

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

F. Débarre



@flodebarre

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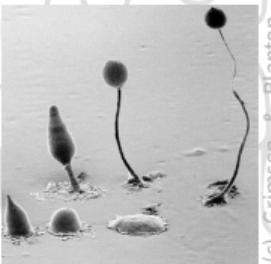








(c) FP



(c) Grimson & Blanton



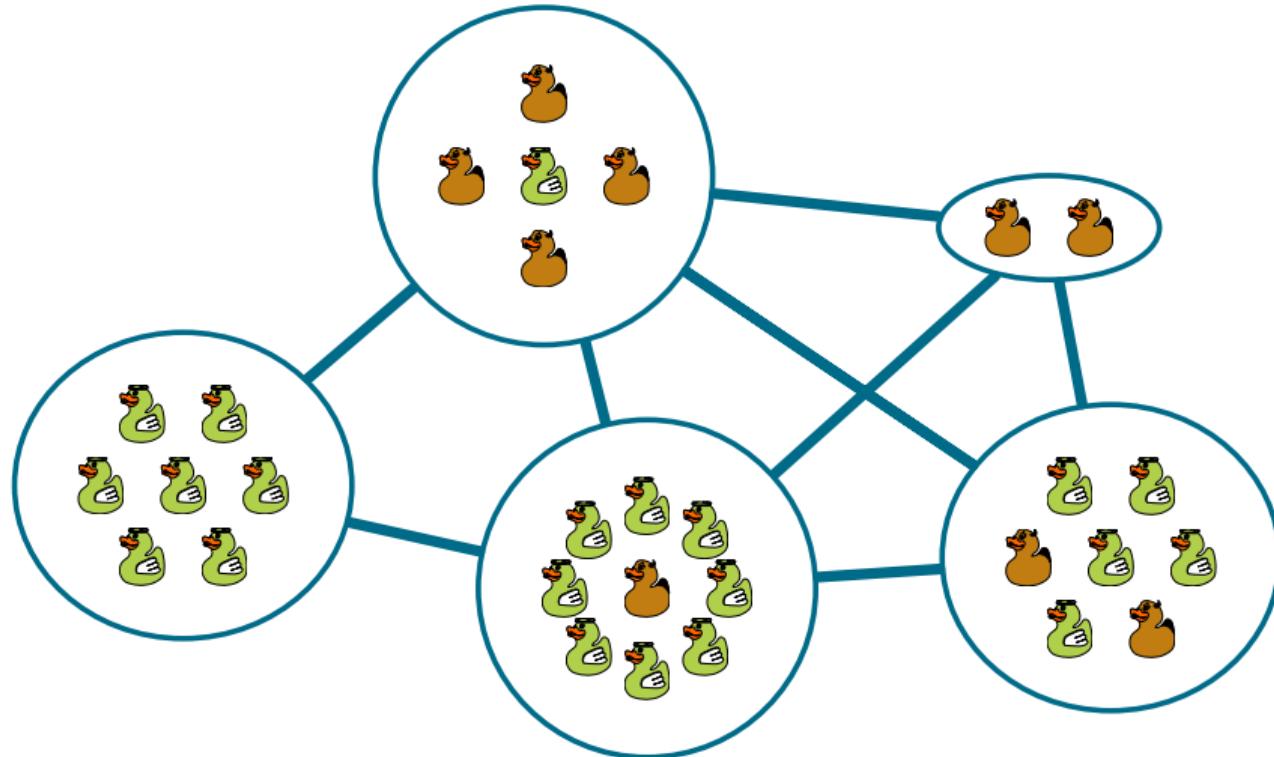
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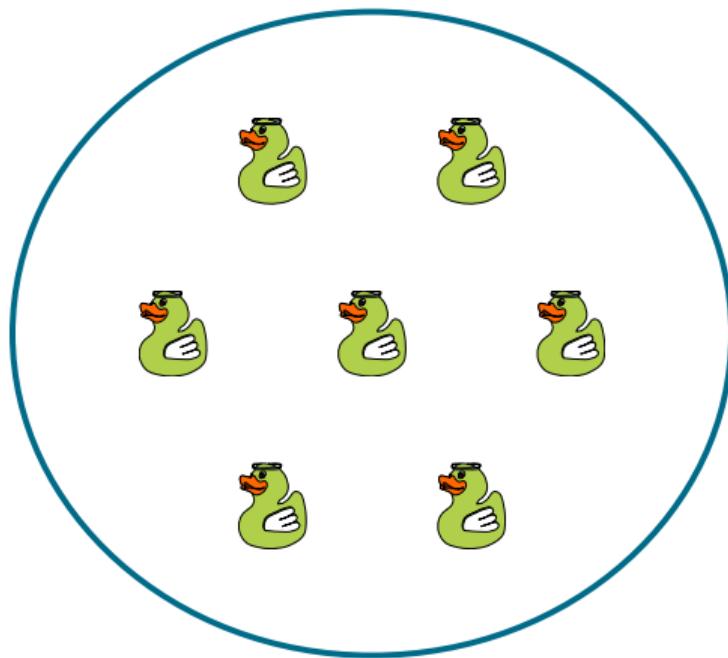
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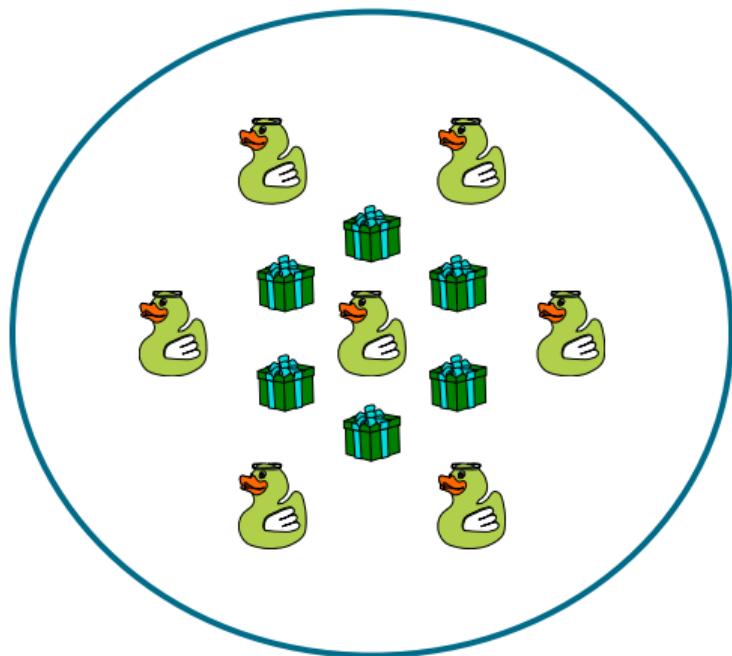
## Spatial structure and altruism



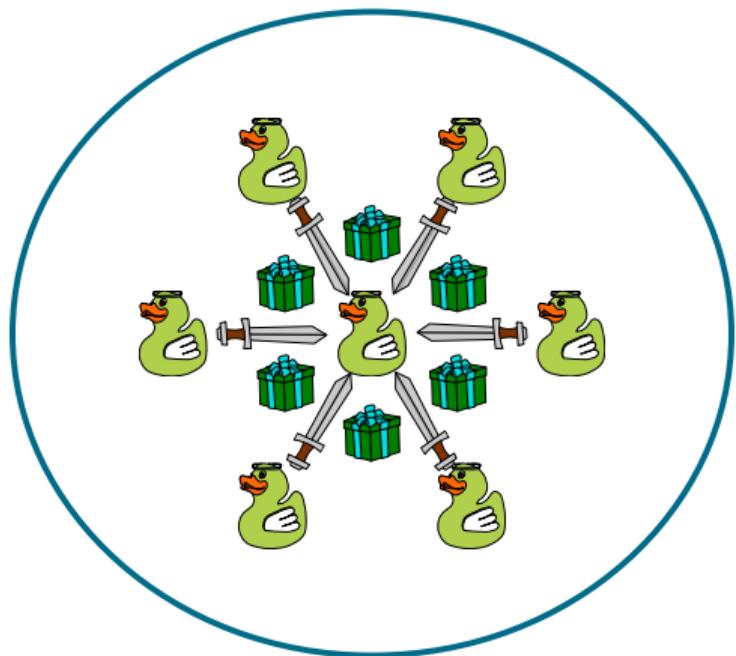
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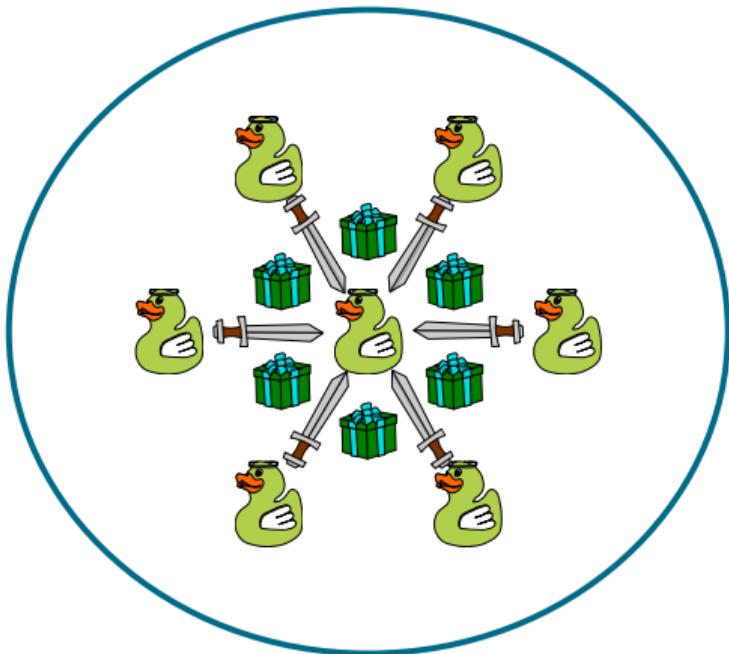
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# Spatial structure and altruism



*Evolutionary Ecology*, 1992, 6, 352–356

## Altruism in viscous populations – an inclusive fitness model

P.D. TAYLOR

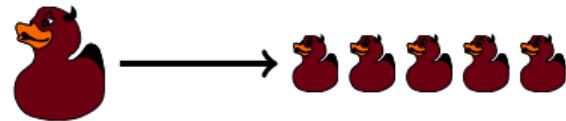
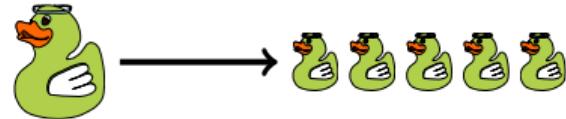
*Department of Mathematics and Statistics, Queen's University, Kingston Ont. K7L 3N6, Canada*

### Summary

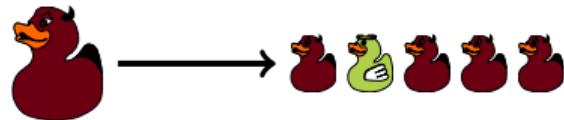
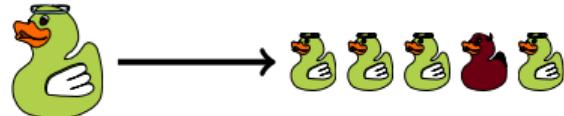
A viscous population (Hamilton, 1964) is one in which the movement of organisms from their place of birth is relatively slow. This viscosity has two important effects: one is that local interactions tend to be among relatives, and the other is that competition for resources tends to be among relatives. 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

## A common feature of models



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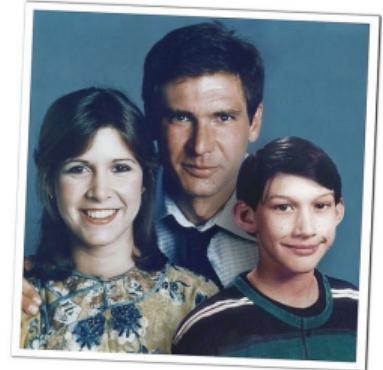


What is the effect of population viscosity  
on the evolution of altruism when parent-  
offspring strategy transmission is **imperfect**?

