(Powerpoint info).

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* Exponential growth.

→ Discrete time model $\quad N_{t+1} = wN_t$

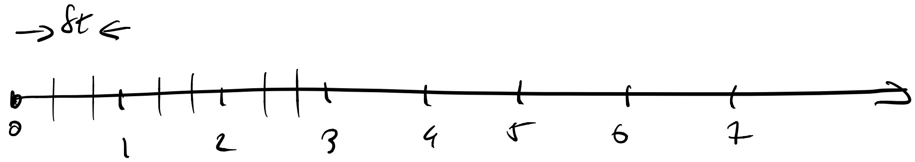
e.g. $w=2 \quad \Rightarrow N_t = N_0 2^t$

* But actually, if we were modelling bacteria, for example, they do not divide at discrete times!
  - → They divide at all times.
  - → A proper description should be stochastic, since bacteria can divide at a random time
  - → But if populations are large we can approximate this using a non-stochastic (deterministic) model.

* Deriving the exponential ODE

→ Start with discrete difference eqn.

$$N_{t+1} = w N_t \quad \to \quad \frac{dN}{dt} = \sigma N.$$



$$\to \quad N_{t+\delta t} = w_{\delta t} N_t$$

→ In our difference eqn, we know want to take $\lim_{\delta t \to 0}$

$$\begin{aligned} N_{t+\delta t} &= w_{\delta t} N_t \\ &= e^{\sigma \delta t} N_t \\ &\approx (1 + \sigma \delta t) N_t \\ &= N_t + \sigma \delta t N_t . \end{aligned}$$

$$\to \quad \delta N_t = N_{t+\delta t} - N_t = \sigma \delta t N_t .$$

$$\to \quad \lim_{\delta t \to 0} \left\{ \frac{\delta N_t}{\delta t} \right\} = \frac{dN}{dt} = \sigma N(t).$$

* $\upsilon = \ln(w)$. $\Rightarrow$ $w = 1 + s$

$\Rightarrow$ if $s \ll 1$ (i.e. $(w-1) \ll 1$)

$$\upsilon = \ln(1+s) \approx s = w - 1$$

* Solution

$$\frac{dN}{N} = \upsilon dt$$

$$\Rightarrow \int_{N_0}^{N} \frac{dN'}{N'} = \upsilon \int_0^t dt'$$

$$\Rightarrow \ln(N/N_0) = \upsilon t$$

$$\Rightarrow N = N_0 e^{\upsilon t}$$

* Alternative way to solve using an integrating factor:

$$\frac{dN}{dt} = \sigma N$$

$$\Rightarrow \frac{dN}{dt} - \sigma N = 0$$

$\times$ by integral of $e^{\int_0^t (-\sigma) dr} = e^{-\sigma t}$

$$\Rightarrow e^{-\sigma t}\frac{dN}{dt} - e^{-\sigma t}\sigma N = 0$$

$$\Rightarrow \frac{d}{dt}\left(Ne^{-\sigma t}\right) = 0$$

$$\Rightarrow Ne^{-\sigma t} = C$$

$$\Rightarrow N = Ce^{\sigma t} \qquad \rightarrow N(0) = C = N_0$$

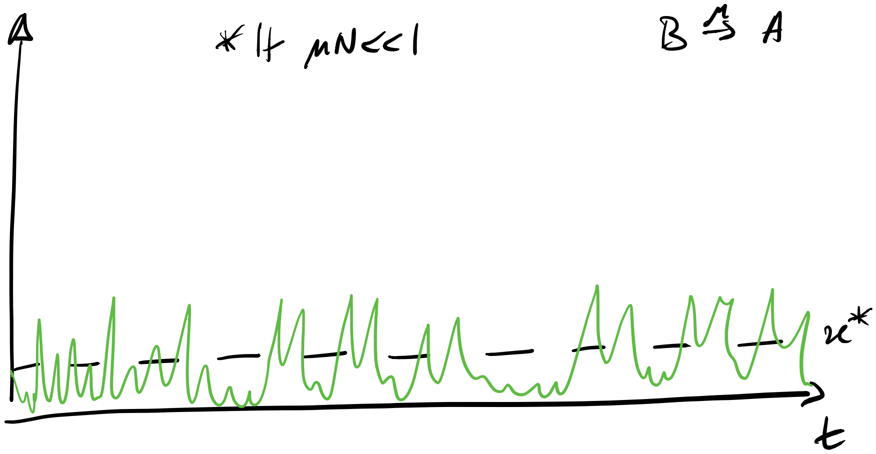
$$= N_0 e^{\sigma t}$$

Mutation - drift balance

$A \xrightarrow{\mu} B \quad w(A) = w(B)$
$B \xrightarrow{\mu} A$

$x = \text{freq}(B) = \frac{n_B}{N}$

* If $\mu N \ll 1$

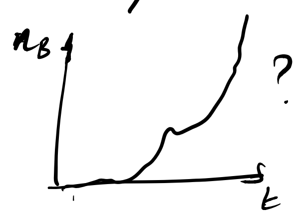


1) assume $n_A + n_B = N$ & $n_A \gg n_B$

2) Mutations enter population at rate μ

$$\frac{dn_B}{dt} = \mu n_A = \mu (N - n_B) - \mu n_B \approx \mu N$$

(What happens ?



)

-> ODE for $x = \frac{n_B}{N}$ $\Rightarrow \frac{dx}{dt} = \frac{d}{dt}\left(\frac{n_B}{N}\right) = \frac{\mu \cancel{N}}{\cancel{N}} = \mu$

$\Rightarrow \frac{dx}{dt} = \mu$ $\quad$ -> Integrate $\int_{x_0}^{x} dx' = \int_0^t \mu dt' = \mu t$

$\Rightarrow x(t) - x_0 = \mu t \Rightarrow x(t) = x_0 + \mu t$

3) As they are rare $\Rightarrow$ they can be lost to genetic drift,

$$\Rightarrow \quad \frac{dx}{dt} \approx \mu - \frac{x}{2N}$$

→ Use integrating factor trick,

$$\frac{dx}{dt} + \frac{x}{2N} = \mu$$

$$\Rightarrow \frac{d}{dt}\left(x e^{t/2N}\right) = \mu e^{t/2N}$$

$$\int d\left(x e^{t/2N}\right) = \mu \int e^{t/2N} dt$$

$$\Rightarrow x e^{t/2N} = 2N\mu e^{t/2N} + C$$

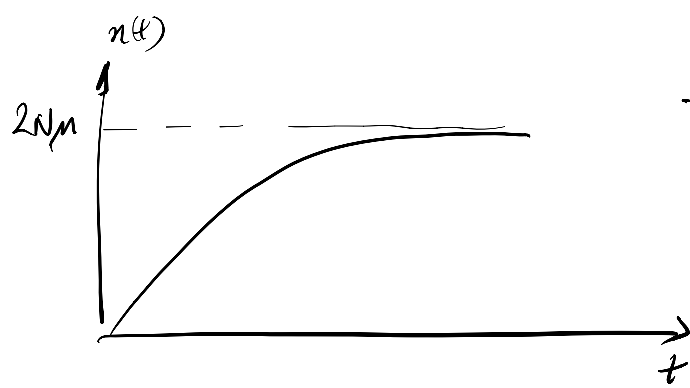
$$x(t) = 2N\mu + C e^{-t/2N}$$

$$x(0) = 2N\mu + C = 0. \Rightarrow C = -2N\mu.$$

$$\Rightarrow x(t) = 2N\mu\left(1 - e^{-t/2N}\right)$$

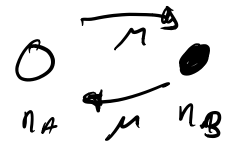
Limits $t \ll \frac{1}{2N} \Rightarrow x(t) \approx 2N\mu\left(1 - (1 - t/2N)\right)$
$\approx \mu t.$

$t \gg 1/2N \Rightarrow x(t) \to 2N\mu.$



→ Used to estimate N_e by measuring π → nucleotide diversity.

Mutation-selection balance.

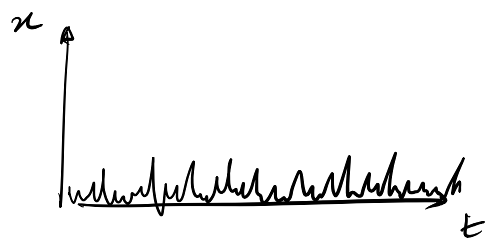


$$x = \frac{n_B}{N}$$

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

→ Not linear can't solve in general.

