

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

F. Débarre



@flodebarre

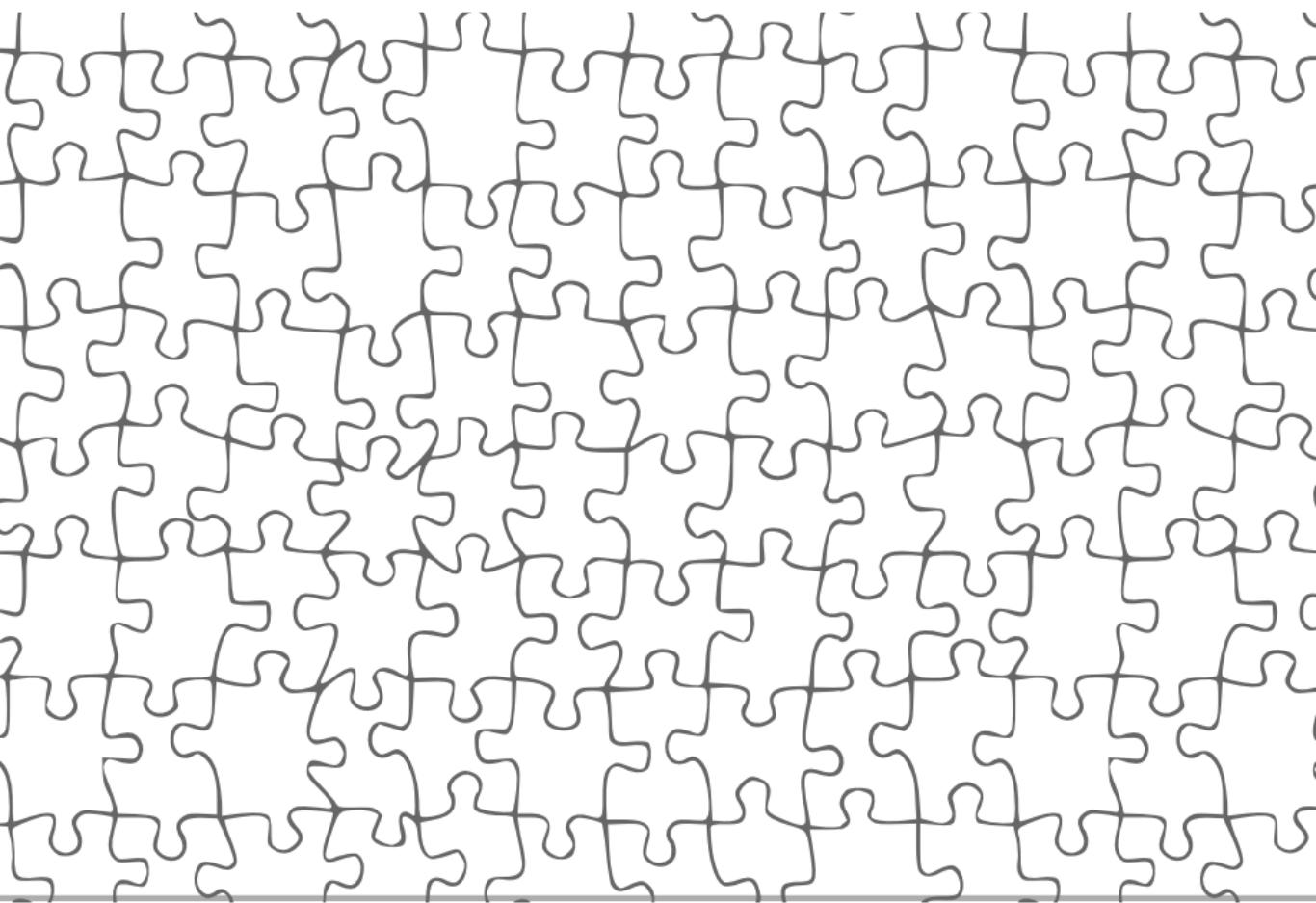
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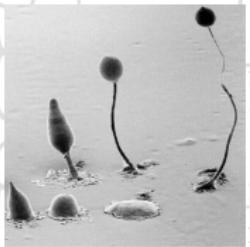
Thematic semester on  
**Cimi**  
Centro International de Matemáticas e Informática  
TOULOUSE

**Mathematics Computer  
science and biology**

**Ecology and evolutionary biology,  
deterministic and stochastic models**







(c) Grimson & Blanton



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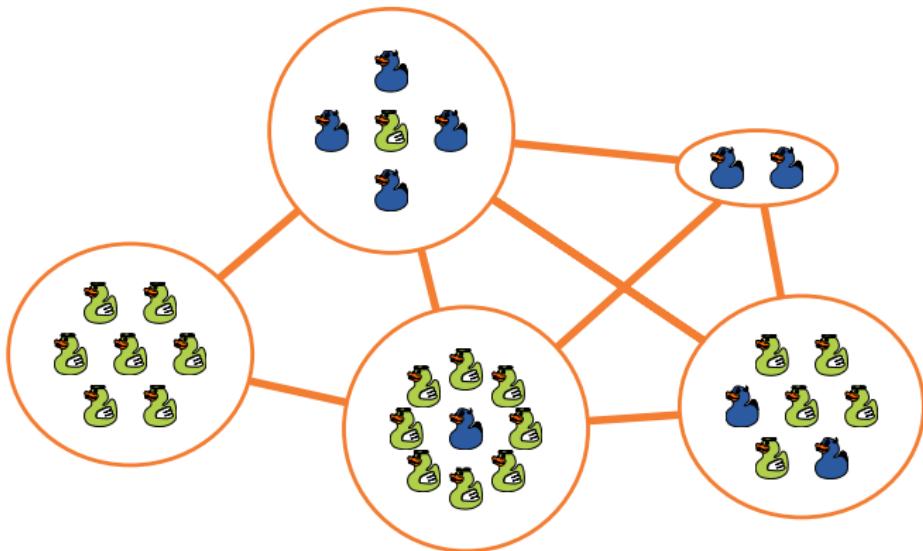
(c) FD



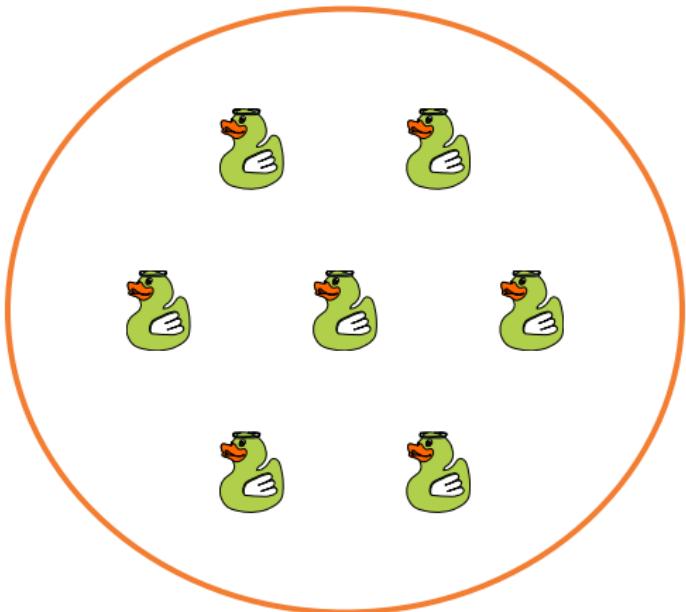
(c) /Picturesforcoloring.com



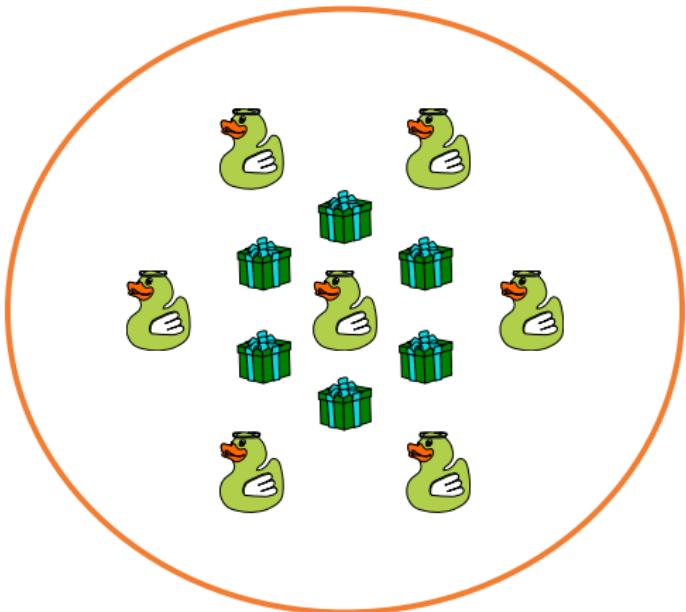
## Spatial structure and altruism



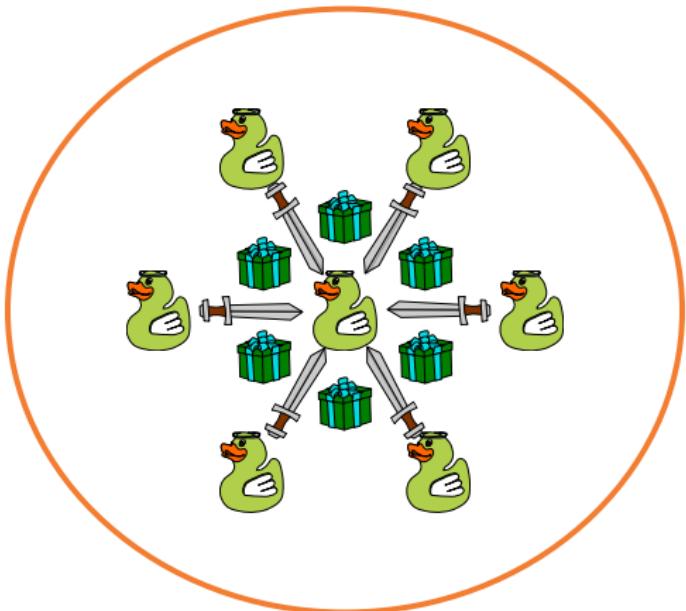
## Spatial structure and altruism



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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