## Fidelity of parent-offspring transmission

### Causes of imperfect strategy transmission

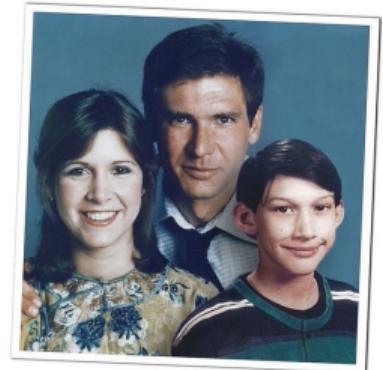
- ▶ Mutation



# Fidelity of parent-offspring transmission

## Causes of imperfect strategy transmission

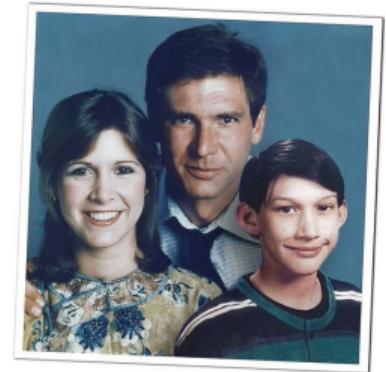
- ▶ Mutation
- ▶ Partial heritability



## Fidelity of parent-offspring transmission

### Causes of imperfect strategy transmission

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- ▶ Partial heritability
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In the model

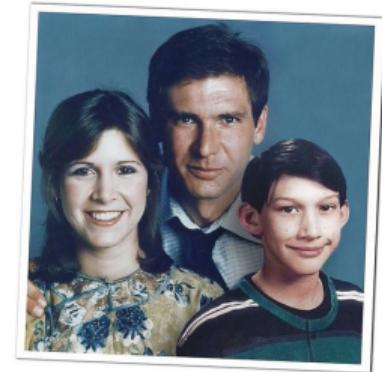
Parent



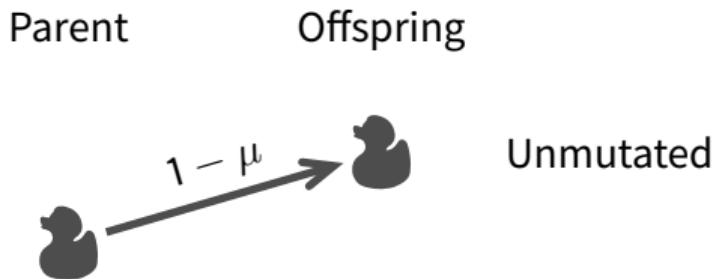
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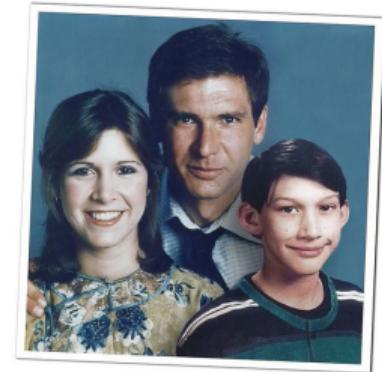
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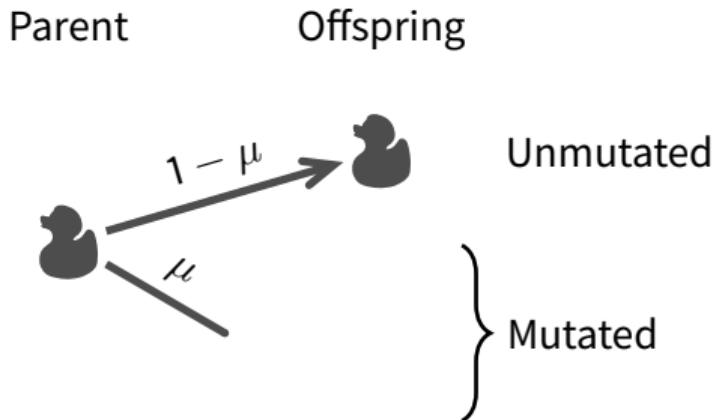
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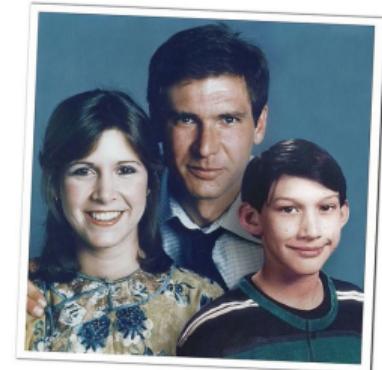
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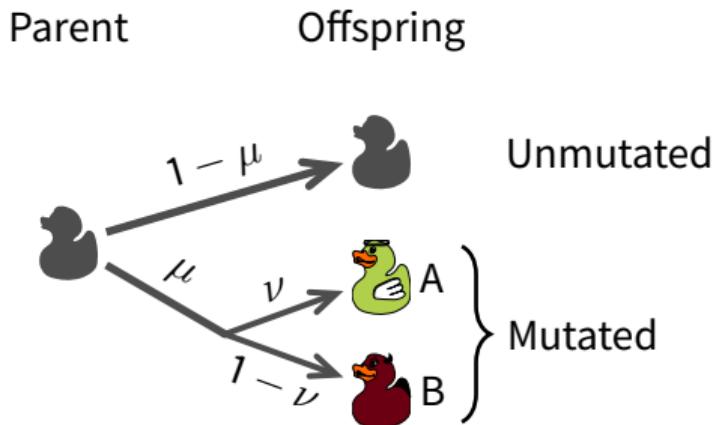
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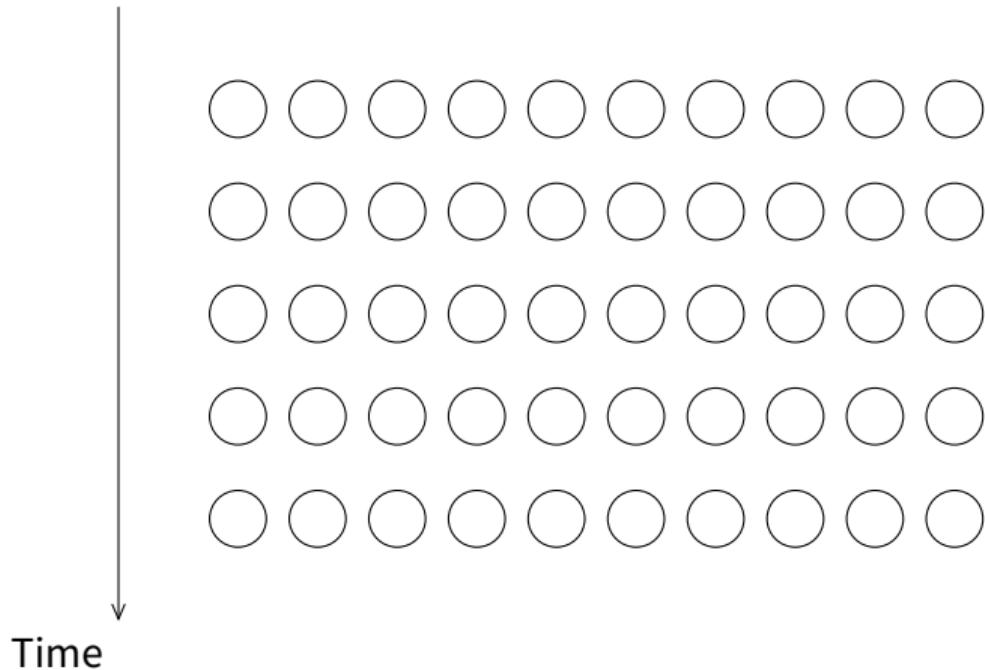
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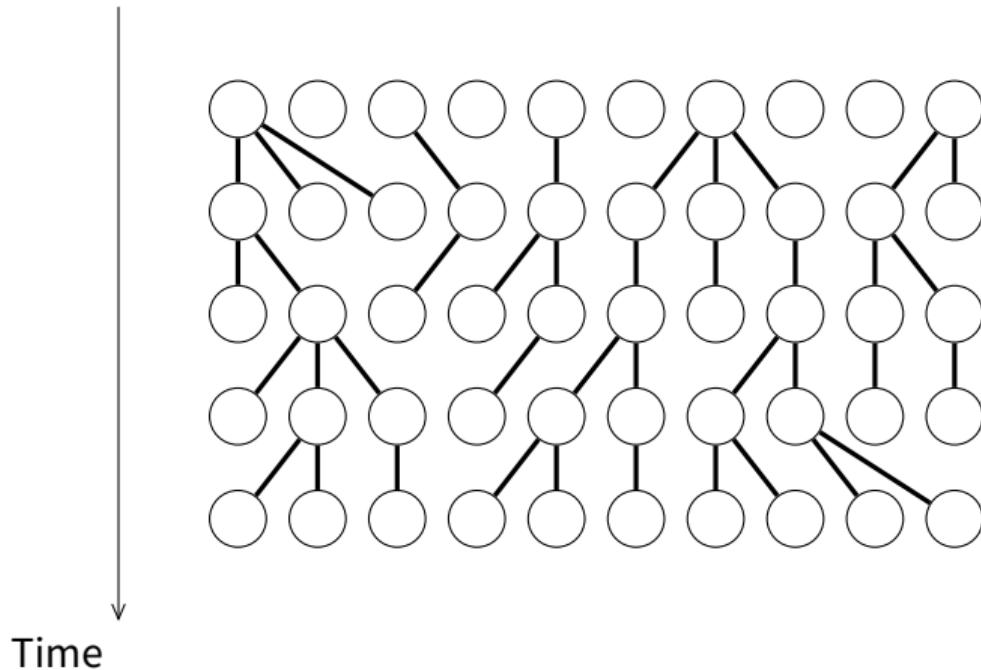
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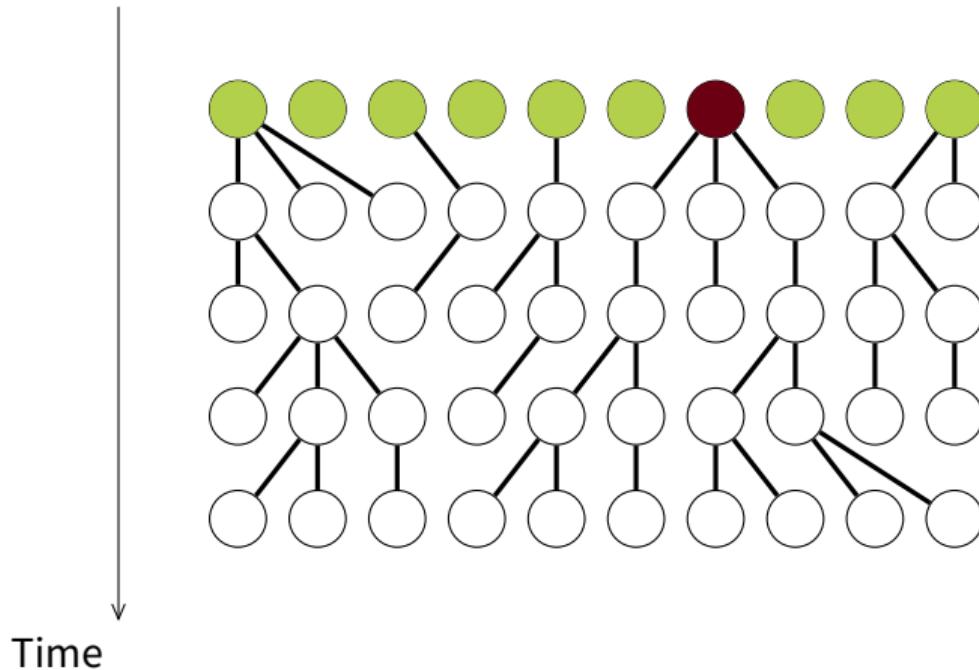
## Genealogy, Identity by descent and Identity in state



