Social evolution in structured populations

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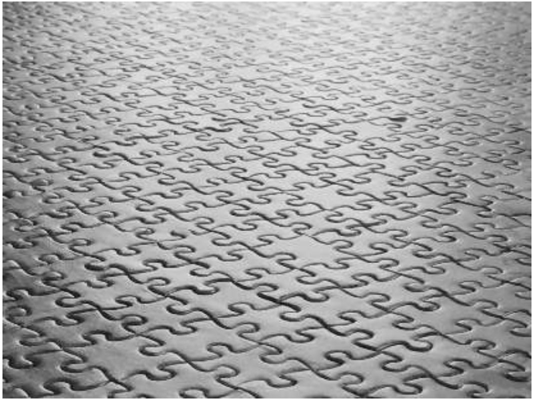
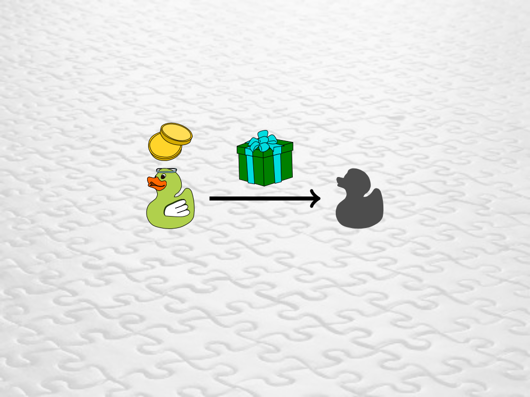
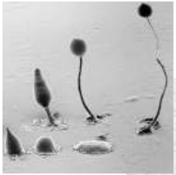
Journée thématique interdisciplinaire maths-bio
Université Paris-Dauphine

4 décembre 2017







(c) Grimson & Blanton

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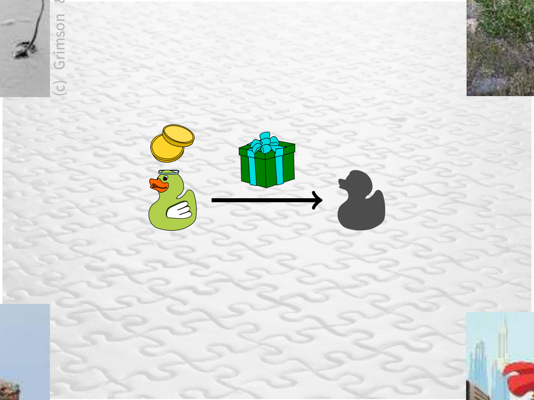

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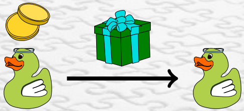
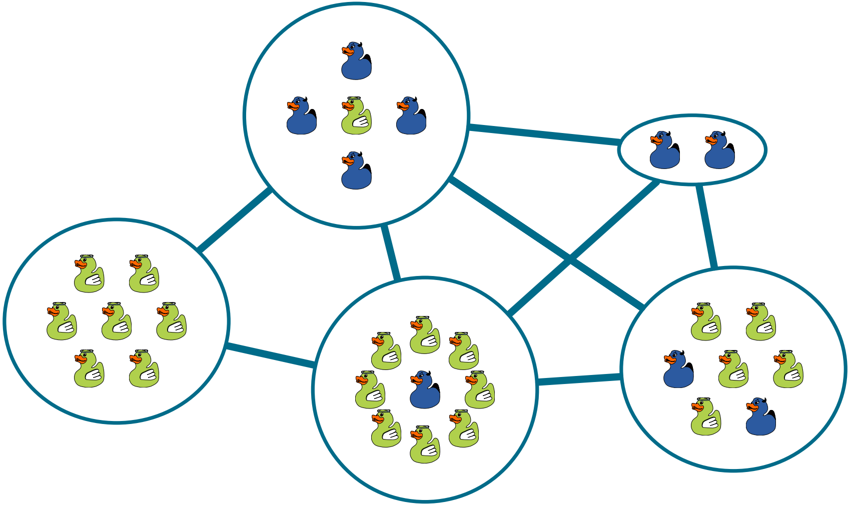