## The choice of life-cycle matters

In homogeneously structured populations,  
with effects of social interactions on **fecundity**:

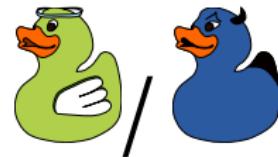
Wright-Fisher



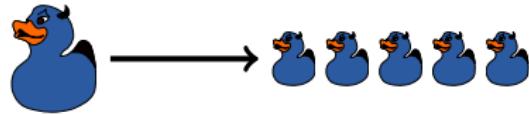
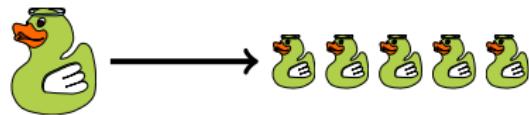
Moran Birth-Death



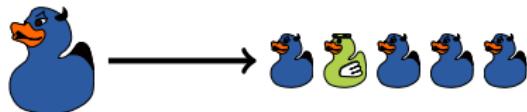
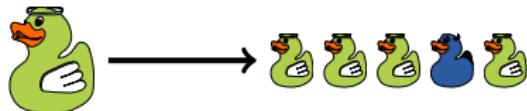
Moran Death-Birth



## A common feature of models



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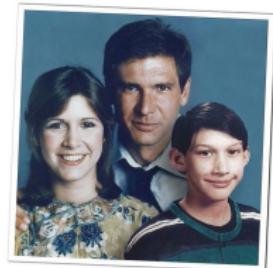


What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

## Fidelity of parent-offspring transmission

### Causes of imperfect strategy transmission

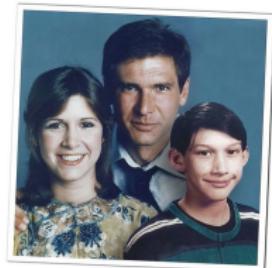
- ▶ Mutation



## Fidelity of parent-offspring transmission

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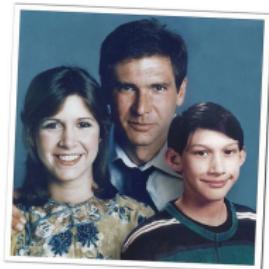
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- ▶ Partial heritability