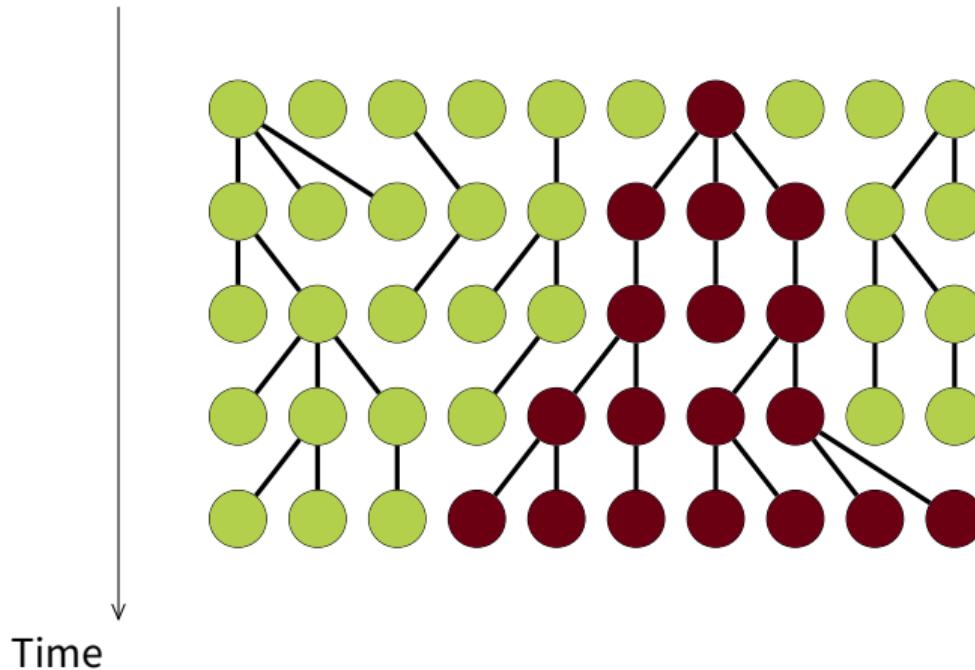
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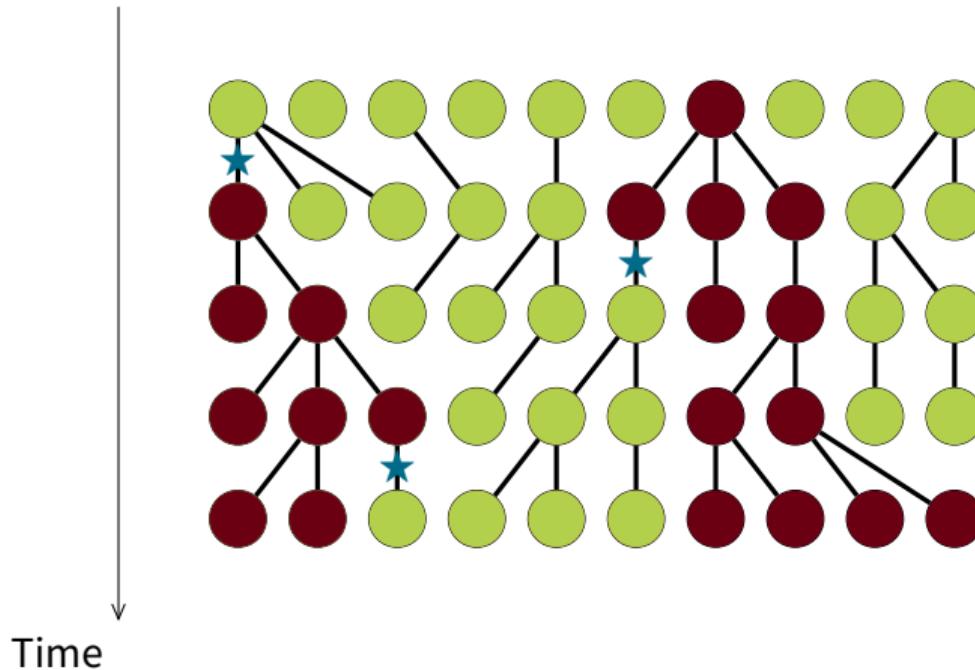
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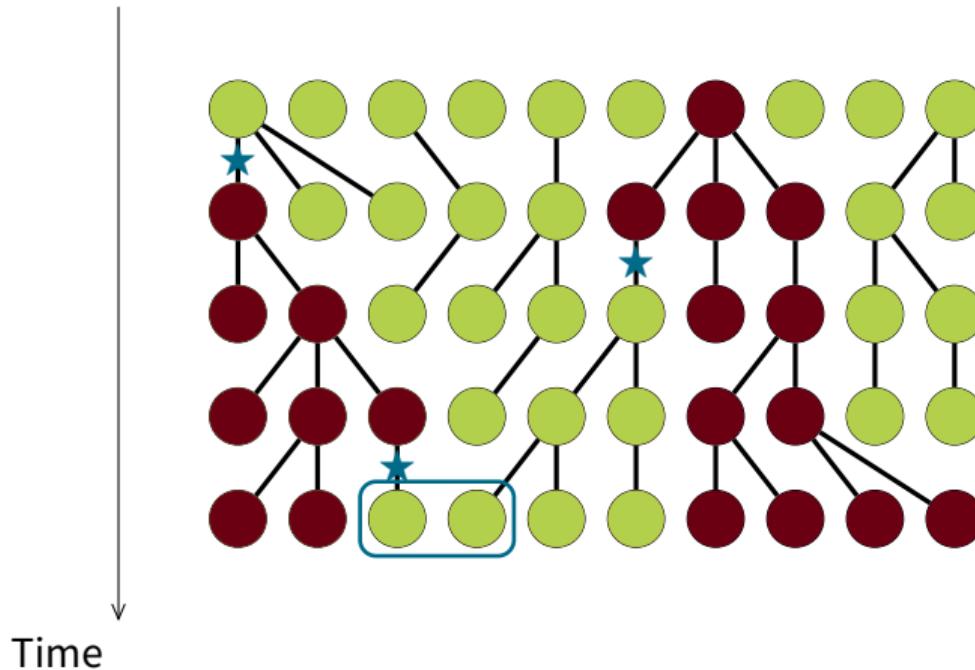
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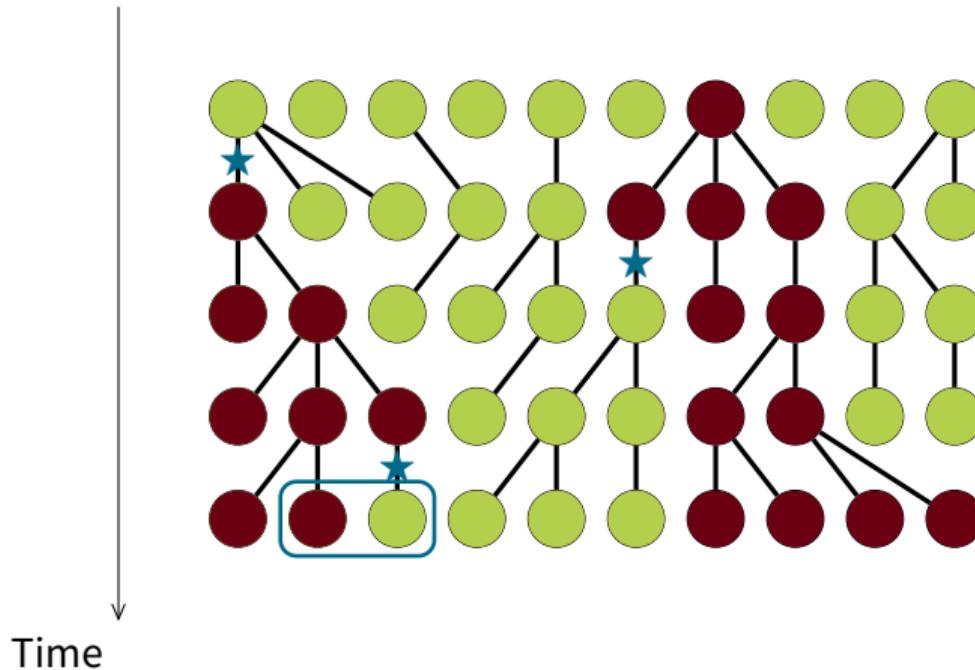
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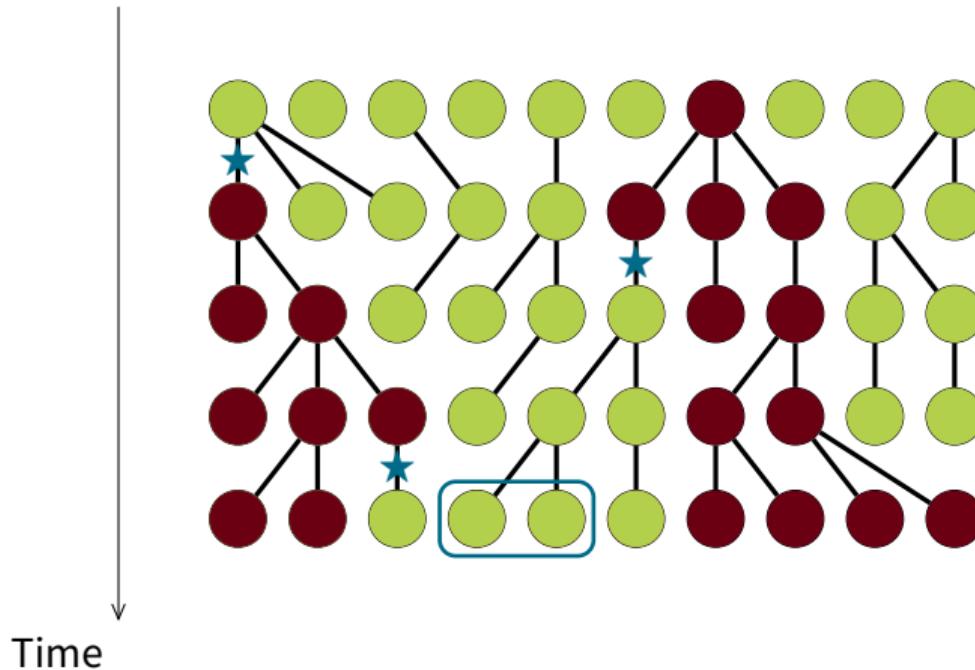
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## Expected state of pairs of sites and identity by descent

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## Expected state of pairs of sites and identity by descent

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

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

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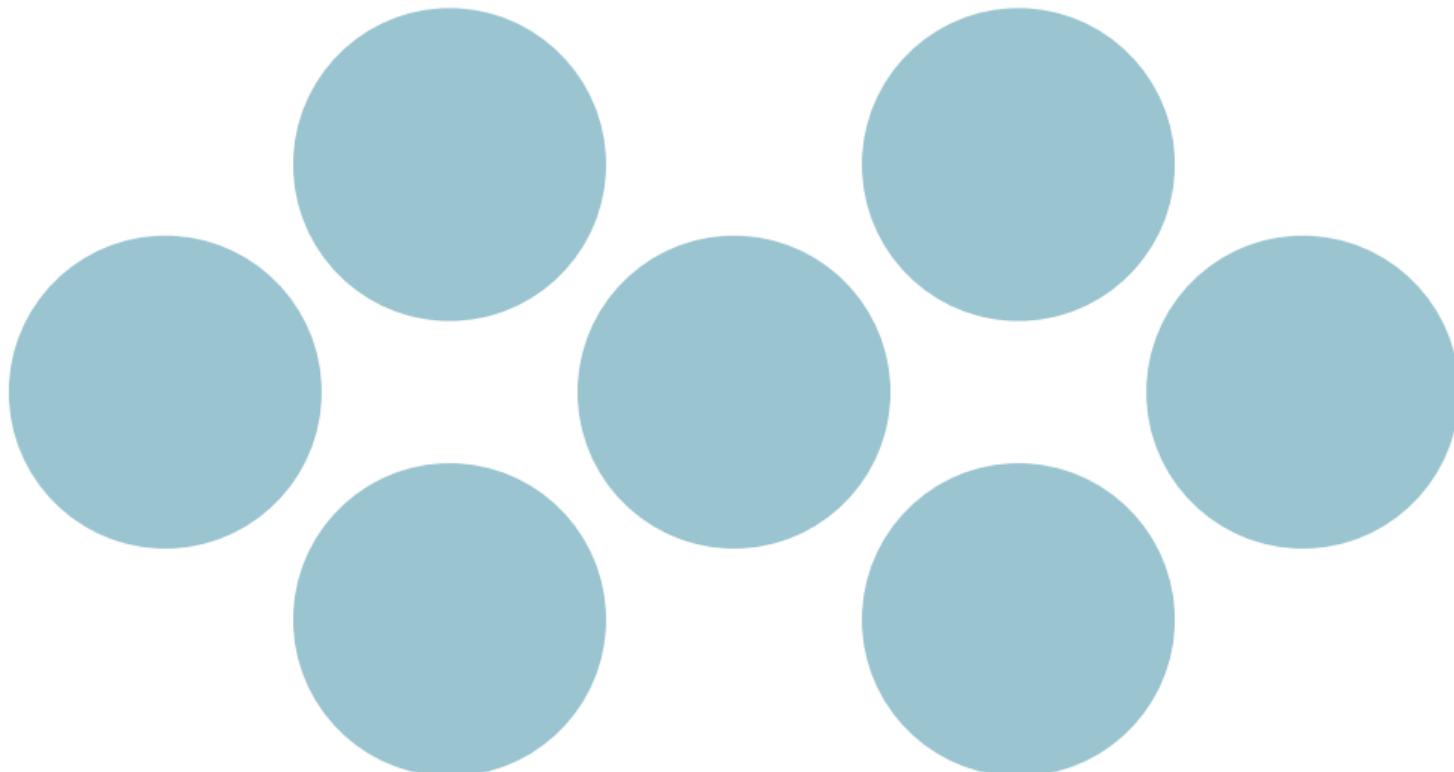
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$Q_{in}$ ,  $Q_{out}$

