

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

F. Débarre



@flodebarre

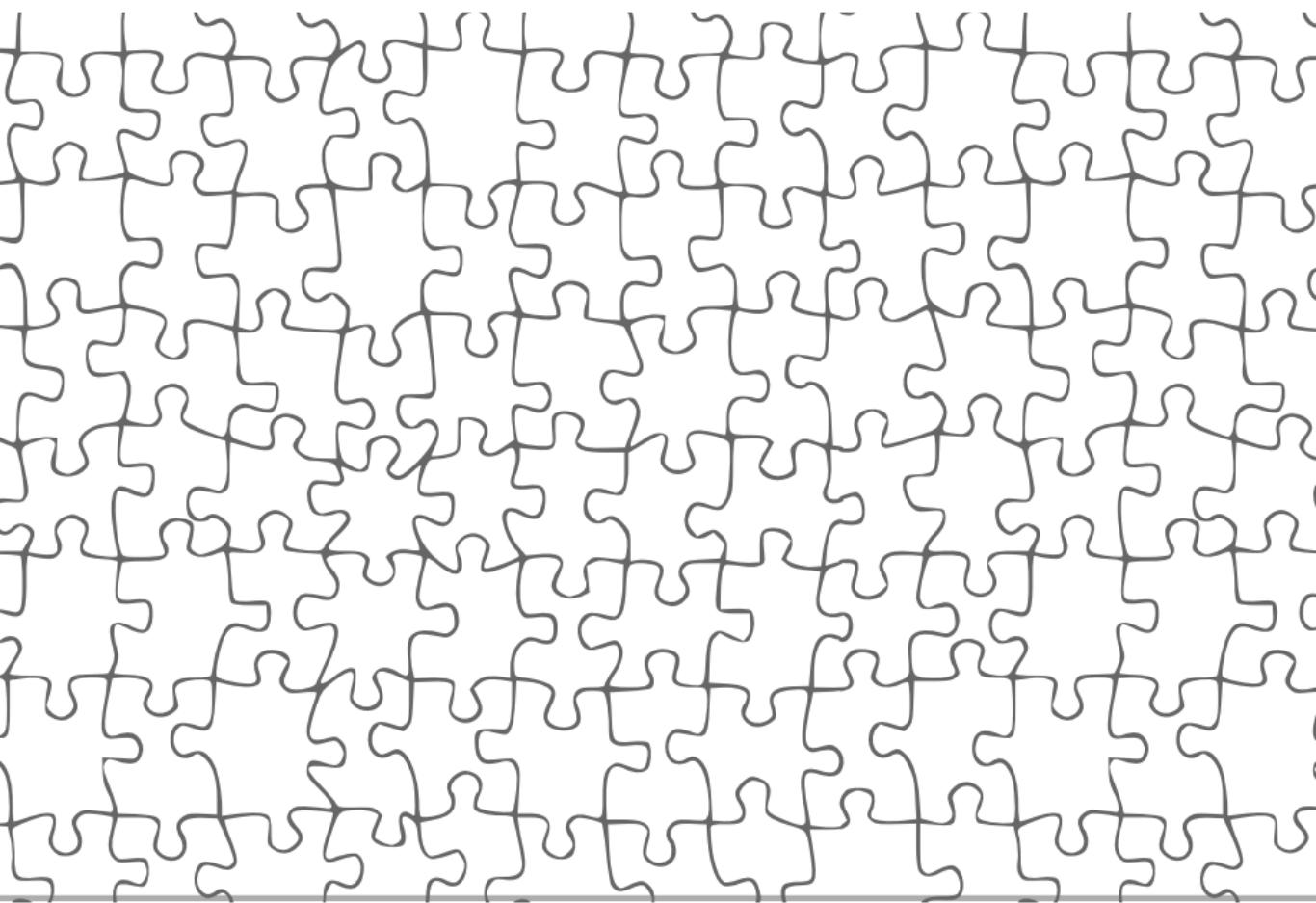
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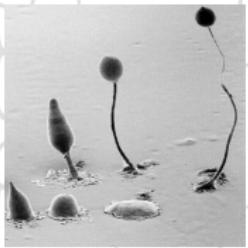
Thematic semester on
Cimi
Centro International de Matemáticas e Informática
TOULOUSE

**Mathematics Computer
science and biology**

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







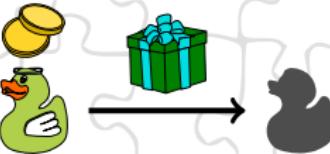
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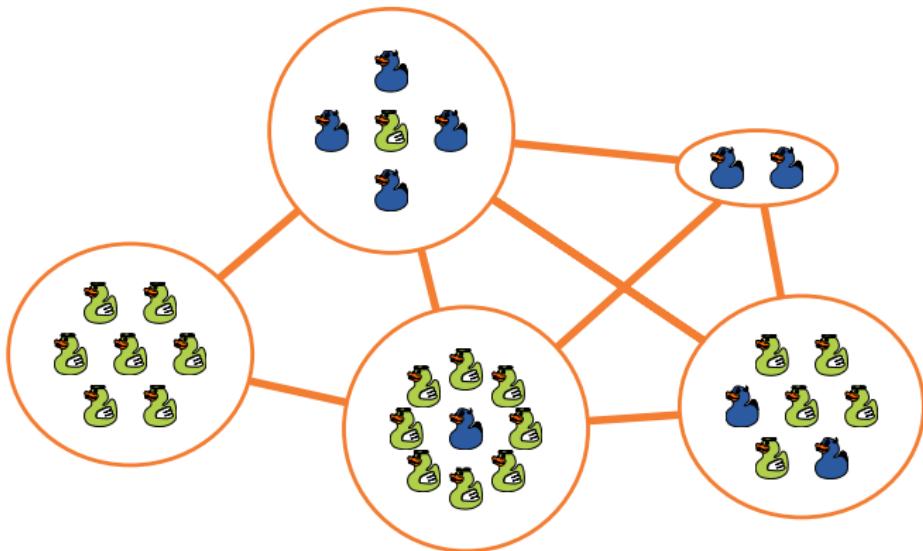
(c) FD



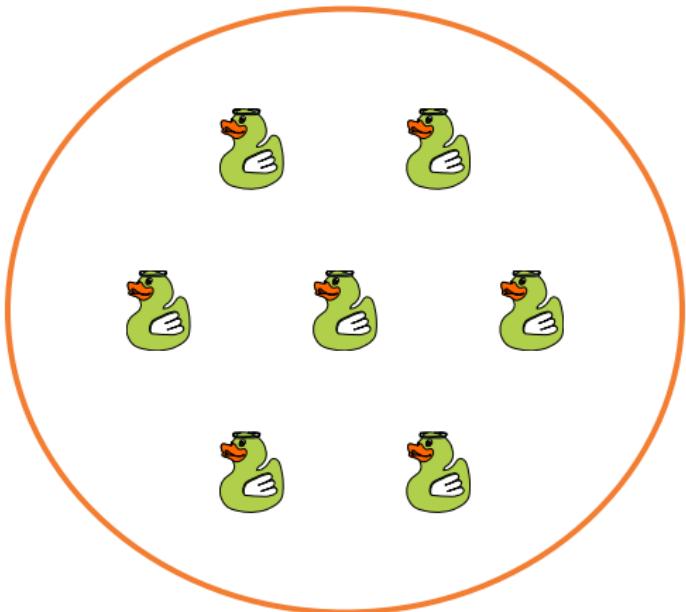
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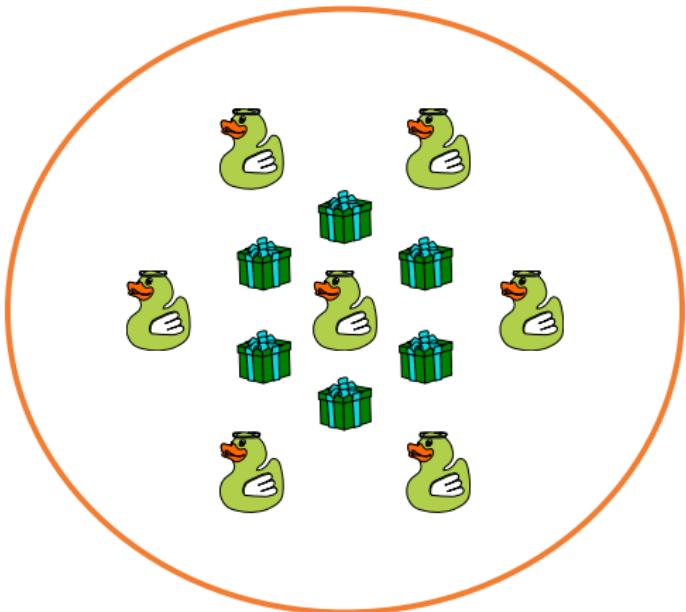
Spatial structure and altruism



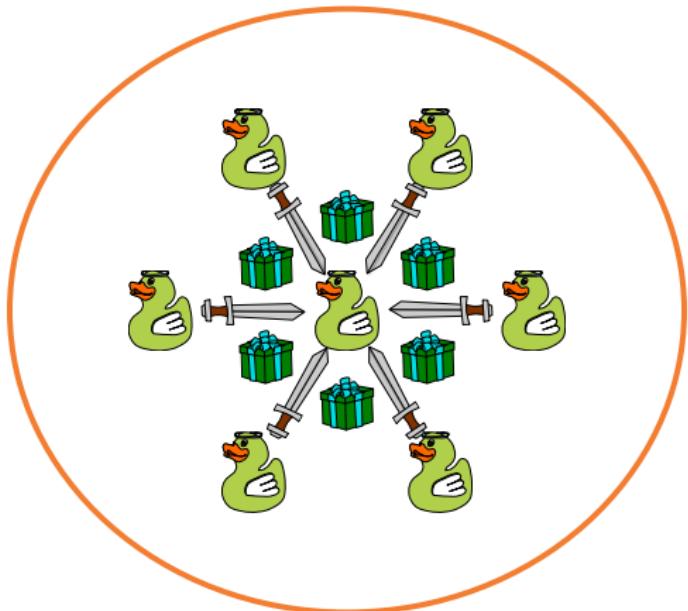
Spatial structure and altruism



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

The choice of life-cycle matters

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

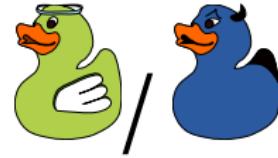
Wright-Fisher



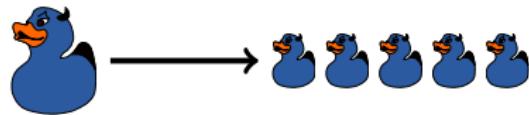
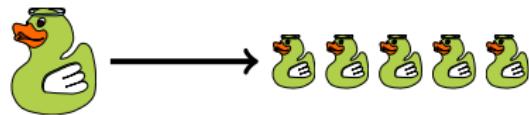
Moran Birth-Death