# Fidelity of parent-offspring transmission

## Causes of imperfect strategy transmission

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



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In the model

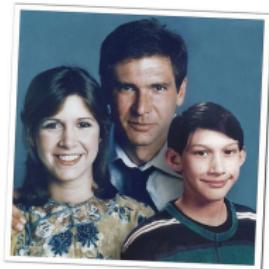
Parent



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In the model

Parent

Offspring

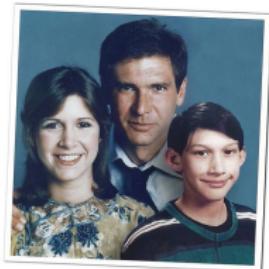


Unmutated

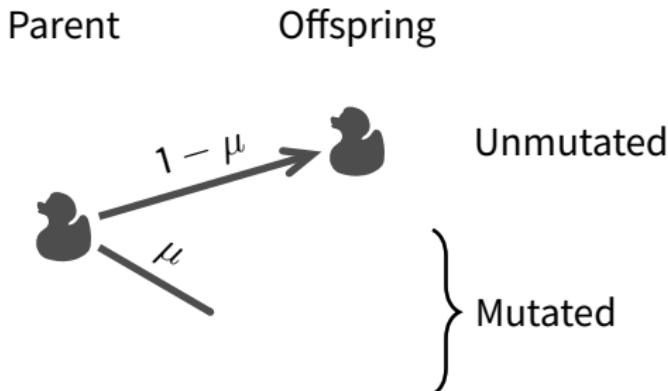
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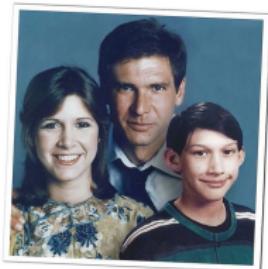
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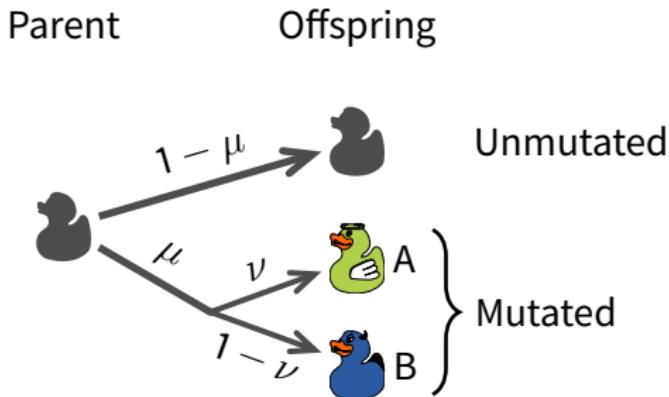
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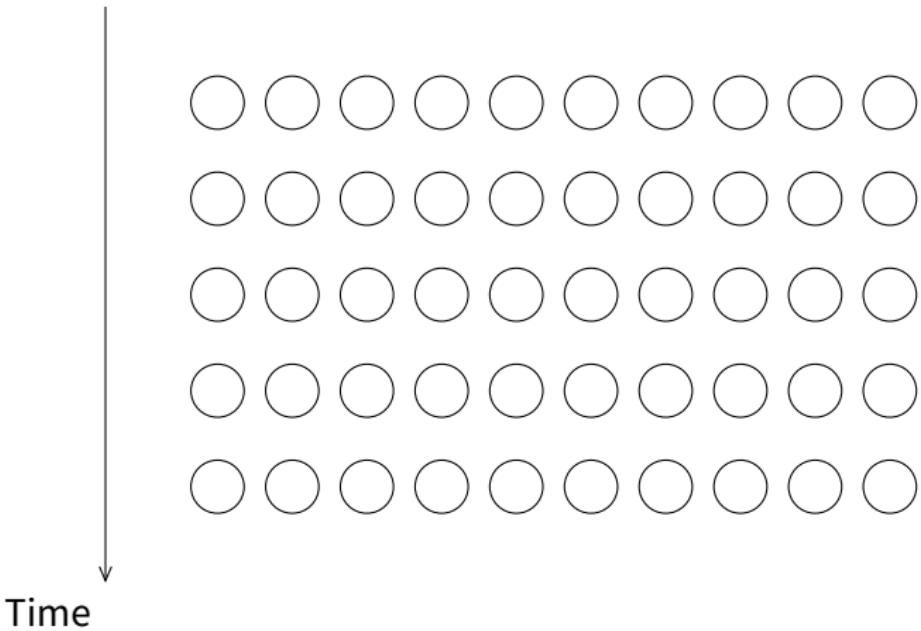
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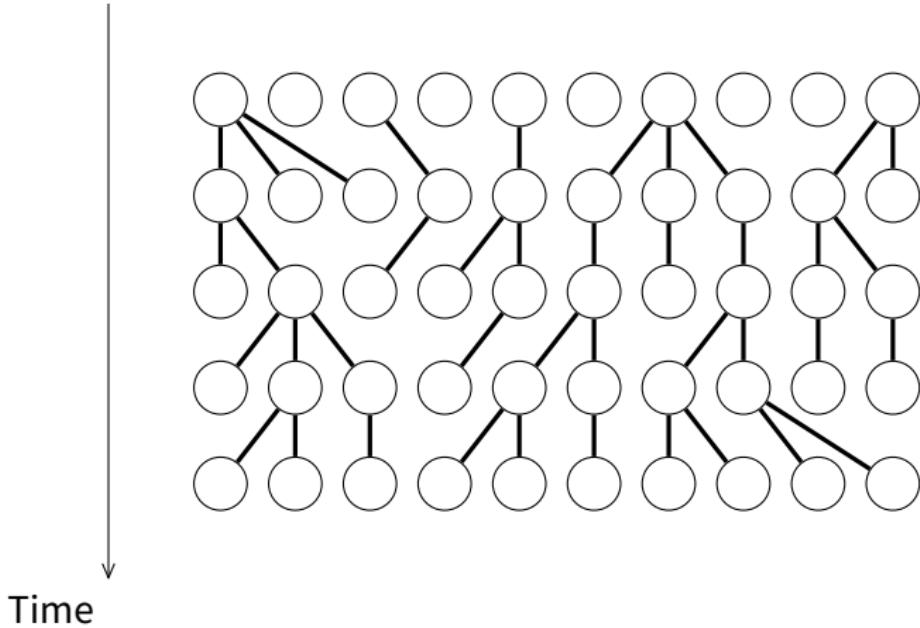
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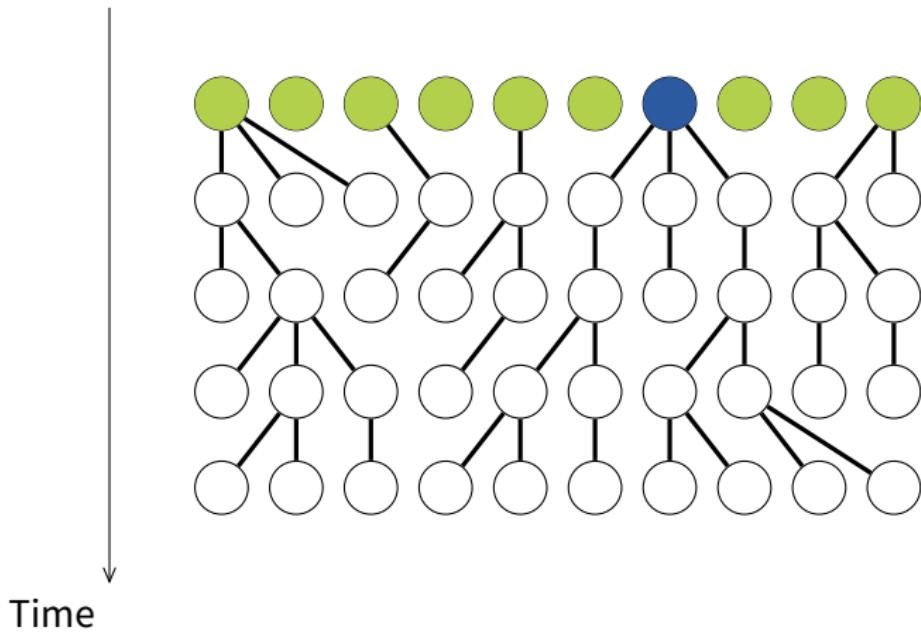
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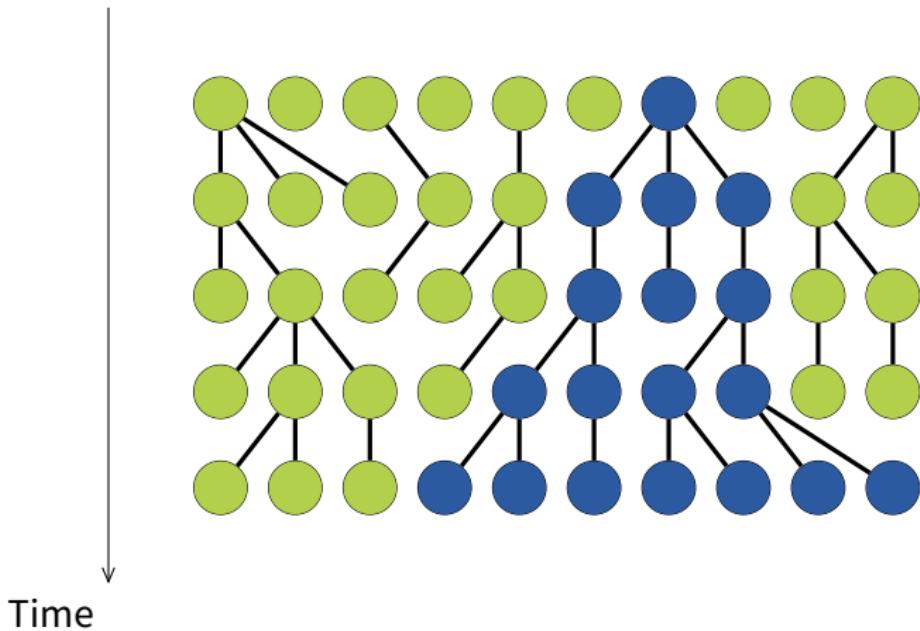
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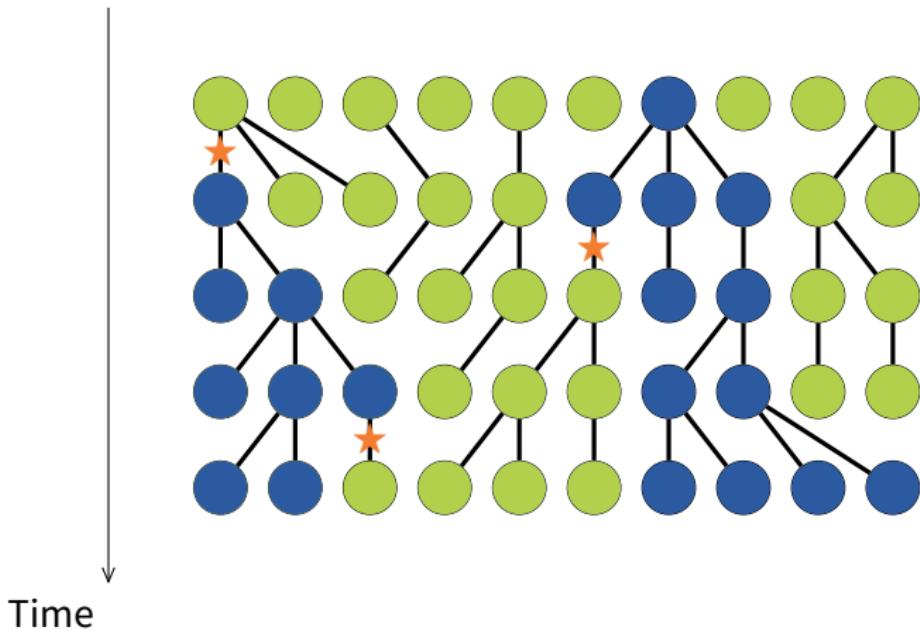
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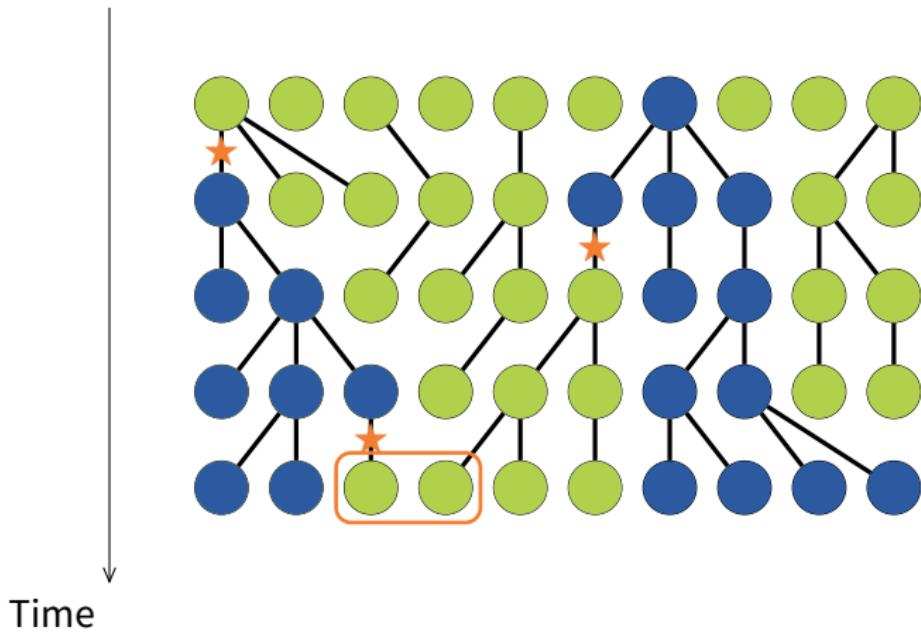
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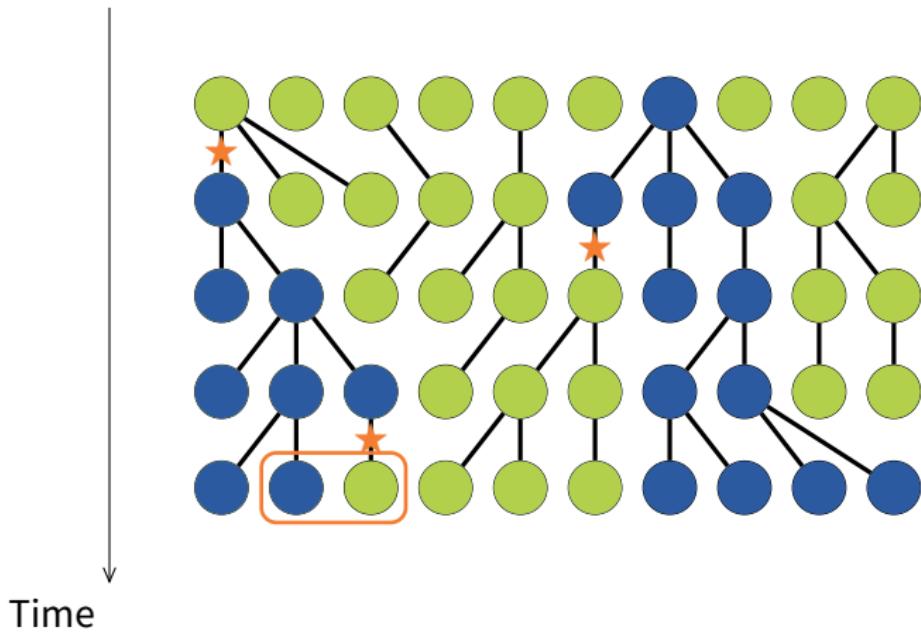
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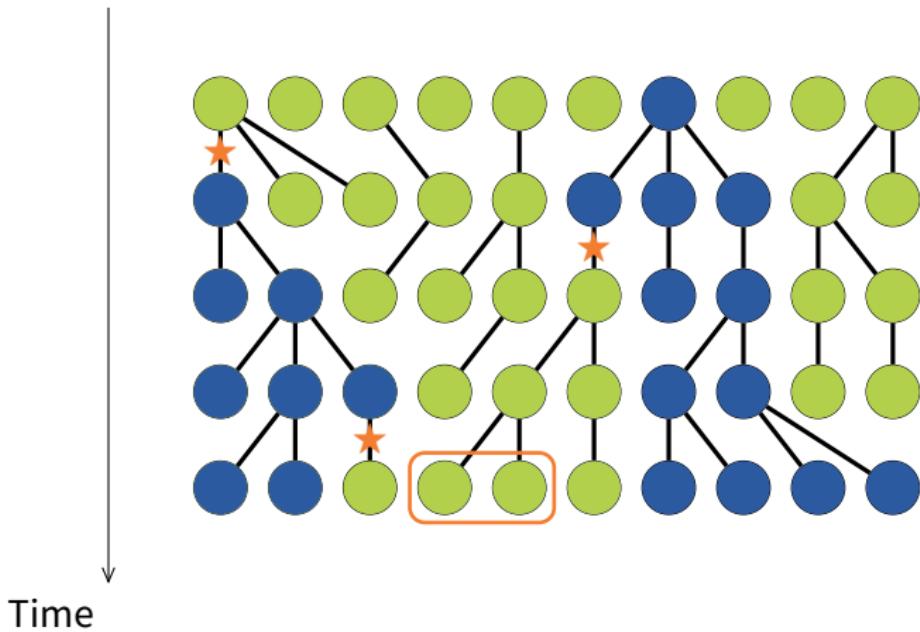
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## Expected state of pairs of sites and identity by descent

