole analysis assumes that $2Ns \geq 1$ & $\geq \ln(2Ns) \geq 0$
 \Rightarrow for $\ln(2Ns) < \frac{1}{2}$ establishment is dominant
* \Rightarrow drift is the most important mechanism, however,
counterintuitively, the time is determined by the selection coeff's
* N does not play a role (Why?)

2) For $\ln(2Ns) > \frac{1}{2}$ deterministic growth due to selection is more important in determining t_{fix} , though the dominance is weak since it grows logarithmically with $2Ns$
(e.g. $2Ns = 10 \Rightarrow \ln(2Ns) = 2.3$
 $2Ns = 10^6 \Rightarrow \ln(2Ns) = 13.8$)

ii) We are ignoring the fact that as the mutant approaches fixation $\kappa \rightarrow 1-\kappa$ is very small, the process of fixation is also stochastic

Question 2 Malthusian selection equations

A continuous time description of selection begins with defining *Malthusian* growth rates for wild type and mutant v_1 and v_2 , respectively. Each population grows as

$$\frac{dn_1}{dt} = v_1 n_1; \quad \frac{dn_2}{dt} = v_2 n_2.$$

- a) If the frequency of the mutant is $x = n_2/(n_1 + n_2)$, using this change of variable and the above ODEs, show that the resulting differential equation for x is

$$\frac{dx}{dt} = (v_2 - v_1)x(1 - x) = \Delta v x(1 - x),$$

- b) If the Wrightian fitness of wild type and mutant are $w_1 = w$ and $w_2 = w(1 + s)$ what is the relationship between Δv and s ?
- c) If an arbitrary constant c is added to each fitness (e.g. I decide to measure fitness of wild type and mutant relative to fitness of another (very closely related) organism or strain), does this change the ODE for x ? If not, why not?

$$2a) \quad \frac{dn_1}{dt} = v_1 n_1 \quad ; \quad \frac{dn_2}{dt} = v_2 n_2 \quad ; \quad n = \frac{n_2}{n_1 + n_2}$$

$$\begin{aligned} \Rightarrow \frac{dn}{dt} &= \frac{d}{dt} \left(\frac{n_2}{n_1 + n_2} \right) \\ &= \frac{1}{n_1 + n_2} \frac{dn_2}{dt} + n_2 \frac{1}{dt} \left(\frac{1}{n_1 + n_2} \right) \\ &= \frac{v_2 n_2}{n_1 + n_2} - \frac{n_2}{(n_1 + n_2)^2} \frac{d}{dt} (n_1 + n_2) \\ &= \frac{n_2}{n_1 + n_2} \left(v_2 - \frac{1}{n_1 + n_2} (v_1 n_1 + v_2 n_2) \right) \\ &= n \left(v_2 - v_1 (1-n) - v_2 n \right) \\ &= n (v_2 - v_1) - (v_2 - v_1) n \\ &= (v_2 - v_1) n (1-n) = \Delta v n (1-n) \end{aligned}$$

b) The relationship between Malthusian fitness & Wrightian fitness
 n

$$\sigma = \ln w$$

i.e. Malthusian fitness is a log-fitness

$$\Rightarrow v_1 = \ln(w_1) \quad \& \quad v_2 = \ln(w_2)$$

$$\begin{aligned}\Delta v = v_2 - v_1 &= \ln w(1+s) - \ln w \\ &= \ln w + \ln(1+s) - \cancel{\ln w} \\ &= \ln(1+s).\end{aligned}$$

[N.B. Note if $s \ll 1$ $\ln(1+s) \approx s$ $\Rightarrow \Delta v \approx s$]

- c) If I add a const c to both v_1 & v_2 , this does not change the difference in fitness $\Delta v = v_2 + c - (v_1 + c) = v_2 - v_1$, & so it does not change the ODE of n .

