

Fidelity of parent-offspring transmission and the evolution of social behavior in subdivided populations.

F. Débarre



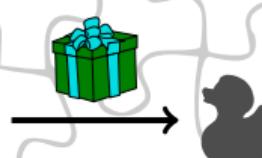
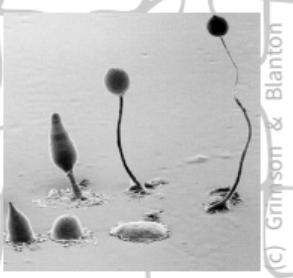
@flodebarre

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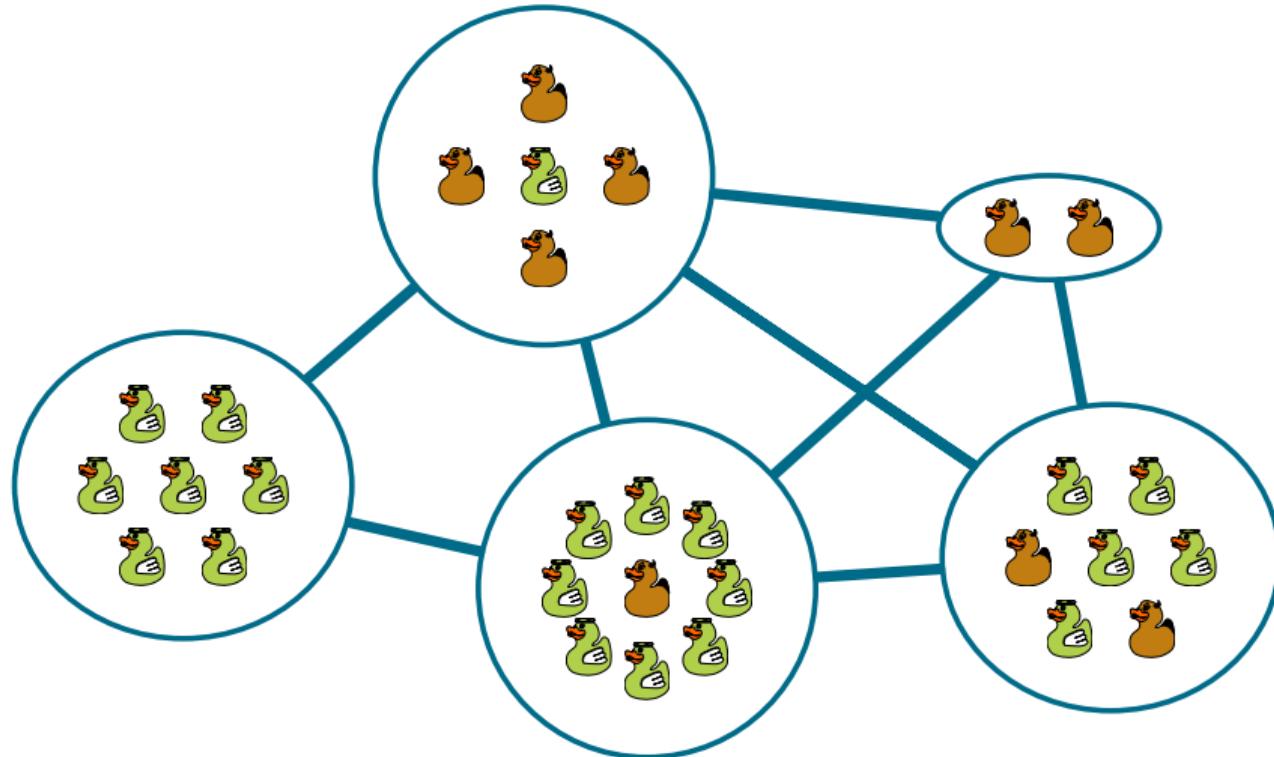




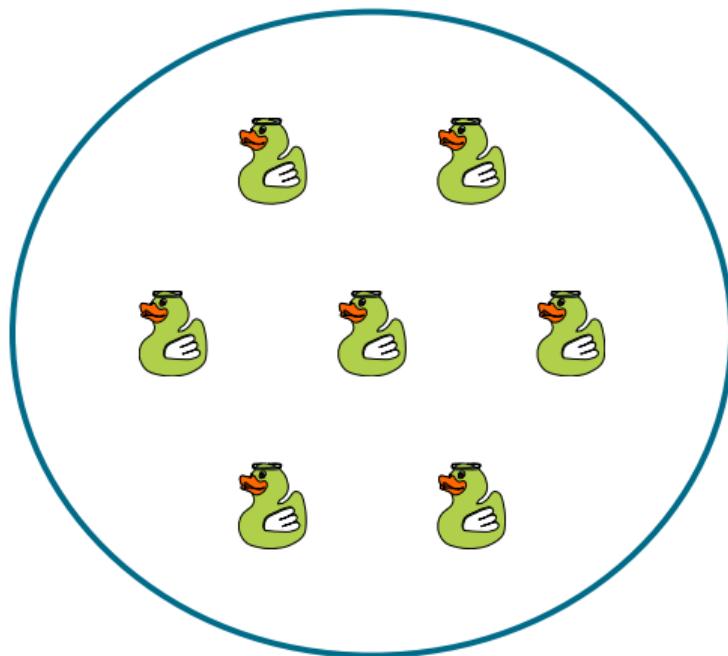




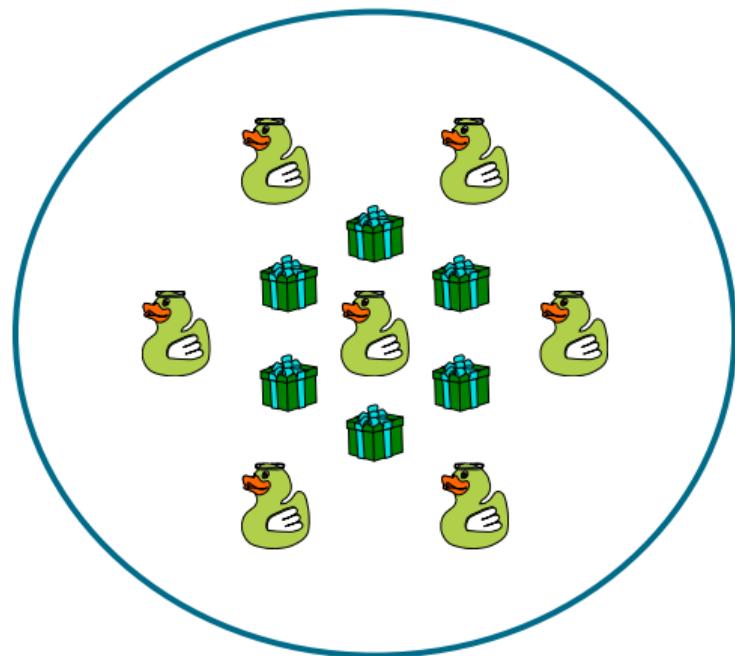
Spatial structure and altruism



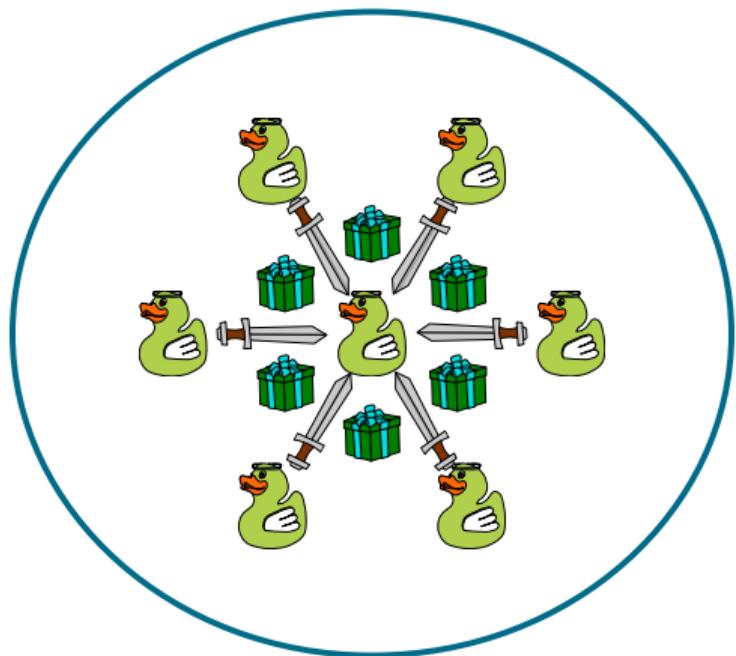
Spatial structure and altruism



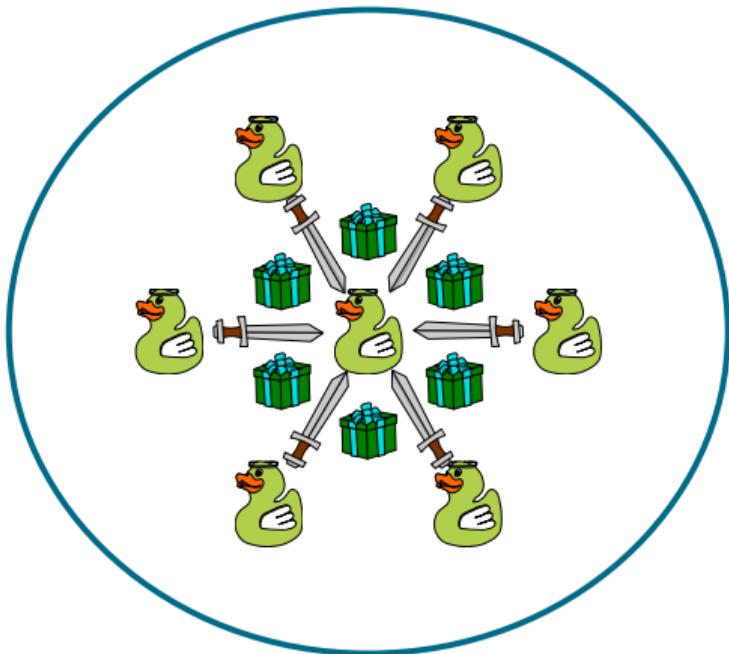
Spatial structure and altruism



Spatial structure and altruism



Spatial structure and altruism



Evolutionary Ecology, 1992, 6, 352–356

Altruism in viscous populations – an inclusive fitness model

P.D. TAYLOR

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Summary

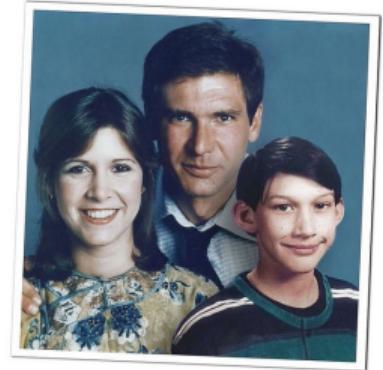
A viscous population (Hamilton, 1964) is one in which the movement of organisms from their place of birth is relatively slow. This viscosity has two important effects: one is that local interactions tend to be among relatives, and the other is that competition for resources tends to be among relatives. The first effect tends to promote and the second to oppose the evolution of altruistic behaviour. In a simulation model of Wilson *et al.* (1992) these two factors appear to exactly balance one another, thus opposing the evolution of local altruistic behaviour. Here I show, with an inclusive fitness model, that the same result holds in a patch-structured population.

Keywords: altruism; inclusive fitness; competition; viscosity

Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

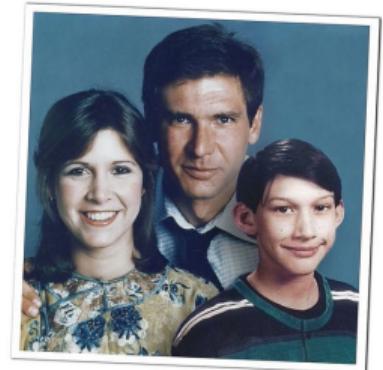
- ▶ Mutation



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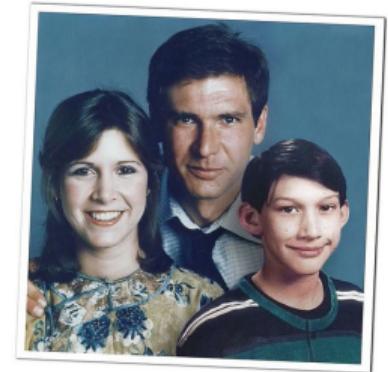
- ▶ Mutation
- ▶ Partial heritability



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Causes of imperfect strategy transmission

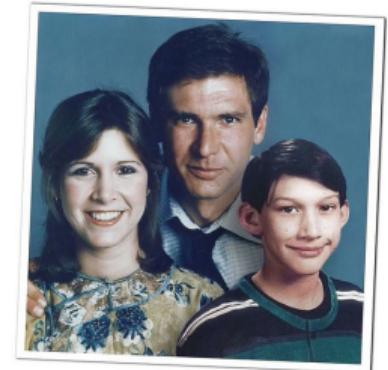
- ▶ Mutation
- ▶ Partial heritability
- ▶ Cultural transmission (vertical)



Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

- ▶ Mutation
- ▶ Partial heritability
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In the model