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

## Population structures

Population of fixed size  $N$

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Dispersal graph

$$\mathcal{D} = (d_{ij})_{1 \leq i,j \leq N}$$

$$\sum_{i=1}^N d_{ij} = \sum_{j=1}^N d_{ji} = 1.$$

# Population structures

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Interaction graph

$$\mathcal{E} = (e_{ij})_{1 \leq i,j \leq N}$$

(any)

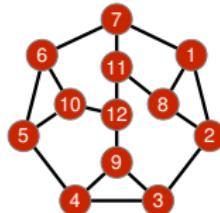
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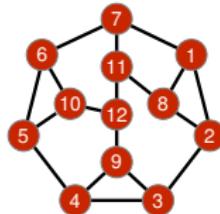
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Evolutionary  
graph theory

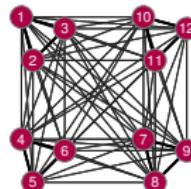
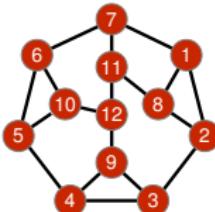
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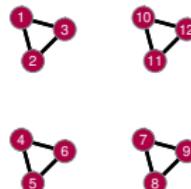
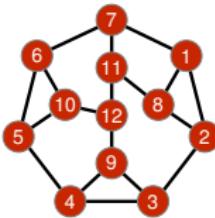
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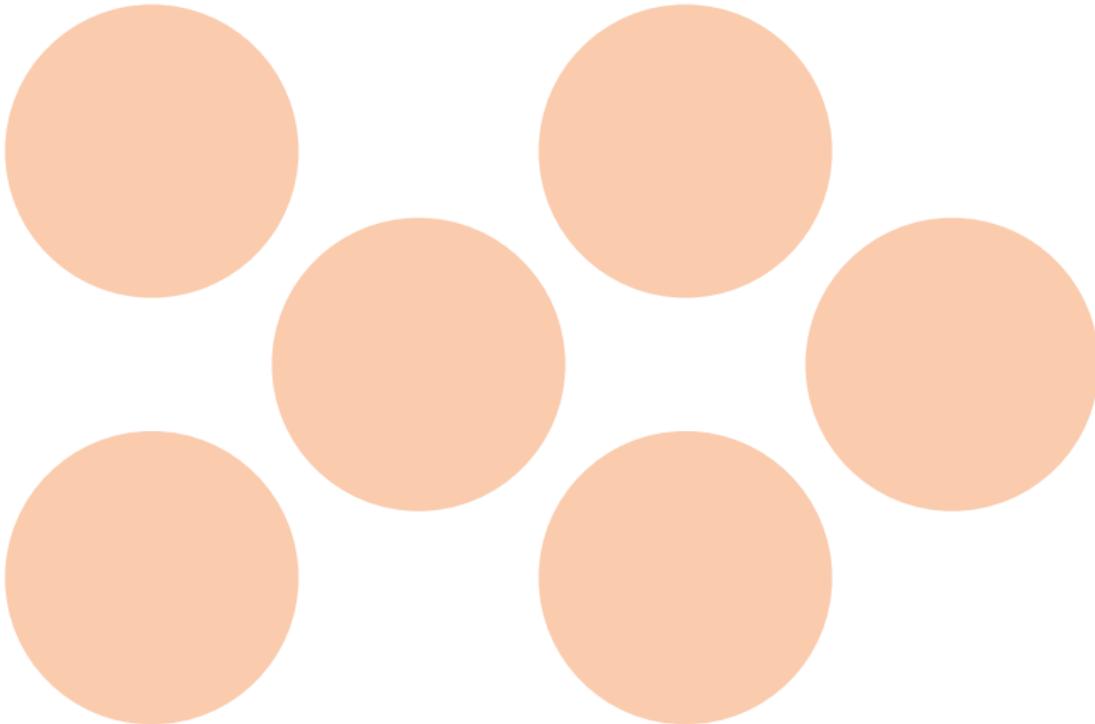


Evolutionary  
graph theory

Subdivided  
populations

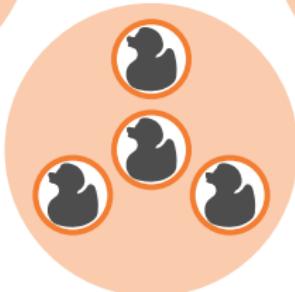
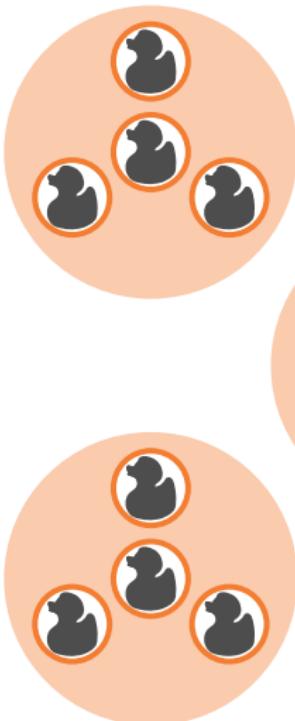
## Subdivided population – Island model

$N_d$  demes



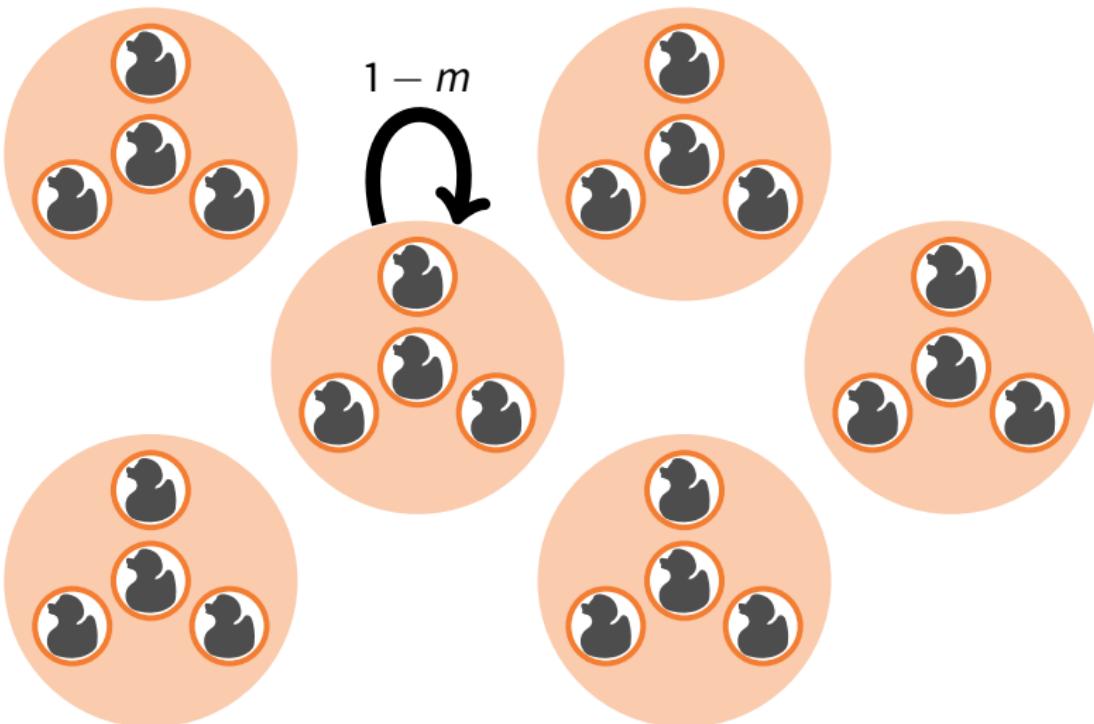
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$N_d$  demes of  $n$  individuals each (total population size  $N = n N_d$ )