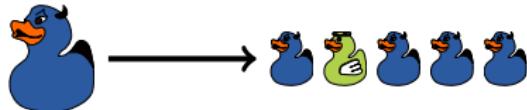
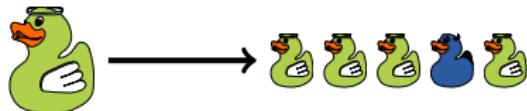
Moran Death-Birth



A common feature of models



A common feature of models

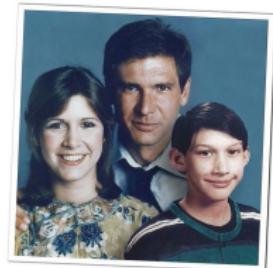


What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

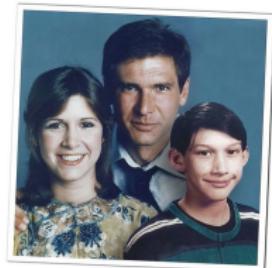
- ▶ Mutation



Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

- ▶ Mutation
- ▶ Partial heritability



Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

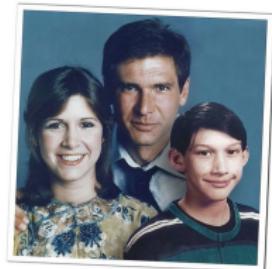
- ▶ Mutation
- ▶ Partial heritability
- ▶ Cultural transmission (vertical)



Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

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In the model

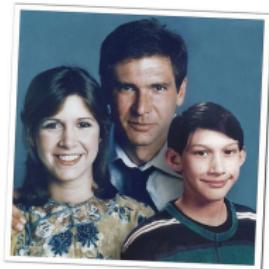
Parent



Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

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In the model

Parent

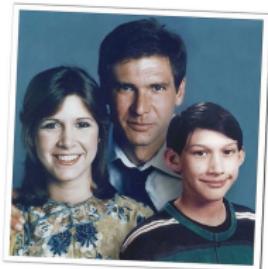
Offspring



Fidelity of parent-offspring transmission

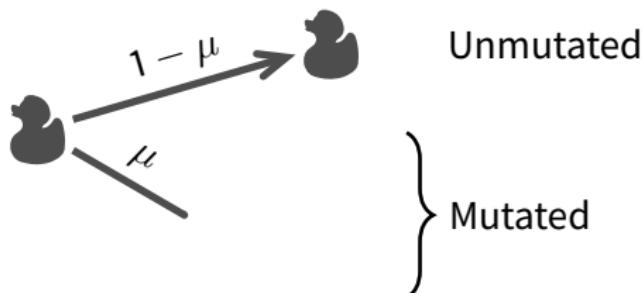
Causes of imperfect strategy transmission

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In the model

Parent Offspring



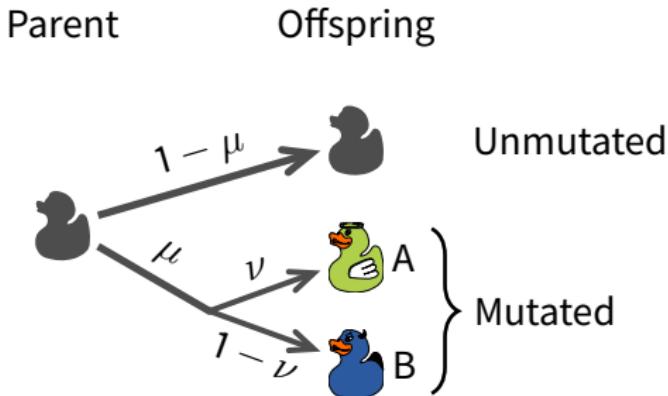
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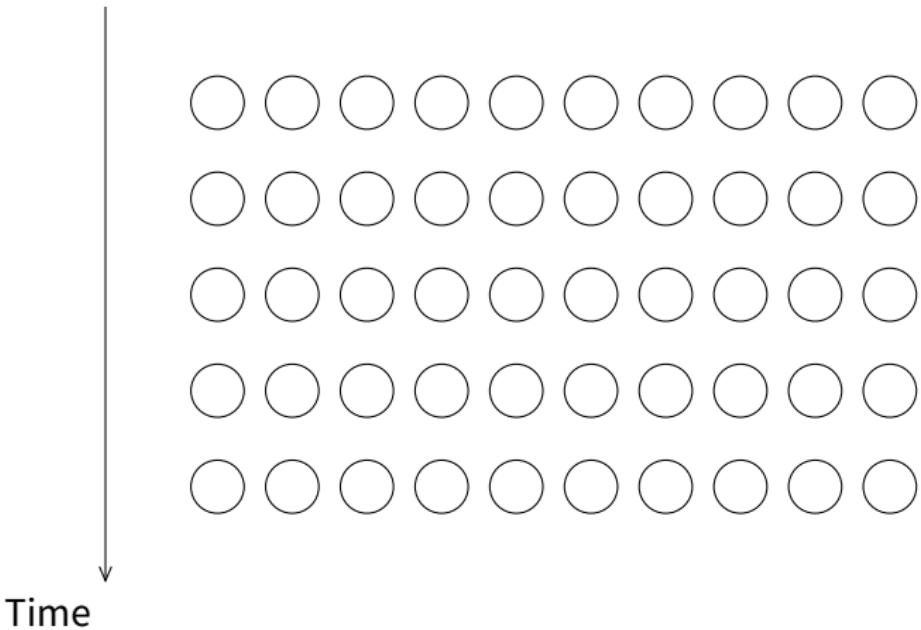
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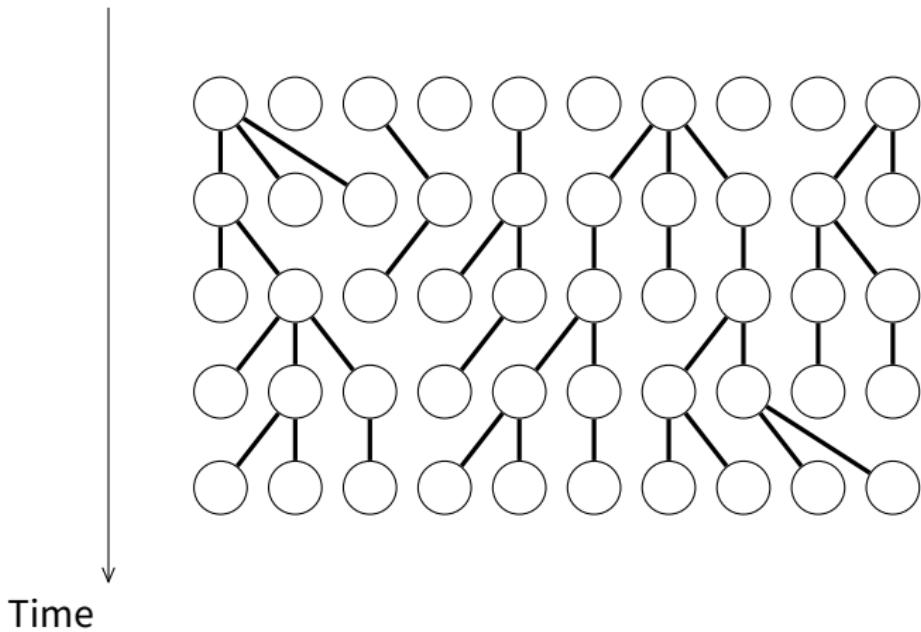
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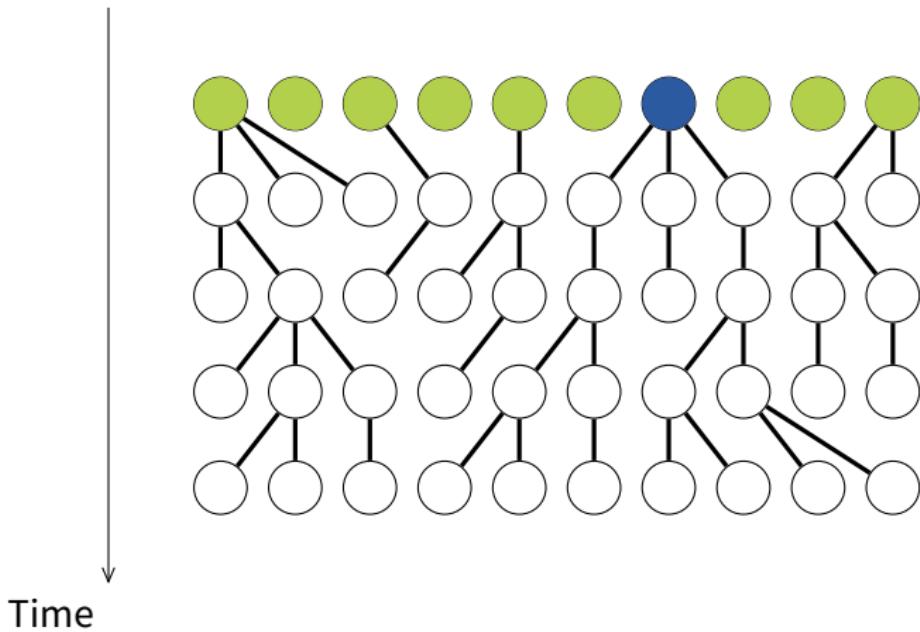
Genealogy, Identity by descent and Identity in state