Assortment / Relatedness

Spatial structure, population viscosity and altruism



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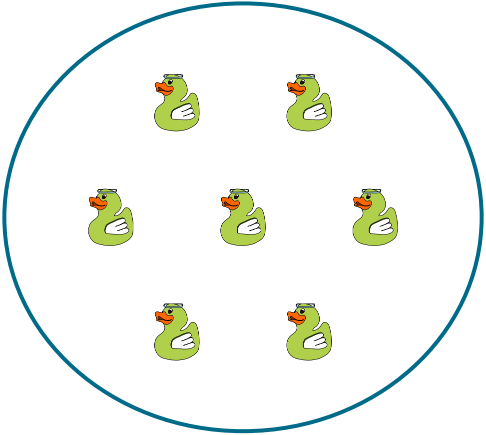

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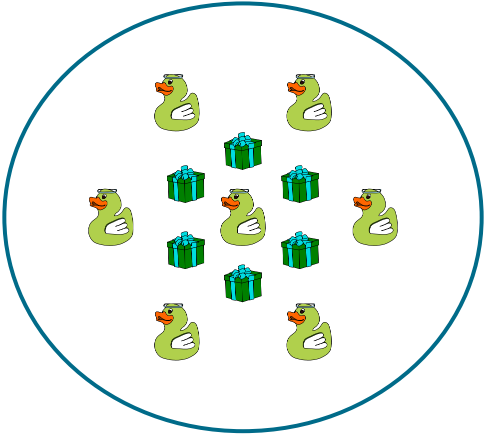

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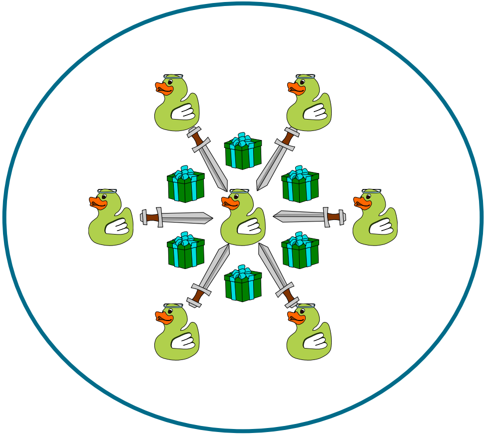

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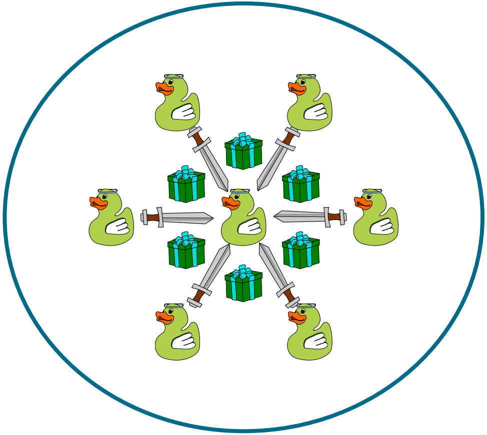