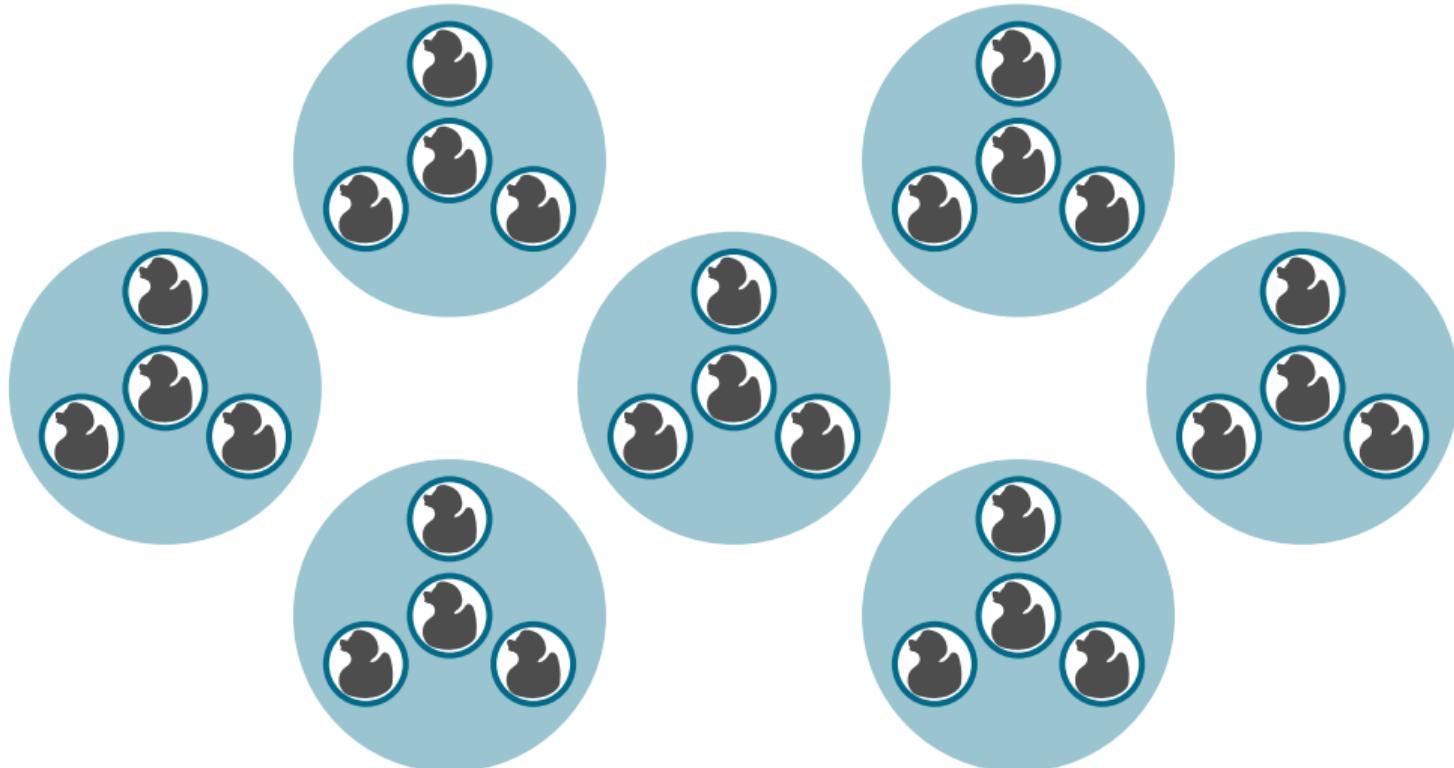
## Subdivided population – Island model

$N_d$  demes



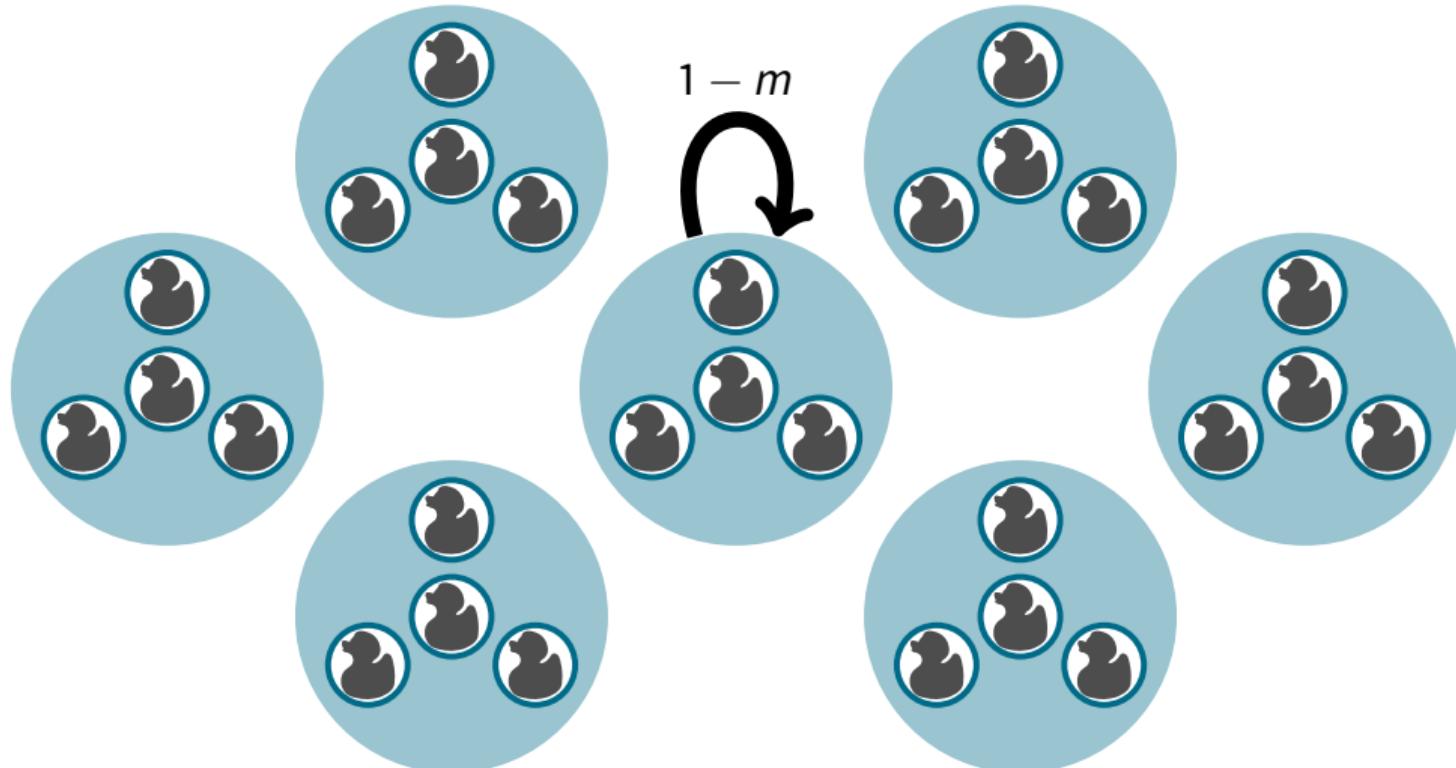
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$N_d$  demes of  $n$  individuals each (total population size  $N = n N_d$ )