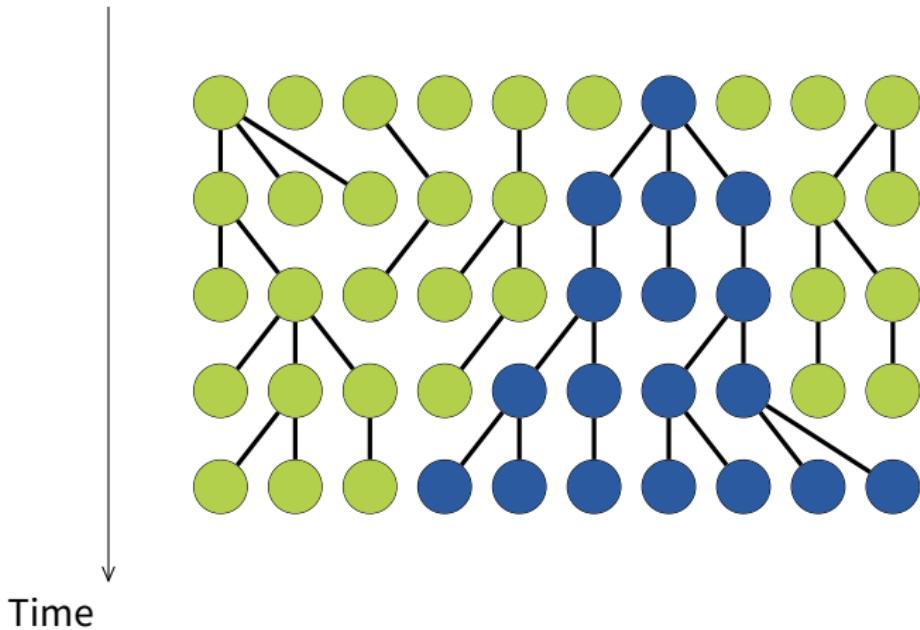
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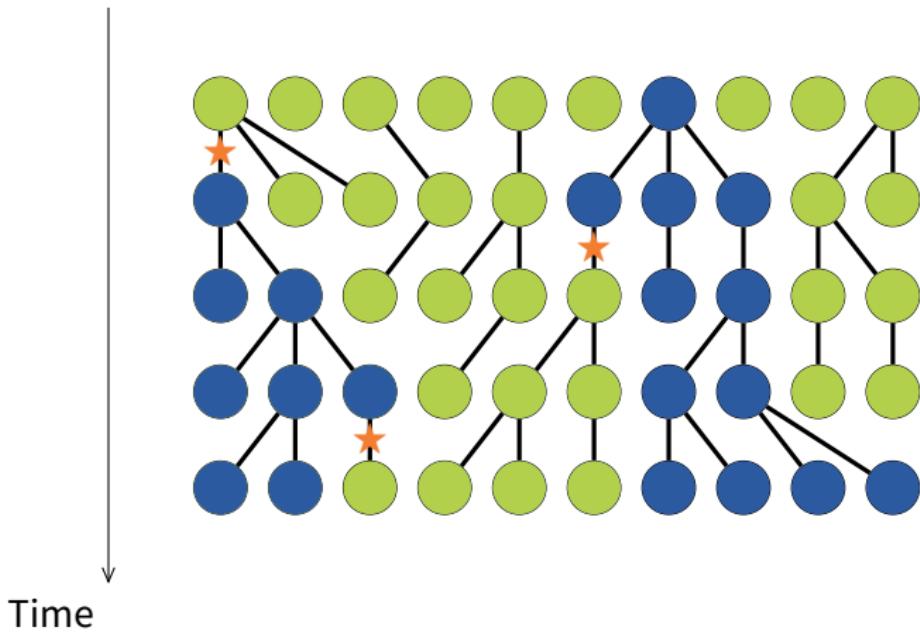
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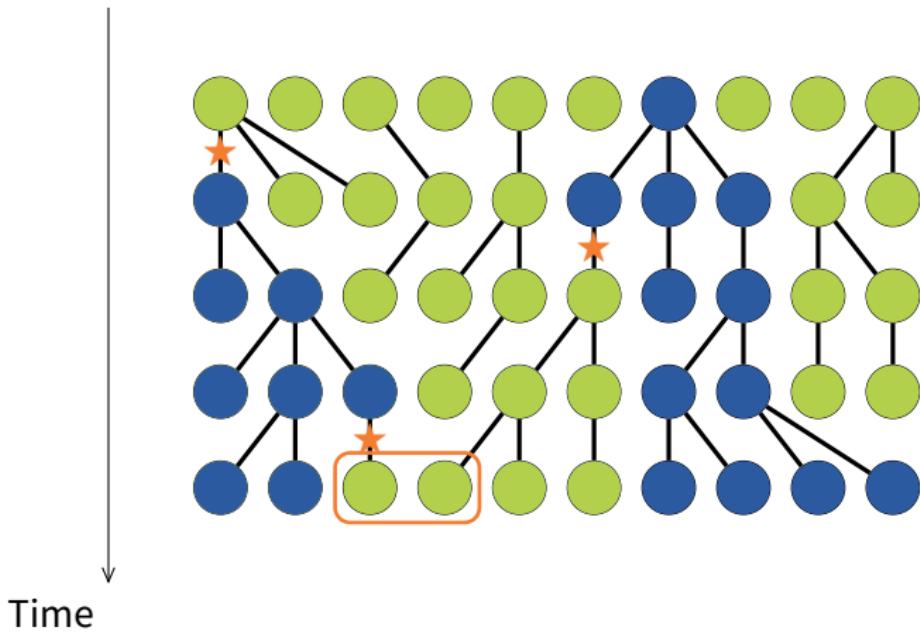
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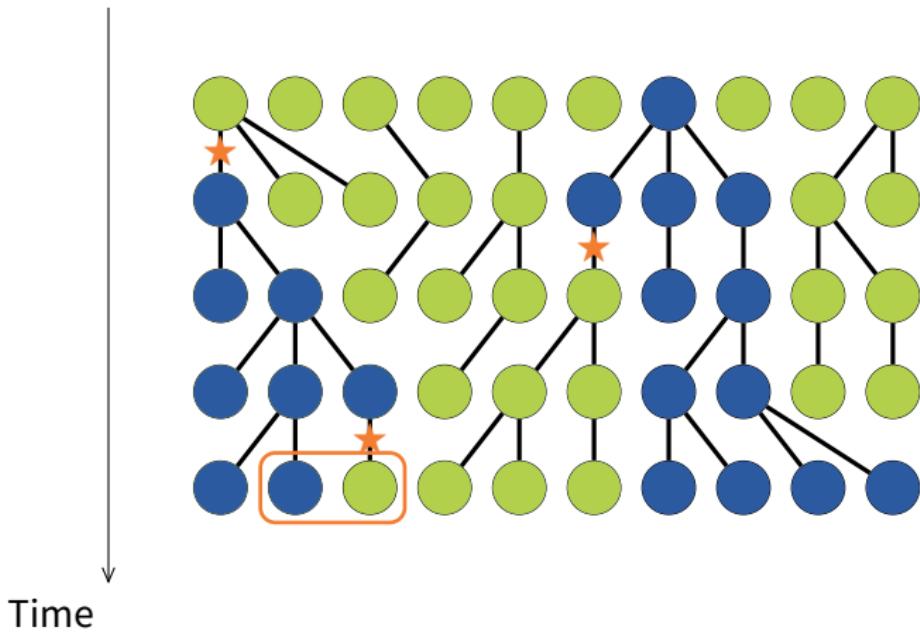
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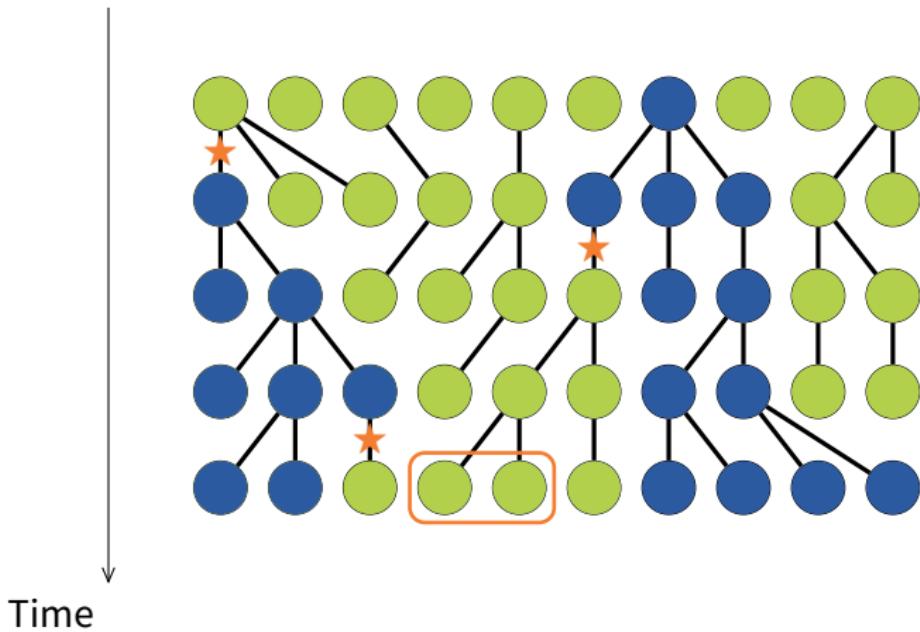
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Genealogy, Identity by descent and Identity in state



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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= Probability that the two
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$$P_{ij} = Q_{ij} \nu$$

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

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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

Population structures

Population of fixed size N

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

Population of fixed size N

Dispersal graph

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Interaction graph

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

(any)

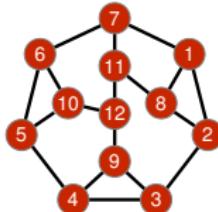
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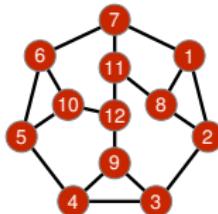
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Evolutionary
graph theory