Evolutionary Ecology, 1992, **6**, 352–356

Altruism in viscous populations – an inclusive fitness model

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

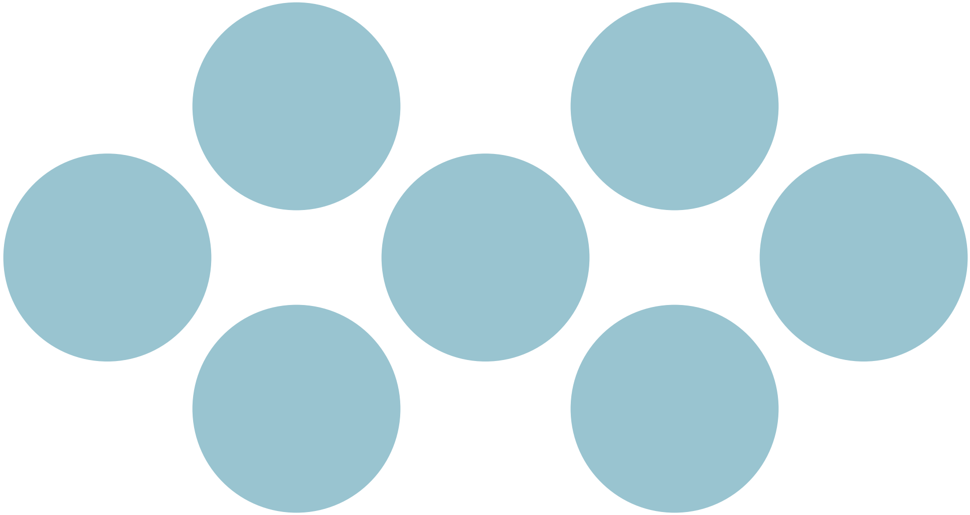
Summary

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

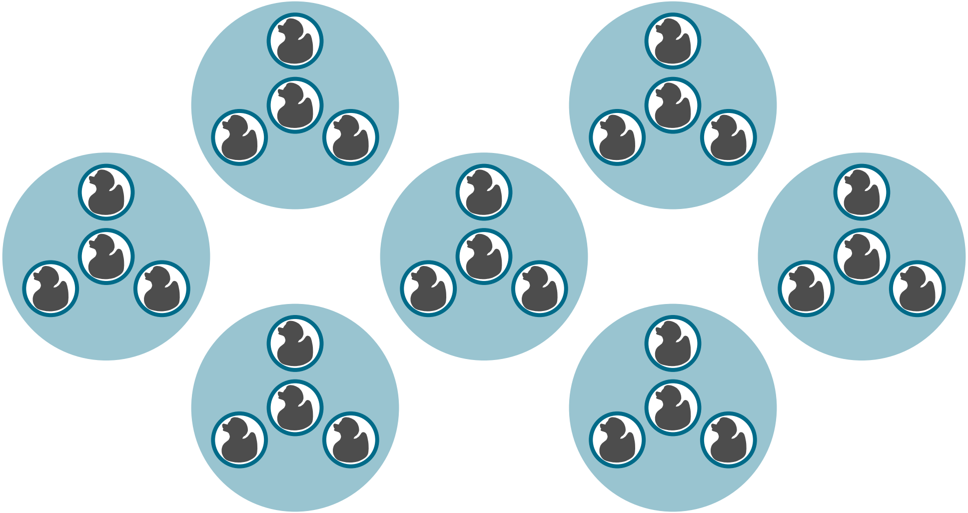
Subdivided population – Island model

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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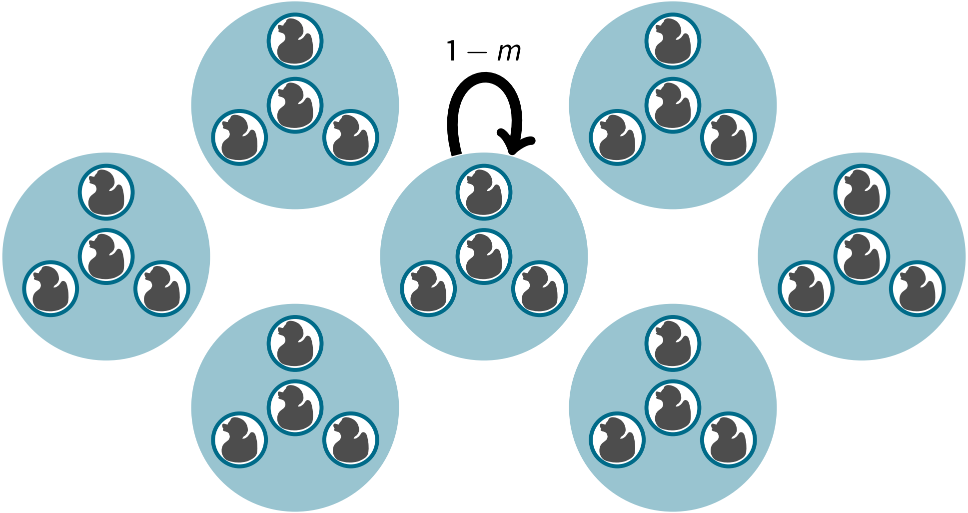