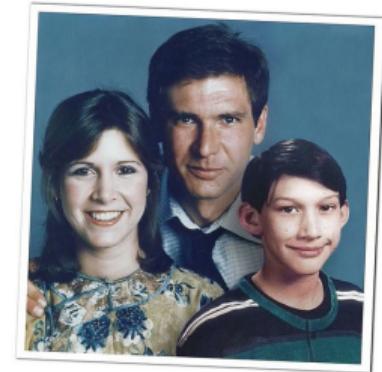
Parent



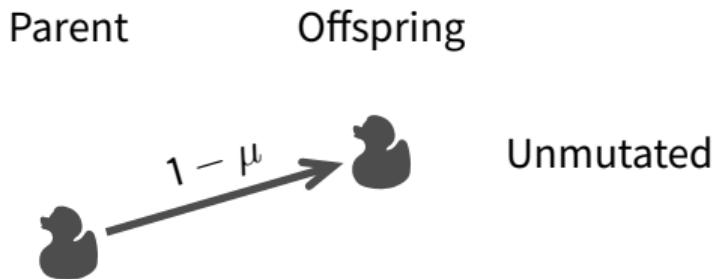
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In the model



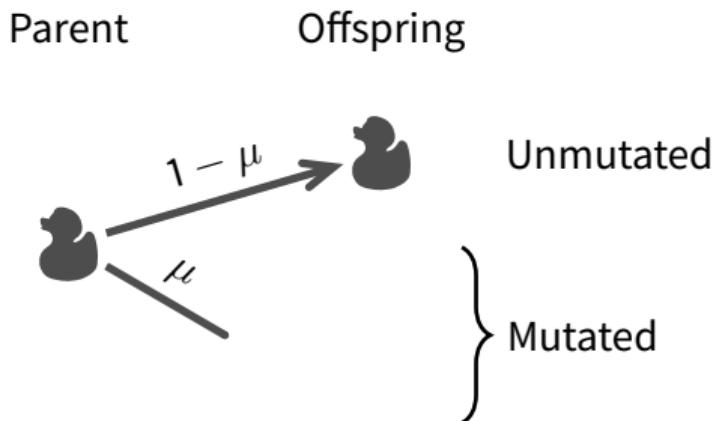
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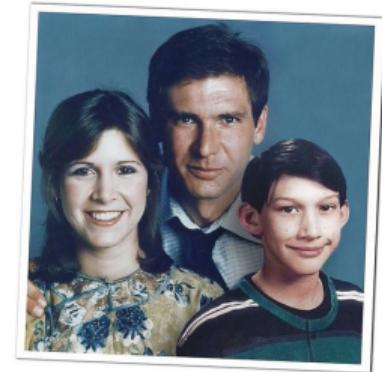
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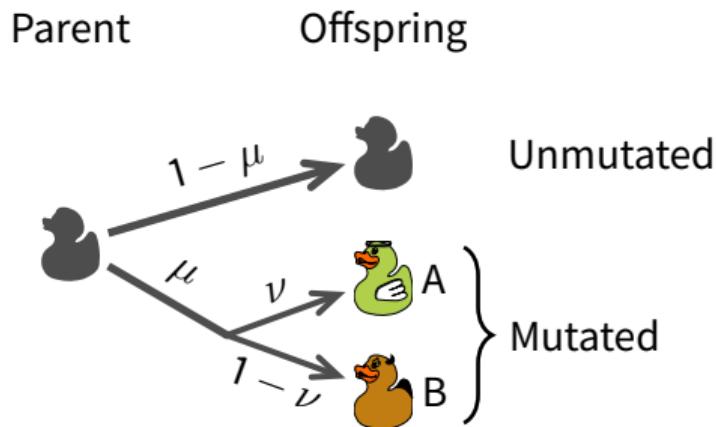
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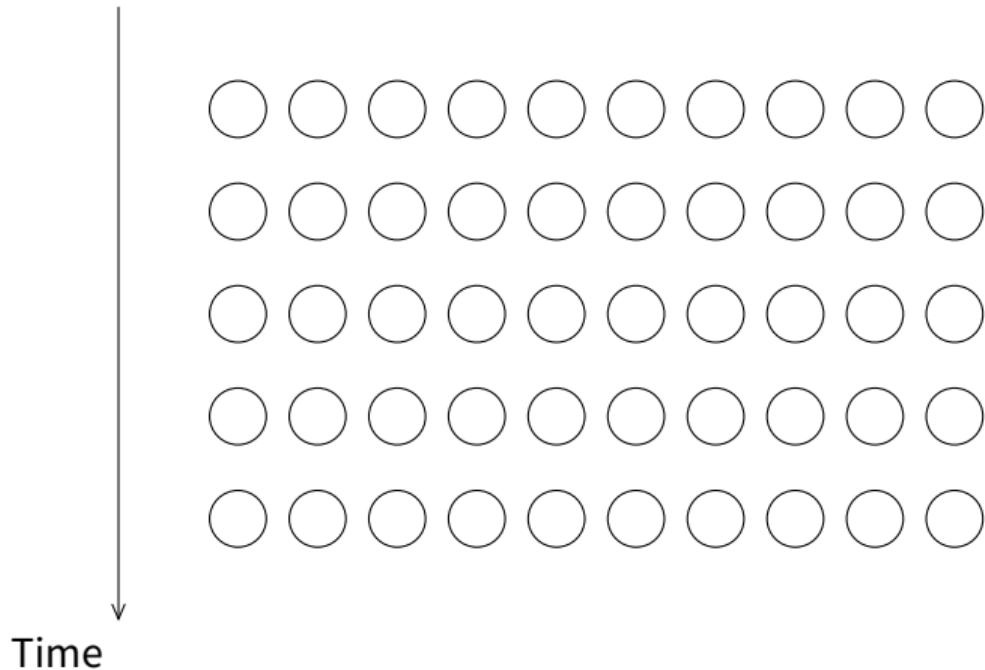
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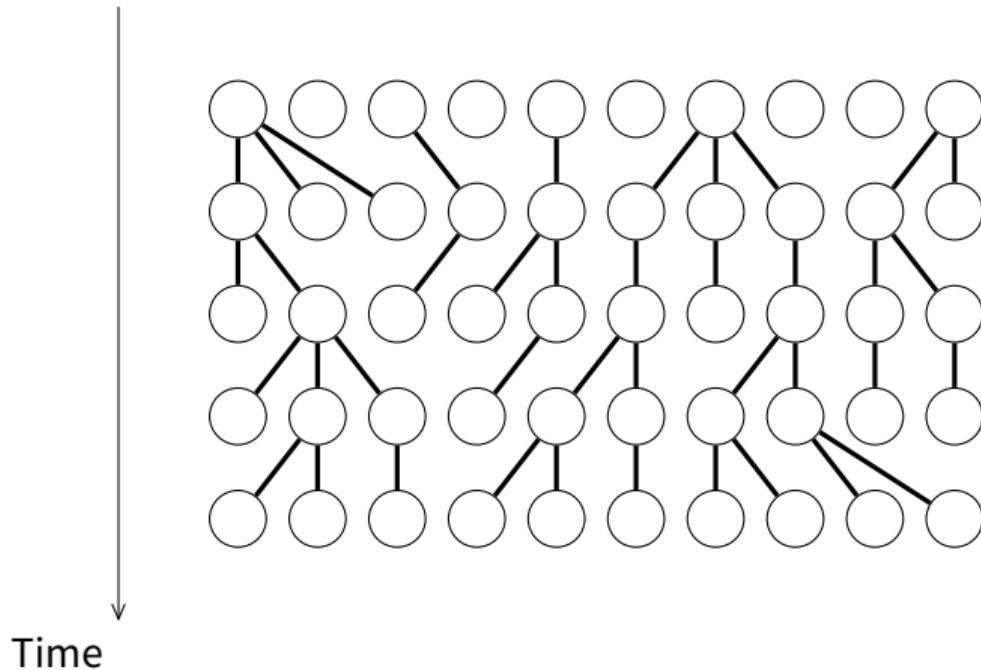
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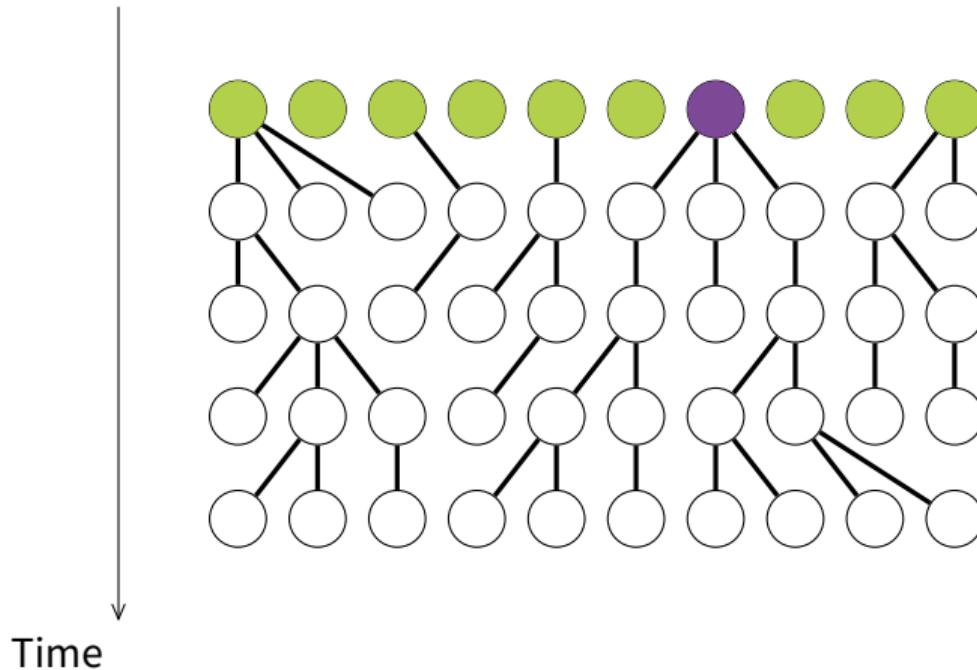
Genealogy, Identity by descent and Identity in state