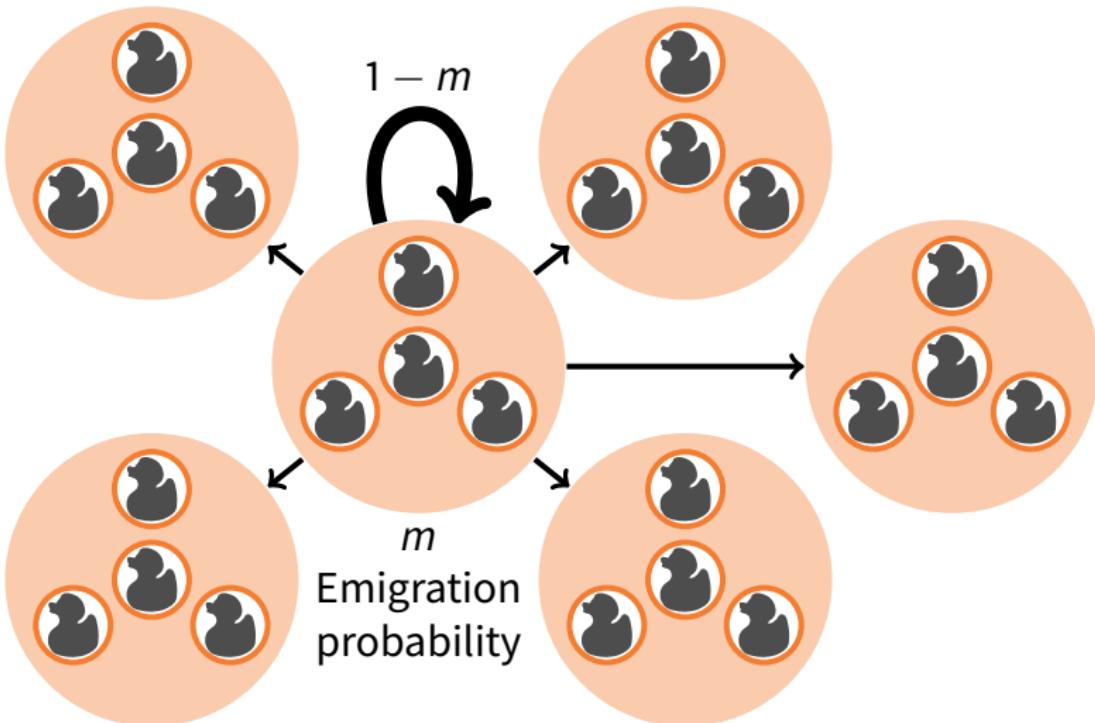
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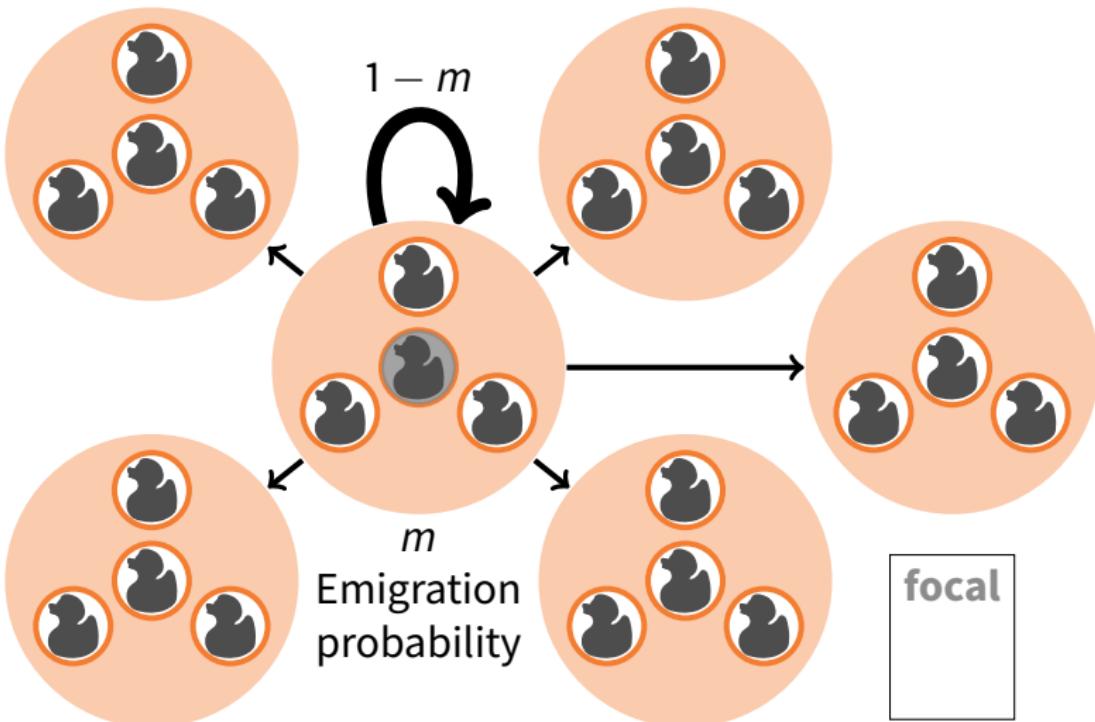
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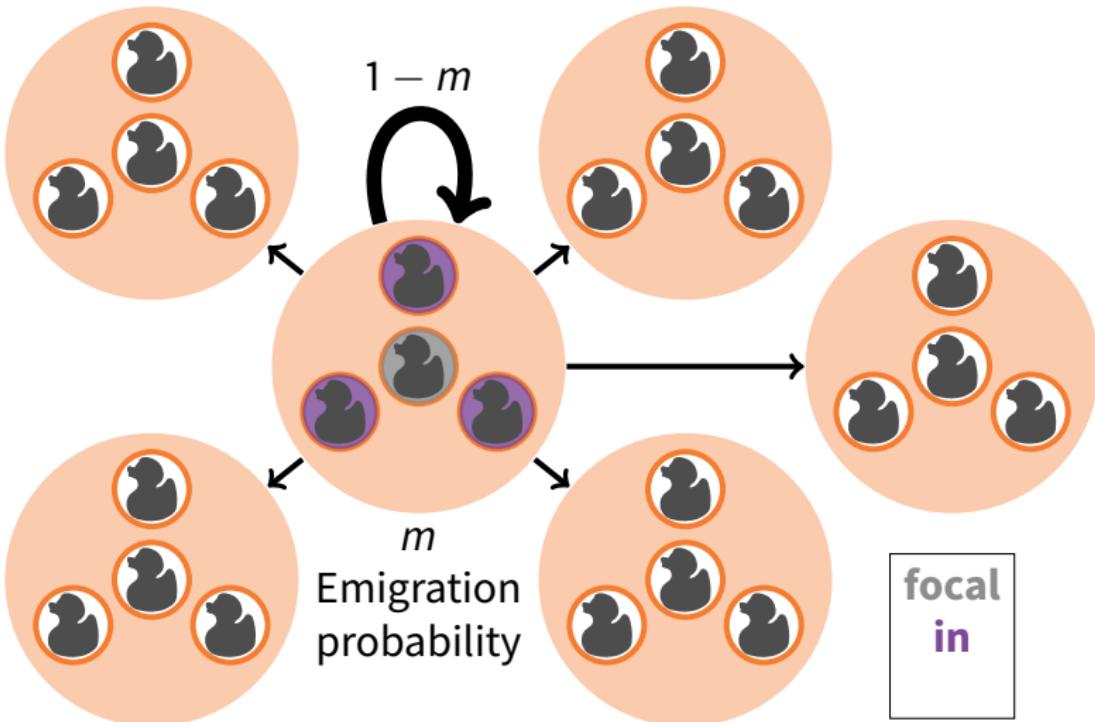
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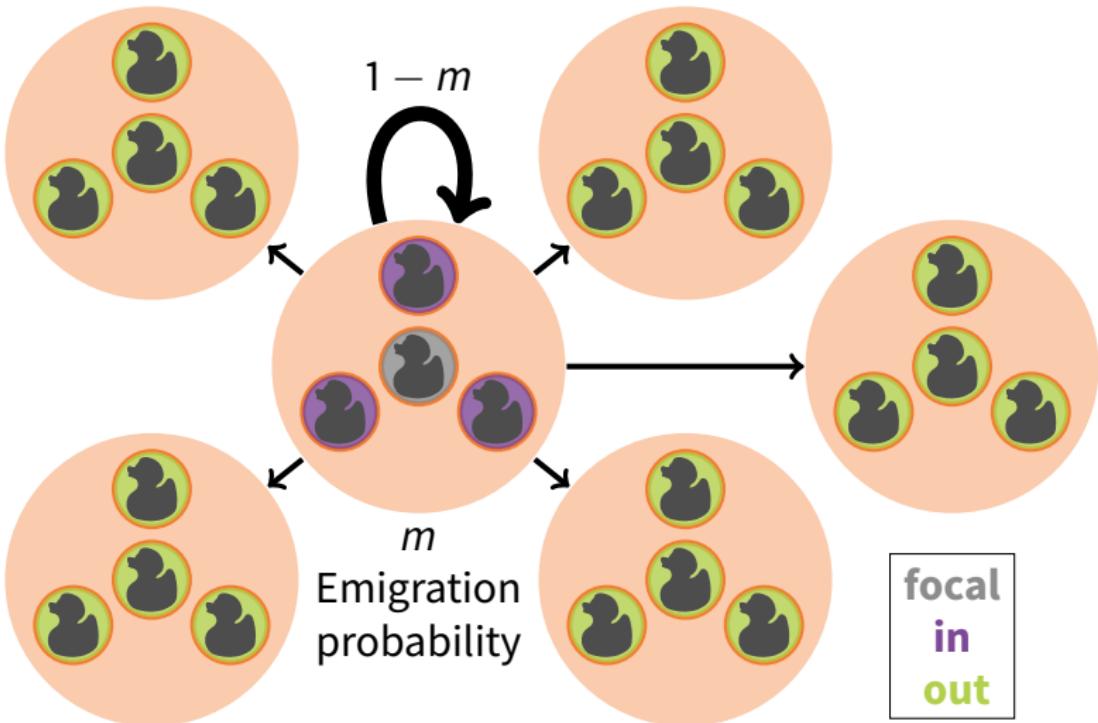
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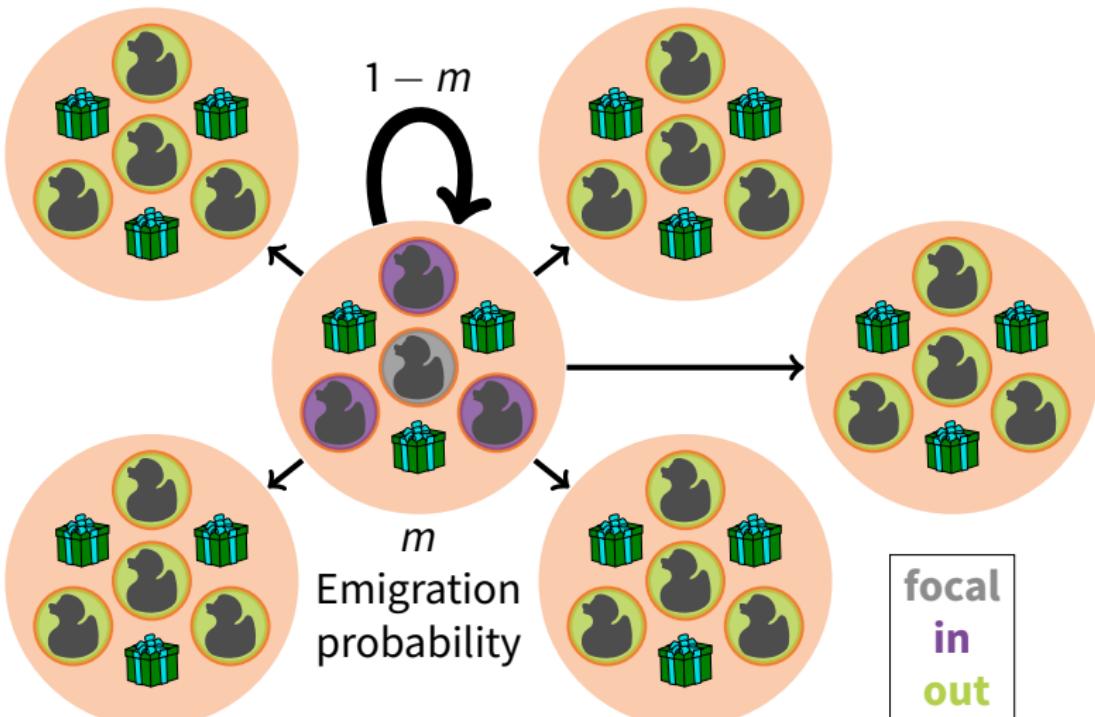
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## Updating the population

