(1)

- Conditional expected frequency

$$E[\bar{X}(t+1) \mid X(t)] = \frac{1}{N}\sum_{i=1}^{N}\left(B_i(1-\mu) + (1-D_i)\right)X_i + \frac{1}{N}\sum_{i=1}^{N} B_i \mu v$$

— mutants

- Take expectation and let $t \to \infty$ (stationary distribution)

$$E[\bar{X}] = \frac{1}{N}E\left[\sum_i \left(B_i(1-\mu) - D_i\right)X_i\right] + \frac{1}{N}E\left[\sum_i B_i \mu v\right] + E[\bar{X}]$$

<u>Note</u>: with our life-cycles, $\sum_i B_i$ does not depend on population composition.

- In the absence of selection, $E_0[X_i] = v$ (mutation bias) and $B_i^0 = D_i^0$.

- Weak selection approximation, first order

$$0 = 0 + \omega\left[\frac{1}{N}E_0\left[\sum_i\left(\frac{\partial B_i}{\partial \omega}(1-\mu) - \frac{\partial D_i}{\partial \omega}\right)X_i\right] + \frac{1}{N}\frac{\partial E}{\partial \omega}\left[\sum_i\left(B_i^0(1-\mu) - D_i^0\right)X_i\right]\right.$$
$$\left. + \frac{1}{N}E_0\left[\frac{\partial \sum_i B_i}{\partial \omega}\mu v\right] + \frac{1}{N}\frac{\partial E}{\partial \omega}\left[\sum_i B_i^0 \mu v\right]\right] + O(\omega^2)$$

$$0 = \omega\left[\frac{1}{N}E_0\left[\frac{\sum_i}{N}\left(\frac{\partial B_i}{\partial \omega}(1-\mu) - \frac{\partial D_i}{\partial \omega}\right)X_i\right] + \frac{-1}{N}\sum_i B_i^* \mu \frac{\partial E(X_i)}{\partial \omega}\right] + O(\omega^2)$$

$$\rightarrow \omega B^* \mu \frac{\partial E[\bar{X}]}{\partial \omega} = \omega\left[E_0\left[\frac{1}{N}\sum_i\left(\frac{\partial B_i}{\partial \omega}(1-\mu) - \frac{\partial D_i}{\partial \omega}\right)X_i\right]\right]_{\omega=0} + O(\omega^2) \quad (1)$$

$$\rightarrow E[\bar{X}] = v + \omega\frac{\partial E[\bar{X}]}{\partial \omega} + O(\omega^2)$$

B^* expected number of offspring of single indiv. at neutrality

Use total derivatives - Charles' version, intermediate variables are phenotypes: $\varphi_i = \delta X_i$ (or ωX_i with my notation)

Let's write $W_i = B_i(1-\mu) - D_i$ (fitness without mutation)

then $\frac{\partial W_i}{\partial \omega} = \sum_{k=1}^{N}\frac{\partial W_i}{\partial \varphi_k} \times \frac{\partial \varphi_k}{\partial \omega} = \sum_k \frac{\partial W_i}{\partial \varphi_k} \times X_k$.

(1) becomes $\omega B^* \mu \frac{\partial E[\bar{X}]}{\partial \omega} = \omega \times \frac{1}{N}\sum_{i,k}\frac{\partial W_i}{\partial \varphi_k}\underbrace{E_0[X_i X_k]}_{} + O(\omega^2)$

expected state of pair of sites written Q_{ik}

(2)

In subdivided population, 3 types of indiv: $\begin{cases} \circ \text{ focal} \\ \text{in, in deme + from focal} \\ \text{out, out of deme} \end{cases}$

$$\sum_k \frac{\partial W_i}{\partial \varphi_k} Q_k = \frac{\partial W_i}{\partial \varphi_0}Q_{ii} + (n-1)\frac{\partial W_i}{\partial \varphi_{in}}Q_{in} + (N-n)\frac{\partial W_i}{\partial \varphi_{out}}Q_{out}.$$

also $\sum_i W_i = \sum_i\left(B_i(1-\mu) - D_i\right) = \underbrace{\sum_i (B_i - D_i)}_{=0} - \underbrace{\sum_i B_i \mu}_{}$

does not depend on the state of the population

so $(N-n)\frac{\partial W_i}{\partial \varphi_{out}} = -\left((n-1)\frac{\partial W_i}{\partial \varphi_{in}} + \frac{\partial W_i}{\partial \varphi_i}\right)$