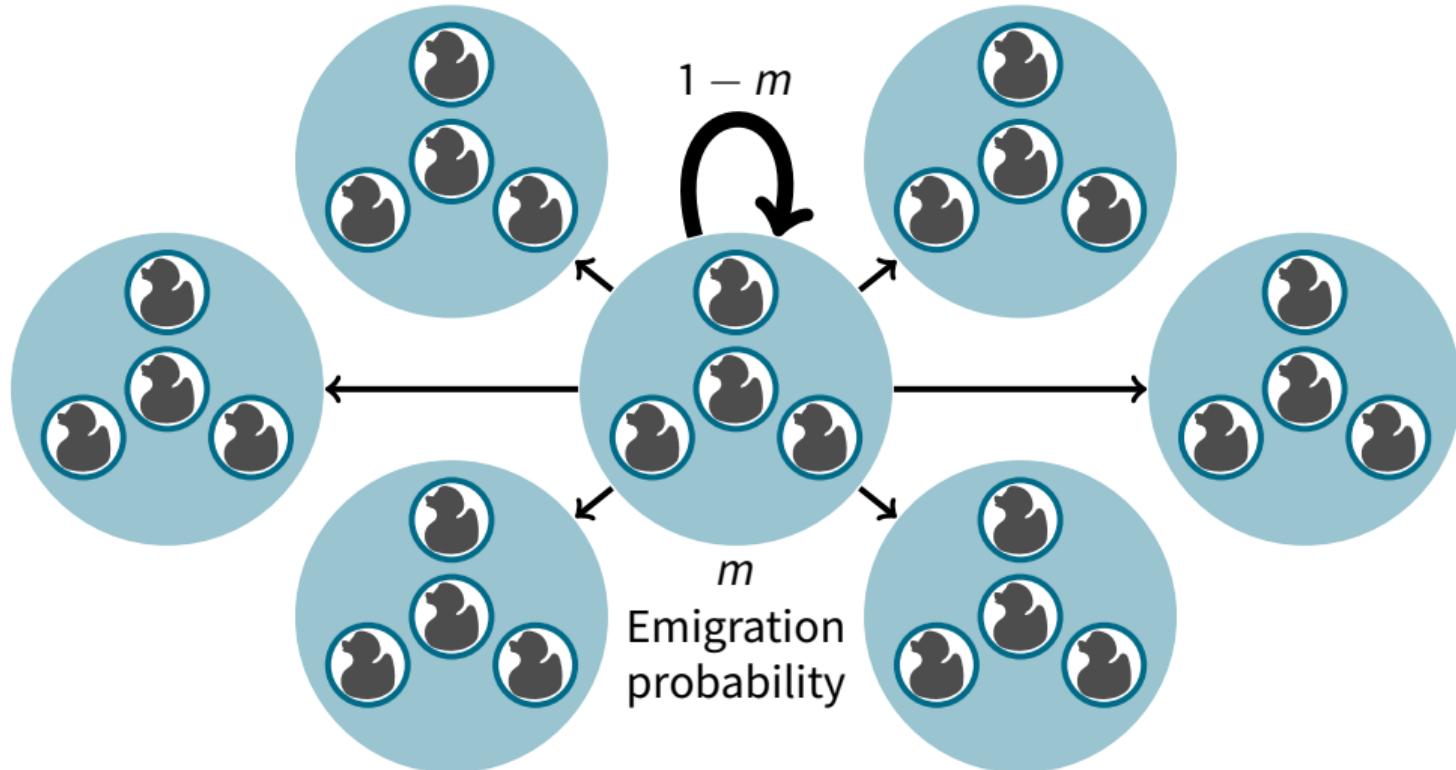
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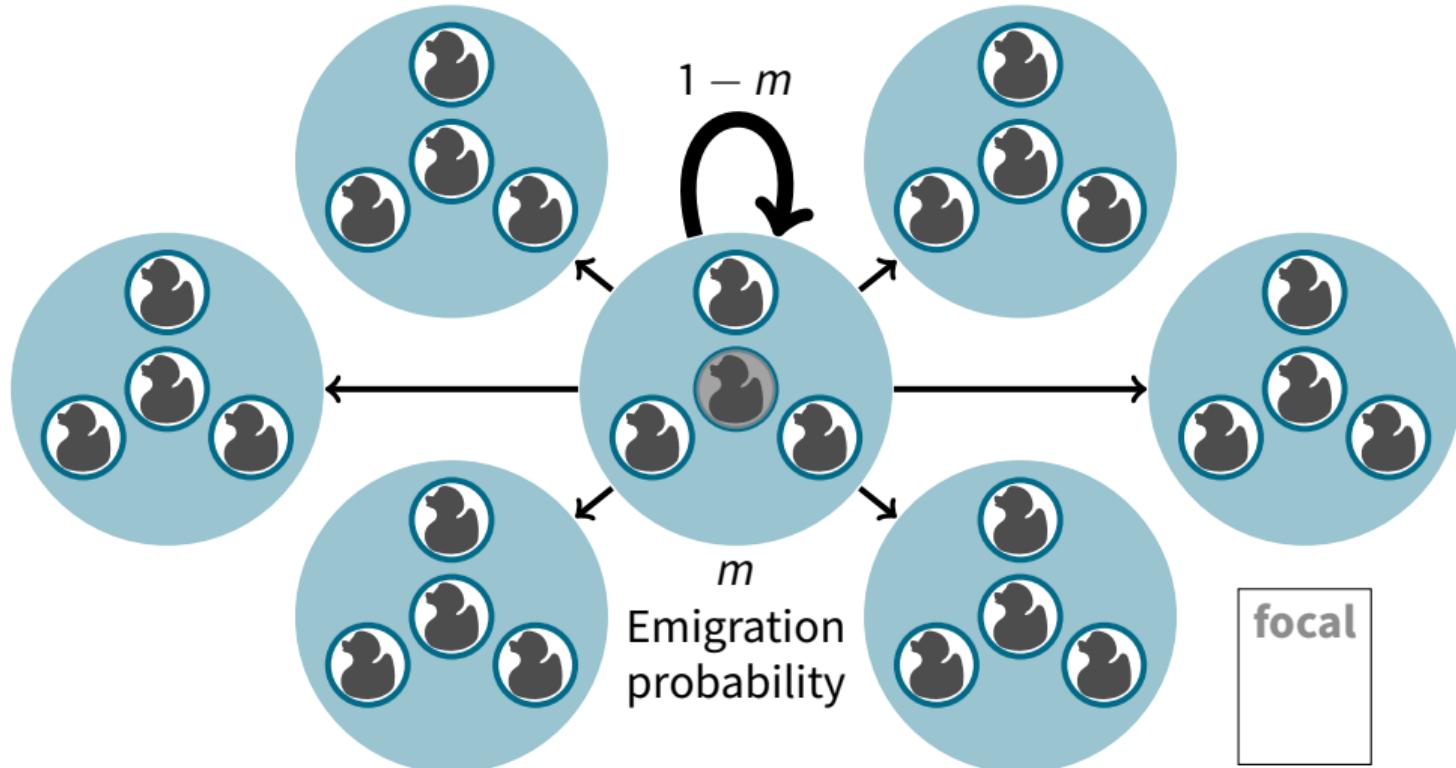
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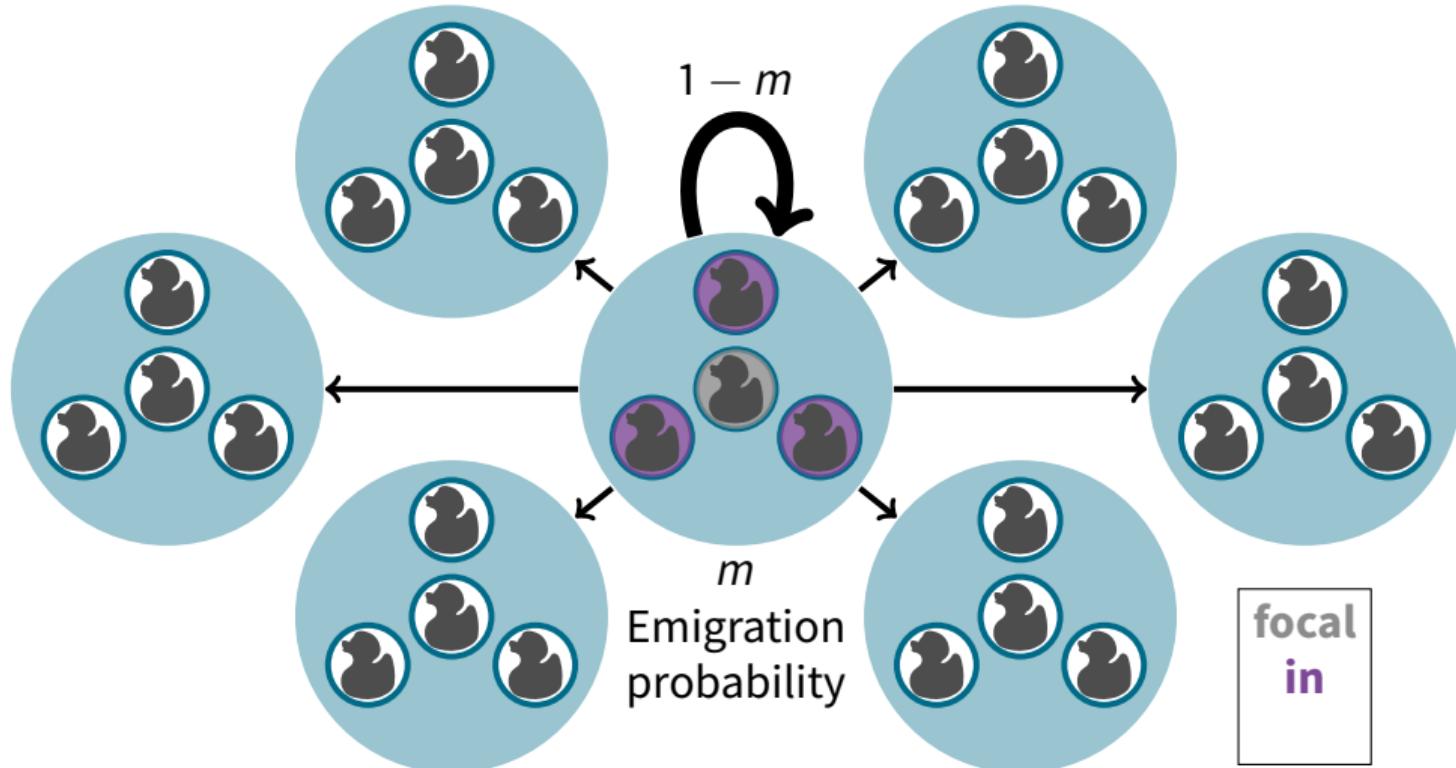
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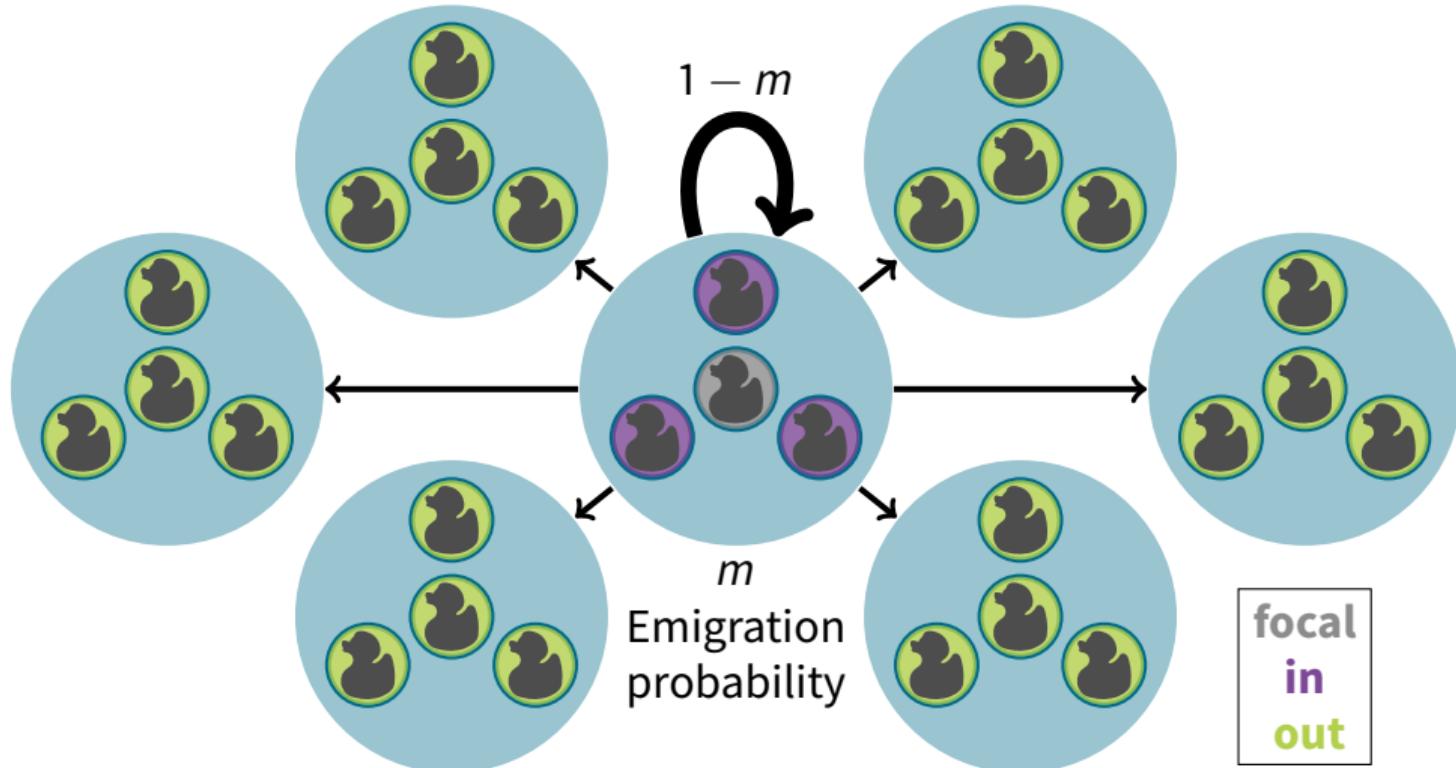
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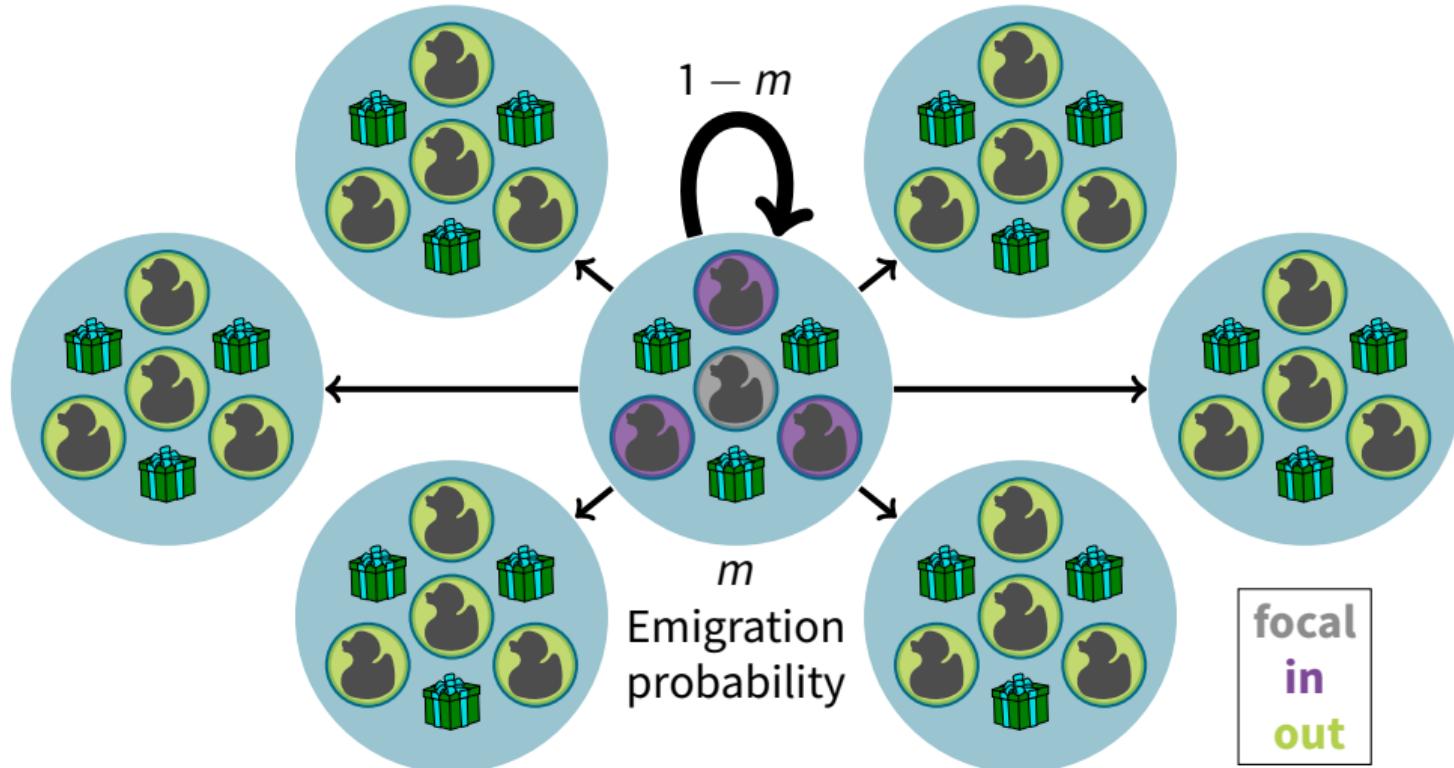
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## Updating the population

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

$$\# \text{[Gravestone]} = \# \text{[Baby Stroller]}$$

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

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

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

## 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

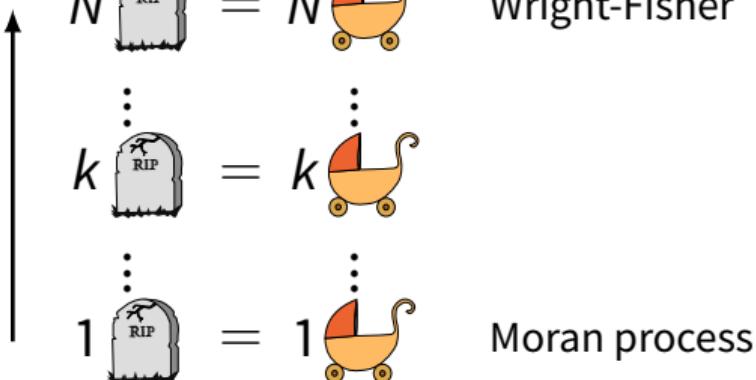
Constant population size ( $N$ ), so  
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$$\# \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = \# \begin{array}{c} \text{babycart} \end{array}$$

Life-cycle

Offspring  
production

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



## Updating the population

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

Life-cycle

Offspring production



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$$k \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = k \begin{array}{c} \text{newborn} \\ \text{stroller} \end{array}$$

Offspring dispersal

$$1 \begin{array}{c} \text{RIP} \\ \text{grave} \end{array} = 1 \begin{array}{c} \text{newborn} \\ \text{stroller} \end{array} \quad \text{Moran process}$$

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Constant population size ( $N$ ), so  
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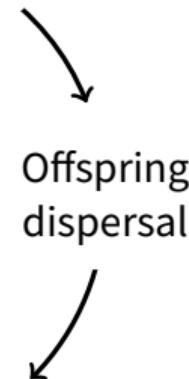
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↑

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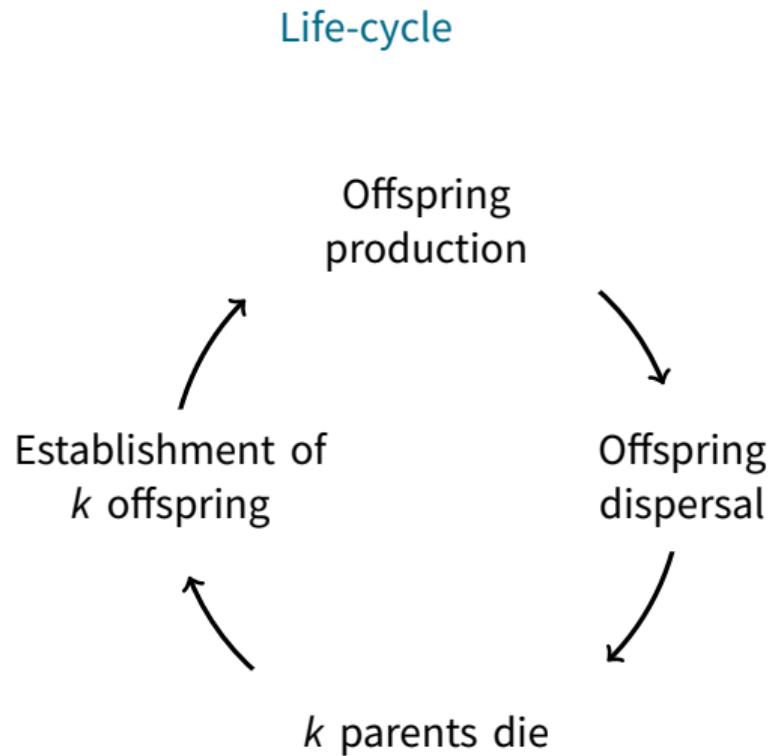
$k$  parents die