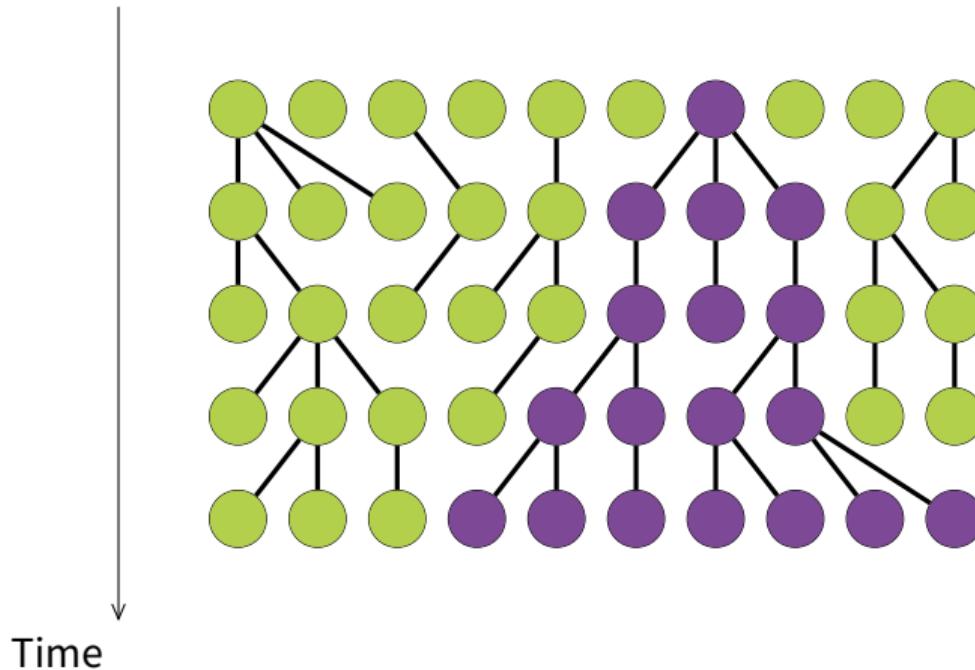
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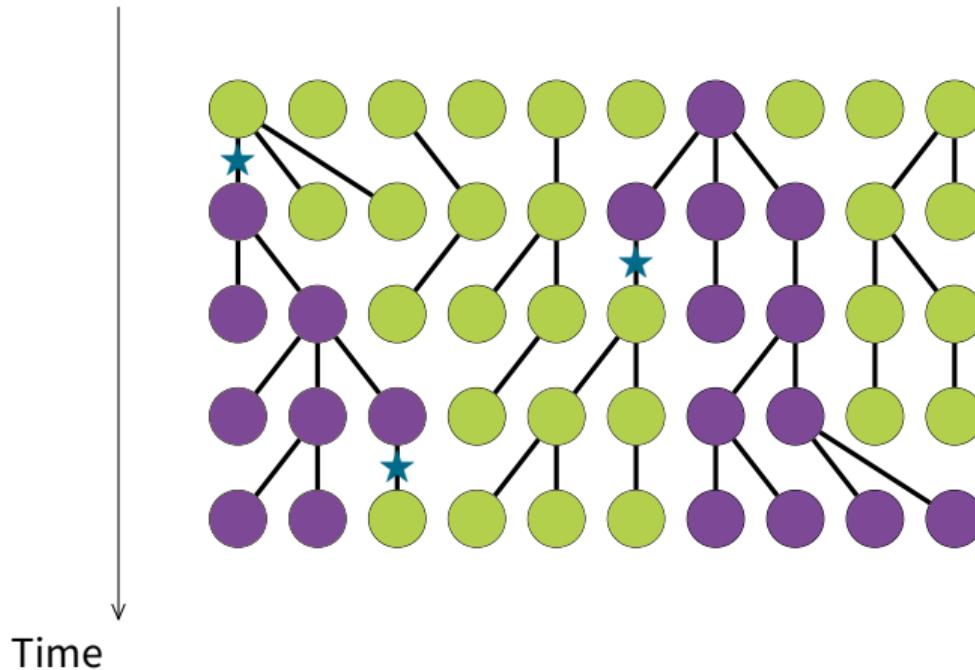
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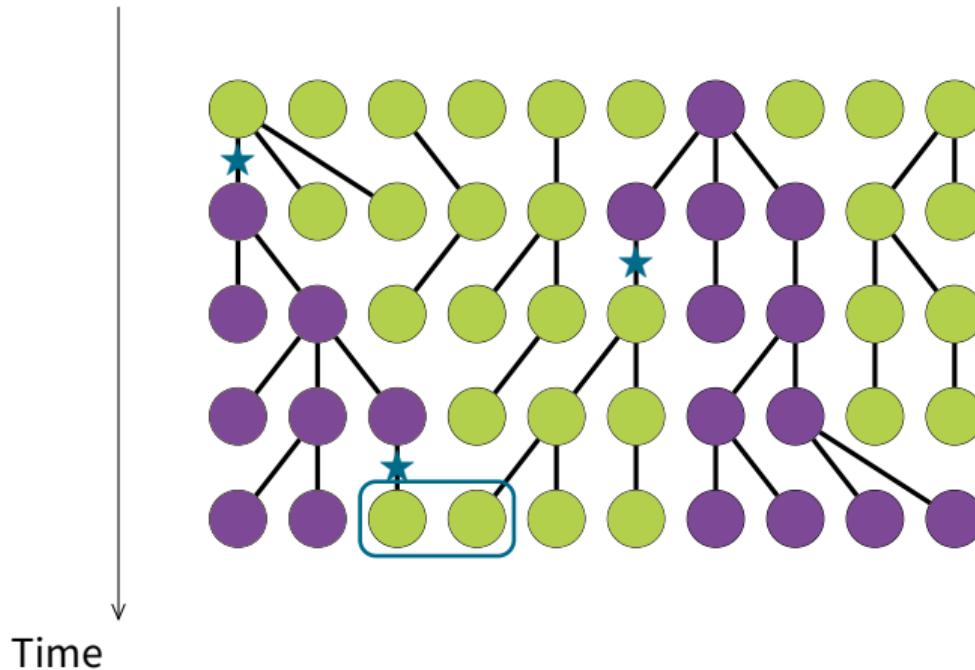
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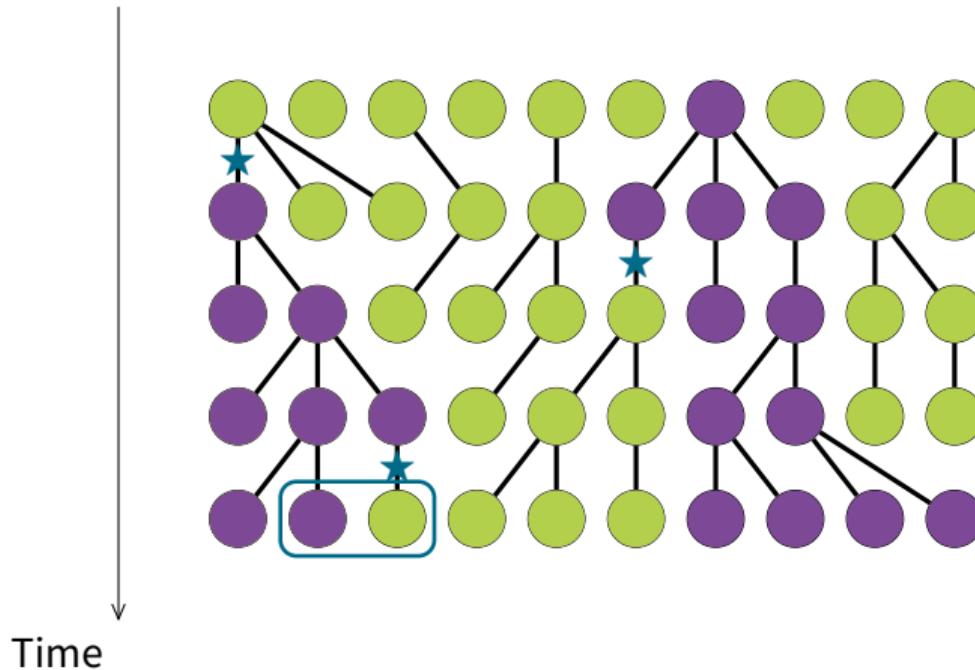
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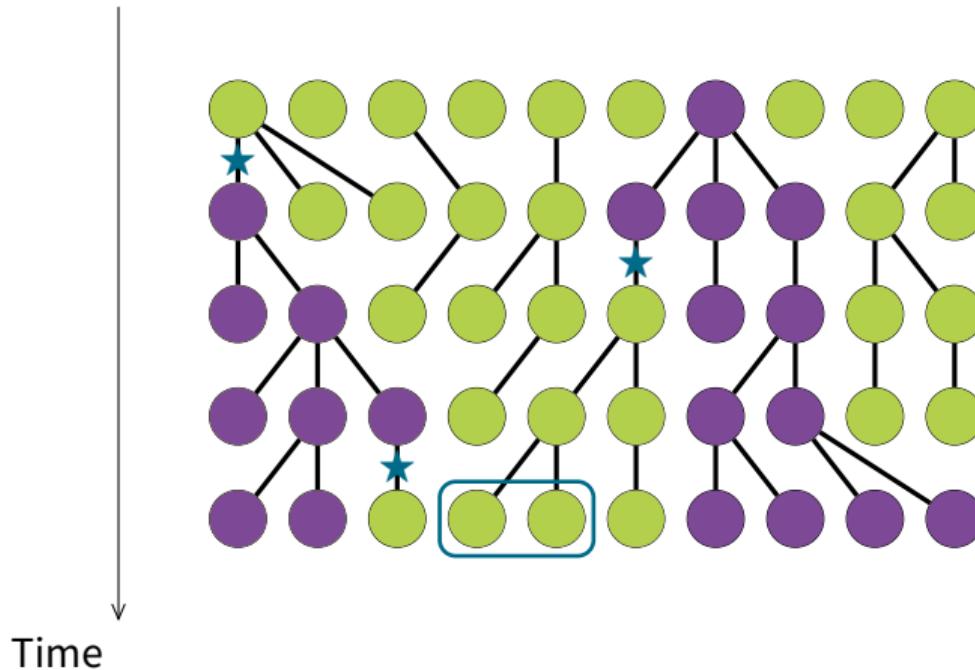
Genealogy, Identity by descent and Identity in state



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Genealogy, Identity by descent and Identity in state



Expected state of pairs of sites and identity by descent

At neutrality (i.e., in the absence of selection, $\delta = 0$),

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P_{ij}
Expected state
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$$P_{ij} = Q_{ij} \nu$$

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Expected state of pairs of sites and identity by descent

At neutrality (i.e., in the absence of selection, $\delta = 0$),

$$P_{ij} = Q_{ij} \nu$$

Diagram illustrating the components of the equation:

- P_{ij} is labeled "Expected state of the i,j pair" and "Probability that the two individuals are altruists".
- Q_{ij} is labeled "Probability that a mutant is an altruist" and "Probability that a given site is occupied by an altruist".
- ν is labeled "Probability that the individuals at sites i and j are identical by descent (no mutation since their common ancestor)".

Expected state of pairs of sites and identity by descent

At neutrality (i.e., in the absence of selection, $\delta = 0$),

$$P_{ij} = Q_{ij} \nu + (1 - Q_{ij})\nu^2$$

Expected state of the i,j pair
= Probability that the two individuals are altruists

Probability that a mutant is an altruist
= Probability that a given site is occupied by an altruist

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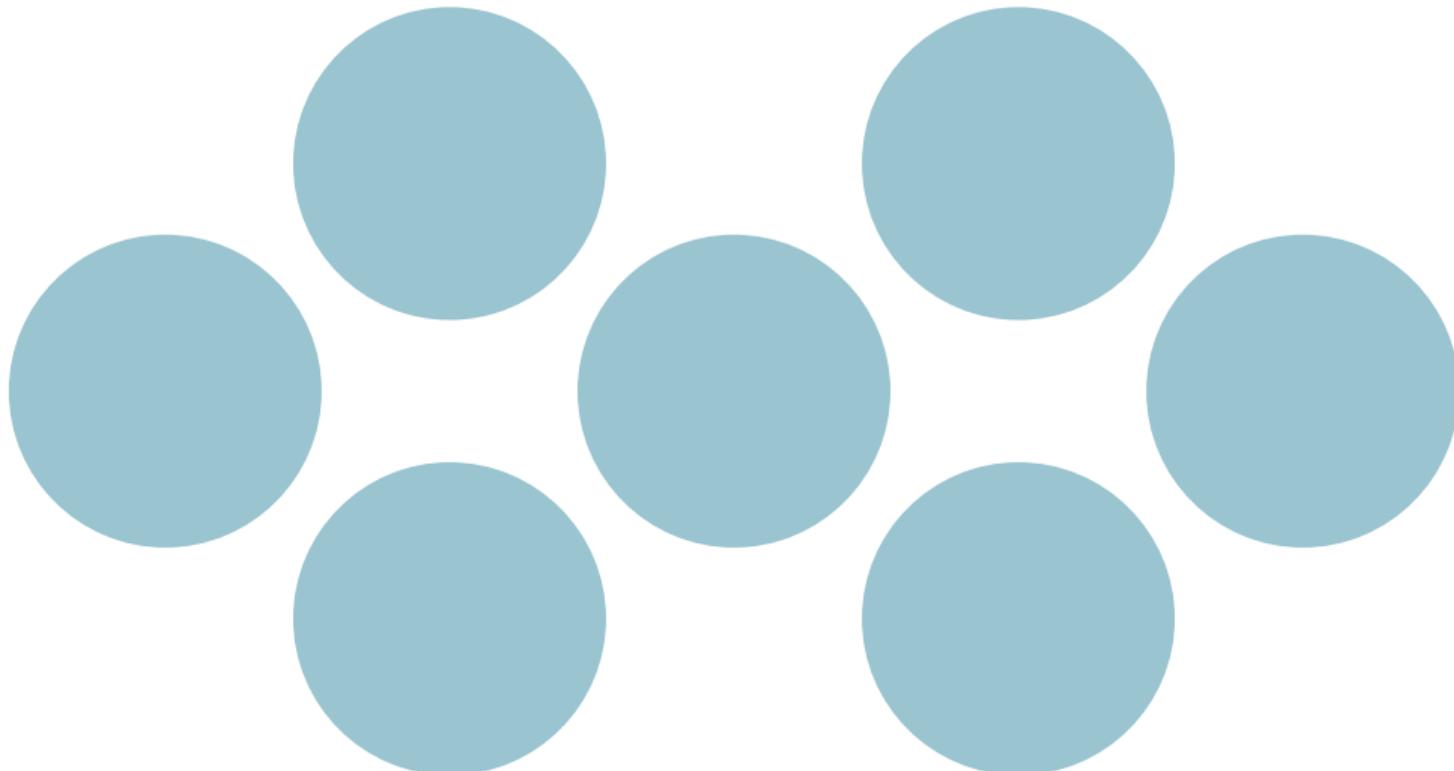
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Q_{in} , Q_{out}