Question 3 Fisher's fundamental theorem of natural selection

In the lectures we derived the equations for the allele frequency in the next generation

$$x_{t+1} = \frac{(1+s)x_t}{\bar{w}},$$

where $\bar{w} = 1 + sx_t$ is the mean (Wrightian) fitness of the population.

- a) Show that $\delta x_t = x_{t+1} - x_t$ is given by

$$\delta x_t = \frac{s x_t (1 - x_t)}{\bar{w}}$$

- b) Show that this can be expressed as

$$\delta x_t = \frac{x_t(1-x_t)}{\bar{w}} \frac{d\bar{w}}{dx} = x_t(1-x_t) \frac{d \ln \bar{w}}{dx}$$

(Hint: for last part, use chain-rule for to show equivalence between LHS and RHS)

- c) This result is often called Fisher's fundamental theorem of natural selection, although Fisher's result was related to a continuous time description and that populations increase their fitness proportional to the genetic variance in fitness. Here, interpret what $\ln \bar{w}$ represents.
- d) For a population that has K -alleles the frequency of the k^{th} allele in the next generation is given by

$$(x_k)_{t+1} = \frac{w_k(x_k)_t}{\bar{w}},$$

Where $\bar{w} = \sum_{k=1}^K w_k \times (x_k)_t$. Show that the change in frequency of the k^{th} allele is given by

$$\delta(x_k)_t = \frac{w_k - \bar{w}}{\bar{w}} (x_k)_t,$$

And interpret what this means for whether the frequency of the k^{th} allele increases or decreases in the population.

$$3a) \quad n_{t+1} = \frac{(1+s)n_t}{\bar{w}} \quad ; \quad \bar{w} = 1 + s n_t$$

$$\begin{aligned} \Rightarrow \delta n_t &= n_{t+1} - n_t = \frac{(1+s)n_t}{\bar{w}} - n_t \\ &= \left(\frac{1+s}{\bar{w}} - 1 \right) n_t \\ &= \frac{1+s-\bar{w}}{\bar{w}} n_t \\ &= \frac{x+s-(x+s n_t)}{\bar{w}} n_t \\ &= \frac{s-s n_t}{\bar{w}} n_t \\ &= \frac{s n_t (1-n_t)}{\bar{w}} \end{aligned}$$

$$b) \quad \begin{cases} \bar{w} = 1 + s n_t \\ \Rightarrow \frac{d\bar{w}}{dn_t} = s \end{cases} \quad \left. \begin{array}{l} \delta n_t = \frac{n_t(1-n_t)}{\bar{w}} \frac{d\bar{w}}{dn_t} \end{array} \right.$$

$$\text{By chain rule} \quad \frac{d \ln f}{du} = \frac{d \ln f}{dt} \frac{df}{dn} = \frac{1}{f} \frac{df}{dn}.$$

$$\Rightarrow \frac{1}{\bar{w}} \frac{d\bar{w}}{dn_t} = \frac{d \ln \bar{w}}{dn_t}$$

$$\Rightarrow \delta n_t = n_t(1-n_t) \frac{1}{\bar{w}} \frac{d\bar{w}}{dn_t} = n_t(1-n_t) \frac{d \ln \bar{w}}{dn_t} //$$

c) $\ln \bar{w}$ represents a function whose derivative gives the direction of change in allele frequencies.
 \rightarrow We know this since $n_k(1-n_k) \geq 0$ & n_k .

d)

$$n_k(t+1) = \frac{w_k n_k(t)}{\bar{w}(t)} \quad ; \quad \bar{w}(t) = \sum_{k=1}^K w_k n_k(t)$$

$$\begin{aligned}\rightarrow \Delta n_k(t) &= n_k(t+1) - n_k(t) \\ &= \frac{w_k n_k(t)}{\bar{w}} - n_k(t) \\ &= \left(\frac{w_k}{\bar{w}} - 1 \right) n_k(t) \\ &= \frac{w_k - \bar{w}}{\bar{w}} n_k(t)\end{aligned}$$

\rightarrow This relation means that the frequency of the k^{th} allele will increase if $w_k - \bar{w} > 0$ & decrease if $w_k - \bar{w} < 0$

Question 4 Diploid selection equations

In the lectures the dynamics of selection was described for haploid organisms. For diploid organisms we need to consider the fitness of genotypes A_1A_1, A_1A_2, A_2A_2 . This question will calculate the equivalent equations for the frequency x_{t+1} of the allele A_2 in the next generation in terms of the frequency in the current generation x_t .