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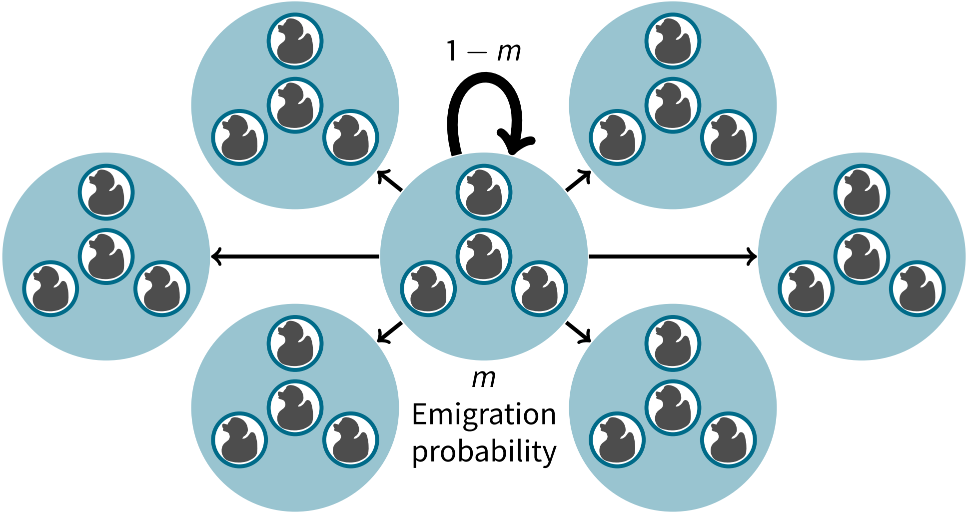

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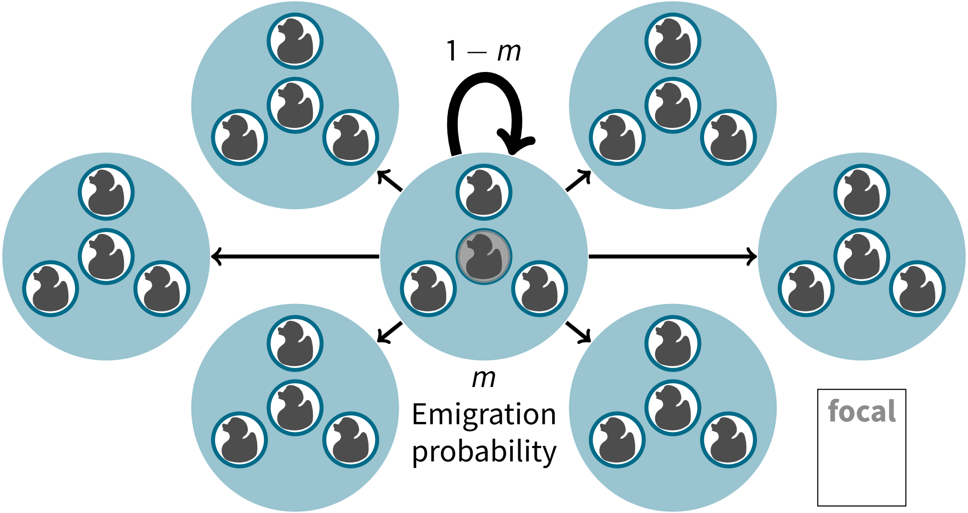