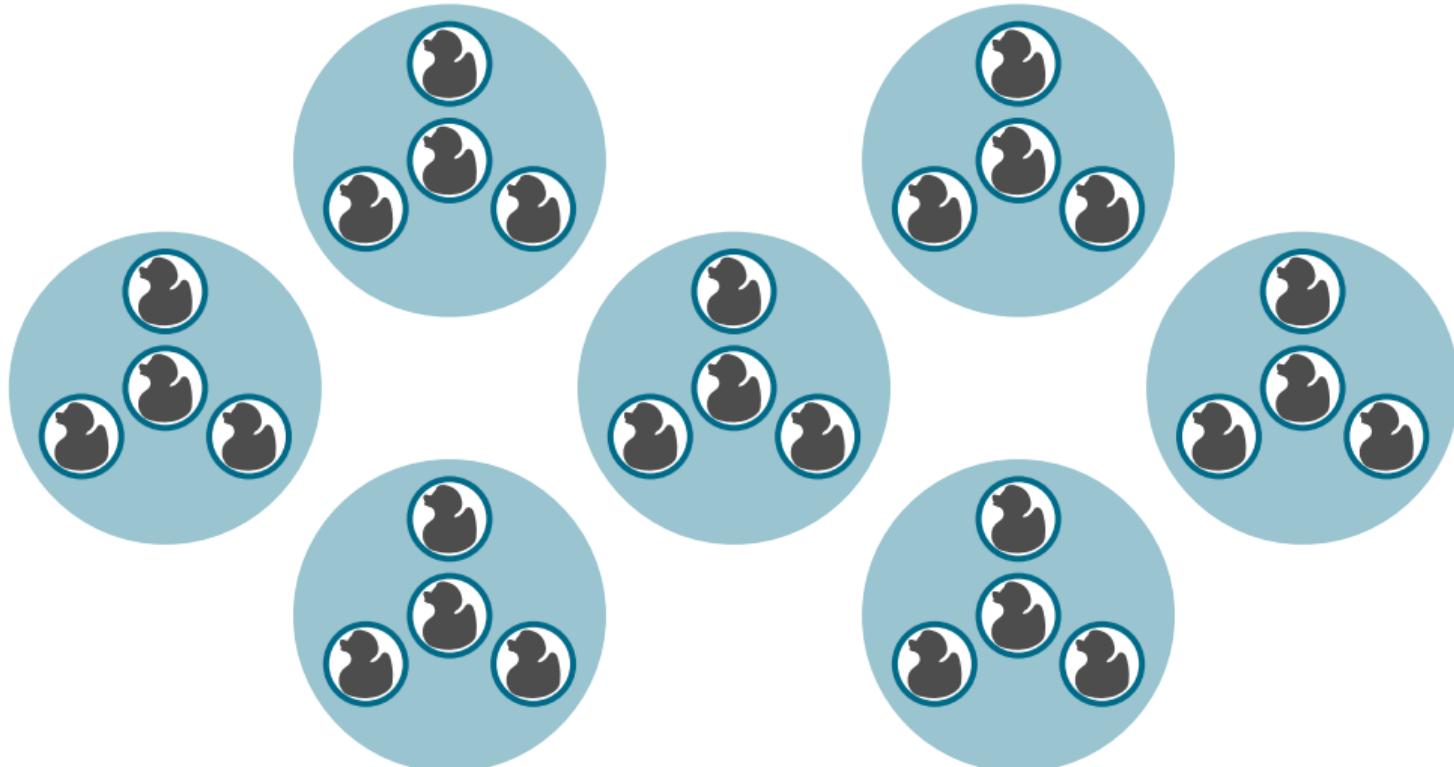
Subdivided population – Island model

N_d demes



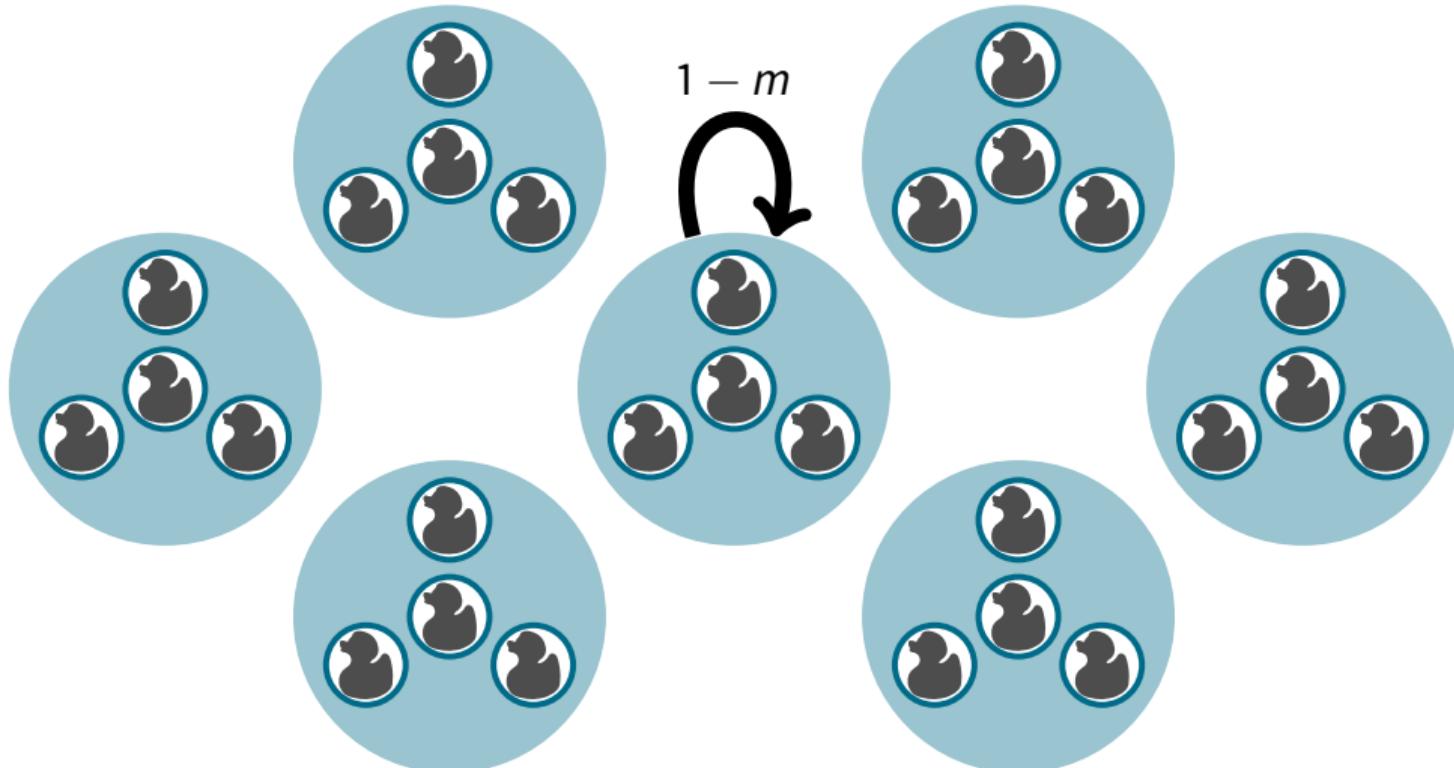
Subdivided population – Island model

N_d demes of n individuals each (total population size $N = n N_d$)



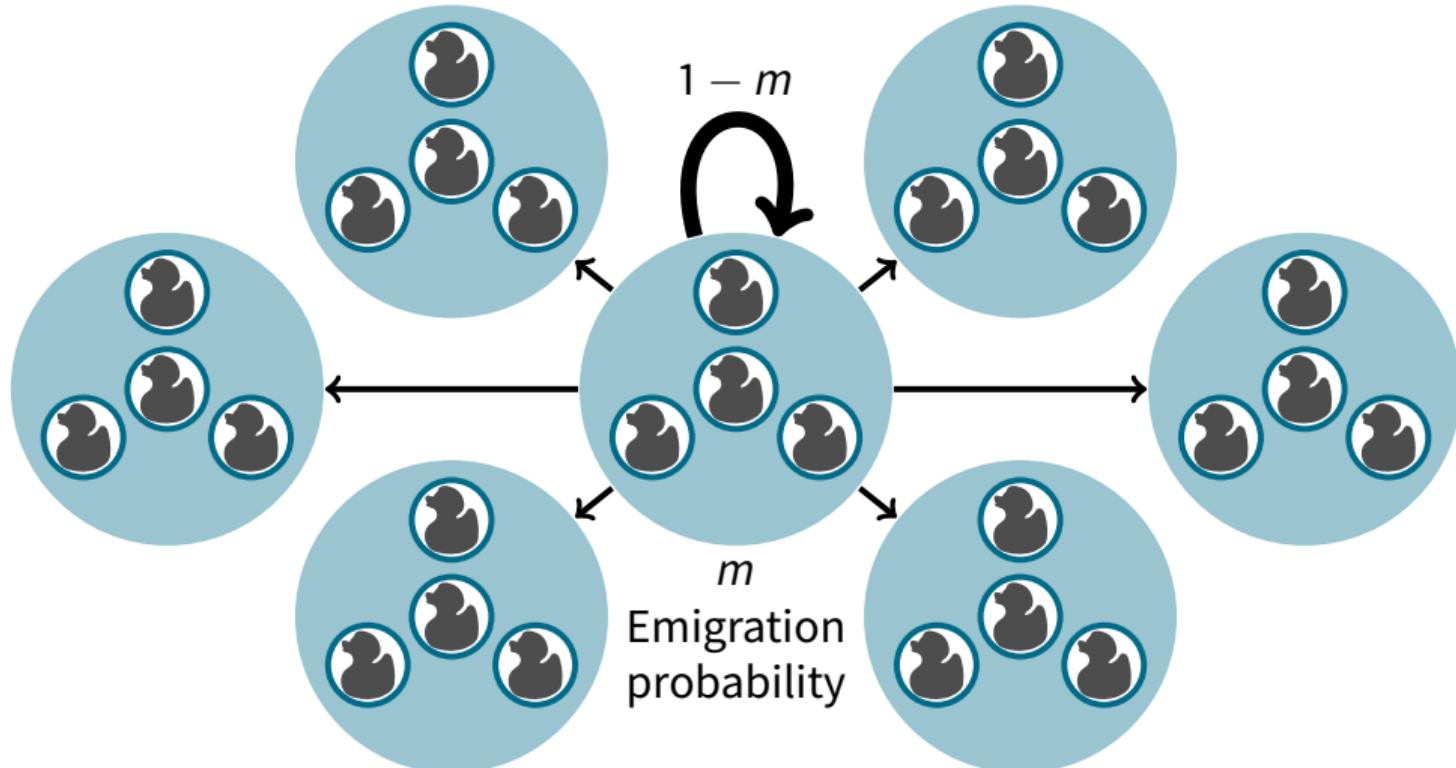
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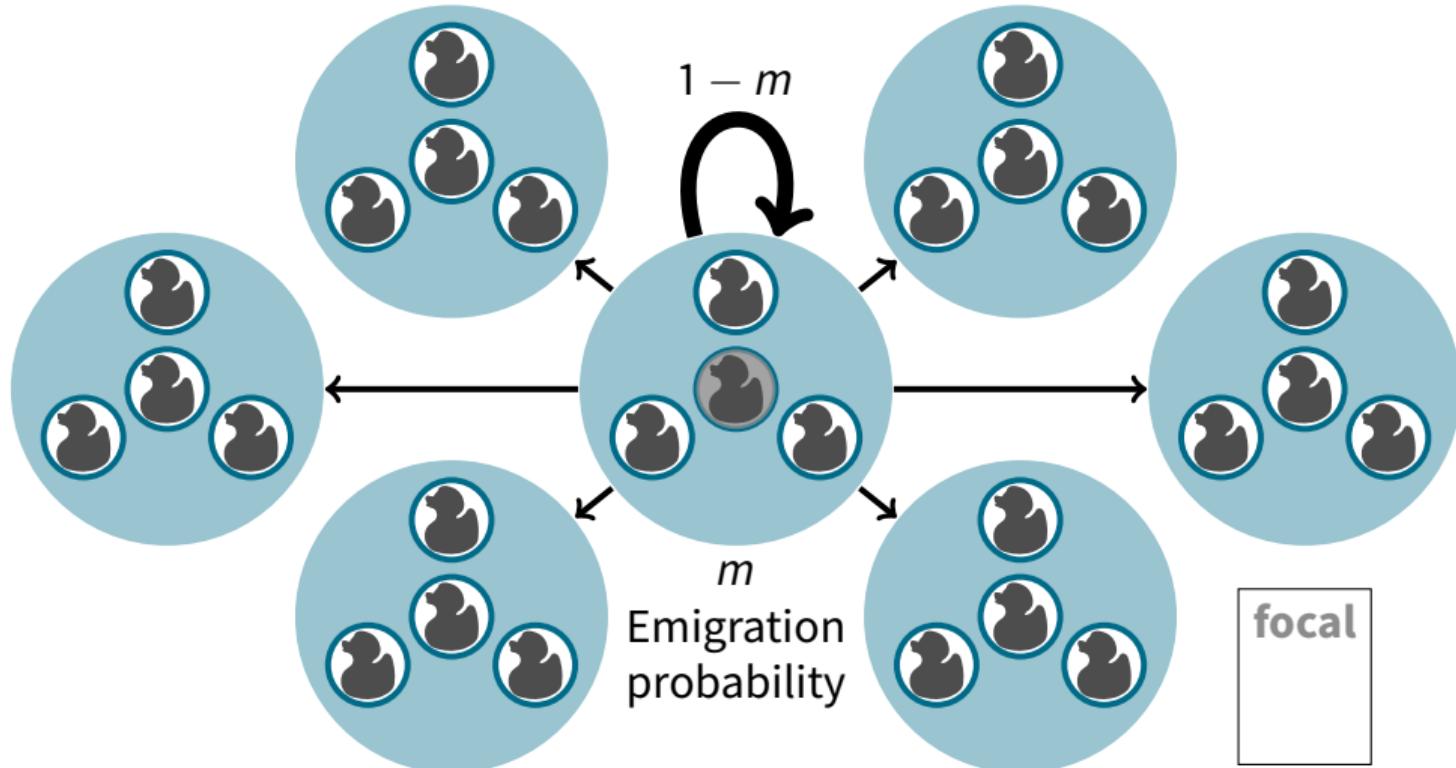
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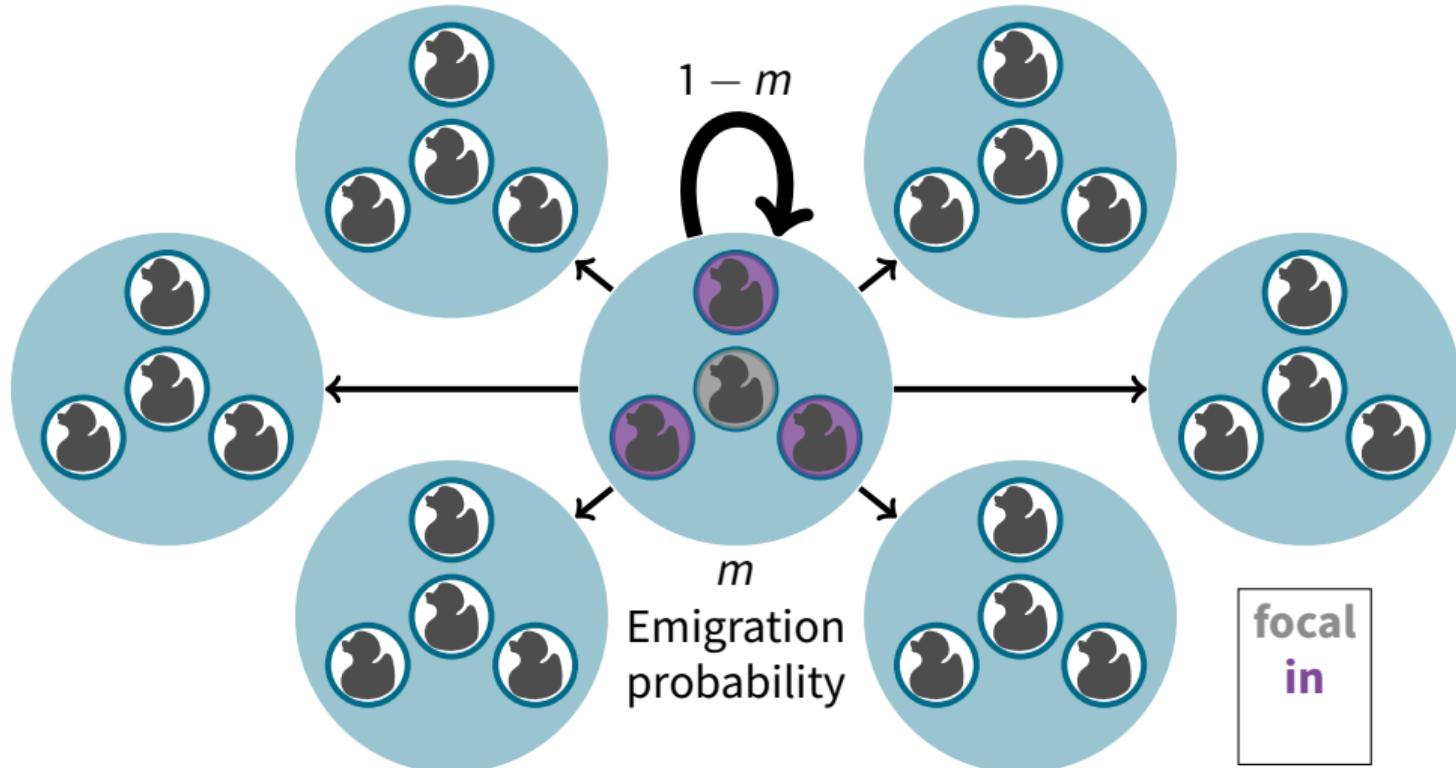
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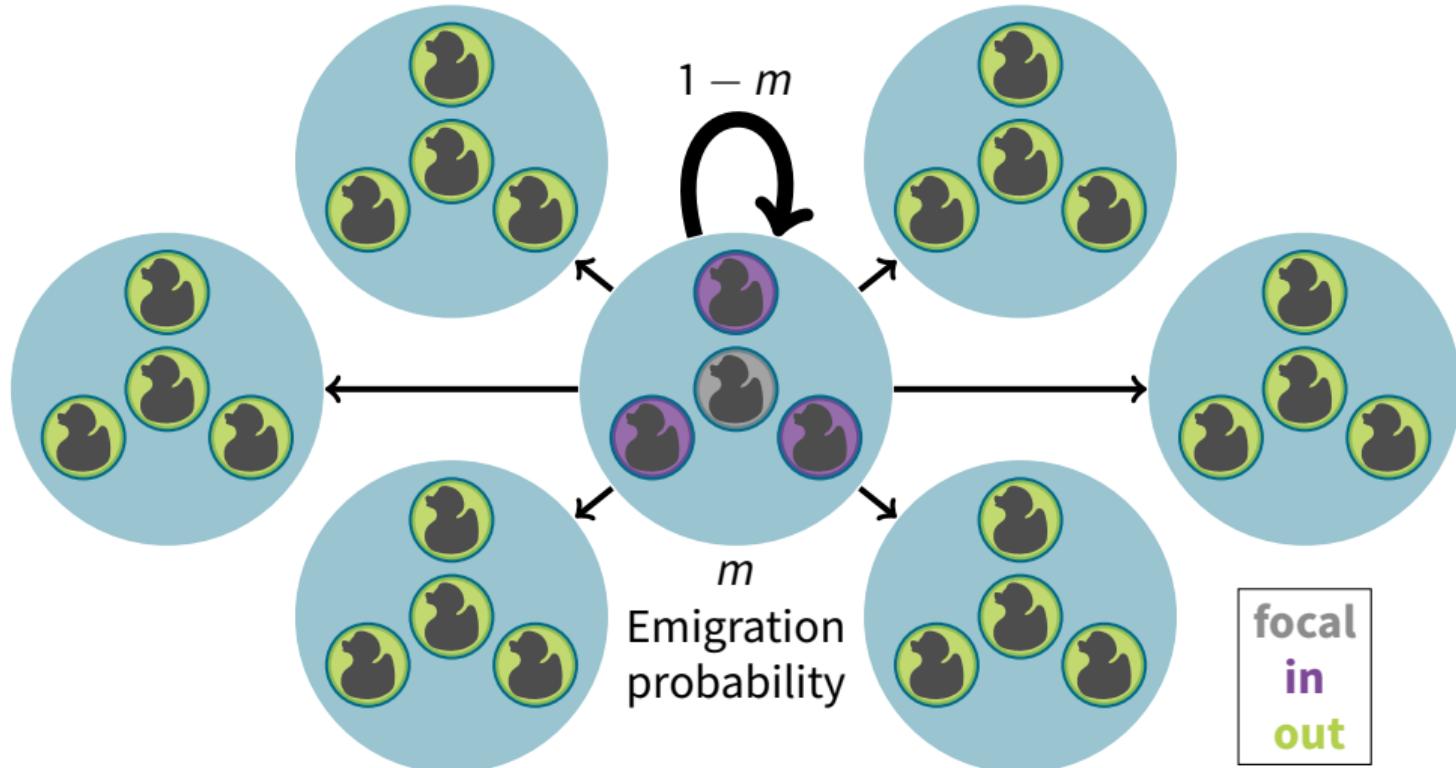
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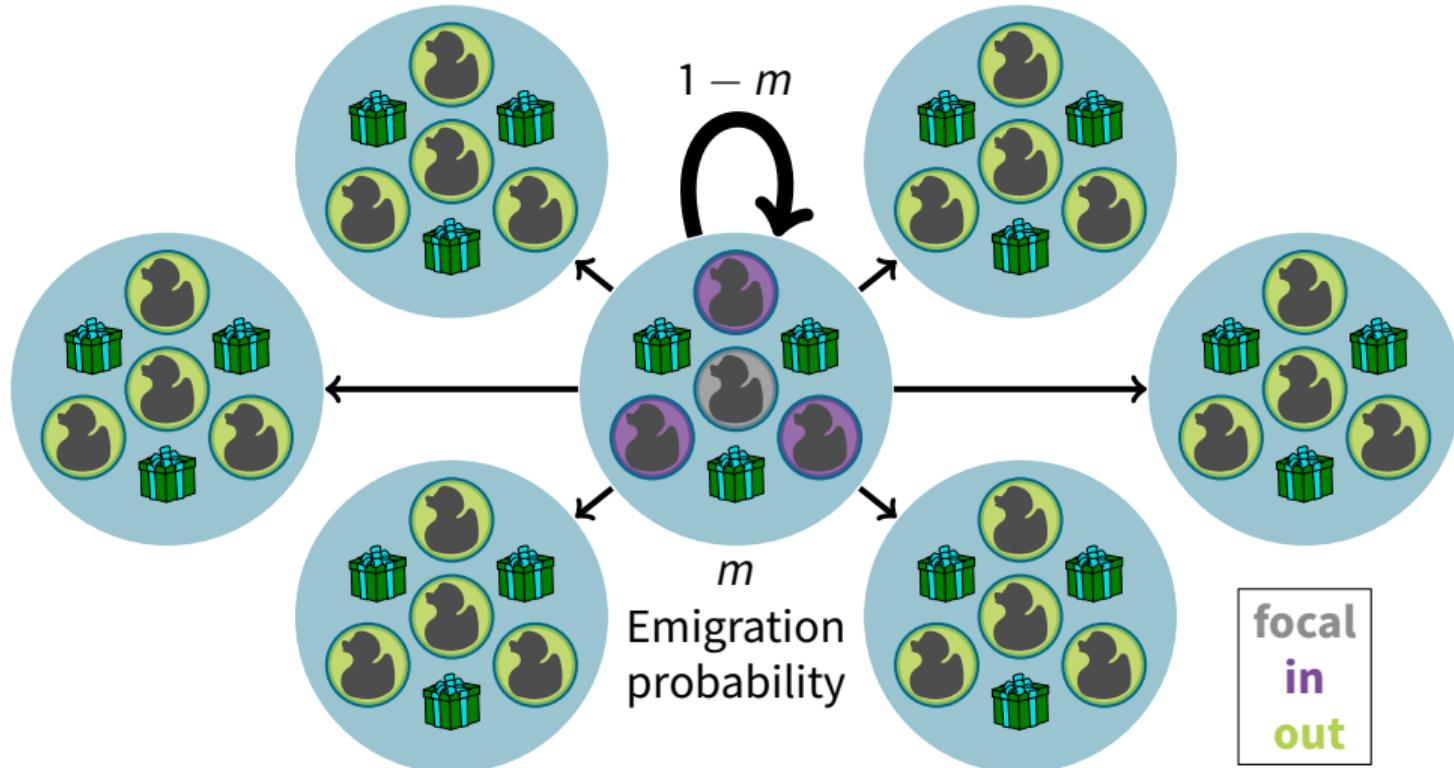
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Updating the population