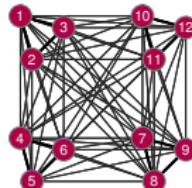
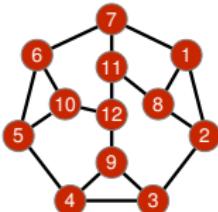
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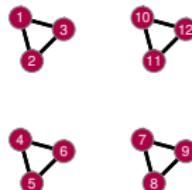
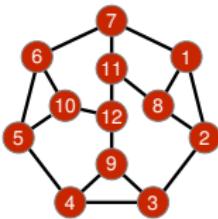
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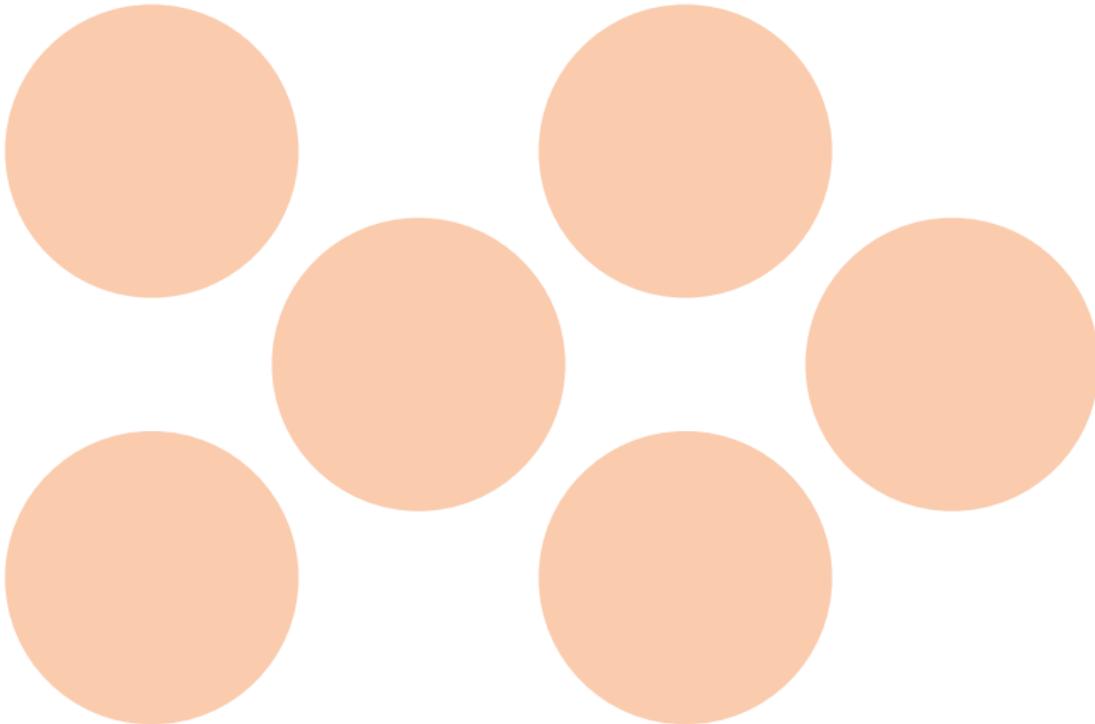