and $\sum_k \frac{\partial W_i}{\partial \varphi_k}Q_k = \frac{\partial W_i}{\partial \varphi_0}(Q_i - Q_{out}) + (n-1)\frac{\partial W_i}{\partial \varphi_{in}}(Q_{in} - Q_{out})$

and so $(1) \Leftrightarrow \omega B^* \mu \frac{\partial E[\bar{X}]}{\partial \omega} = \omega \times \frac{1}{N}\sum_i\left(\underbrace{\frac{\partial W_i}{\partial \varphi_0}}_{-C} + \underbrace{(n-1)\frac{\partial W_i}{\partial \varphi_{in}}}_{B}\underbrace{\frac{(Q_{in} - Q_{out})}{Q_{ii} - Q_{out}}}_{R \text{ pairwise relatedness}}\right)(Q_i - Q_{out})$

+ same behavior for all sites in expectation

<u>Note</u> $Q_{ij} = \mathcal{Q}_{ij}v + (1-\mathcal{Q}_{ij})v^2$ so that $R = \frac{\mathcal{Q}_{in} - \mathcal{Q}_{out}}{1 - \mathcal{Q}_{out}}$.

Then we decompose again the terms using total derivatives and fecundities as intermediate variables

$$\frac{\partial W_i}{\partial \ldots} = \sum_{l=1}^{N}\frac{\partial W_i}{\ldots}\frac{\partial f_l}{\ldots} \begin{cases} \text{if } l=k: -c \\ \text{if } l \neq k, \text{ same deme}: \frac{b}{n-1} \\ \ldots 0 \end{cases}$$

$(n-1)\frac{\partial W_i}{\partial f_{in}} \times \frac{b}{n-1}$

$\ldots 0$

(3)

(DB) Moran DB & WF differ by $1/N$

$B_i = \frac{1}{N}\sum_j \frac{f_i d_{ij}}{\sum_k f_k d_{kj}}$ $\quad D_i = \frac{1}{N}$ $\quad \frac{\partial D_i}{\partial f} = 0.$

$$\frac{\partial B_i}{\partial f_i} = \frac{1}{N}\sum_j\left(\frac{d_{ij} \times 1 - d_{ij} \times d_{ij}}{1^2}\right) = \frac{1}{N}\left(1 - \sum_j d_{ij}^2\right)$$
$$= \frac{1}{N}\left(1 - \left(n\frac{(1-m)^2}{n^2} + (N-n)\frac{m^2}{(N-n)^2}\right)\right)$$

$$\frac{\partial B_i}{\partial f_{in}} = \frac{1}{N}\sum_i\left(\cancel{d_{ij}} - d_{ij}\,d_{ij}\right) = \frac{1}{N}\left(0 - \left(\frac{(1-m)^2}{n} + \frac{m^2}{N-n}\right)\right)$$

would be $\neq$ if dself $\neq$ din; no self. replacⁿ.

$B^* = 1/N$

<u>Moran Birth Death</u> $\quad B_i = \frac{f_i}{\sum_k f_k} \quad D_i = \sum_k d_{ki}\frac{f_k}{\sum_l f_l}$

$$\frac{\partial B_i}{\partial f_i} = \frac{1 \times N - 1 \times 1}{N^2} = \frac{1}{N} - \frac{1}{N^2}. \qquad \frac{\partial D_i}{\partial f_i} = \sum_k d_{ki}\frac{\delta_{ki} 1 \times N - 1 \times 1}{N^2}$$

$$\frac{\partial B_i}{\partial f_{in}} = -\frac{1}{N^2} \qquad \frac{\partial D_i}{\partial f_{in}} = \sum_k d_{ki}\frac{\delta_{kj}N - 1}{N^2} = \frac{d_{ji}}{N} - \frac{1}{N^2} \qquad \frac{\partial D_i}{\partial f} = \frac{d_{ii}}{N^2} - \frac{1}{N^2}.$$

(DB) $\omega\frac{B^*}{N}\mu\frac{\partial E[\bar{X}]}{\partial \omega} = \frac{\omega \times (1-\mu)}{N}\left((1 - \text{comp})(-c) + b \times (\cancel{1} - \text{comp}) + \frac{R}{(n-1)}\left[\frac{b}{n-1}(1-\text{comp}) + (-c) \times (-\text{comp}) + \frac{n-2}{n-1}b(-\text{comp})\right]\right)$

$$= \frac{\omega(1-\mu)}{N}\left(\left(-c - \text{comp}(b-c)\right) + R \times \left(b - \frac{\text{comp}}{(n-1)}(b-c)\right)\right)$$

with $\text{comp} = \frac{(1-m)^2}{n} + \frac{m^2}{N-n}$