Constant population size (N), so
between two time steps,

$$\# \text{[grave]} = \# \text{[stroller]}$$

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$$\begin{array}{c} \uparrow \\ N \text{ [grave]} = N \text{ [stroller]} \\ \vdots \\ k \text{ [grave]} = k \text{ [stroller]} \\ \vdots \\ 1 \text{ [grave]} = 1 \text{ [stroller]} \end{array}$$

Updating the population

Constant population size (N), so
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$$\# \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = \# \begin{array}{c} \text{orange baby carriage} \end{array}$$

$$N \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = N \begin{array}{c} \text{orange baby carriage} \end{array} \quad \text{Wright-Fisher}$$

$$k \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = k \begin{array}{c} \text{orange baby carriage} \end{array}$$

$$1 \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = 1 \begin{array}{c} \text{orange baby carriage} \end{array} \quad \text{Moran process}$$

Updating the population

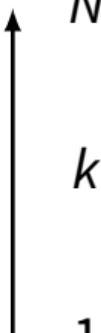
Constant population size (N), so
between two time steps,

$$\# \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = \# \begin{array}{c} \text{babycart} \end{array}$$

Life-cycle

Offspring
production

$$N \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = N \begin{array}{c} \text{babycart} \end{array} \quad \text{Wright-Fisher}$$



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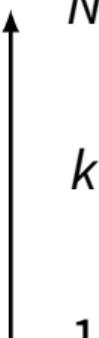
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Life-cycle

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$$k \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = k \begin{array}{c} \text{orange baby carriage} \end{array}$$

Offspring dispersal

$$1 \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = 1 \begin{array}{c} \text{orange baby carriage} \end{array} \quad \text{Moran process}$$

Updating the population

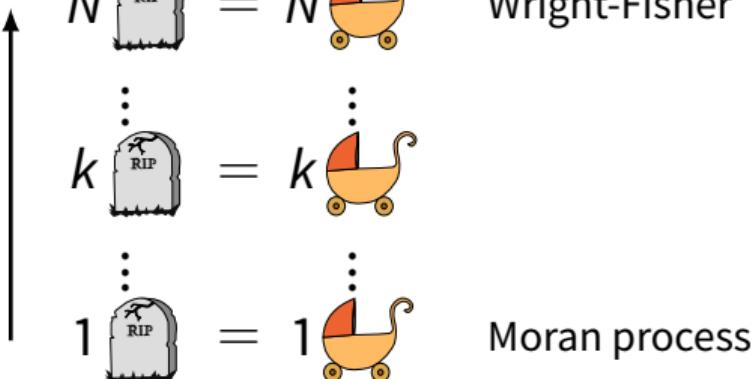
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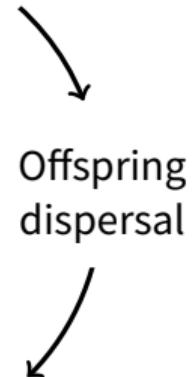
Life-cycle

Offspring production

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Moran process



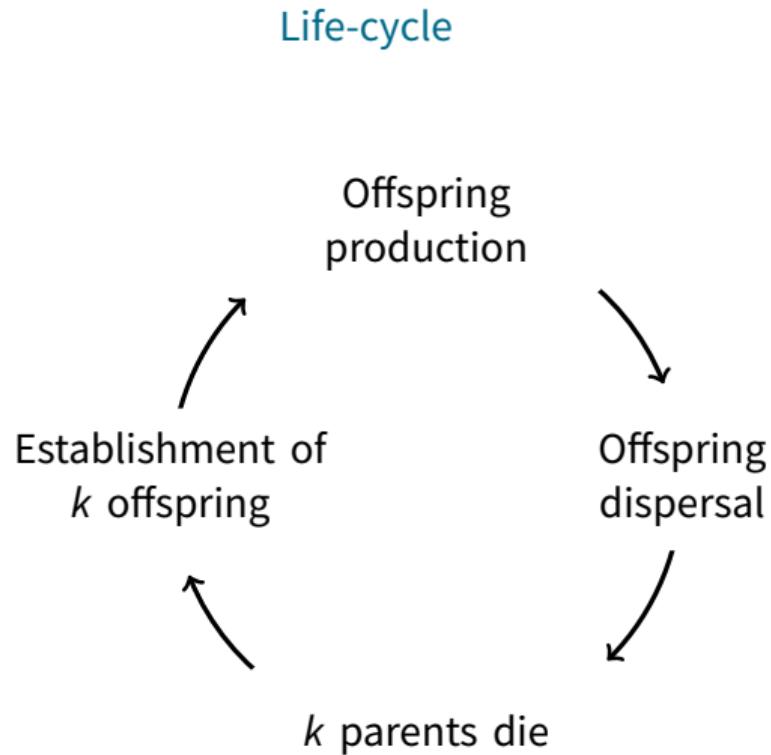
k parents die

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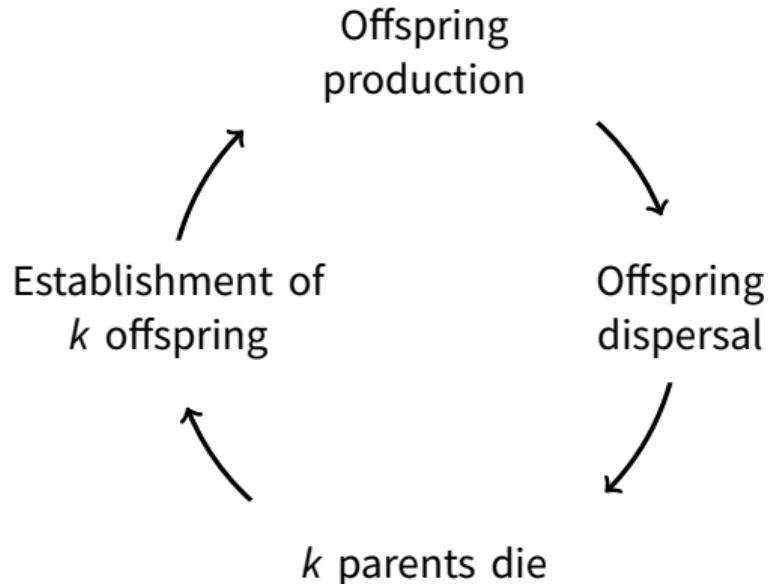
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Life-cycle
“Death-Birth” updating