Evolutionary
graph theory

Subdivided
populations

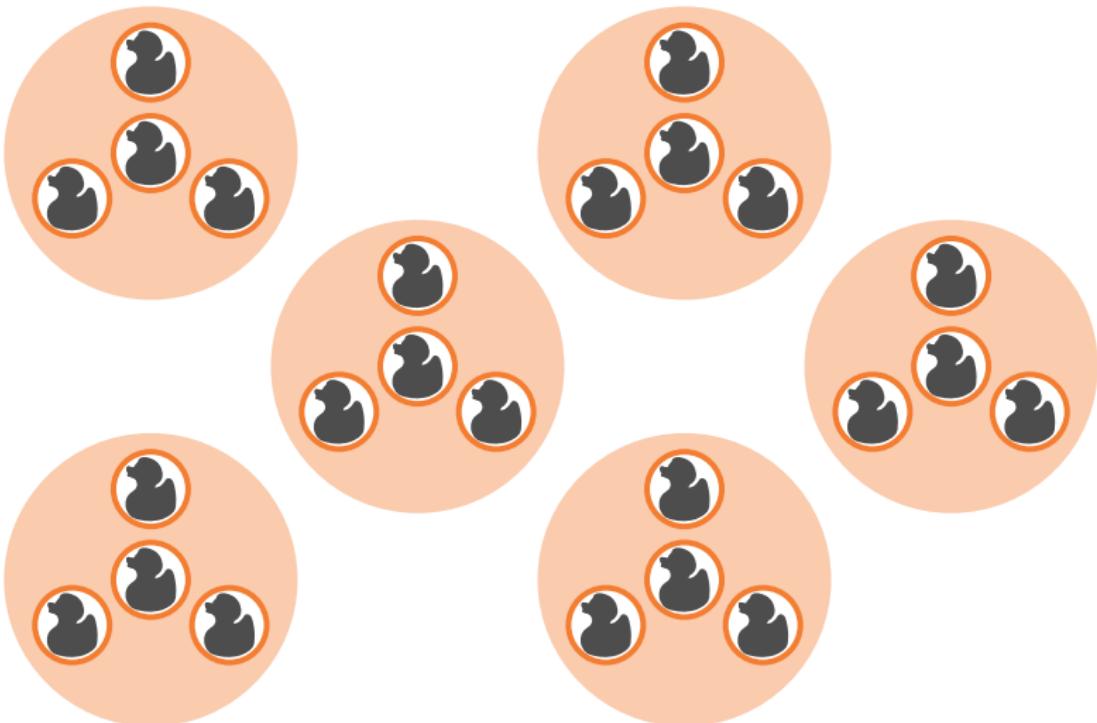
Subdivided population – Island model

N_d demes



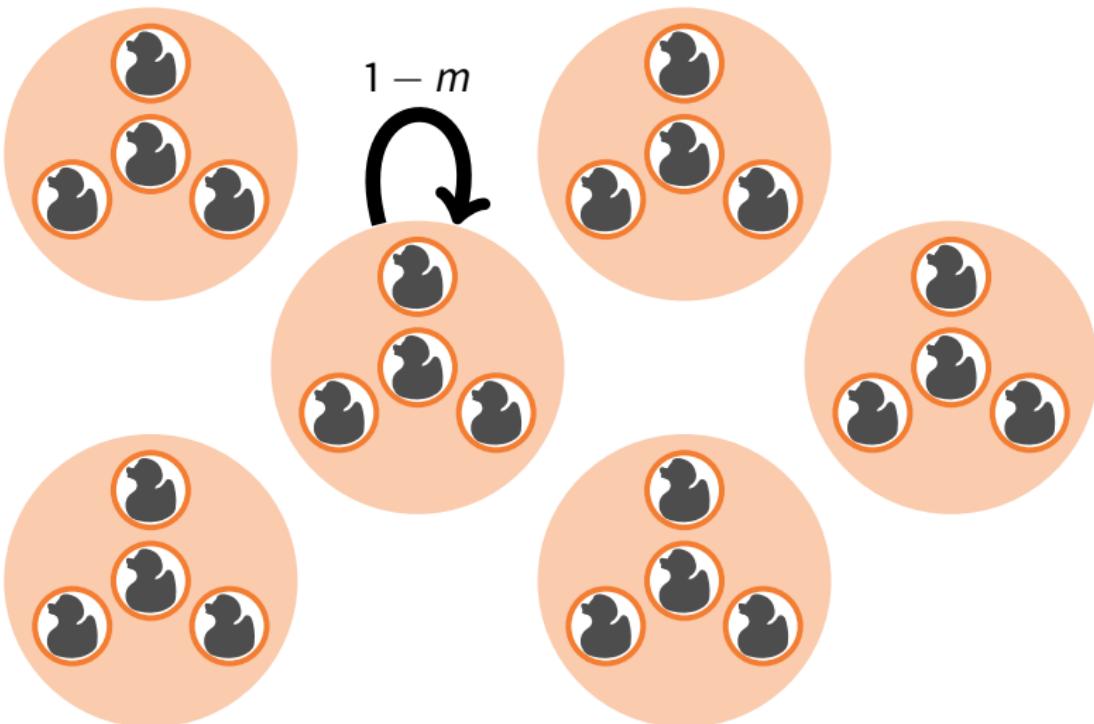
Subdivided population – Island model

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



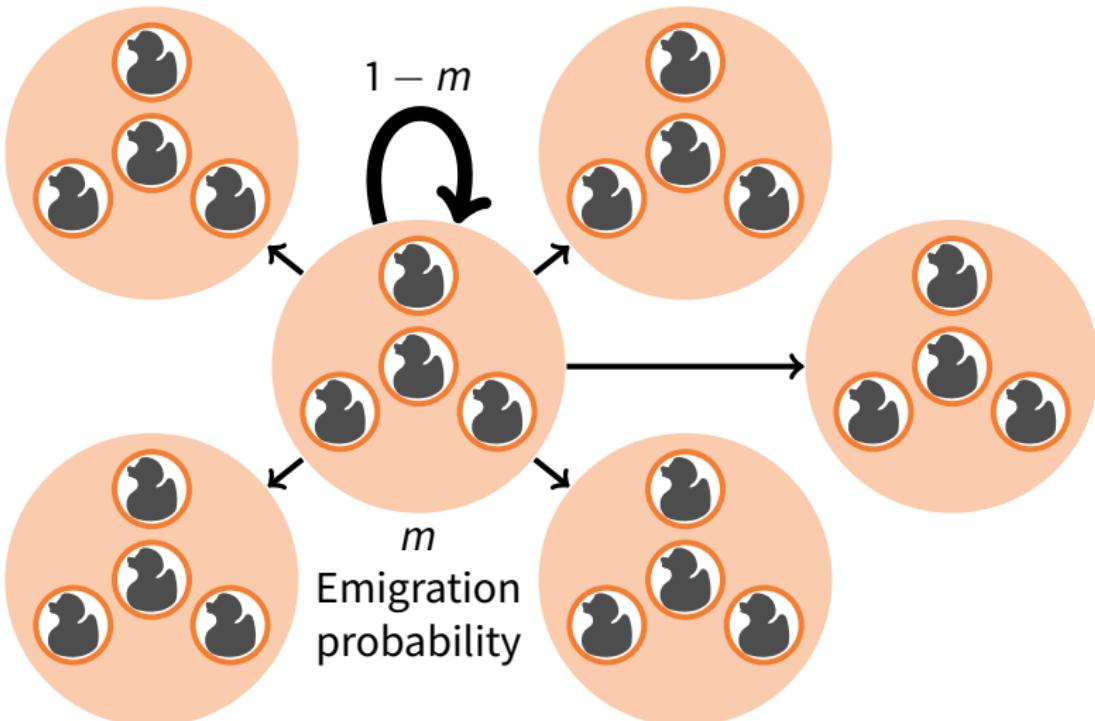
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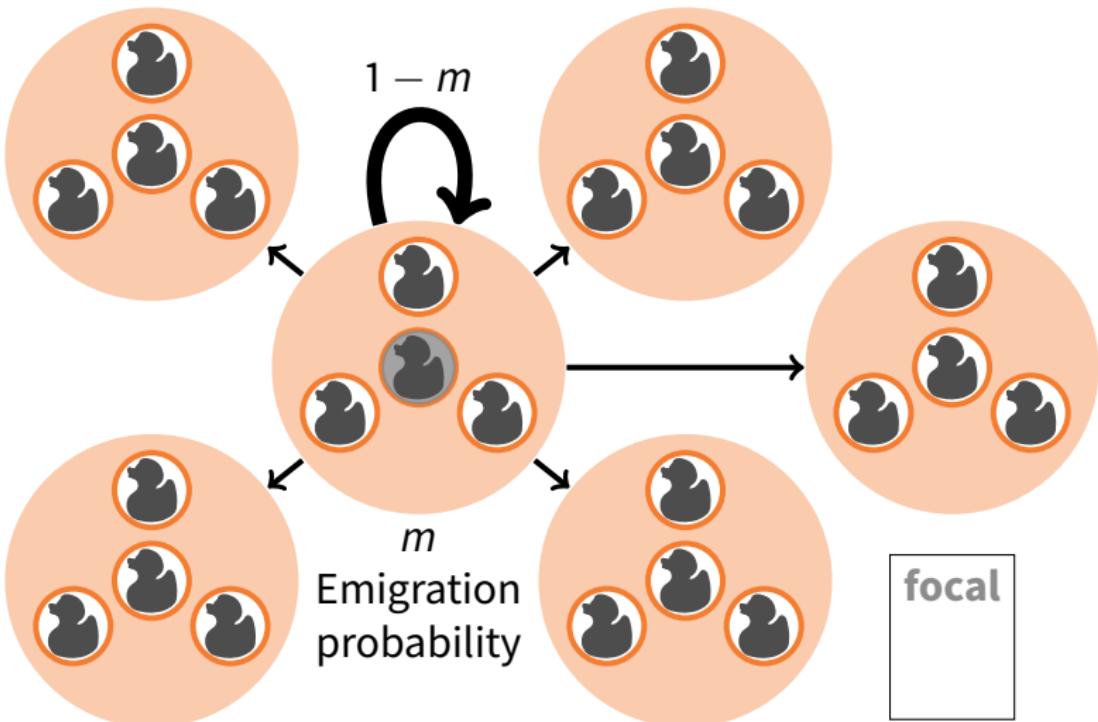
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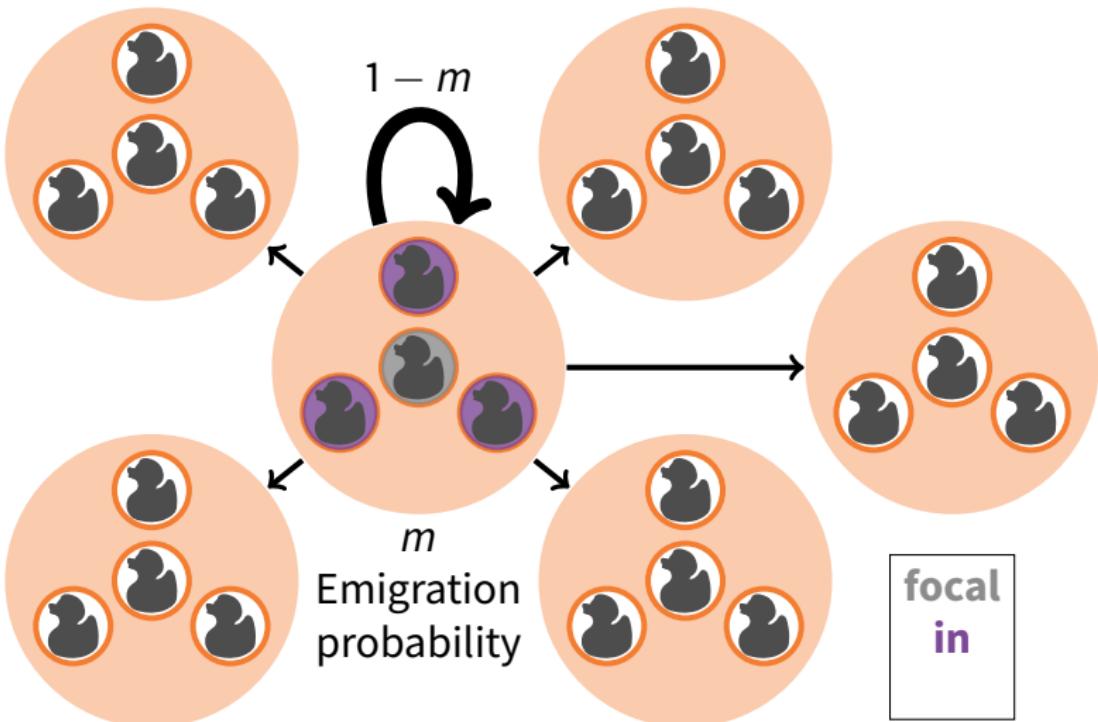
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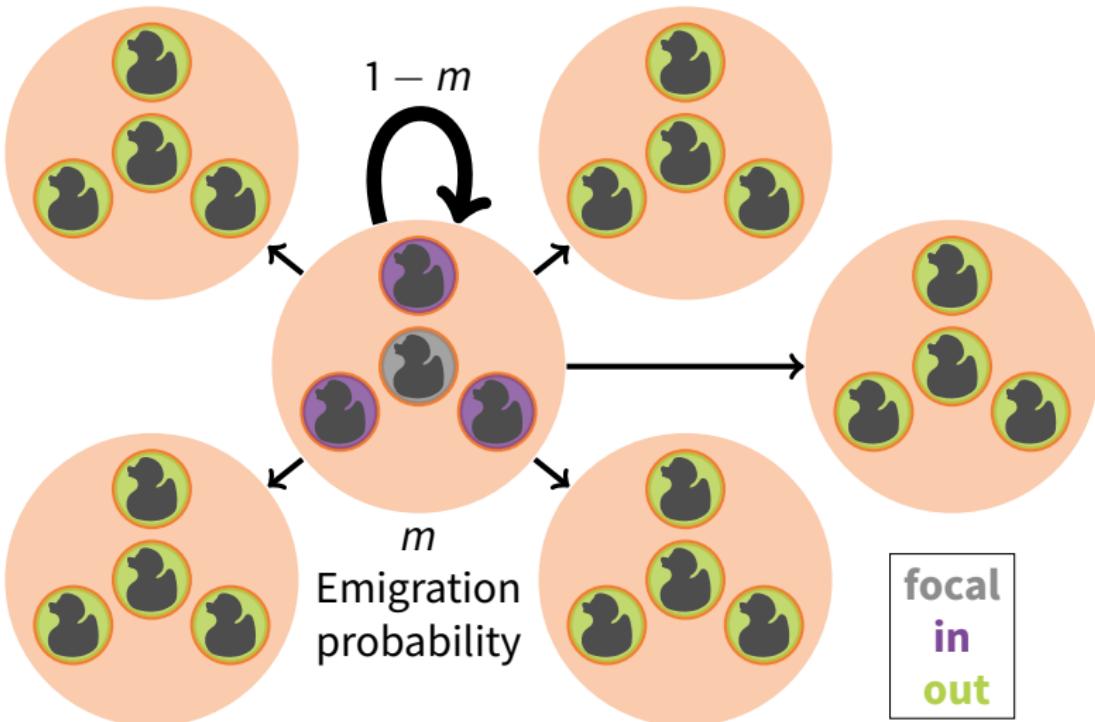
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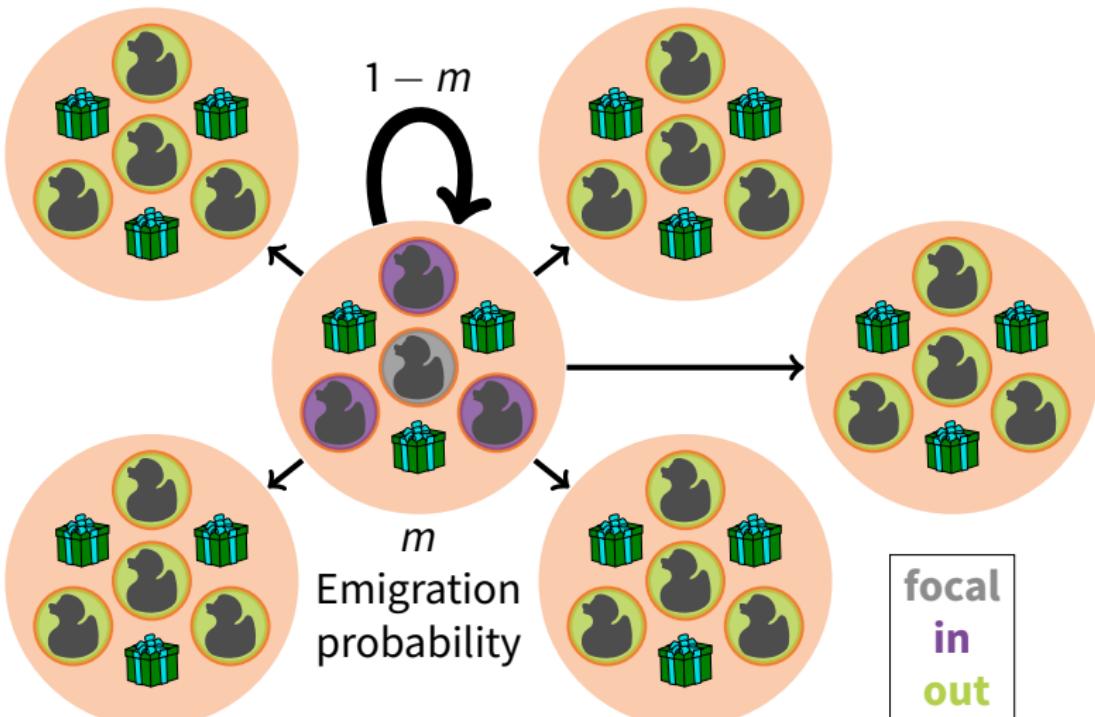
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Updating the population

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

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

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

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

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

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Moran process

Updating the population

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

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

Life-cycle

Wright-Fisher

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

Offspring production

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

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

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Updating the population

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

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Life-cycle

Wright-Fisher

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

Offspring production

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



Offspring dispersal

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

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

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



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

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

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

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

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,

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Life-cycle
“Death-Birth” updating

Wright-Fisher

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

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

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Moran process

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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

Phenotype

$$\phi_i = \delta X_i.$$

Social interactions affect fecundity

In a deme with k 



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

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

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Selection is weak

$$\delta \ll 1.$$

Calculations

Notation

$B_i = B_i(\mathbf{X}, \delta)$: expected # of offspring of individual i ;

$D_i = D_i(\mathbf{X}, \delta)$: probability that i dies.