- a) If the absolute viability fitness of each of the genotypes A_1A_1, A_1A_2, A_2A_2 is w_{11}, w_{12}, w_{22} , respectively, in generation t , what are the zygotic frequencies of i) the A_1A_1 genotype, ii) the A_1A_2 genotype, and iii) the A_2A_2 genotype in terms of the allele frequency x_t . Check that the sum of i), ii) and iii) equal 1.
- b) If N_t is the total zygotic population size, what are the number of individuals in adulthood after viability selection with i) n_{11} , with A_1A_1 genotype, ii) n_{12} , with A_1A_2 genotype, and iii) n_{22} with A_2A_2 genotype.
- c) Assuming random fusion of gametes and the Hardy-Weinberg law these will also be the number of zygotes in the next generation. Using the zygotic frequencies in a) show that the total population size in next generation is $N_{t+1} = \bar{w}N_t$, where \bar{w} is the mean viability fitness of zygotes in generation t .
- d) Given your answer to b) and bii) above, what is i) the total number of copies n_1 of the A_1 allele and ii) n_2 of A_2 in the population?
- e) Using your answer to c) what is the total number of chromosomes $2N_{t+1}$? Express your answer in terms of x_t , using your results to b).
- f) Hence, using your answer to c) & d) show the frequency x_{t+1} of the A_2 allele in the next generation in terms of the absolute fitness of genotypes and x_t is

$$x_{t+1} = \frac{w_{22}x_t^2 + w_{12}x_t(1-x_t)}{w_{11}(1-x_t)^2 + 2w_{12}x_t(1-x_t) + w_{22}x_t^2} = \frac{w_{22}x_t^2 + w_{12}x_t(1-x_t)}{\bar{w}}$$

- g) Now let the absolute fitness of each genotype be decomposed into a density-dependent part $w(N)$ and a relative fitness for each genotype:
 $w_{11} = w(N) \times 1; w_{12} = w(N) \times (1 + hs); w_{22} = w(N) \times (1 + s)$,
where s is the selective advantage of the homozygotes A_2A_2 , hs is the selective advantage of the heterozygotes A_1A_2 , and where h is the dominance coefficient of heterozygotes. Show that

$$x_{t+1} = \frac{(1+s)x_t^2 + (1+hs)x_t(1-x_t)}{1 + 2hsx_t(1-x_t) + sx_t^2}$$

- h) Show that

$$\delta x_t = x_{t+1} - x_t = \frac{s(h + (1 - 2h)x)}{1 + 2hsx_t(1 - x_t) + sx_t^2} x_t(1 - x_t)$$

And that if $s \ll 1$

$$\lim_{\delta t \rightarrow 0} \left\{ \frac{\delta x_t}{\delta t} \right\} = \frac{dx}{dt} \approx s(h + (1 - 2h)x)x(1 - x)$$

This is the ODE continuous time description of the dynamics of selection for diploid populations.

Q4.

Let $n \equiv N_t$

freq of genotype assumes alleles are randomly distributed in individuals

a) i) $(1-x)^2$; ii) $2x(1-x)$; & iii) x^2

$$(1-x)^2 + 2x(1-x) + x^2 = 1 + x^2 - 2x + 2x - 2x^2 + x^2 \\ = 1 //$$

b) i) $n_{11} = N_t \times w_{11} (1-x)^2$;
ii) $n_{12} = N_t w_{12} \times 2x(1-x)$
iii) $n_{22} = N_t w_{22} x^2$

c) $N_{t+1} = n_{11} + n_{12} + n_{22} = N_t (w_{11}(1-x)^2 + 2w_{12}x(1-x) + w_{22}x^2)$
 $= \bar{w} N_t$

d) Each homozygote has 2 copies of allele & each heterozygote 1 copy of each.