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

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

## Updating the population

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

$$\# \text{[Grave]} = \# \text{[Pram]}$$

$$N \text{ [Grave]} = N \text{ [Pram]}$$

$$\vdots \\ k \text{ [Grave]} = k \text{ [Pram]}$$

$$\vdots \\ 1 \text{ [Grave]} = 1 \text{ [Pram]}$$

## Updating the population

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

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

Wright-Fisher

$$N \text{ [Grave]} = N \text{ [Baby Stroller]}$$

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Moran process

## Updating the population

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

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

Life-cycle

Wright-Fisher

$$N \text{ [Gravestone]} = N \text{ [Stroller]}$$

Offspring production

$$k \text{ [Gravestone]} = k \text{ [Stroller]}$$

$$1 \text{ [Gravestone]} = 1 \text{ [Stroller]}$$

Moran process

## Updating the population

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

$$\# \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} = \# \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array}$$

Life-cycle

$$N \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} = N \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array}$$

Offspring production

$$k \begin{array}{c} \vdots \\ \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} \end{array} = k \begin{array}{c} \vdots \\ \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} \end{array}$$



Offspring dispersal

$$1 \begin{array}{c} \vdots \\ \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} \end{array} = 1 \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array}$$

Moran process

## Updating the population

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

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Life-cycle

$$N \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array} = N \begin{array}{|c|} \hline \text{RIP} \\ \hline \end{array}$$

Offspring production

$$k \begin{array}{|c|} \hline \vdots \\ \hline \text{RIP} \\ \hline \end{array} = k \begin{array}{|c|} \hline \vdots \\ \hline \text{RIP} \\ \hline \end{array}$$



Offspring dispersal

$$1 \begin{array}{|c|} \hline \vdots \\ \hline \text{RIP} \\ \hline \end{array} = 1 \begin{array}{|c|} \hline \vdots \\ \hline \text{RIP} \\ \hline \end{array}$$

$k$  parents die

Moran process

## Updating the population

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

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

Life-cycle

Wright-Fisher

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

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

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Moran process

Offspring production

Establishment of  
 $k$  offspring

Offspring dispersal

$k$  parents die

## Updating the population

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

$$\# \text{[Grave]} = \# \text{[Stroller]}$$

Life-cycle  
“Death-Birth” updating

Wright-Fisher

$$N \text{ [Grave]} = N \text{ [Stroller]}$$

$$k \text{ [Grave]} = k \text{ [Stroller]}$$

$$1 \text{ [Grave]} = 1 \text{ [Stroller]}$$

Moran process

Offspring production

Establishment of  
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$k$  parents die

## Population

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

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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  $k$  :

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

$$f_{\text{blue}} = 1 + \delta \left( b \frac{k}{n-1} \right).$$



# Social interactions

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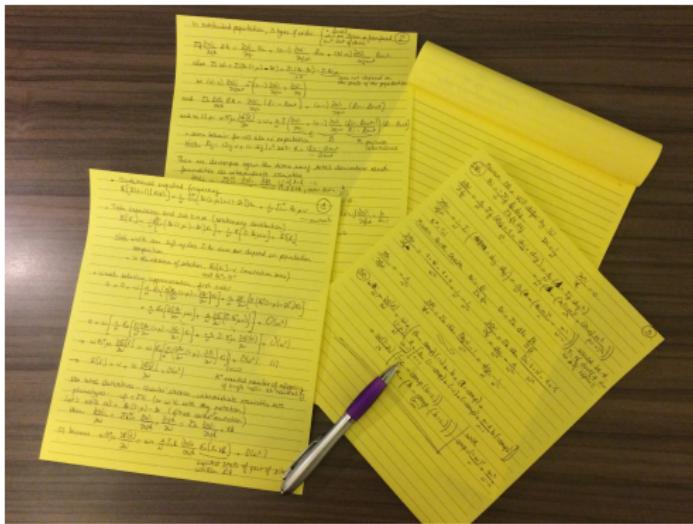
$$f_{\text{blue}} = 1 + \delta \left( b \frac{k}{n-1} \right).$$



Selection is weak

$$\delta \ll 1.$$

## “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

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

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium      Selection  
strength

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## Expected frequency of altruists in the population

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

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

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

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$\mathcal{B}$

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$R$

$\mathcal{B}$

## Expected frequency of altruists in the population

Mutation-drift  
equilibrium

Selection  
strength

Population variance  
Variance in the state of one site

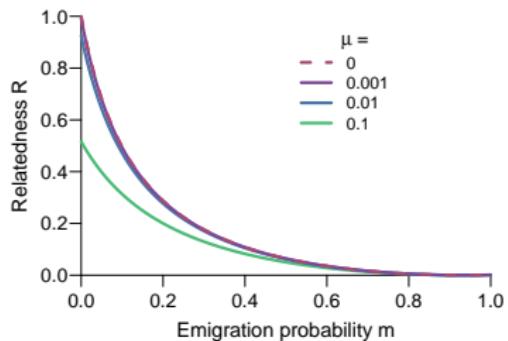
$$\mathbb{E}[\bar{X}] = \nu + \delta \nu(1 - \nu) \frac{1 - \mu}{\mu} (1 - Q_{\text{out}}) \times$$
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$R$        $B$

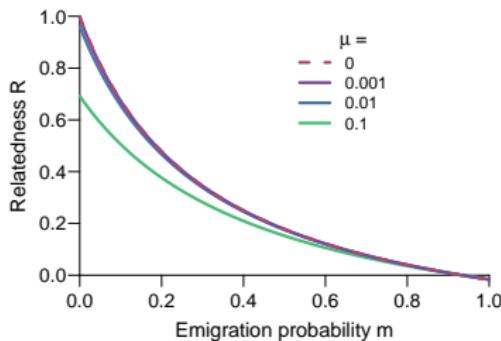
How does relatedness  $R$  change with the emigration probability  $m$ ?