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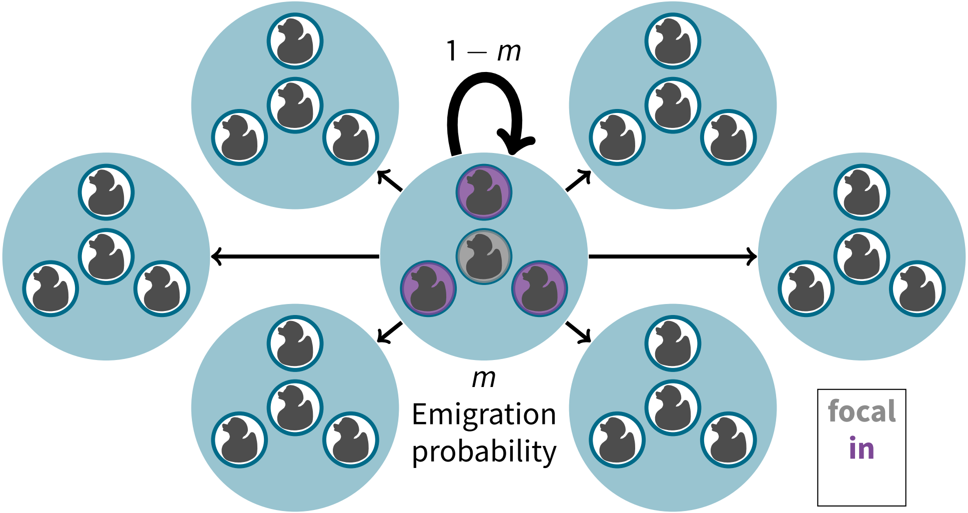

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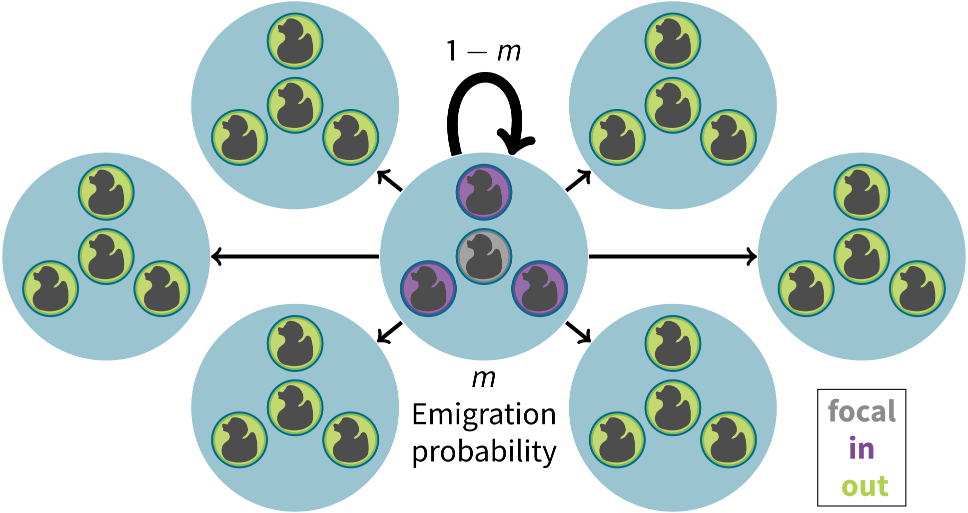

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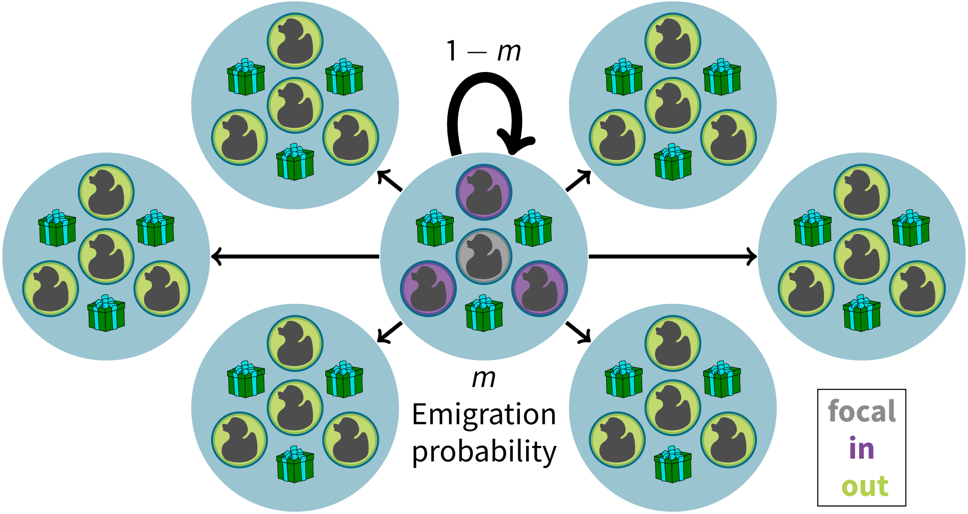