\Rightarrow i) $n_1 = 2n_{11} + n_{12} = 2N_t (w_{11}(1-x)^2 + w_{12}x(1-x))$
ii) $n_2 = 2n_{22} + n_{12} = 2N_t (w_{22}x^2 + w_{12}x(1-x))$

e) Total # of chromosomes = # copies of A_1 + # copies of A_2

$$\Rightarrow N_{t+1} = n_1 + n_2 = 2n_{11} + 2n_{12} + 2n_{22}$$

$$= 2(N_t w_{11}(1-x)^2 + 2N_t w_{12}x(1-n) + N_t w_{22}x^2)$$

$$= 2N_t (w_{11}(1-x)^2 + 2w_{12}x(1-x) + w_{22}x^2)$$

f) $\Rightarrow n_t = \frac{n_2}{2N_t} \quad \left(= \frac{\# \text{ chromosomal copies of } A_2}{\# \text{ chromosomes}} \right)$

$$= \frac{2N_t (w_{22}x^2 + w_{12}x(1-x))}{2N_t (w_{11}(1-x)^2 + 2w_{12}x(1-x) + w_{22}x^2)}$$

g) $w_{11} = 1 ; w_{12} = 1+s ; w_{22} = 1+s$

$$\Rightarrow \bar{w} = (1-x)^2 + 2n(1-x)(1+s) + x^2(1+s)$$

$$= (1-x)^2 + 2n(1-x) + n^2 + 2nsx(1-x) + sx^2$$

$$= 1 + 2nsx(1-x) + sx^2$$

$$\& w_{22}x^2 + w_{12}x(1-x) = (1+s)x^2 + (1+s)x(1-x)$$

$$\Rightarrow n_{t+1} = \frac{(1+s)x^2 + (1+s)x(1-x)}{1 + 2nsx(1-x) + sx^2}$$

$$\begin{aligned}
x_{t+1} - x_t &= \frac{(1+s)x^2 + (1+h_s)x(1-x)}{1 + 2h_s x(1-x) + sx^2} - x \\
&= x \left[\frac{(1+s)x + (1+h_s)(1-x)}{1 + 2h_s x(1-x) + sx^2} - 1 \right] \\
&= x \frac{(1+s)x + (1+h_s)(1-x) - 1 - 2h_s x(1-x) - sx^2}{1 + 2h_s x(1-x) + sx^2} \\
&= x \frac{x + sx - sx^2 + h_s x + hs(1-x) - 1 - 2hs x(1-x)}{1 + 2h_s x(1-x) + sx^2} \\
&= x \left(\frac{sx(1-x) + hs(1-x)[1-2x]}{1 + 2h_s x(1-x) + sx^2} \right) \\
&= s \left(\frac{x^2(1-x) + hs(1-x)[1-2x]}{1 + 2h_s x(1-x) + sx^2} \right) \\
&= \frac{s x(1-x)(x + h(1-2x))}{1 + 2h_s x(1-x) + sx^2} \\
&= \frac{s x(1-x)((1-2h)x + h)}{1 + 2h_s x(1-x) + sx^2}
\end{aligned}$$

$$h) \text{ if } s \ll 1 \quad \bar{w} = 1 + 2hn(1-n) + sn^2 \approx 1$$

$$\Rightarrow \delta u_r \approx s([1-2h]n+h)n(1-n)$$

$$\Delta \frac{\delta u_r}{\delta t} \approx s \left(h + \frac{[1-2h]}{\delta t} n(1-n) \right) = s(h + (1-2h)n(1-n))$$