→ What if mutant is deleterious $s<0$?

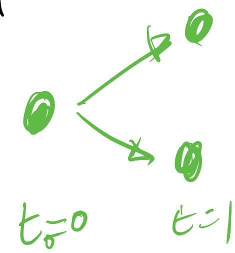


→ x is always small

$$\to \quad \frac{dx}{dt} = -s_d\, x(1-x) + \mu(1-2x)$$
$$= -s_d x + \cancel{s_d x^2} + \mu - 2\mu x$$
$$\approx -(s_d+2\mu)x + \mu$$

→ this we can solve! (tutorial)

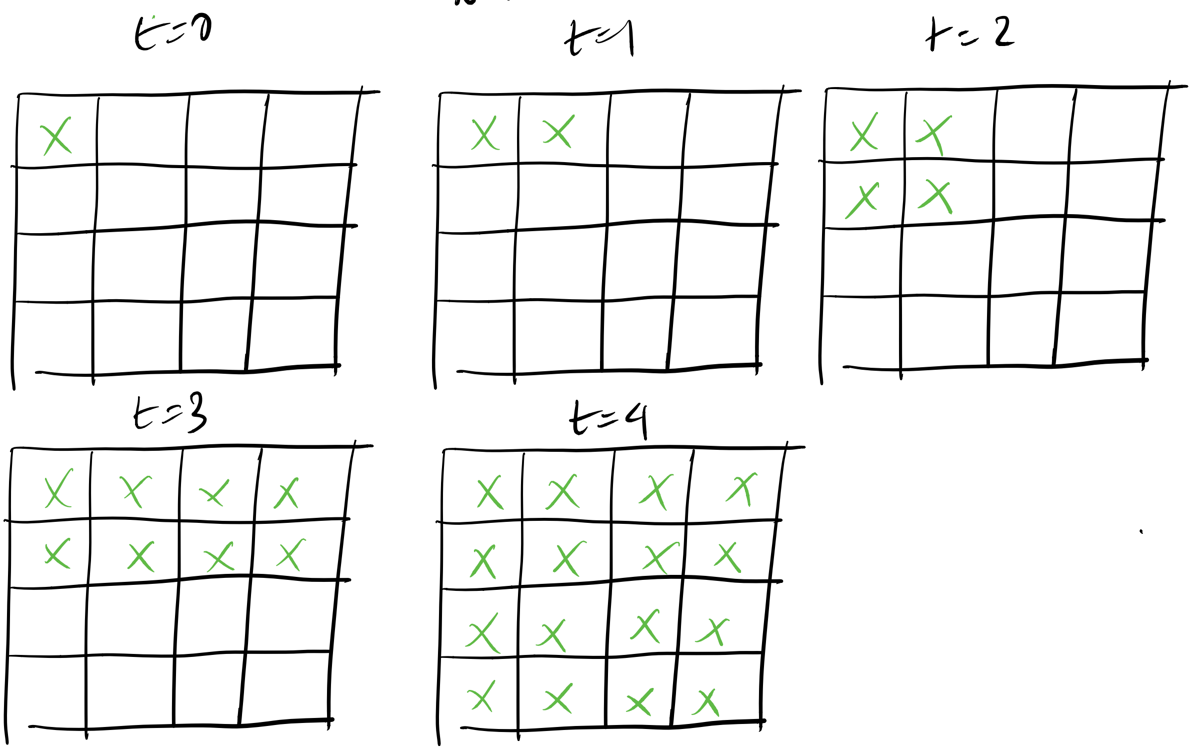
Finite carrying capacity



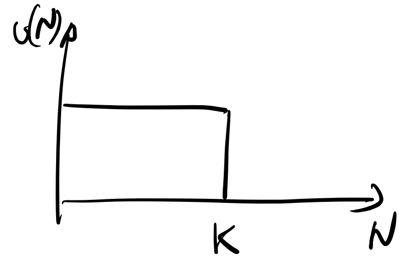
$$\frac{dN}{dt} = r_K(N)\,N$$

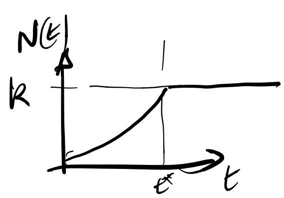
$\square$ = food needed for 1 person to survive per generation