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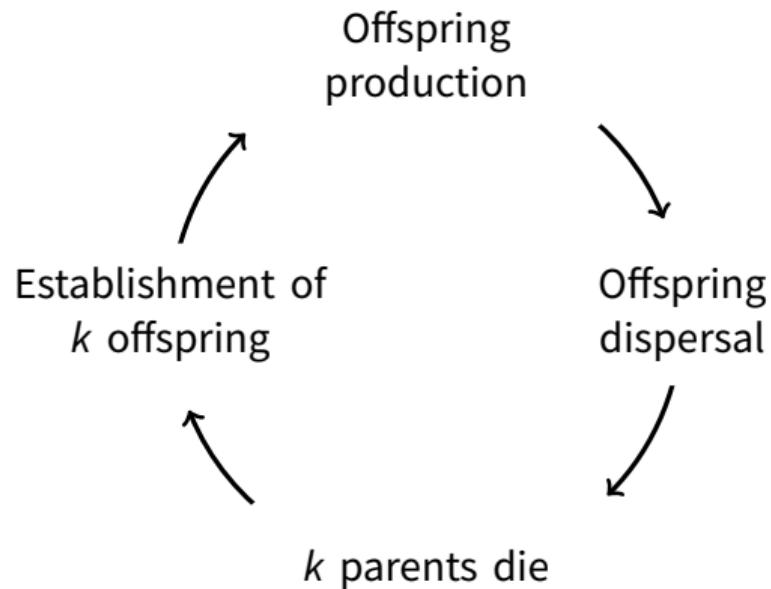
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Life-cycle  
“Death-Birth” updating



## Population

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

## Population

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

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  $k$  

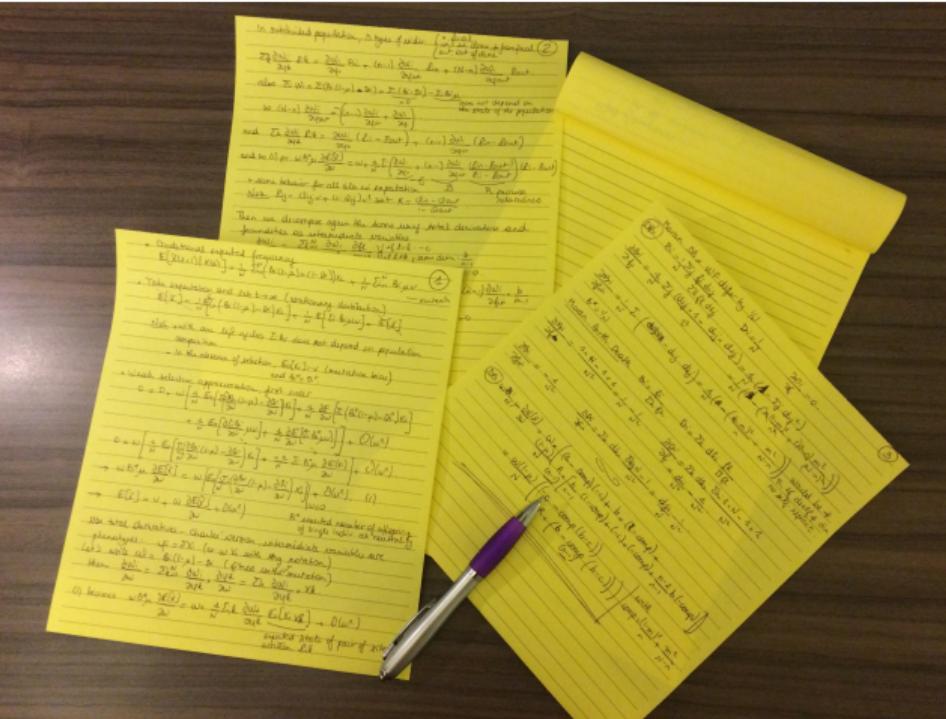
$$f_{\text{green}} = 1 + \omega \left( b \frac{k-1}{n-1} - c \right),$$
$$f_{\text{red}} = 1 + \omega \left( b \frac{k}{n-1} \right).$$



Selection is weak

$$\omega \ll 1.$$

# “Field site”



## 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

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

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

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

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

Mutation-drift equilibrium   Selection strength   Population variance  
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$\mathcal{B}$

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equilibrium

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$\mathcal{R}$        $\mathcal{B}$

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

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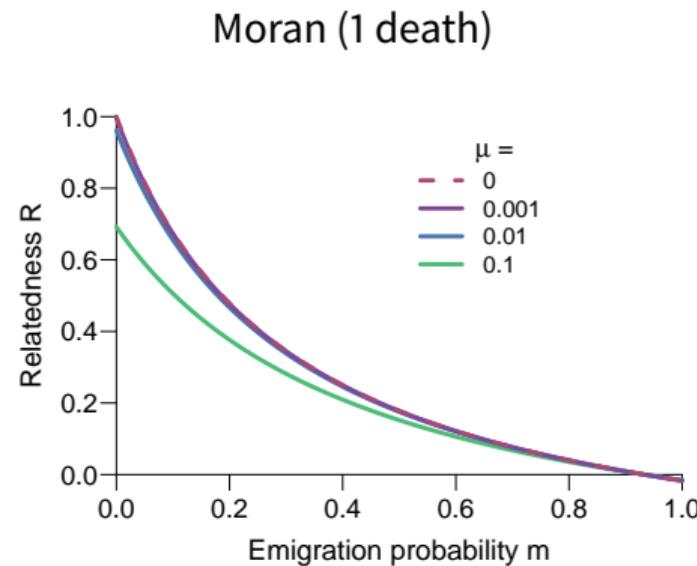
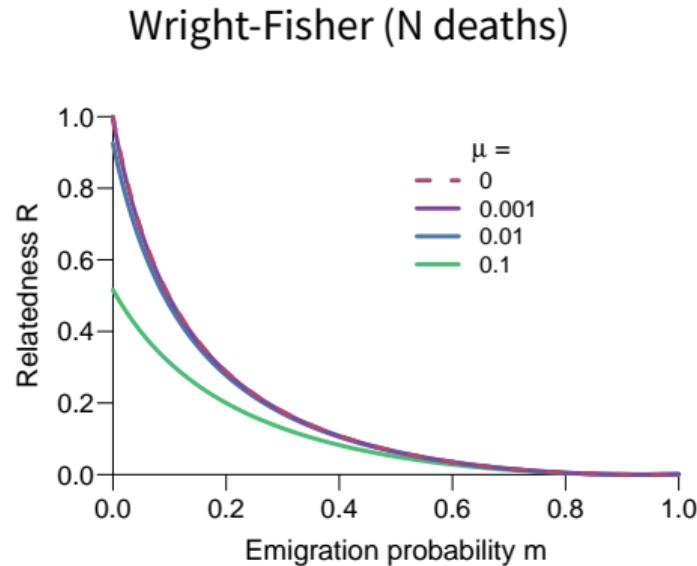
Mutation-drift equilibrium      Selection strength      Population variance  
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$$(n = 4, N_d = 15)$$

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

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Mutation-drift equilibrium   Selection strength   Population variance  
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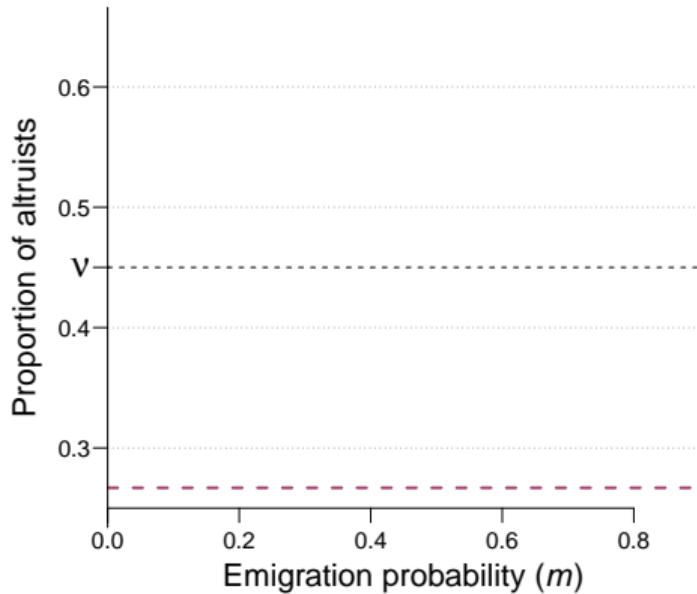
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## Effect of the emigration probability $m$ on the expected proportion of altruists

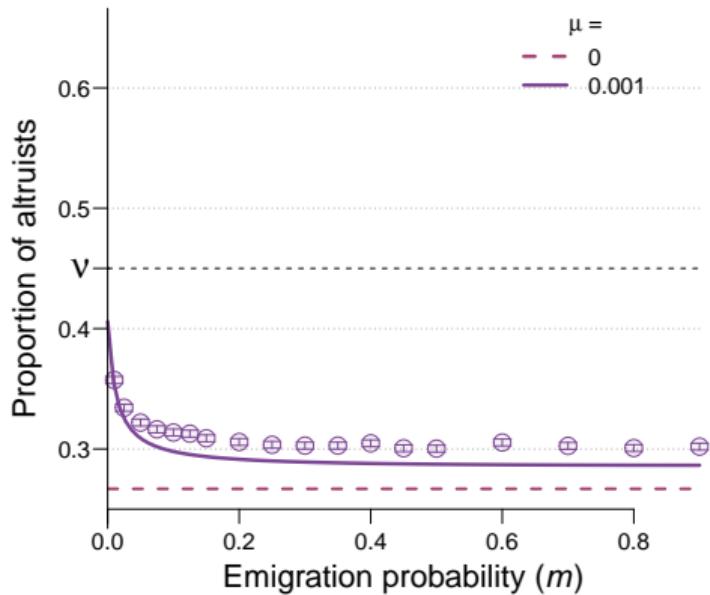
Wright-Fisher ( $N$  deaths &  $N$  births)



