

## Expected frequency of altruists in the population

$$\begin{aligned} \mathbb{E}[\bar{X}] = & \nu + \delta \nu(1-\nu) \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times \\ & \left( -c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right. \\ & \left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right] \right) \end{aligned}$$

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium

$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1-\nu) \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times$$
$$\left( -c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right.$$
$$\left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right] \right)$$

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium

Selection  
strength

$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1-\nu) \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times$$

$$\left( -c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right.$$

$$\left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right] \right)$$

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium

Selection  
strength

Population variance  
Variance in the state of one site

$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1-\nu) \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times$$

$$\left( -c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right.$$

$$\left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right] \right)$$

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Variance in the state of one site

$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1 - \nu) \frac{1 - \mu}{\mu} (1 - Q_{\text{out}}) \times$$

$$\left( -c - (b - c) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{n(N_d - 1)} \right) - c \right.$$

$$\left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b - c)(n - 1) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{n(N_d - 1)} \right) \right] \right)$$

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$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1-\nu) \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times$$

$$\left( -c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) - c \right.$$

$$\left. + \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right) \right] \right)$$

$\mathcal{B}$

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium

Selection  
strength

Population variance  
Variance in the state of one site

$$\mathbb{E}[\bar{X}] = \underbrace{\nu}_{\text{Mutation-drift equilibrium}} + \underbrace{\delta}_{\text{Selection strength}} \underbrace{\nu(1-\nu)}_{\text{Population variance}} \frac{1-\mu}{\mu} (1-Q_{\text{out}}) \times$$

$$\left( \underbrace{-c - (b-c) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right)}_{\text{Purple box}} - \underbrace{c}_{\text{Purple italic}} \right.$$

$$+ \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{\text{Blue box } R} \left[ \underbrace{b - (b-c)(n-1) \left( \frac{(1-m)^2}{n} + \frac{m^2}{n(N_d-1)} \right)}_{\text{Green box } B} \right] \Bigg)$$

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$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1 - \nu) \frac{1 - \mu}{\mu} (1 - Q_{\text{out}}) \times$$

$$\left( -c - (b - c) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{n(N_d - 1)} \right) - c \right)$$

$$+ \frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}} \left[ b - (b - c)(n - 1) \left( \frac{(1 - m)^2}{n} + \frac{m^2}{n(N_d - 1)} \right) \right]$$

$R$

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