$K = 16$



$$r(N) = r \quad \text{if} \quad N \le K$$
$$\quad\;\; = 0 \quad \text{if} \quad N > K.$$

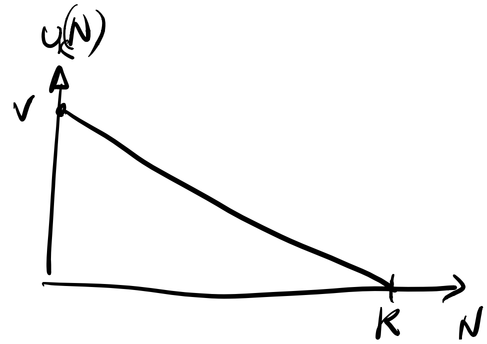




$$K = N_0 e^{r t^*}$$
$$t^* = \frac{1}{r} \ln\left(\frac{K}{N_0}\right)$$

* Logistic growth. :

→ More realistic



→ E.g. When lots of spare food it is easier to find

$$\Rightarrow \quad r_K(N) = r\left(1 - \frac{N}{K}\right) \quad \begin{cases} r & \text{for } N = 0 \\ 0 & \text{for } N = K \end{cases}$$

→ this is a rate of individuals added per individual per unit time.

$$\Rightarrow \quad \frac{dN}{dt} = r_K(N)\, N = r N \left(1 - N/K\right)$$

+ Solution :

$$\frac{dN}{N(1 - N/K)} = r\, dt.$$

$$\Rightarrow \quad \int_{N_0}^{N} \frac{dN'}{N'(1 - N'/K)} = \int_0^t r\, dt'$$

$\rightarrow$ Use Partial fractions:

$$\int_{N_0}^{N} dN \left(\frac{A}{N'} + \frac{B}{1 - N'/K} \right) = rt$$

$$\frac{A(1 - N'/K) + BN'}{N'(1 - N'/K)}$$

$\Rightarrow A = 1$ & $B = 1/K$

$$\int_{N_0}^{N} dN' \left(\frac{1}{N'} + \frac{1/K}{1 - N/K} \right) = rt.$$

$$\Rightarrow \Big[\ln|N'| - \ln|K - N'| \Big]_{N_0}^{N}$$

$$\Rightarrow \ln\left(\frac{|N||K-N_0|}{|N_0||K-N|} \right) = rt.$$

$$\ln\left(\frac{N}{N_0} \frac{(K-N_0)}{(K-N)} \right) = rt$$

$\frac{|N|}{|N_0|} \rightarrow \frac{N}{N_0}$ as $N > 0$, $N_0 > 0$

$\frac{|K-N_0|}{|K-N|} \rightarrow \frac{K-N_0}{K-N}$

as if $N_0 < K \Rightarrow N \leq K$

& $N_0 > K \Rightarrow N \geq K$.

$$\Rightarrow N(K - N_0) = N_0(K - N)e^{rt}$$

$$= N_0 K e^{rt} - N_0 N e^{rt}$$

$$\Rightarrow N(K - N_0 + N_0 e^{rt}) = N_0 K e^{rt}$$

$$\Rightarrow N(t) = \frac{N_0 K e^{rt}}{K - N_0(1 - e^{rt})}$$

$$= \frac{N_0 e^{rt}}{1 - N_0/K(1 - e^{rt})}$$

* Does it do "what it says on tin"

$$N(t=0) = N_0$$

$$N(t\to\infty) = \frac{\cancel{N_0 e^{\sigma t}}}{\frac{\cancel{N_0}}{K}\cancel{e^{\sigma t}}} = K$$

→ When $N(t) \ll K$, growth should be exponential, & $t \ll \frac{1}{\sigma}$.

$t \ll \frac{1}{\sigma}$ $\quad e^{\sigma t} \approx 1 + \sigma t$

$$\Rightarrow N(t) = \frac{N_0 e^{\sigma t}}{1 - \frac{N_0}{K}(1-(1+\sigma t))} = \frac{N_0 e^{\sigma t}}{1 + \frac{N_0}{K}\sigma t}$$

⇒ if $\frac{N_0 \sigma t}{K} \ll 1$

$$N(t) \approx N_0 e^{\sigma t}$$