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

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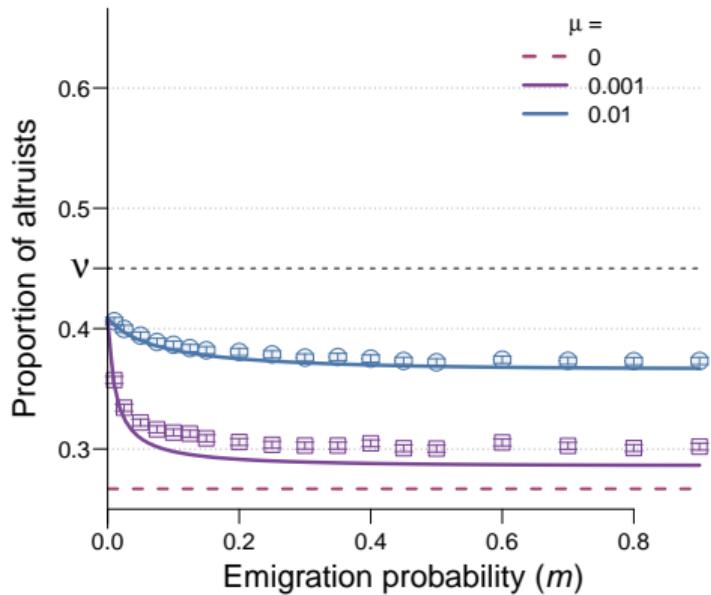
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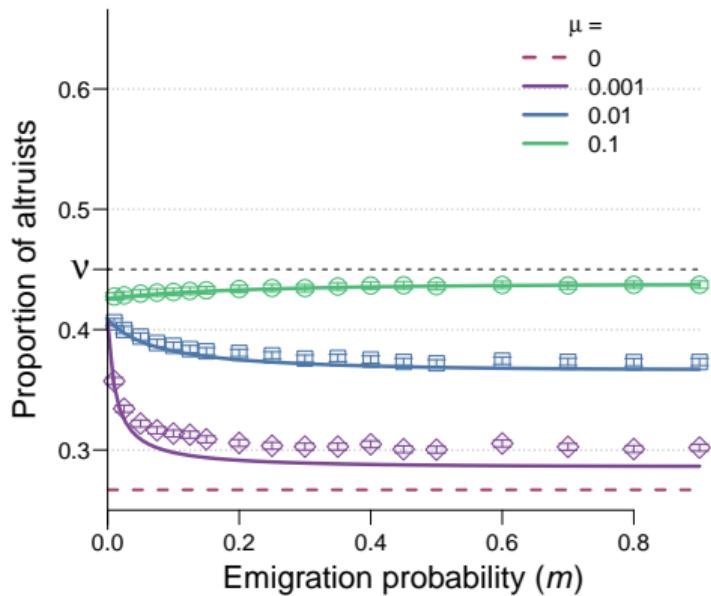
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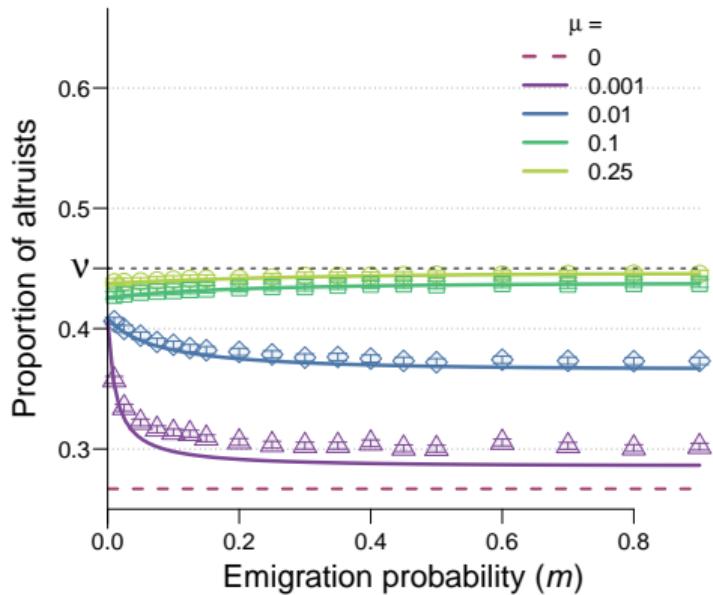
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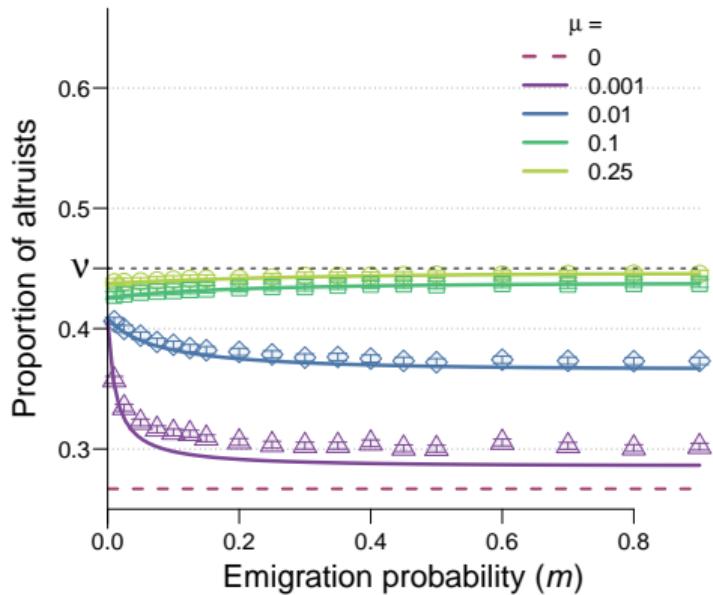
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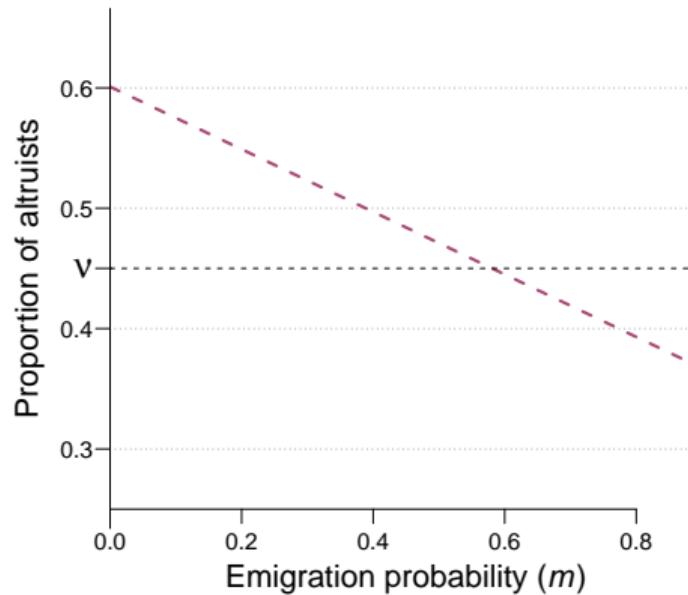
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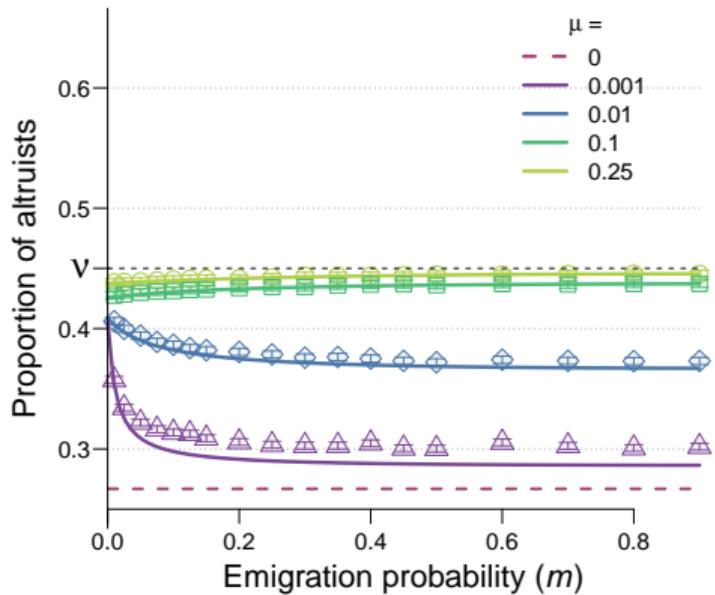
Moran Death-Birth (1 death & 1 birth)



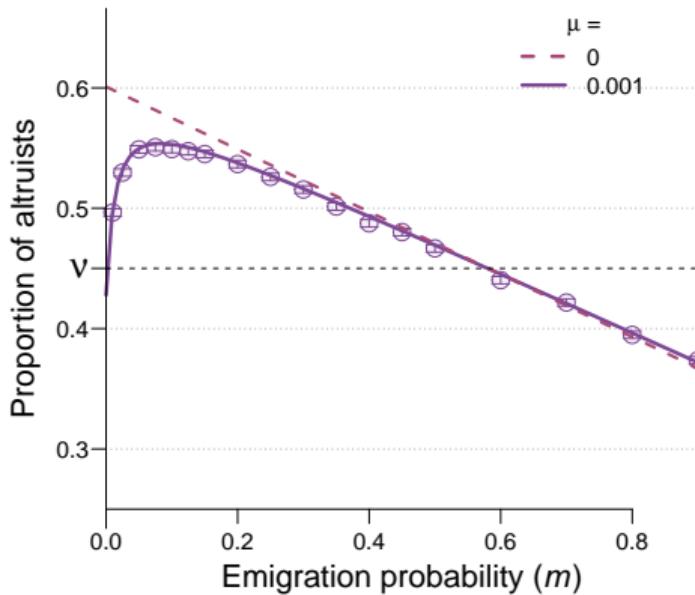
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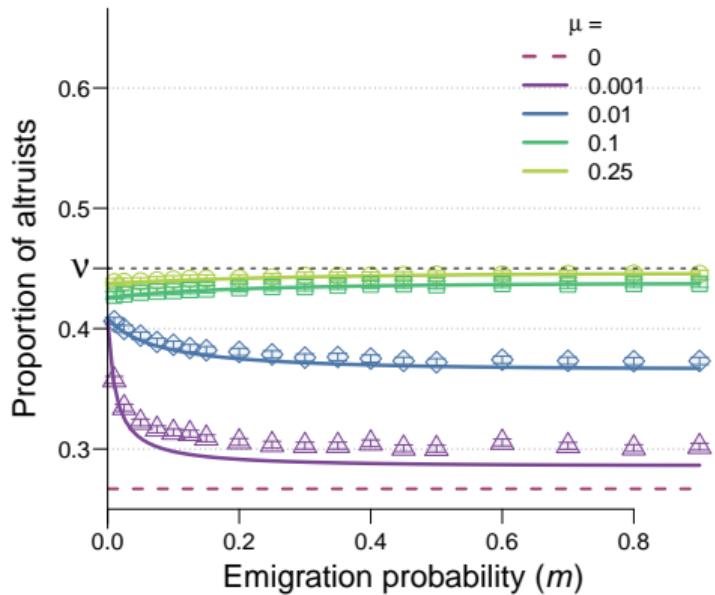
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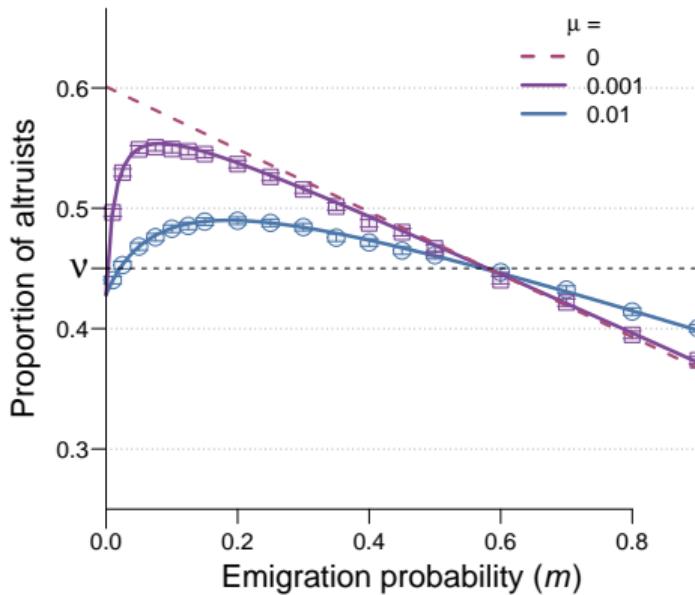
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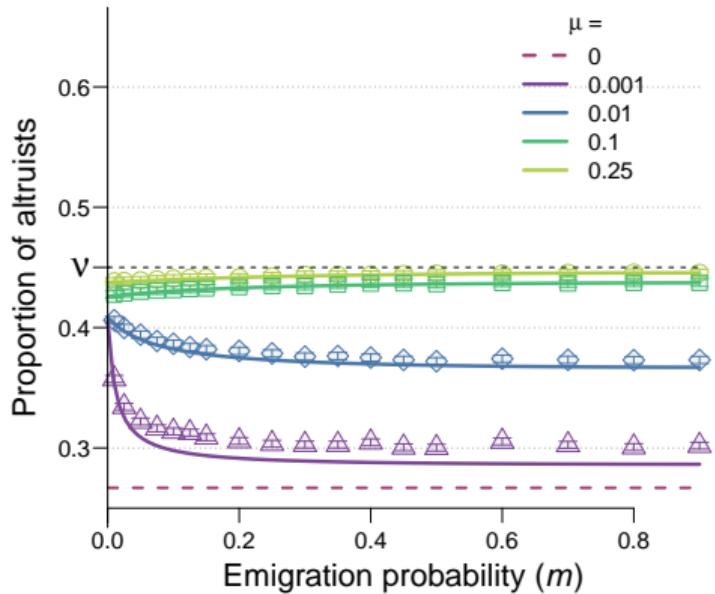
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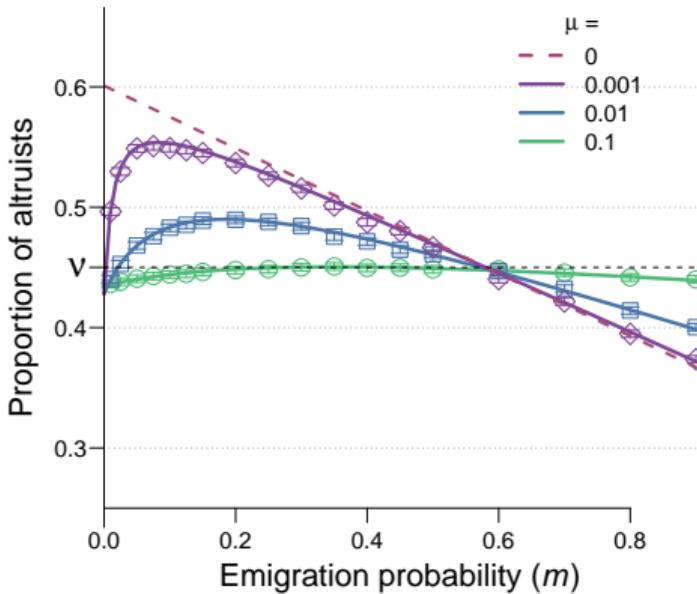
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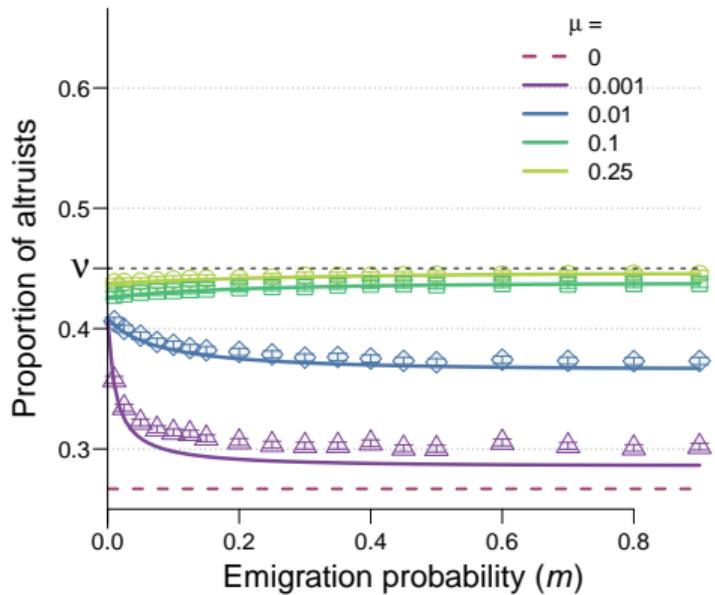
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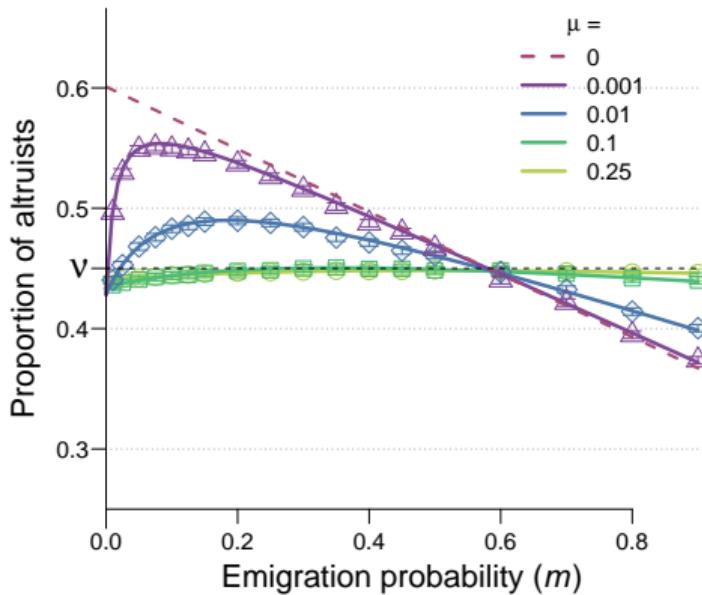
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Is the result robust?