The choice of life-cycle matters

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

$=\#$.

Ohtsuki et al. 2006; Taylor, Day & Wild 2007; Taylor, Lillicrap, Cownden 2010

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Wright-Fisher	Moran Birth-Death	Moran Death-Birth
N & N	1 & 1	1 & 1

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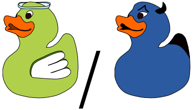

In homogeneously structured populations,
with effects of social interactions on **fecundity**.

Ohtsuki et al. 2006; Taylor, Day & Wild 2007; Taylor, Lillicrap, Cownden 2010

A common feature of models

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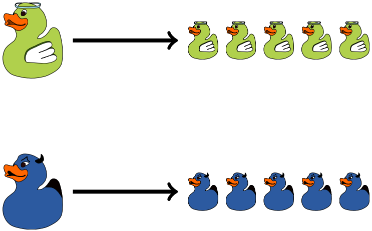

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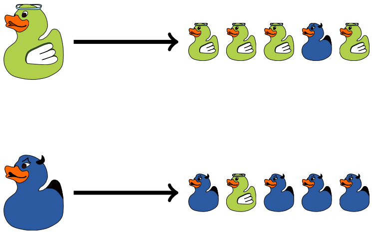

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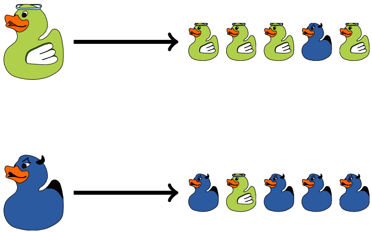

What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

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In the model

Parent Offspring

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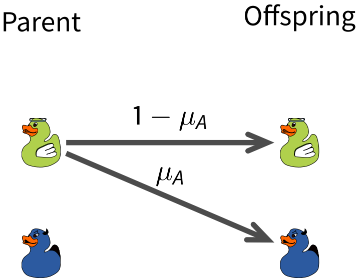

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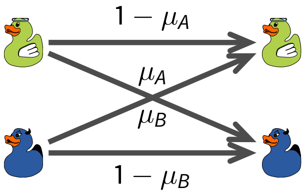

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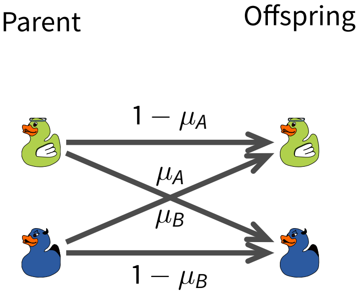

$$\mu = \mu_A + \mu_B$$
$$\nu = \frac{\mu_B}{\mu_A + \mu_B}$$

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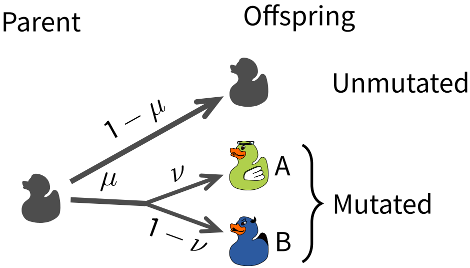

$$\mu = \mu_A + \mu_B$$
$$\nu = \frac{\mu_B}{\mu_A + \mu_B}$$

Notation

$\mathbf{X}(t)$; $\quad X_i(t) = \begin{cases} 1 \\ 0 \end{cases}$

- 1: if site i occupied by  at time t $(1 \leq i \leq N)$
- 0: if site i occupied by  at time t $(1 \leq i \leq N)$