Population

$$X_i(t) = \begin{cases} 1 & \text{if site } i \text{ occupied by } \text{🐍 at time } t (1 \leq i \leq N) \\ 0 & \text{if site } i \text{ occupied by } \text{🐢 at time } t (1 \leq i \leq N) \end{cases}$$

Population

$$X_i(t) = \begin{cases} 1 & \text{if site } i \text{ occupied by } \text{green person icon} \text{ at time } t (1 \leq i \leq N) \\ 0 & \text{if site } i \text{ occupied by } \text{orange person icon} \text{ at time } t (1 \leq i \leq N) \end{cases}$$

We are interested in $\mathbb{E}[\bar{X}]$,
the expected (\mathbb{E}) proportion (\bar{X}) of altruists in the population.

Social interactions

Social interactions affect fecundity

In a deme with k 

$$f_{\text{green}} = 1 + \omega \begin{pmatrix} b \frac{k-1}{n-1} & -c \end{pmatrix},$$
$$f_{\text{brown}} = 1 + \omega \left(b \frac{k}{n-1} \right).$$



Selection is weak

$$\omega \ll 1.$$

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

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

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Mutation-drift equilibrium Selection strength Population variance
equilibrium Selection strength Variance in the state of one site

Expected frequency of altruists in the population

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

\mathcal{B}

Mutation-drift
equilibrium

Selection
strength

Population variance
Variance in the state of one site

Expected frequency of altruists in the population

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

\mathcal{R} \mathcal{B}

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Variance in the state of one site

Expected frequency of altruists in the population

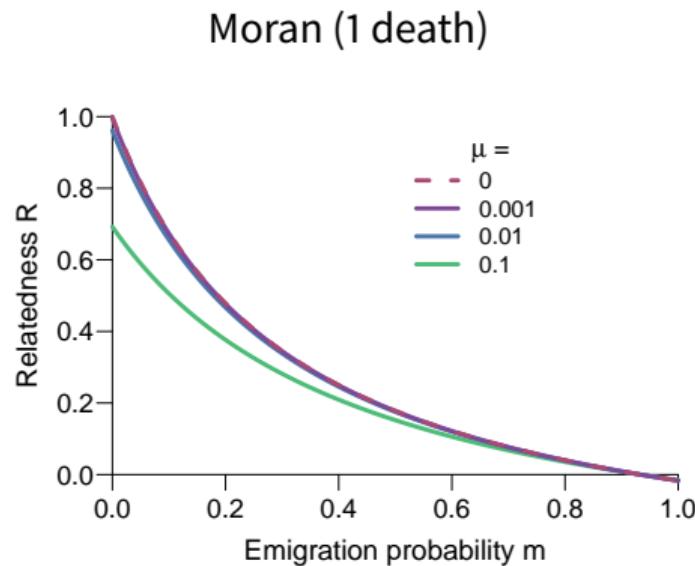
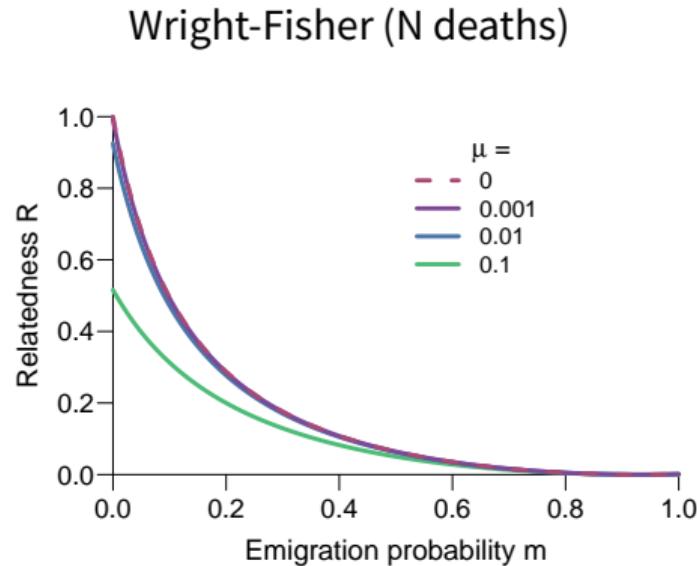
Mutation-drift equilibrium Selection strength Population variance
Variance in the state of one site

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

R \mathcal{B}

How does relatedness R change with the emigration probability m ?

How does relatedness R change with the emigration probability m ?



$$(n = 4, N_d = 15)$$

Expected frequency of altruists in the population

Mutation-drift equilibrium Selection strength Population variance
Variance in the state of one site

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

$R \searrow \mathcal{B}$

Expected frequency of altruists in the population

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

$R \searrow \mathcal{B}$

Mutation-drift equilibrium Selection strength Population variance
equilibrium Selection strength Variance in the state of one site

Expected frequency of altruists in the population

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

$R \searrow \quad \mathcal{B} \nearrow$

Mutation-drift equilibrium Selection strength Population variance
equilibrium Selection strength Variance in the state of one site

Expected frequency of altruists in the population

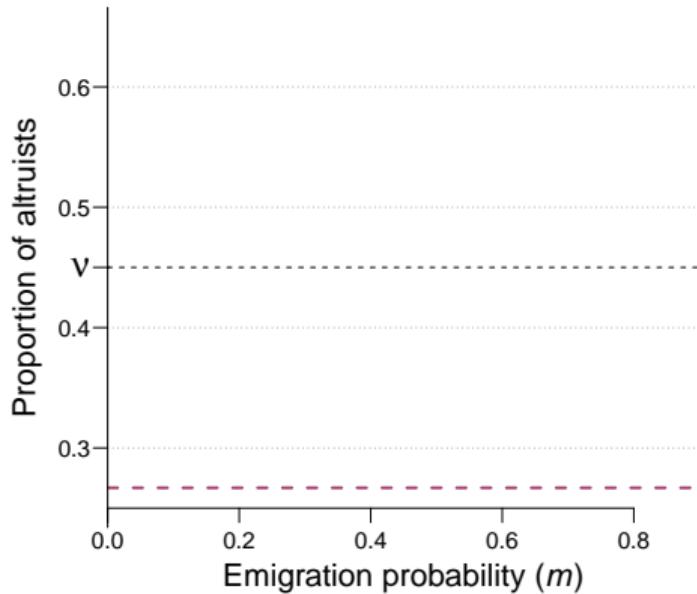
Mutation-drift equilibrium Selection strength Population variance
Variance in the state of one site

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

$R \searrow \quad \mathcal{B} \nearrow$

Effect of the emigration probability m on the expected proportion of altruists

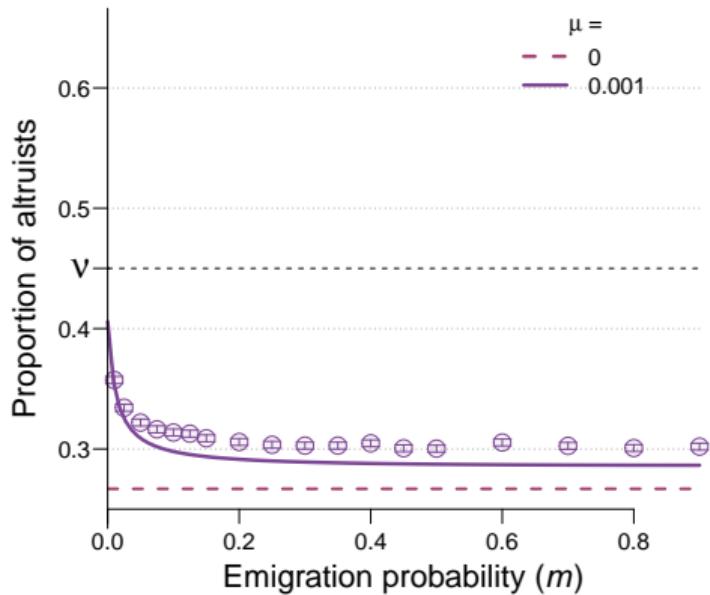
Wright-Fisher (N deaths & N births)



$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

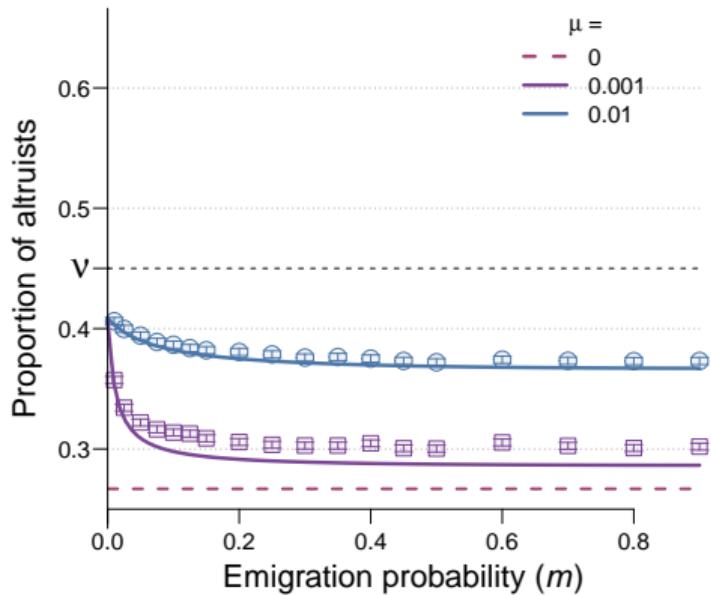
Wright-Fisher (N deaths & N births)



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Effect of the emigration probability m on the expected proportion of altruists

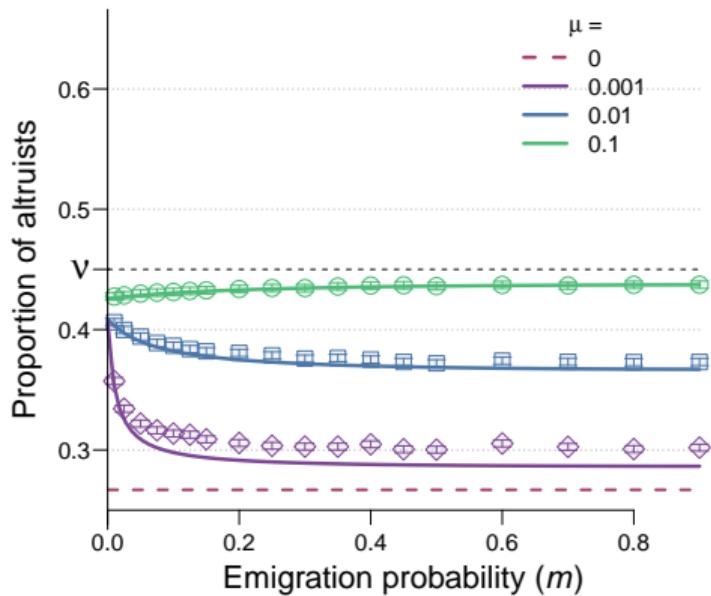
Wright-Fisher (N deaths & N births)



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Effect of the emigration probability m on the expected proportion of altruists

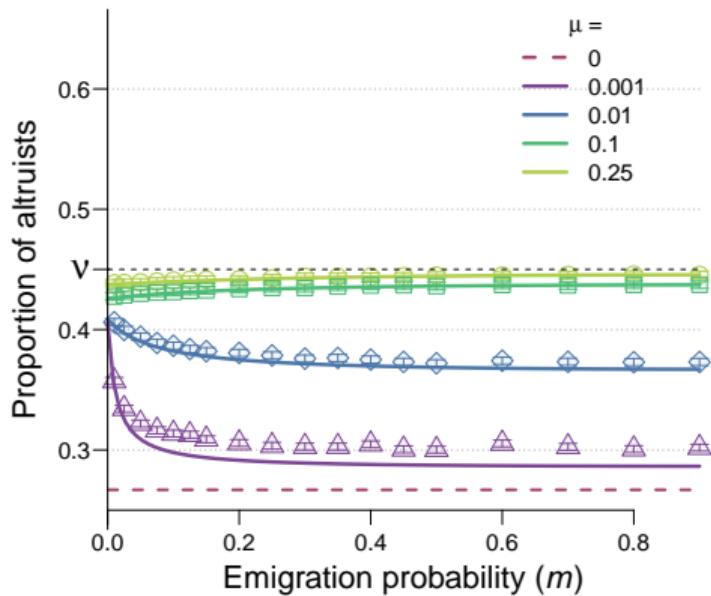
Wright-Fisher (N deaths & N births)