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Notation

$B_i = B_i(\mathbf{X}, \delta)$: expected # of offspring of individual i ;

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- Expected proportion of altruists at $t + 1$ in the proportion of altruists, conditional on the state of the population at time t :

$$\mathbb{E}[\bar{X}(t+1)|\mathbf{X}(t)] = \frac{1}{N} \sum_{i=1}^N [B_i(1 - \mu)X_i + (1 - D_i)X_i + B_i\mu\nu]$$

Calculations

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- Take expectation and let $t \rightarrow \infty$; stationary distribution ξ

$$0 = \frac{1}{N} \sum_{X \in \Omega} \left[\underbrace{\sum_{i=1}^N B_i(1 - \mu) - D_i}_{W_i} X_i + \sum_{i=1}^N B_i\mu\nu \right] \xi(\mathbf{X}, \delta, \mu)$$

Calculations (2)

- Selection is weak ($\delta \ll 1$) and reproductive values are all equal:

$$0 = \frac{\delta}{N} \sum_{i=1}^N \left[\sum_{X \in \Omega} \frac{\partial W_i}{\partial \delta} X_i \xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega} \mu B^* X_i \frac{\partial \xi}{\partial \delta} \right] + O(\delta^2),$$

which we rewrite as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \mathbb{E}_0 \left[\frac{\partial W_i}{\partial \delta} X_i \right] + O(\delta^2).$$

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$$0 = \frac{\delta}{N} \sum_{i=1}^N \left[\sum_{X \in \Omega} \frac{\partial W_i}{\partial \delta} X_i \xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega} \mu B^* X_i \frac{\partial \xi}{\partial \delta} \right] + O(\delta^2),$$

which we rewrite as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \mathbb{E}_0 \left[\frac{\partial W_i}{\partial \delta} X_i \right] + O(\delta^2).$$

- Using partial derivatives: phenotypes

$$\frac{\partial W_i}{\partial \delta} = \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} \frac{\partial \phi_k}{\partial \delta} = \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} X_k.$$

Calculations (2)

- Selection is weak ($\delta \ll 1$) and reproductive values are all equal:

$$0 = \frac{\delta}{N} \sum_{i=1}^N \left[\sum_{X \in \Omega} \frac{\partial W_i}{\partial \delta} X_i \xi(\mathbf{X}, 0, \mu) - \sum_{X \in \Omega} \mu B^* X_i \frac{\partial \xi}{\partial \delta} \right] + O(\delta^2),$$

which we rewrite as

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \mathbb{E}_0 \left[\frac{\partial W_i}{\partial \delta} X_i \right] + O(\delta^2).$$

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- We obtain

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \sum_{k=1}^N \frac{\partial W_i}{\partial \phi_k} \underbrace{\mathbb{E}_0 [X_i X_k]}_{P_{ik}} + O(\delta^2).$$

Calculations (3)

- In a subdivided population,

$$\frac{\partial W_i}{\partial \phi_i} + (n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}} + (N - n) \frac{\partial W_i}{\partial \phi_{\text{out}}} = 0,$$

Calculations (3)

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- ▶ So

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-C} + \underbrace{(n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}}}_{B} \underbrace{\frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}}}_R \right) (P_{ii} - P_{\text{out}}) + O(\delta^2).$$

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- So

$$\delta \mu B^* \frac{\partial \mathbb{E}[\bar{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^N \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-c} + \underbrace{(n - 1) \frac{\partial W_i}{\partial \phi_{\text{in}}}}_{B} \underbrace{\frac{P_{\text{in}} - P_{\text{out}}}{P_{ii} - P_{\text{out}}}}_R \right) (P_{ii} - P_{\text{out}}) + O(\delta^2).$$

- Then further decompose with partial derivatives:

$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^N \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k}$$

$$\frac{\partial f_\ell}{\partial \phi_\ell} = -c; \quad \frac{\partial f_\ell}{\partial \phi_{\text{in}}} = \frac{b}{n-1}; \quad \frac{\partial f_\ell}{\partial \phi_{\text{out}}} = 0.$$

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

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

Expected frequency of altruists in the population

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

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

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

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\mathcal{B}

Expected frequency of altruists in the population

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

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

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

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

R

\mathcal{B}

Expected frequency of altruists in the population

Mutation-drift
equilibrium

Selection
strength

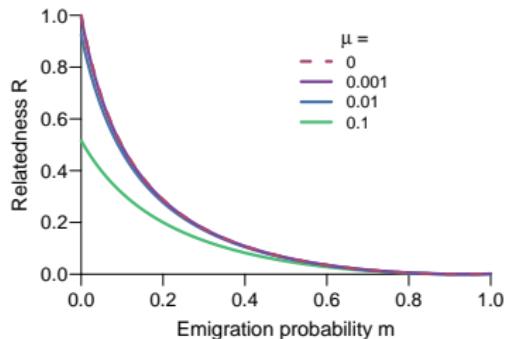
Population variance
Variance in the state of one site

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

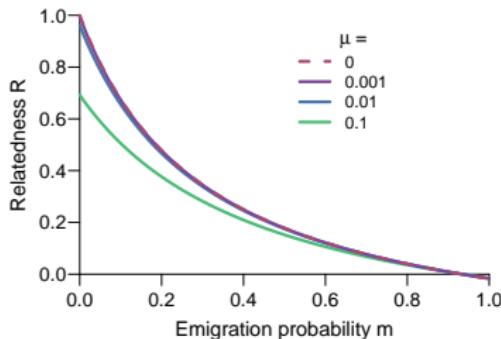
How does relatedness R change with the emigration probability m ?

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
equilibrium

Selection
strength

Population variance
Variance in the state of one site

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

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

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

R

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

R ↘

\mathcal{B}

Expected frequency of altruists in the population

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

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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

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

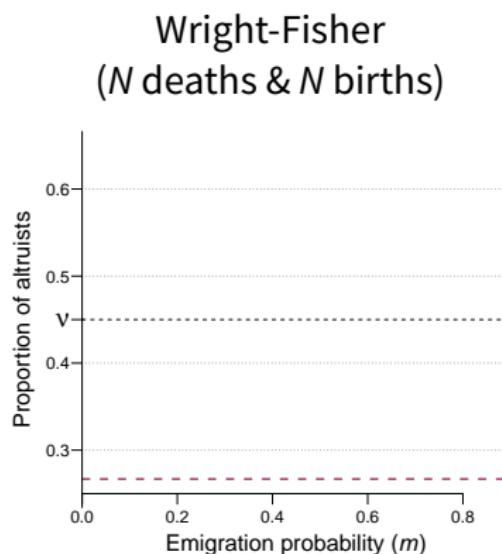
$$\left(-c - (b - c) \left(\frac{(1 - m)^2}{n} + \frac{m^2}{n(N_d - 1)} \right) - \mathcal{C} \right) \nearrow$$

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R

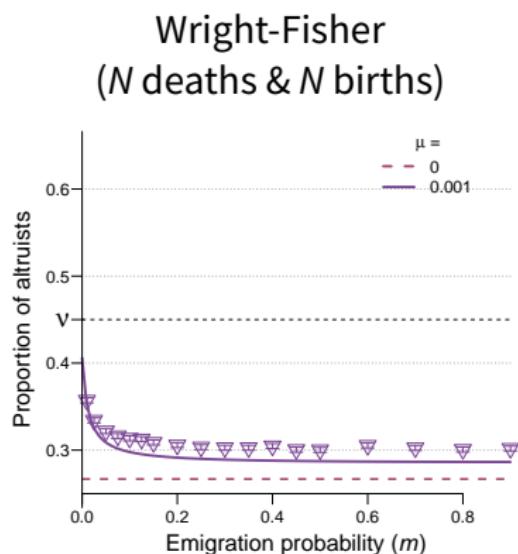
\mathcal{B}

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



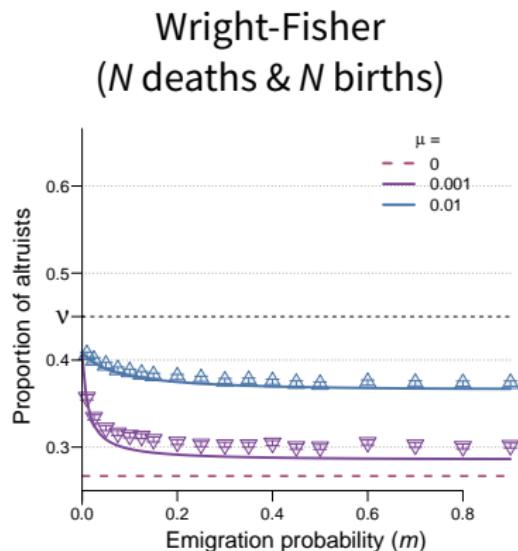
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