# How does relatedness $R$ change with the emigration probability $m$ ?

Wright-Fisher ( $N$  deaths)



Moran (1 death)



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

## Expected frequency of altruists in the population

Mutation-drift  
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Population variance  
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$R$

$B$

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$\mathcal{B}$

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$R$  ↘

$\mathcal{B}$  ↗

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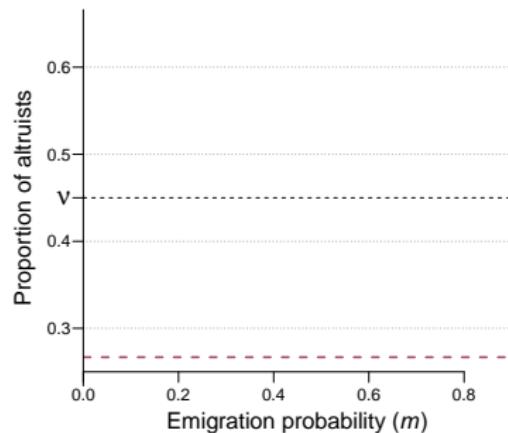
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$R$

$\mathcal{B}$

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

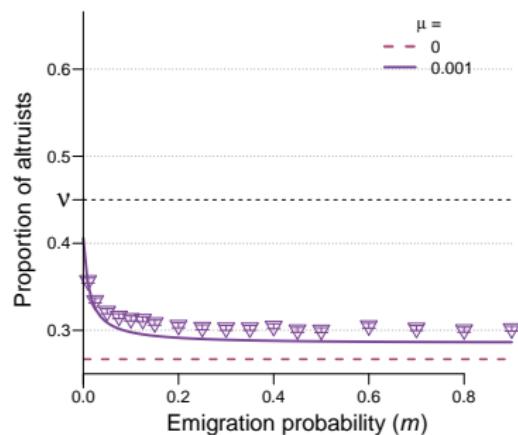
Wright-Fisher ( $N$  deaths &  $N$  births)



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

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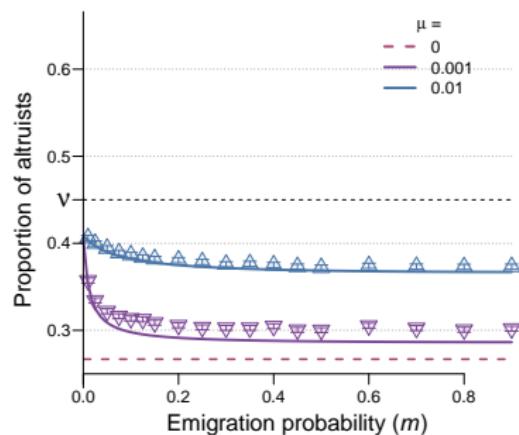
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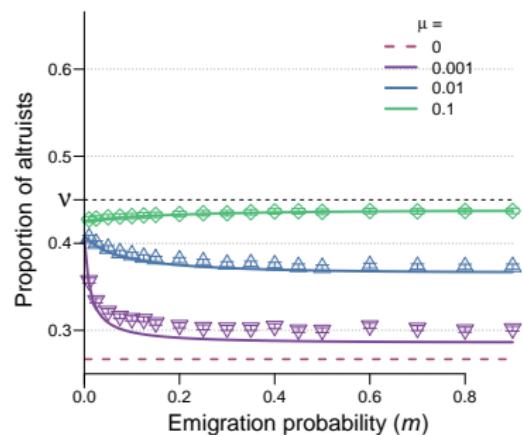
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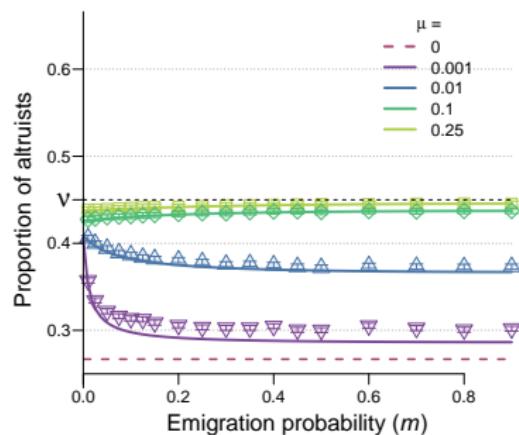
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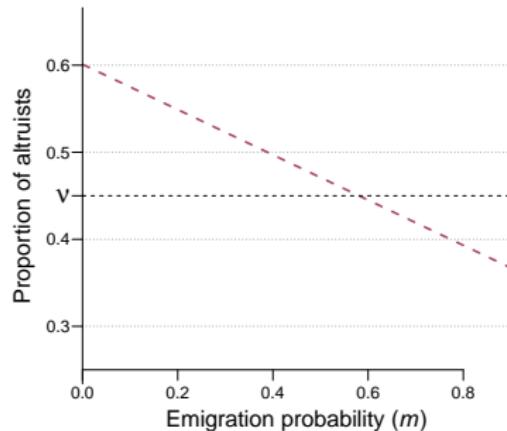
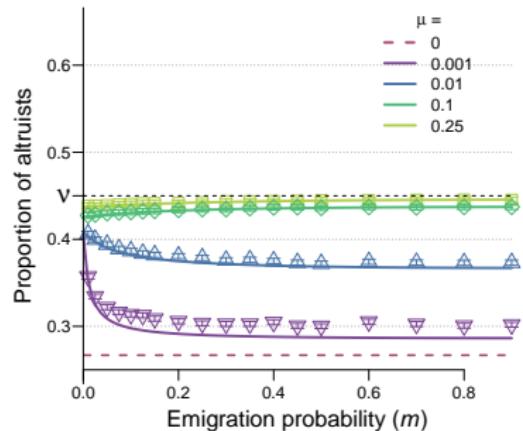
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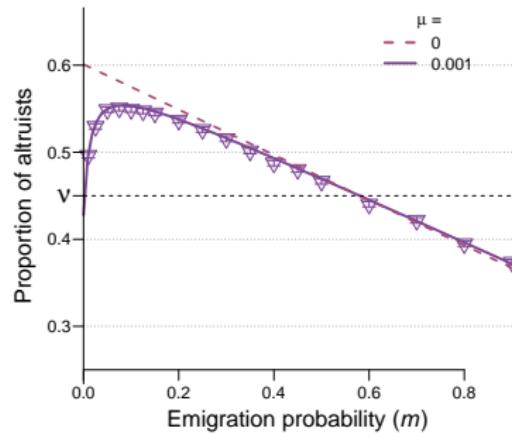
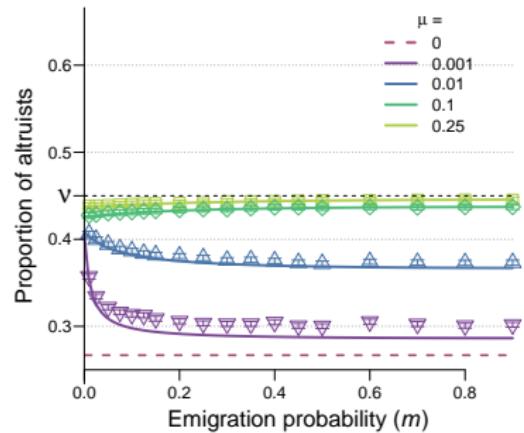
Wright-Fisher ( $N$  deaths &  $N$  births) Moran Death-Birth (1 death & 1 birth)