$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

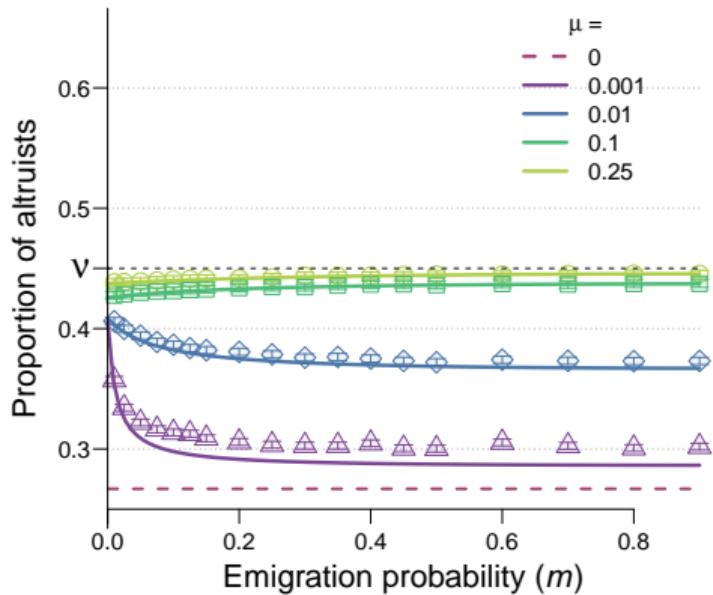
Wright-Fisher (N deaths & N births)



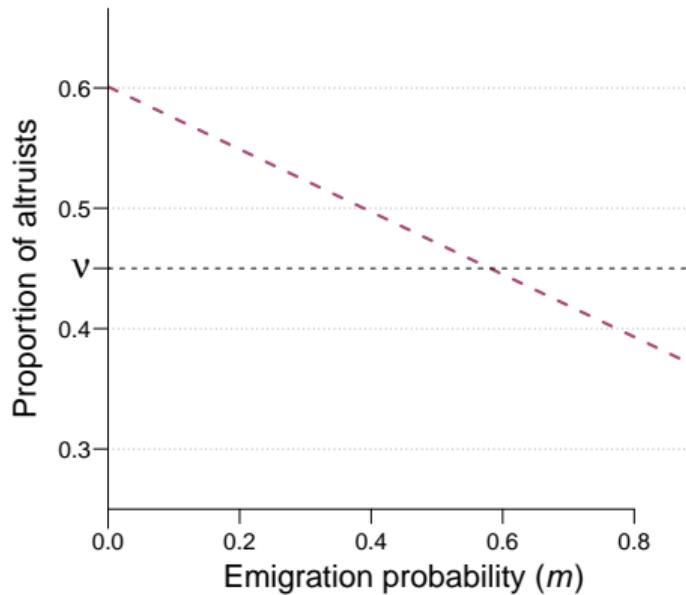
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher (N deaths & N births)



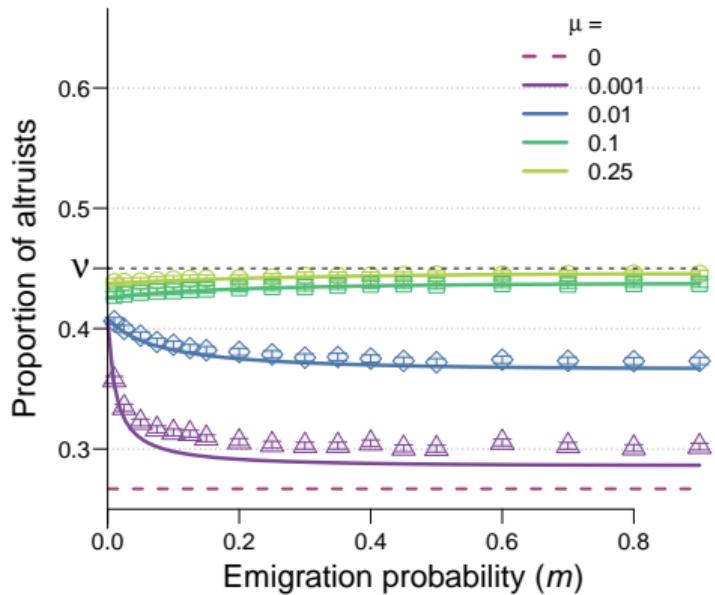
Moran Death-Birth (1 death & 1 birth)



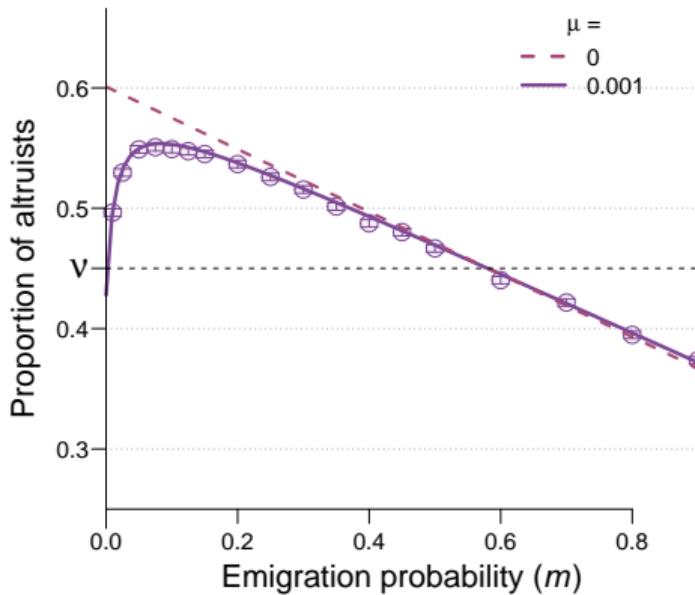
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher (N deaths & N births)



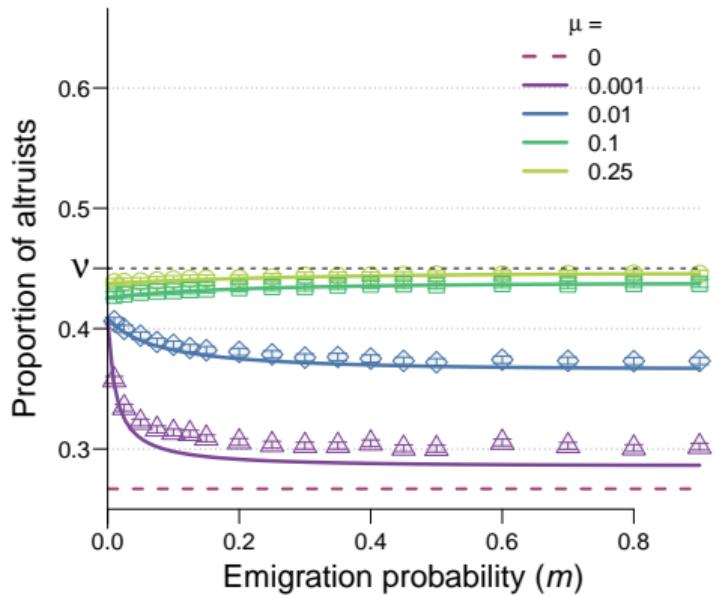
Moran Death-Birth (1 death & 1 birth)



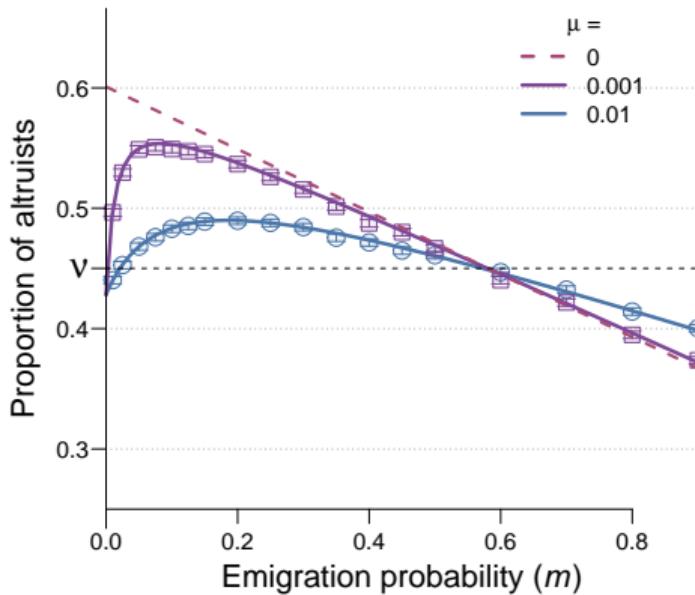
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher (N deaths & N births)



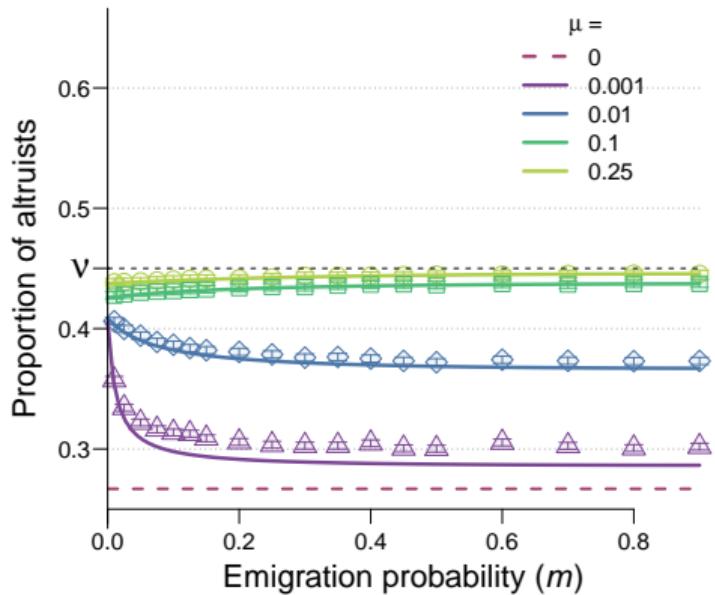
Moran Death-Birth (1 death & 1 birth)



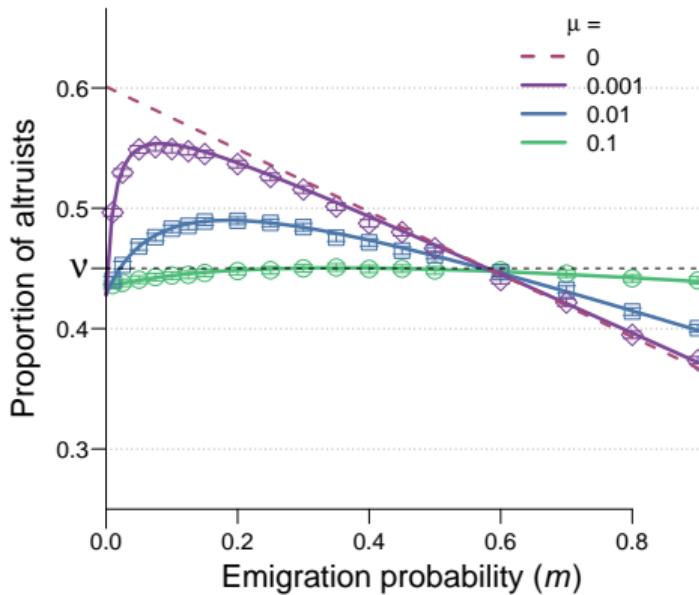
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher (N deaths & N births)



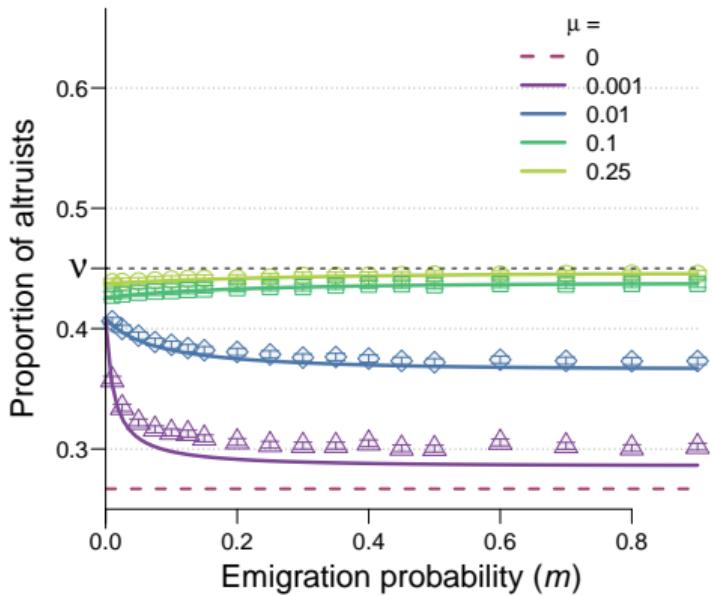
Moran Death-Birth (1 death & 1 birth)



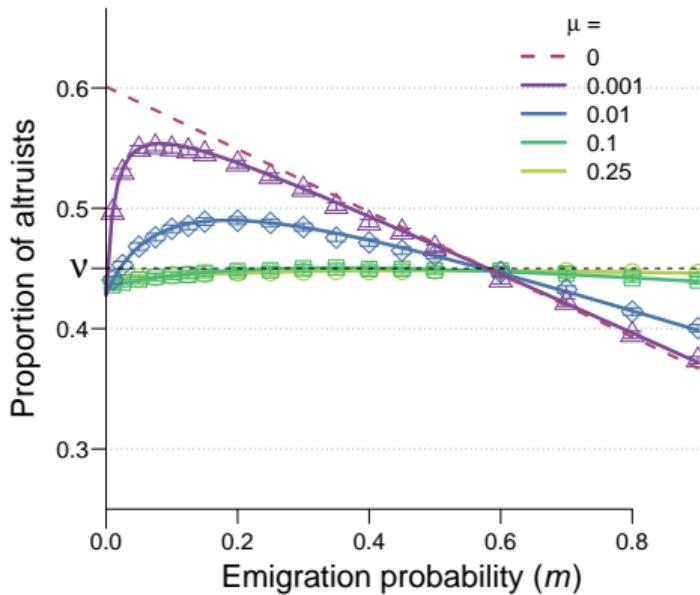
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher (N deaths & N births)



Moran Death-Birth (1 death & 1 birth)



$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Is the result robust?