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



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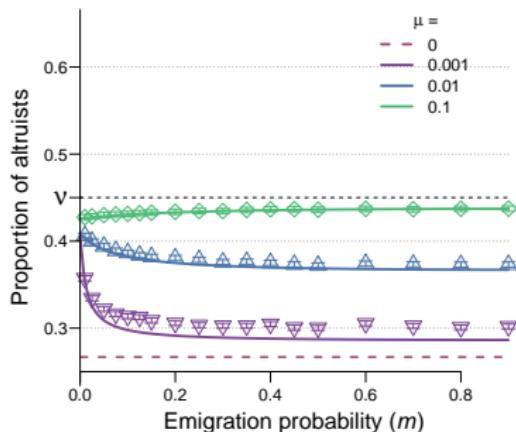
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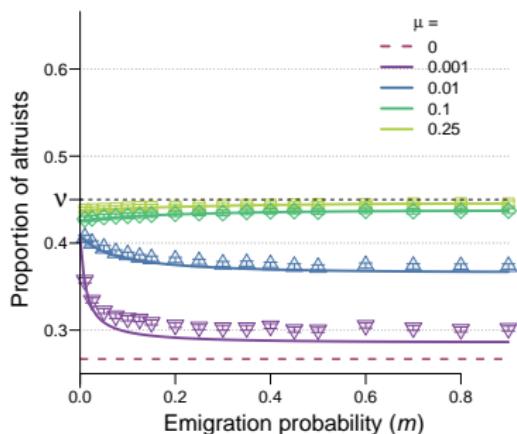
Wright-Fisher
(N deaths & N births)



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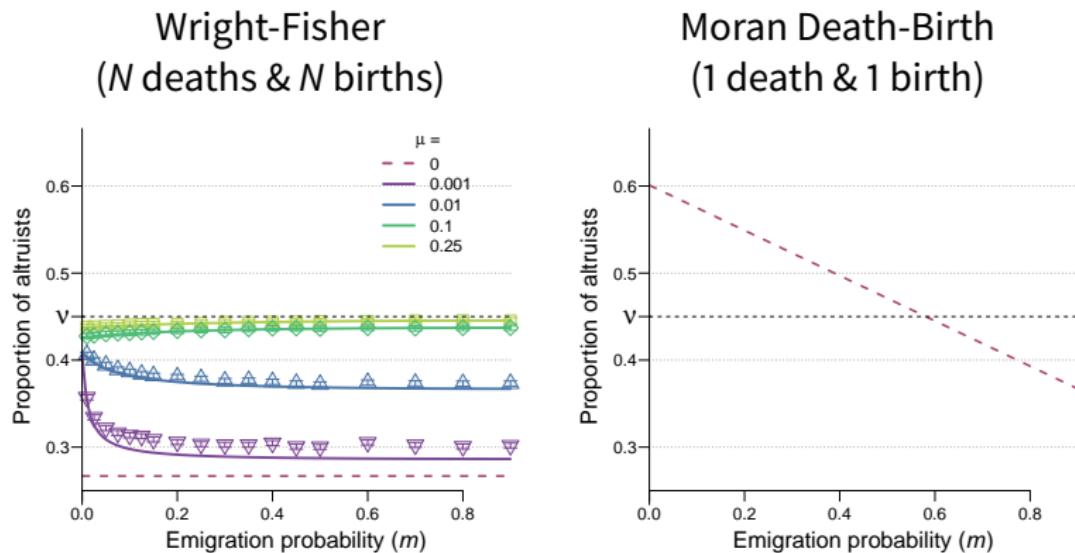
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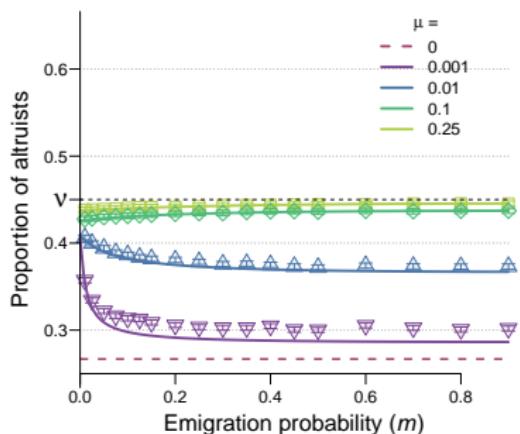
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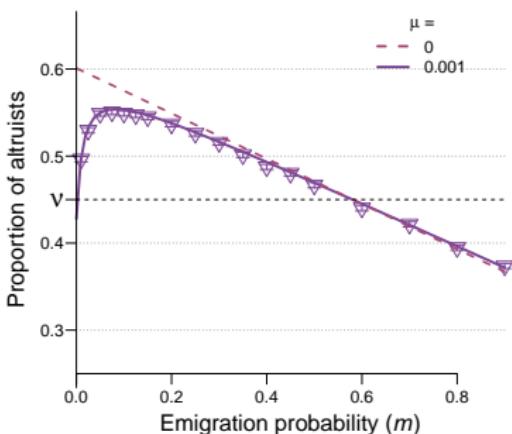
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

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

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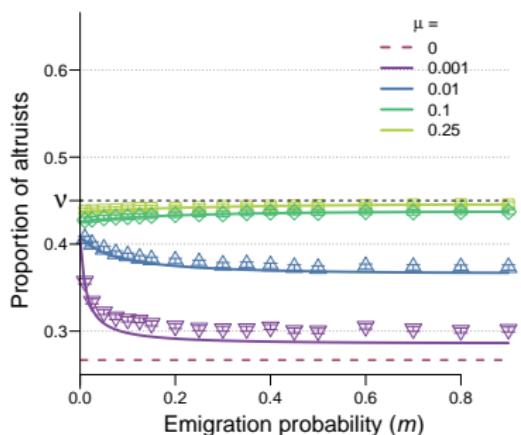
Moran Death-Birth
(1 death & 1 birth)



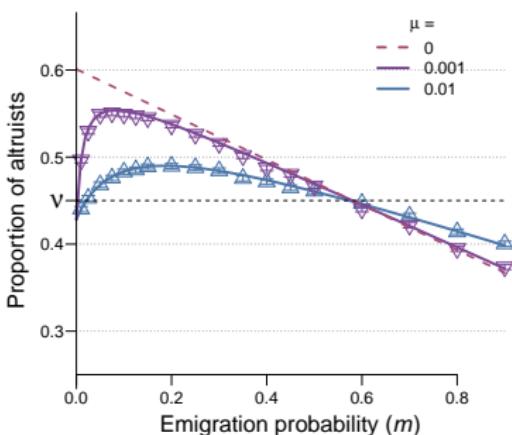
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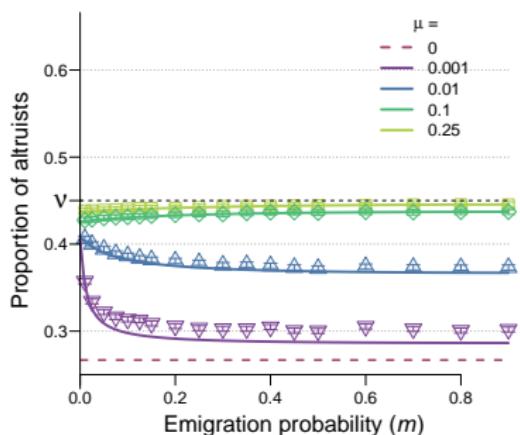
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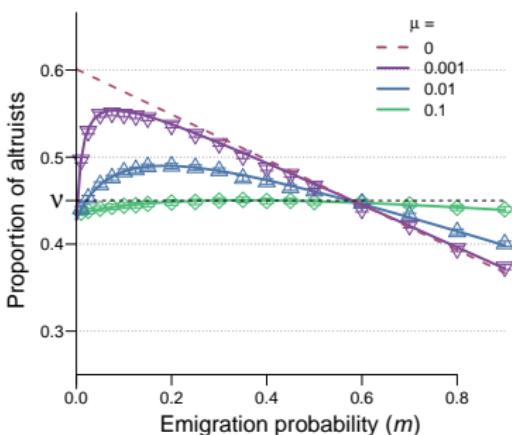
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Effect of the emigration probability m on the expected proportion of altruists

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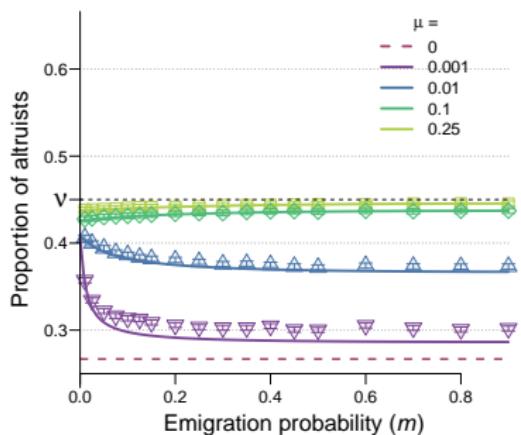
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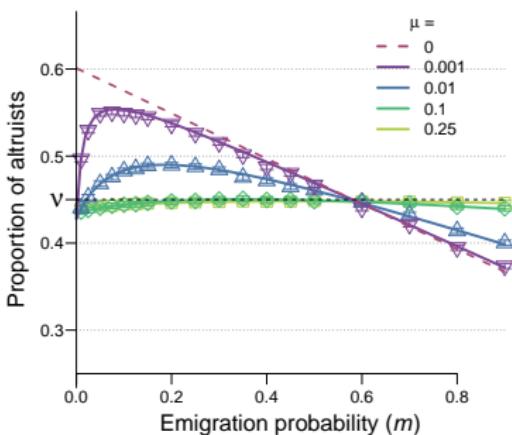
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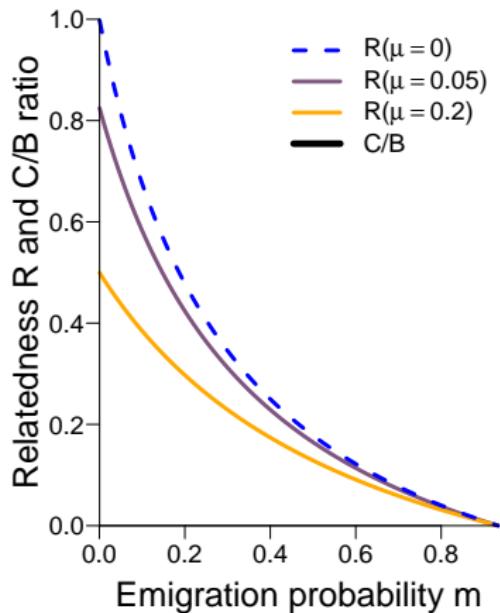
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