(since $\delta t=1$, for a single generation and by taking $s \ll 1$
effective growth per unit time is RHS)

$$\Rightarrow \lim_{\delta t \rightarrow 0} \left\{ \frac{\delta u_r}{\delta t} \right\} = \frac{du}{dt} = s(h + [1-2h])n(1-n)$$

Question 5 Diploid mutation-selection balance in deterministic population genetics

An ODE that describes deleterious selection on a mutant allele and mutation between mutant and wild type alleles for diploid individuals with dominance coefficient h is

$$\frac{dx}{dt} = -s_d(h + (1 - 2h)x)x(1 - x) + \mu(1 - 2x)$$

where $x(t)$ is the frequency of the mutant allele that has selective advantage $s = -s_d$ ($s_d > 0$) and μ the mutation rate and we assume there is incomplete dominance ($0 \leq h \leq 1$).

- a) For which values of s_d is the ODE above valid as a good description for discrete dynamics
- b) If h is not small, $\mu \ll s_d$ and $x \ll 1$, show that the approximate ODE is

$$\frac{dx}{dt} = -hs_dx + \mu,$$

and that the fixed point is

$$x^* \approx \frac{\mu}{hs_d}.$$

- c) However, this is not correct when $h \rightarrow 0$. In this case the ODE becomes

$$\frac{dx}{dt} \approx -s_d(h + x)x(1 - x) + \mu(1 - 2x).$$

Again, make the approximation that $x \ll 1$ to show that the fixed point is given by

$$\begin{aligned} x^* &= \frac{-(hs_d + 2\mu) \pm \sqrt{(hs_d + 2\mu)^2 + 4\mu s_d}}{2s_d} \\ &= -\left(\frac{h}{2} + \frac{\mu}{s_d}\right) + \sqrt{\left(\frac{h}{2} + \frac{\mu}{s_d}\right)^2 + \frac{\mu}{s_d}}. \end{aligned}$$

Why do we take the positive square root? Why can we not ignore the term $-2\mu x$ in this calculation, when we could in a)?

- d) Plot x^* vs h (x^* on a log scale) for $\frac{\mu}{s_d} = 10^{-3}$ and $0 \leq h < 1$ from b) and from c). What do you notice?
- e) Show from the answer to c) that

$$\lim_{h \rightarrow 0} x^* \approx \sqrt{\frac{\mu}{s_d}},$$

& confirm that the y -intercept of your plot corresponds to this value. (Hint: $\sqrt{x} \gg x$ for $x \ll 1$).

The mutational load is a measure of how far the population is from optimum. Here if there were no mutations, the wildtype would fix and the mutational load would be $\mathcal{L} = 0$. Assuming that the optimum has fitness 1, then in general the mutational load is given by

$$\mathcal{L} = 1 - \bar{w},$$

where \bar{w} is the mean fitness:

- f) Show that the mean fitness is

$$\bar{w} = 1 - 2hs_dx(1 - x) - s_dx^2$$

And so, the mutational load is

$$\mathcal{L} = 2hs_dx(1 - x) + s_dx^2.$$

- g) For finite (non-zero) h , show that the mutational load is

$$\mathcal{L} \approx 2\mu$$

- h) For the case that $h \rightarrow 0$, show that the mutational load is

$$\mathcal{L} \approx \mu$$

- i) Explain why the mutational load does not depend on how deleteriousness of the allele s_d .

Q5

- a) When $s_d \ll 1$, then the continuous dynamics of this ODE will be a good approximation of the discrete dynamics.

b) $\frac{dx}{dt} = -s_d(h + (1-2h)x)x(1-x) + \mu(1-2x)$

1) $h \gg (1-2h)x$ for $x \ll 1$

2) $1-x \approx 1$ for $x \ll 1$

$$\Rightarrow \frac{dx}{dt} \approx -s_d h x + \mu(1-2x) = \mu - (s_d h + 2\mu)x$$

But 3) $\mu \ll s_d \Rightarrow s_d h + 2\mu \approx s_d h$.