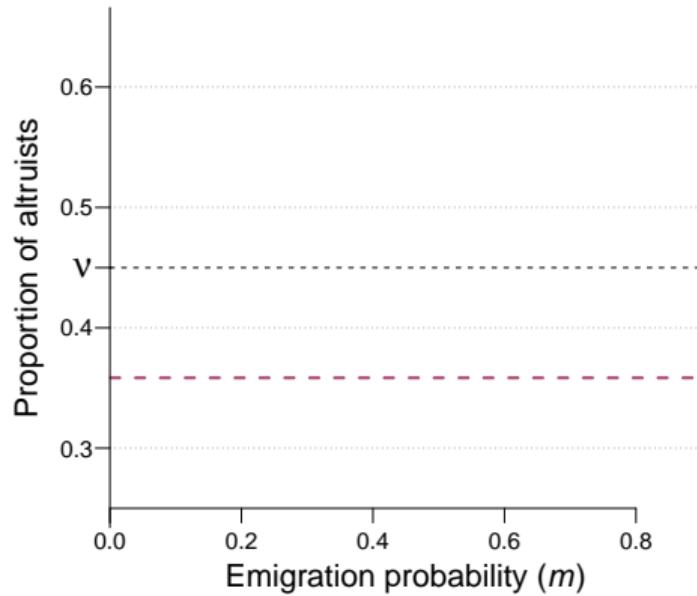
Another life-cycle

Moran Birth-Death (1 birth & 1 death)

$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Another life-cycle

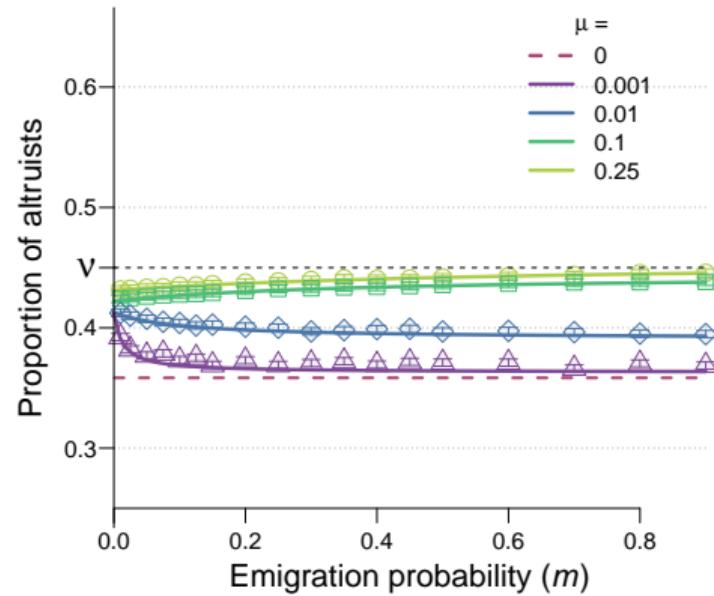
Moran Birth-Death (1 birth & 1 death)



$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

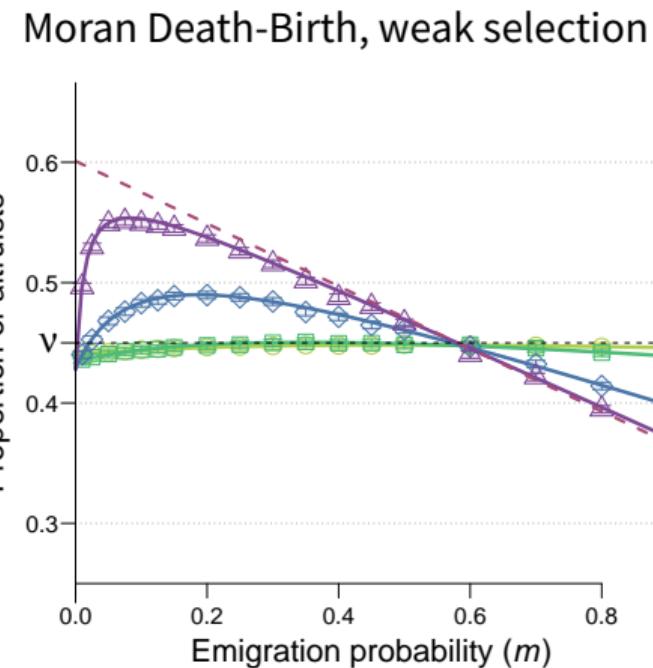
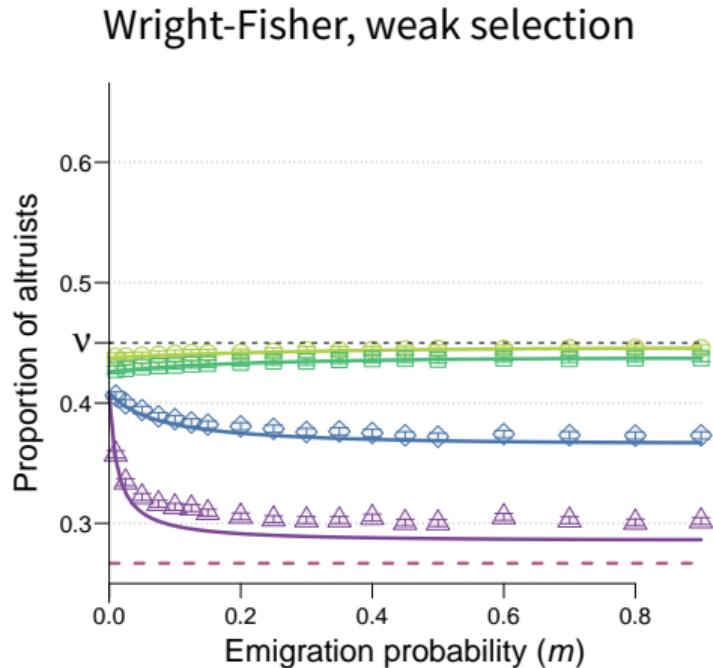
Another life-cycle

Moran Birth-Death (1 birth & 1 death)



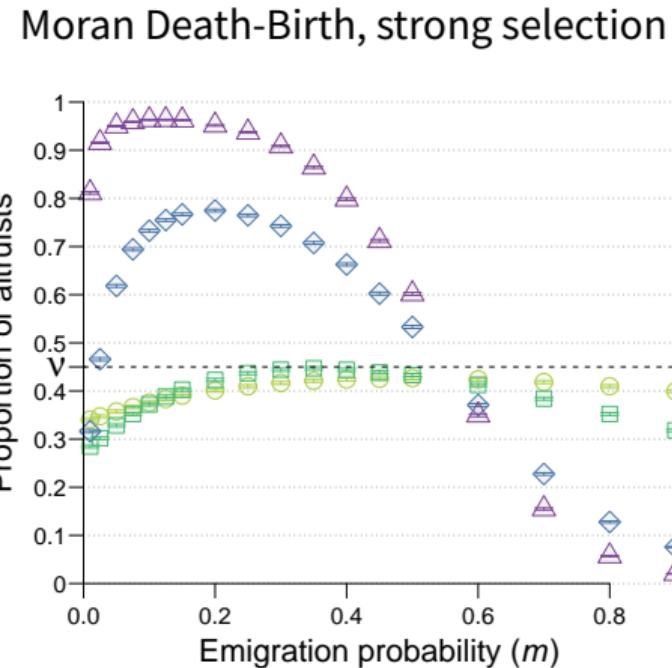
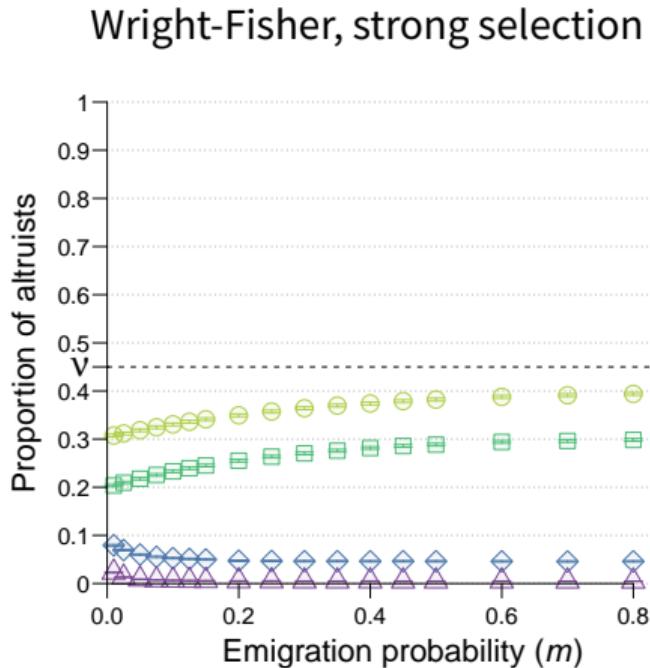
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Strong selection



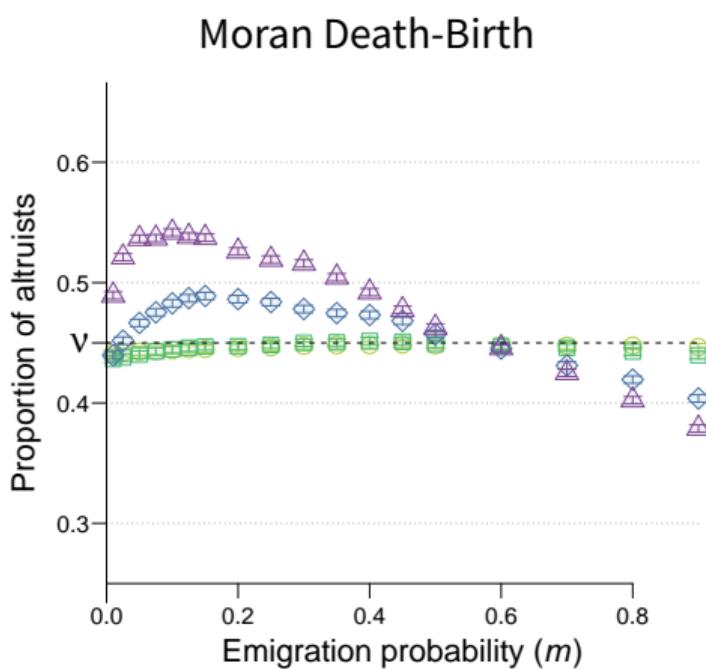
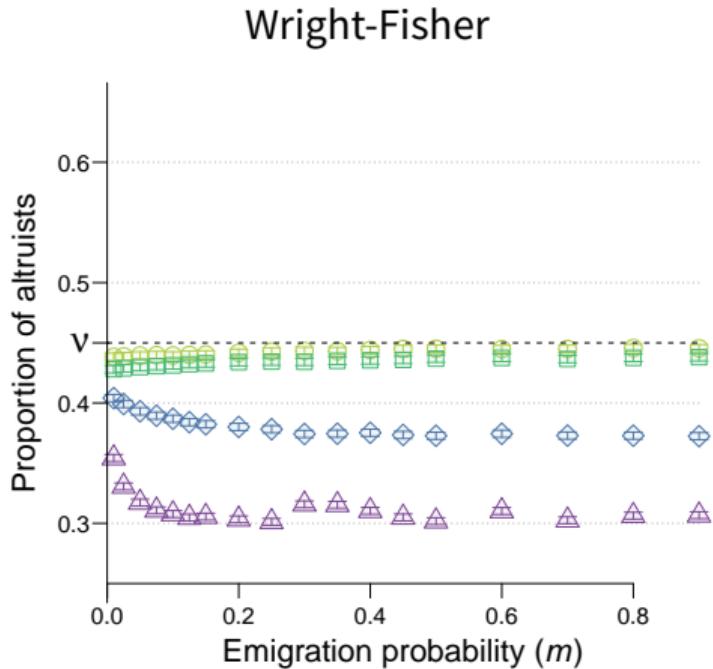
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

Strong selection



$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.1)$$

Heterogeneous deme sizes ($\bar{n} = 4$ as before, but $2 \leq n \leq 5$)



$$(b = 15, c = 1, \bar{n} = 4, N_d = 15, \delta = 0.005)$$

Take-Home Messages

- ▶ Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- ▶ $\mathbb{E}[\bar{X}] > \nu \Leftrightarrow \mathcal{B}R > \mathcal{C} \Leftrightarrow b\kappa > c$.
- ▶ In subdivided populations, $\mathbb{E}[\bar{X}]$ can increase with the emigration probability m when strategy transmission is imperfect ($\mu > 0$).
- ▶ This result seems to hold under stronger selection and in heterogeneous populations.

Funding & Thanks



ANR-14-ACHN-0003-01

L. Kruuk & J. Reid
+ Ch. Mullon
for comments

and thank you for
your attention!