How to explain this result? (Moran Death-Birth)

$$-\mathcal{C} + \mathcal{B}R > 0 \Leftrightarrow R > \mathcal{C}/\mathcal{B}$$

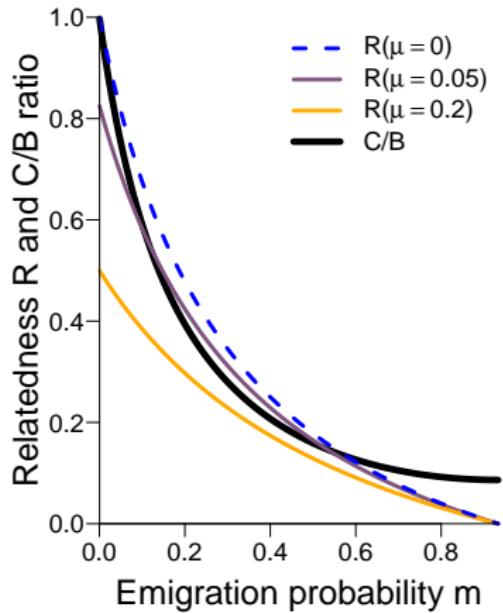
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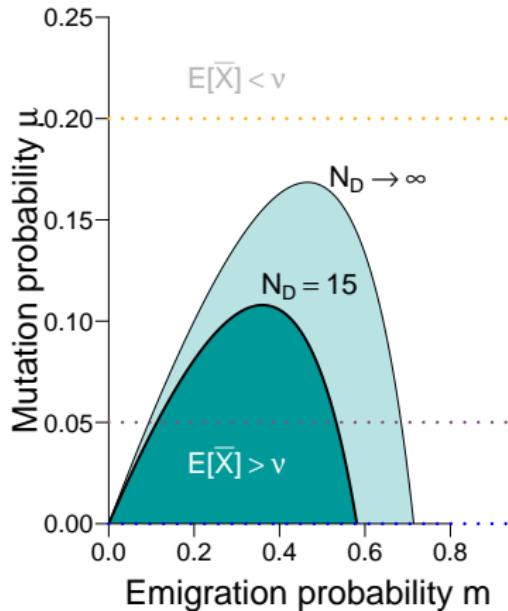
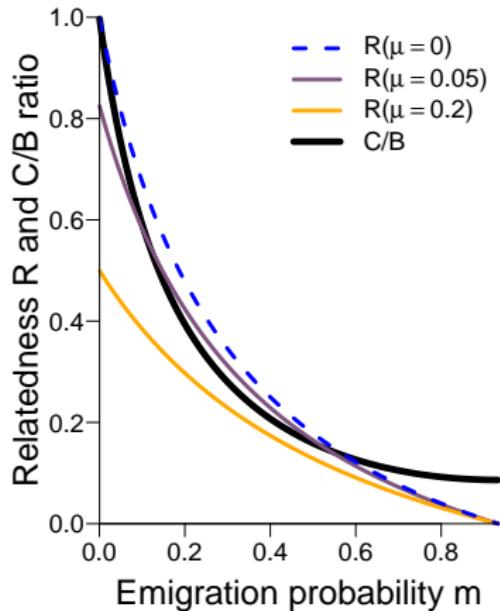
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Is the result robust?

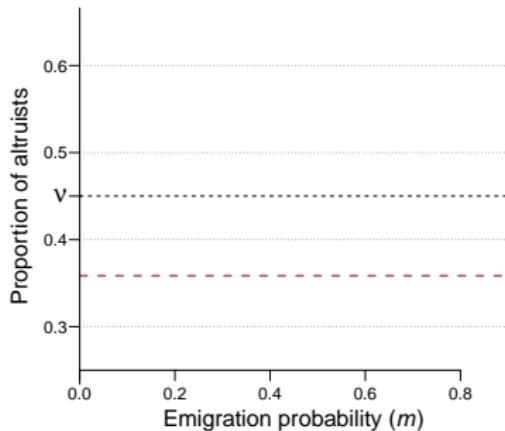
Another life-cycle

Moran Birth-Death
(1 birth & 1 death)

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

Another life-cycle

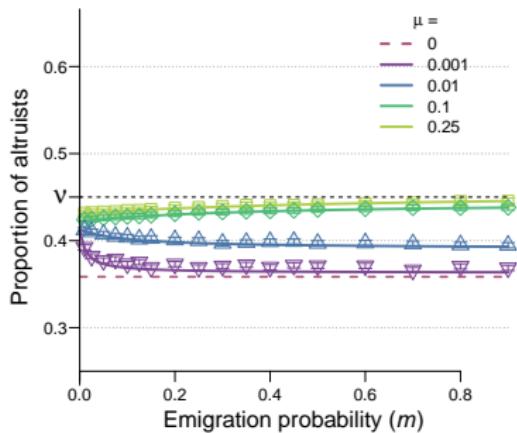
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Another life-cycle

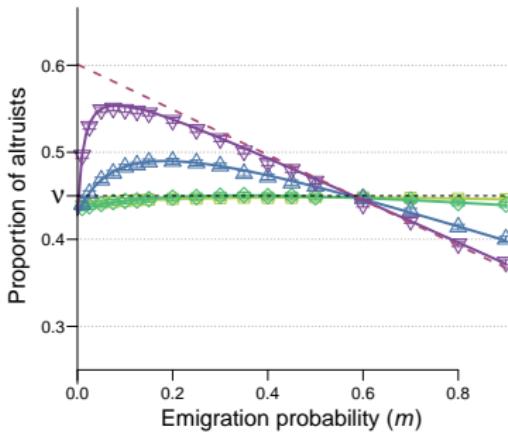
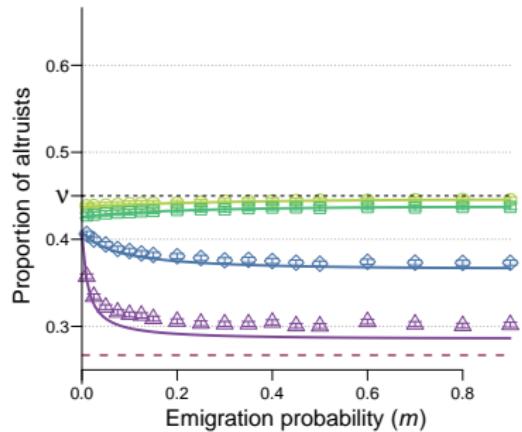
Moran Birth-Death
(1 birth & 1 death)



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

Strong selection

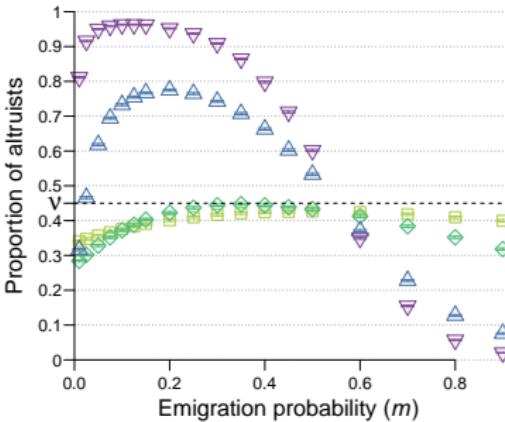
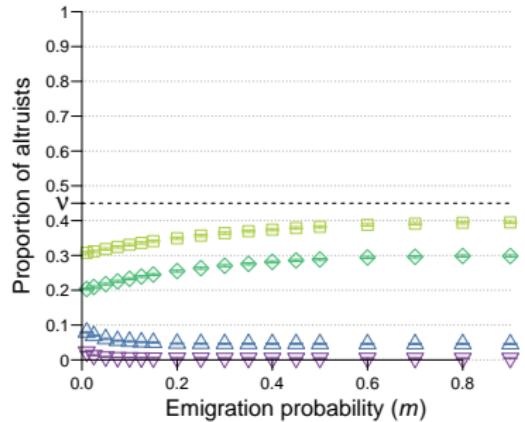
Wright-Fisher, weak selection Moran Death-Birth, weak selection



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Strong selection

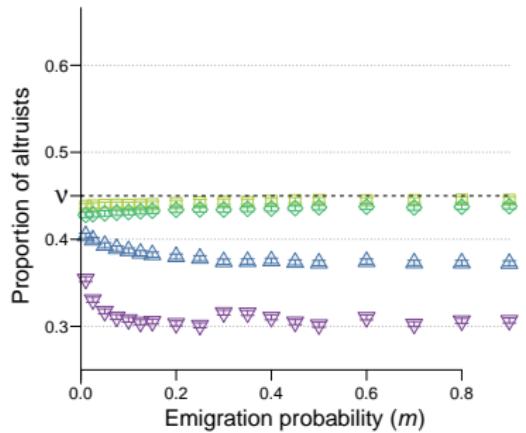
Wright-Fisher, strong selection | Moran Death-Birth, strong selection



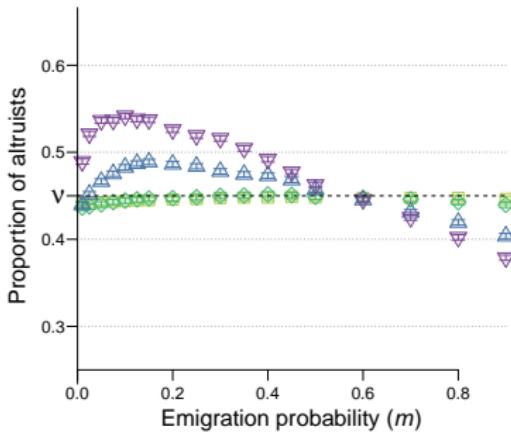
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.1)$$

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

Wright-Fisher



Moran Death-Birth



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

Political implications

When strategy transmission is imperfect, too small emigration probabilities can prevent the evolution of altruistic behavior

Take-Home Messages

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Funding & Thanks



R. Aguilée,
M. Costa,
G. Faye,
S. Gandon,
S. Mirrahimi,

Ch. Mullon,
S. Lion

and thank you
for your attention!