$$\Rightarrow \frac{dx}{dt} \approx -s_d h x + \mu$$

fixed point given by $\frac{dx}{dt} = 0$,

$$\Rightarrow \frac{dx^*}{dt} = -s_d h x^* + \mu = 0,$$

$$\Rightarrow s_d h x^* = \mu$$

$$\Rightarrow x^* = \mu / h s_d$$

c) When $h \rightarrow 0$ or $h \ll 1$ & $n \ll 1$

the terms h & $(1-2h)n$ could be of order the same magnitude; however, $1-2h \approx 1$, if $h \ll 1$

$\Rightarrow 1) 1-2h \approx 1 \text{ as } h \ll 1$

$2) 1-n \approx 1 \text{ as } n \ll 1$

$$\Rightarrow \frac{dn}{dt} \approx -S_d(h+n)n + \mu(1-2n)$$

We can't let $1-2n \approx 1$ since we are effectively approximating the RHS to 2nd order in n (i.e. up to n^2)
 & we need to keep track of all constant terms (n^0)
 all linear terms (n^1)
 & all quadratic terms (n^2).

i.e. $\frac{dn}{dt} = \mu - S_d h n - 2\mu n - S_d n^2$
 + $\underbrace{-2\mu n}_{\text{constant}}$ $\underbrace{- S_d n^2}_{\text{quadratic}}$

\Rightarrow In order to ignore the $2\mu n$ term we need $2\mu \ll S_d h$,

but although we know $\mu \ll S_d$, as $h \rightarrow 0$ ($h \ll 1$), then we can't say that $2\mu \ll S_d h$, as both μ & h are small.

[for part b) it was true that $2\mu \ll S_d h$, because we specified that h is not small].

\rightarrow The same is true if we quadratic term $s_d n^2$, even though $x \ll 1$, since $h \ll 1$, & $\mu \ll s_d$

we don't know that $s_d n^2$ will be much smaller than $s_d h x$ OR much smaller than $2\mu n$

\rightarrow In other words, $s_d n^2$, $s_d h x$ & $2\mu n$, all have terms which are (small thing) \times (small thing), so they could be the same order of magnitude.

$$\text{Fixed point: } \frac{dn}{dt} \approx -s_d(h+n)n + \mu(1-2n)$$

$$= \mu - (s_d h + 2\mu)n - s_d n^2$$

$$\Rightarrow \frac{dn}{dt} = 0 \Rightarrow s_d n^2 + (s_d h + 2\mu)n - \mu = 0$$

This is a quadratic eqn $a n^2 + b n + c = 0$
with solution

$$n^* = \frac{-b \pm \sqrt{b^2 - 4ac}}{2a}$$

$$\text{Here } a = s_d ; b = s_d h + 2\mu ; c = -\mu$$

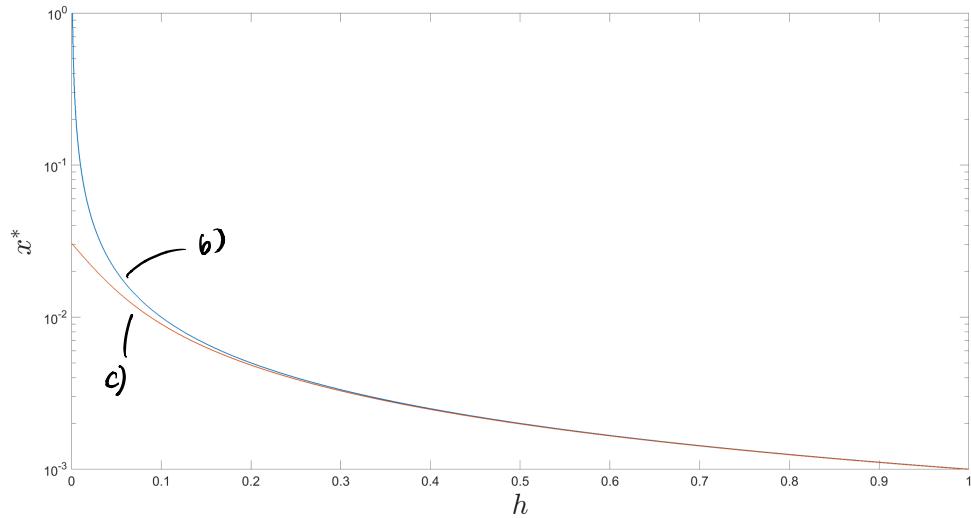
$$\Rightarrow n^* = \frac{-(s_d h + 2\mu) \pm \sqrt{(s_d h + 2\mu)^2 + 4s_d \mu}}{2s_d}$$