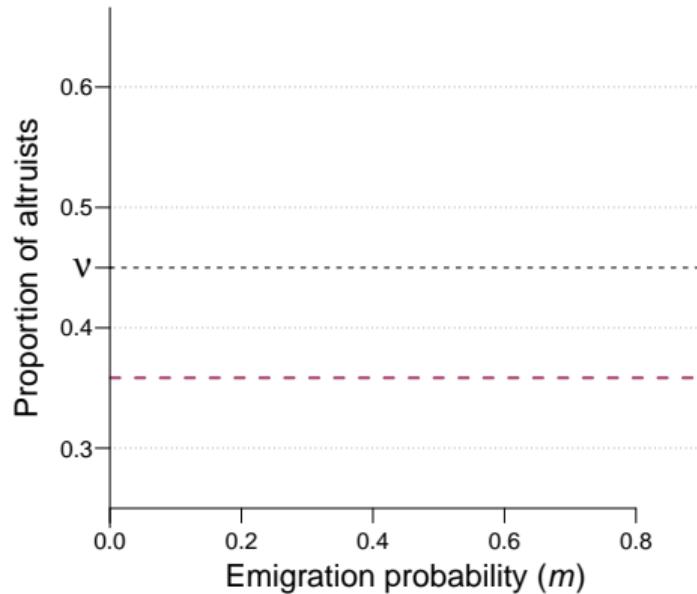
## Another life-cycle

Moran Birth-Death (1 birth & 1 death)

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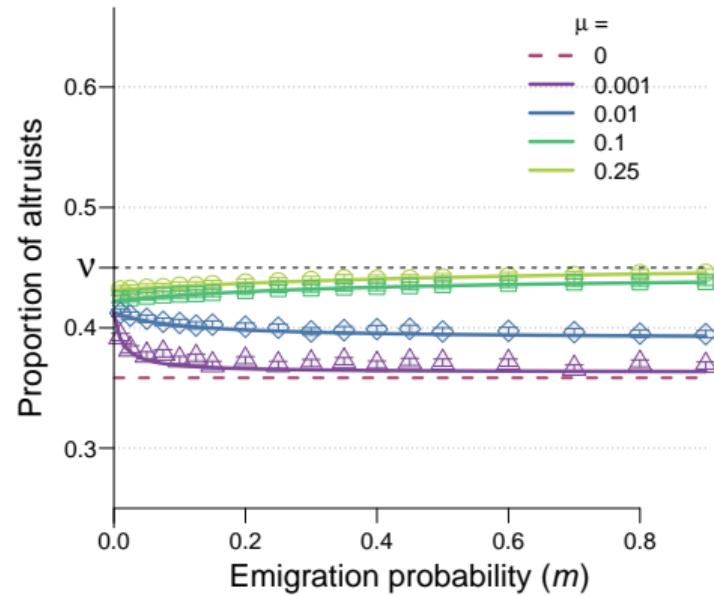
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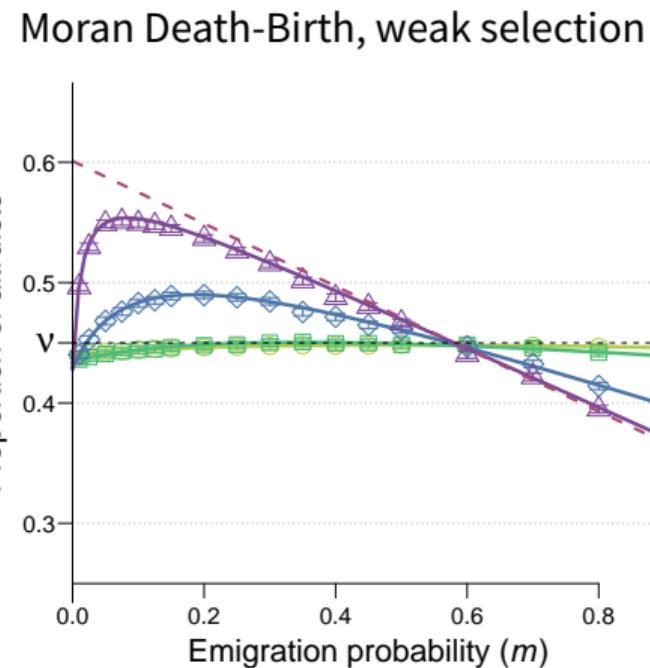
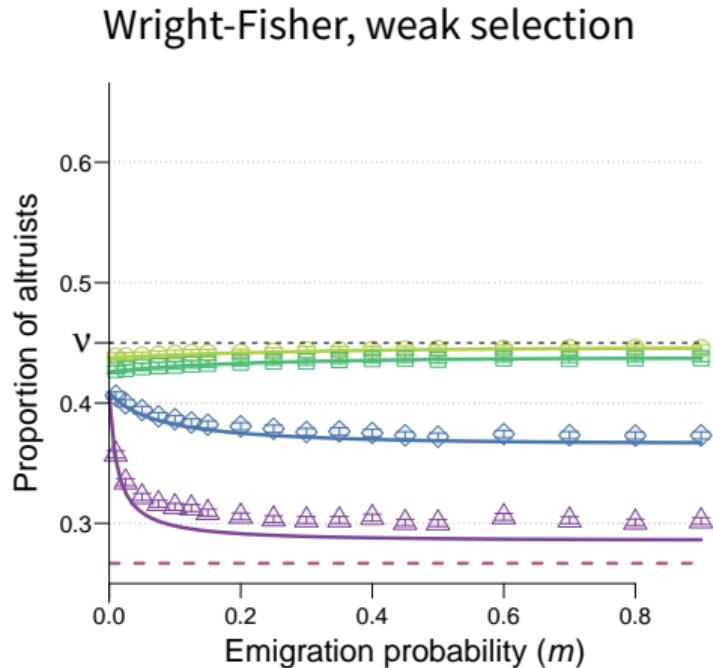
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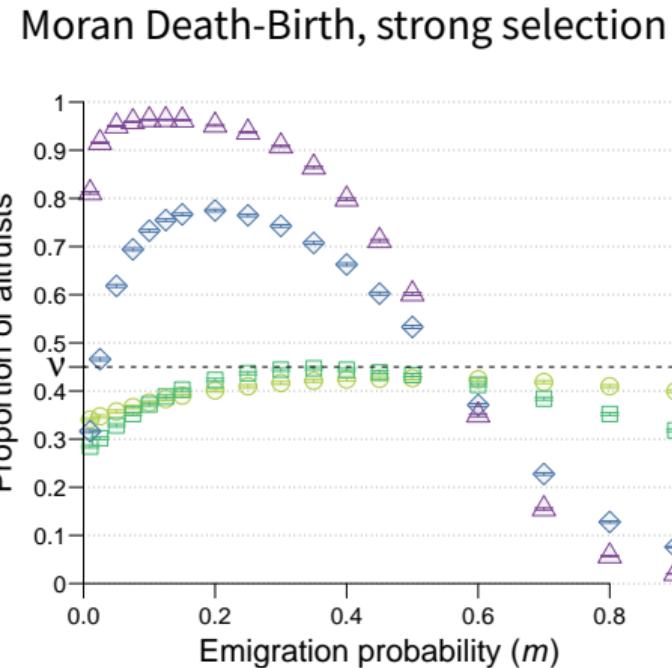
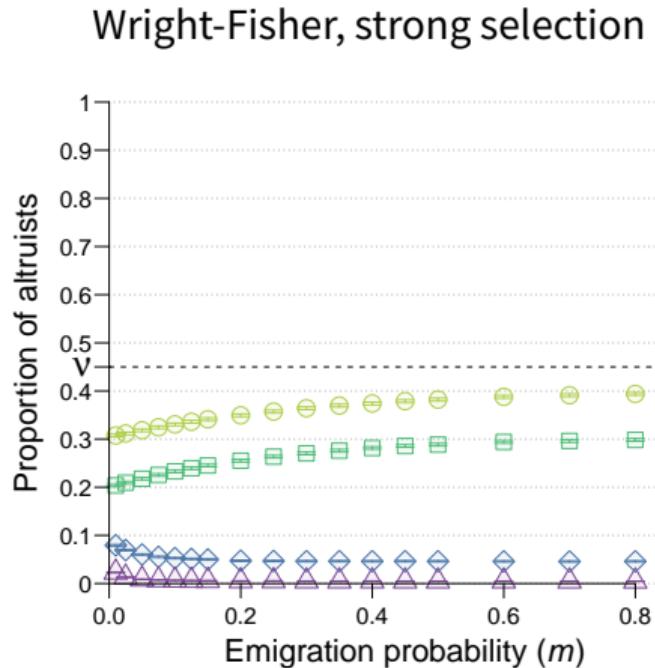
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## Strong selection



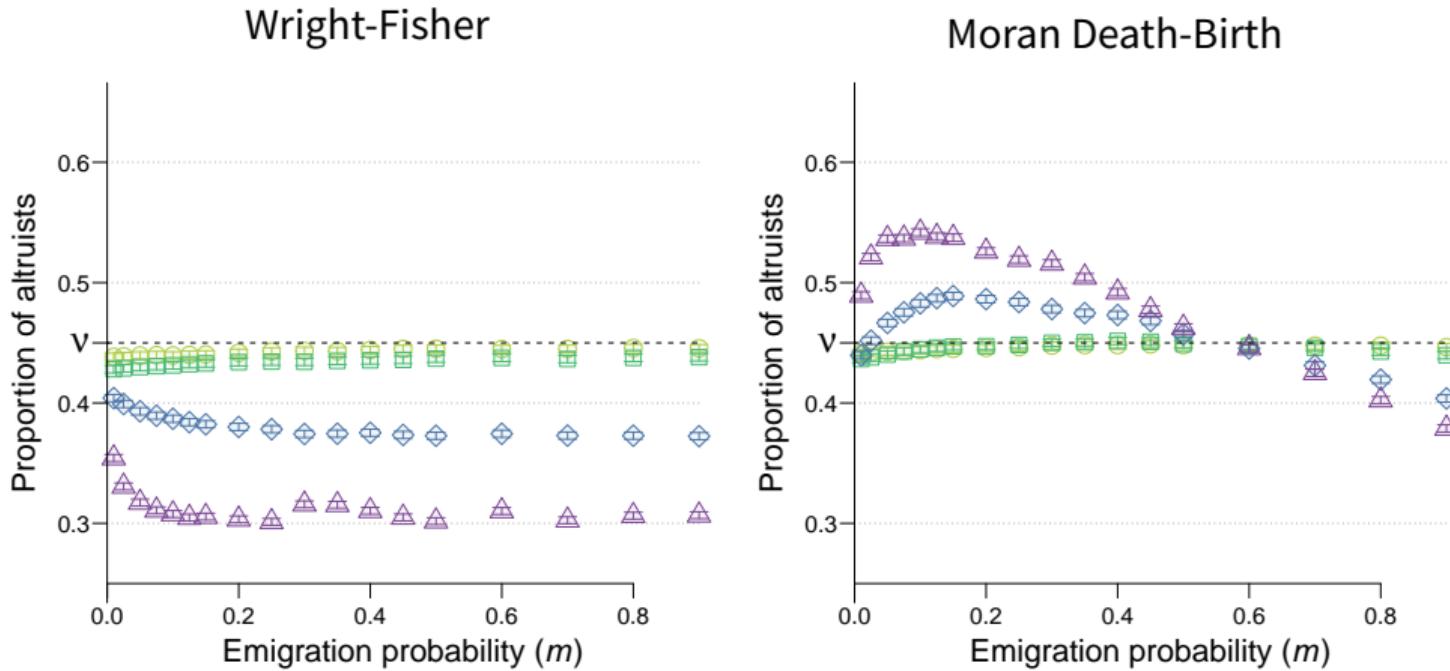
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## Strong selection



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

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



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

From theory to reality...

## Take-Home Messages

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## Funding & Thanks



ANR-14-ACHN-0003-01

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

and thank you for  
your attention!