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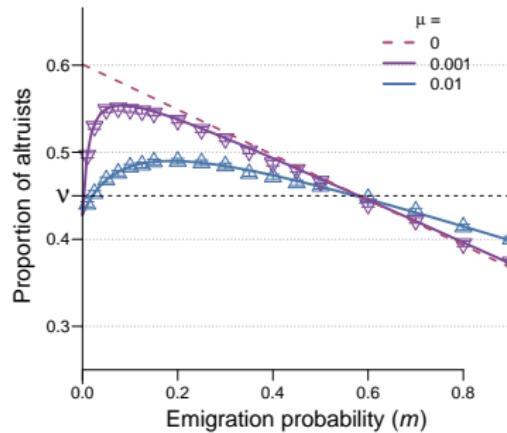
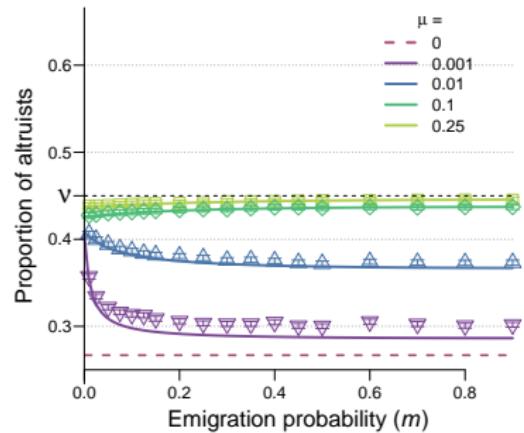
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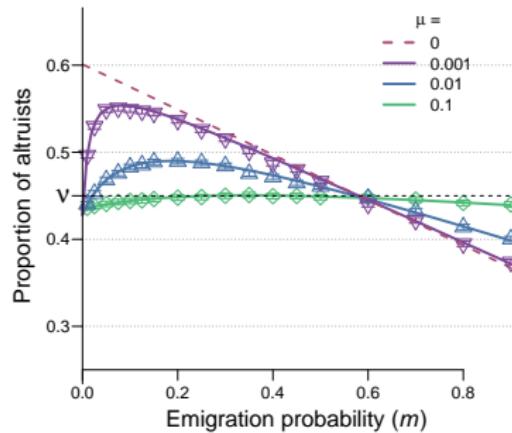
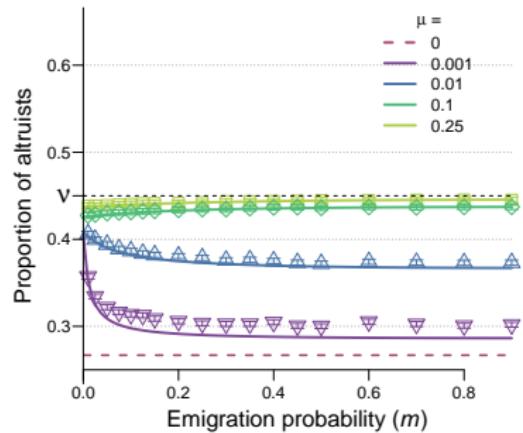
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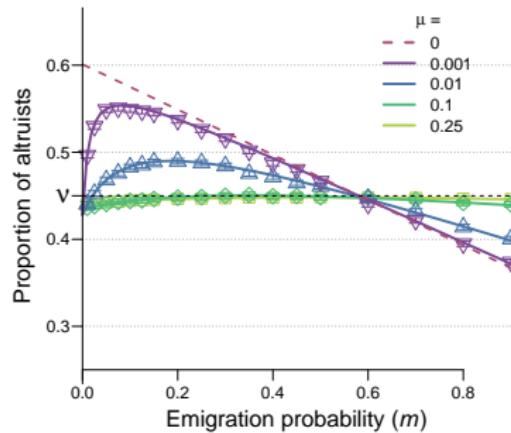
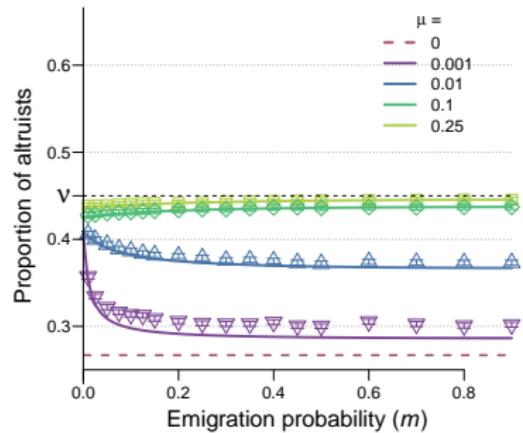
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Is the result robust?

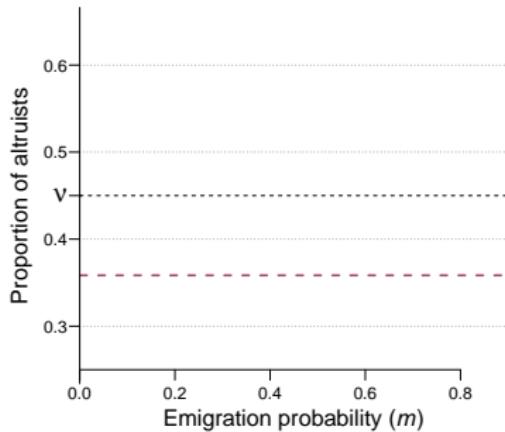
## Another life-cycle

Moran Birth-Death (1 birth & 1 death)

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

## Another life-cycle

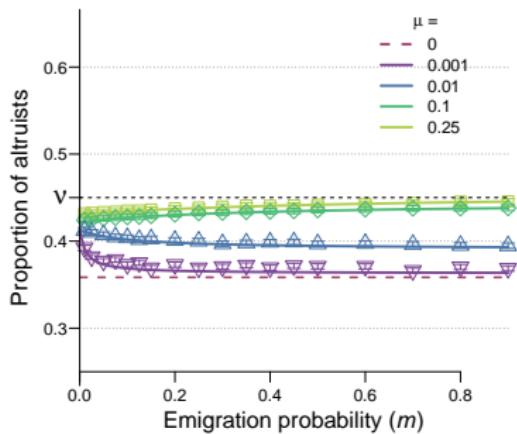
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## Another life-cycle

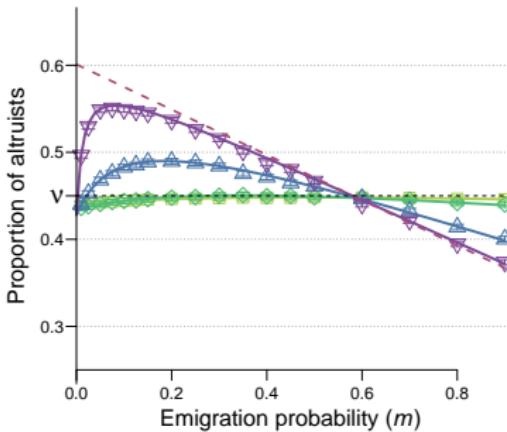
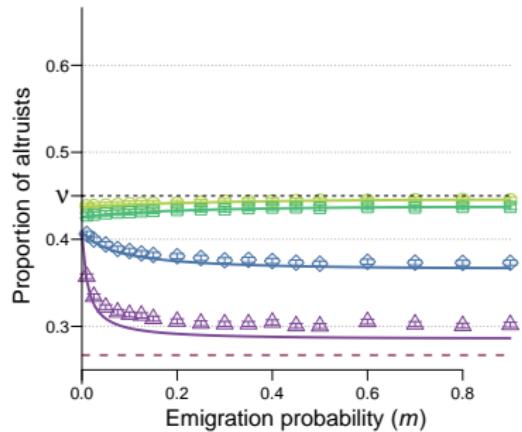
### Moran Birth-Death (1 birth & 1 death)



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

## Strong selection

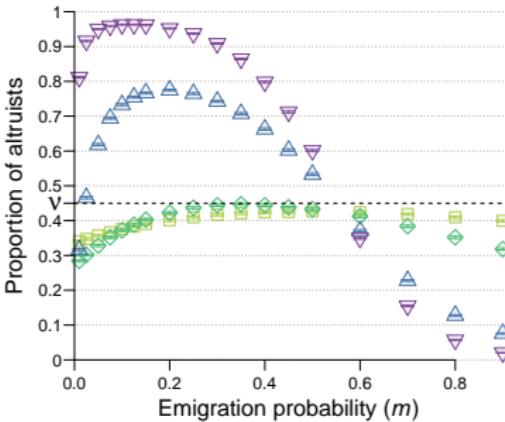
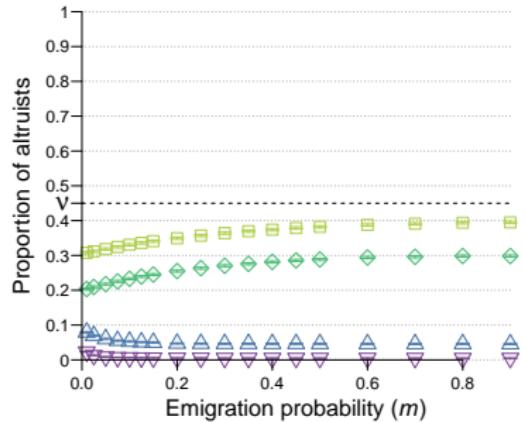
Wright-Fisher, weak selection Moran Death-Birth, weak selection



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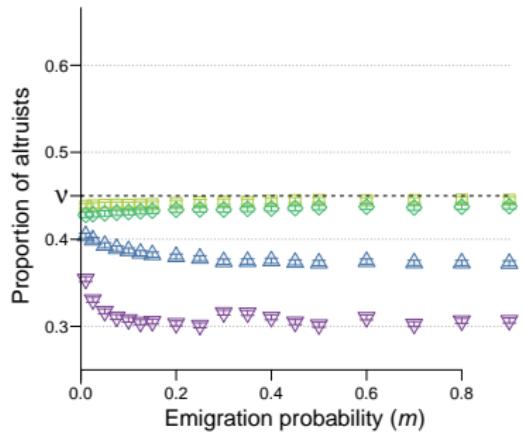
Wright-Fisher, strong selection | Moran Death-Birth, strong selection



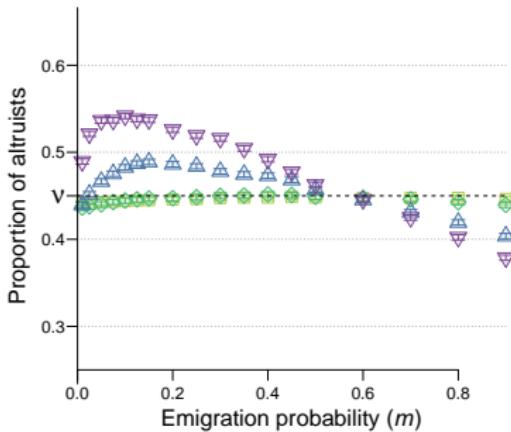
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.1)$$

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

Wright-Fisher



Moran Death-Birth



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

From theory to reality...

## 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)

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## Funding & Thanks



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

and thank you  
your attention