$$= -\left(\frac{h}{2} + \frac{\mu}{s_d}\right) \pm \sqrt{\left(\frac{h}{2} + \frac{\mu}{s_d}\right)^2 + \frac{4\mu s_d}{s_d^2}}$$

$$= -\left(\frac{h}{2} + \frac{M}{S_d}\right) + \sqrt{\left(\frac{h}{2} + \frac{M}{S_d}\right)^2 + \frac{M}{S_d}}$$

→ We take the +ve square root since the negative one will give negative solutions to x^* , which is not possible !!

d)



→ For large values of h the approximator in b) $x^* = \frac{M}{h S_d}$ works very well, but for small values of h , we need to use the better approximation in c)

e)

$$\begin{aligned}
 \lim_{h \rightarrow 0} \left\{ \frac{du}{dx} \right\} &= -M/S_d + \sqrt{\left(\frac{M}{S_d}\right)^2 + M/S_d} \\
 &= -\frac{M}{S_d} + \sqrt{\frac{M}{S_d}(1 + M/S_d)} \quad M/S_d \ll 1 \\
 &= -\frac{M}{S_d} + \sqrt{\frac{M}{S_d}}.
 \end{aligned}$$

$\approx \sqrt{\frac{M}{S_d}}$ ($\sqrt{x} \gg x$ for $x \ll 1$)

f)

$$L = 1 - \bar{w} \quad + \text{some higher-order terms where } w_1 = 1 \\
 w_{12} = 1 - hS_d \quad \& \quad w_{22} = 1 - S_d.$$

$$\begin{aligned}
 \bar{w} &= w_{11}(1-n)^2 + 2w_{12}n(1-n) + w_{22}n^2 \\
 &= (1-\cancel{n}^2 + 2(1-hS_d)n(1-n) + (1-\cancel{n})n^2) \\
 &= (1-n^2 + 2n(1-n) + n^2 - 2hS_dn(1-n) - S_dn^2) \\
 &= 1 + \cancel{n^2} - 2\cancel{n} + 2n - \cancel{2n^2} + \cancel{n^2} - 2hS_dn(1-n) - S_dn^2 \\
 &= 1 - 2hS_dn(1-n) - S_dn^2
 \end{aligned}$$

$$\Rightarrow L = 1 - \bar{w}$$

$$= 2hS_dn(1-n) + S_dn^2$$

g) if $n^* = M_{fsd}$. (i.e. h finite)

$$\begin{aligned}
 L &\approx 2h s_d n^* && (\text{since } n^* \ll 1, \text{ we can ignore quadratic terms}) \\
 &= 2h s_d \times \frac{M}{h s_d} \\
 &= 2\mu
 \end{aligned}$$

h) But as $h \rightarrow 0$ $L \approx s_d n^2$

$$n^2 \approx \sqrt{\frac{M}{s_d}} \Rightarrow L \approx s_d \left(\sqrt{\frac{M}{s_d}} \right)^2 = \mu$$

i) The nutritional load L does not depend on how debtors the number is, s_d , since for a given freq. the load would increase with s_d , but the fixed point freq. decreases as we increase s_d & in both regimes ($h < c$ & $h \neq 0$), we find a perfect cancellation of effects.