Notation

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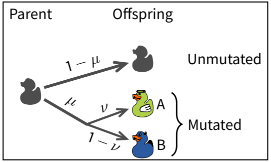

$$\mathbb{E}[Y_i] \qquad = (1-\mu)\,X_i + \mu\nu \times 1 + \mu(1-\nu) \times 0.$$

Expected trait of the
offspring of individual i

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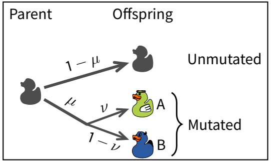

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Expected trait of the offspring of individual i

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$$\mathbf{X}(t); \quad X_i(t) = \begin{cases} 1 & \text{if site } i \text{ occupied by [green duck] at time } t \ (1 \leq i \leq N) \\ 0 & \text{if site } i \text{ occupied by [blue duck] at time } t \ (1 \leq i \leq N) \end{cases}$$

Proportion of altruists in the population:

$$\overline{X} = \frac{1}{N} \sum_{i=1}^{N} X_i.$$

We want to compute $\mathbb{E}[\overline{X}]$,
the expected proportion of altruists in the population.

Social interactions

Phenotype

$$\phi_i = \delta X_i,$$

and we assume that $\delta \ll 1$. (Selection is weak.)

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Social interactions affect fecundity

At the first order in δ,

$$f_i = 1 + \delta \left(\mathrm{b} \sum_{j \in \mathcal{D}_i \setminus i} \frac{X_j}{n-1} - \mathrm{c} \; X_i \right) .$$

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Proportion of altruists
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The cost is only paid
by altruists

Calculations

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

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

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

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

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Calculations (2)

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

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

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which we rewrite as

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

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- Using partial derivatives: phenotypes

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

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- We obtain

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

Calculations (3)

- In a subdivided population,

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

Rousset & Billiard (2000)

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- Then further decompose with partial derivatives:

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

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Calculations (3)

- In a subdivided population,

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

- So

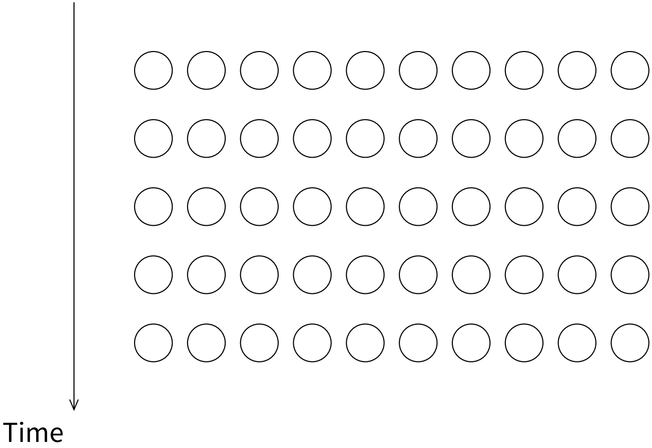
$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-\mathcal{C}} + \underbrace{(n-1)\frac{\partial W_i}{\partial \phi_{\text{in}}}}_{\mathcal{B}} \underbrace{\frac{P_{\text{in}} - P_{\text{out}}}{P_{ii}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

- Then further decompose with partial derivatives:

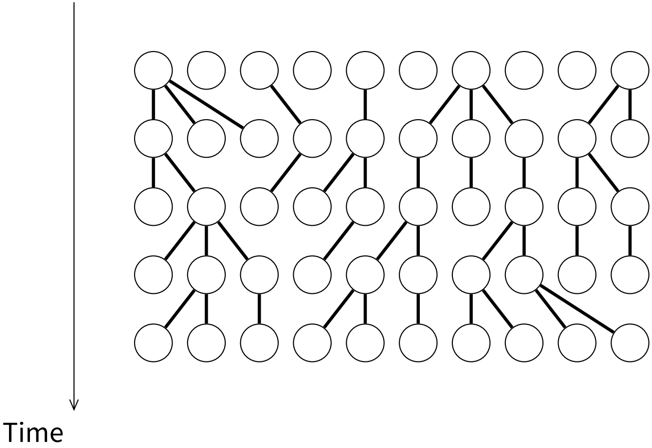
$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^{N} \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k} \quad \text{and} \quad \frac{\partial f_\ell}{\partial \phi_\ell} = -\mathrm{c}; \quad \frac{\partial f_\ell}{\partial \phi_{\text{in}}} = \frac{\mathrm{b}}{n-1}; \quad \frac{\partial f_\ell}{\partial \phi_{\text{out}}} = 0.$$

Rousset & Billiard (2000)

Genealogy, Identity by descent and Identity in state



Genealogy, Identity by descent and Identity in state



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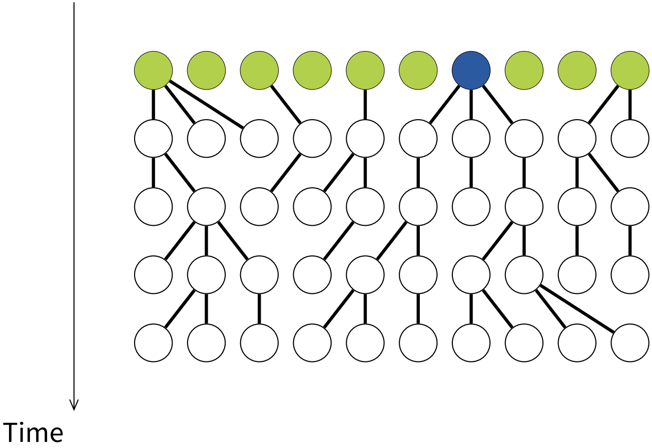

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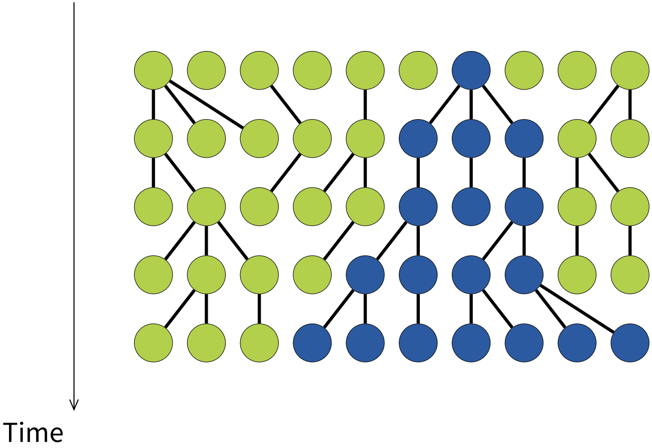
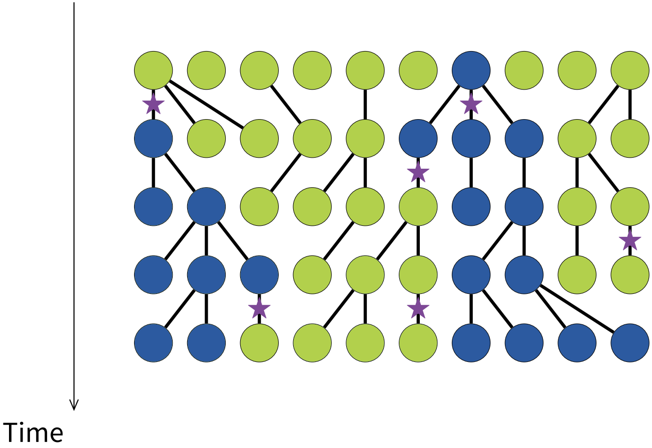
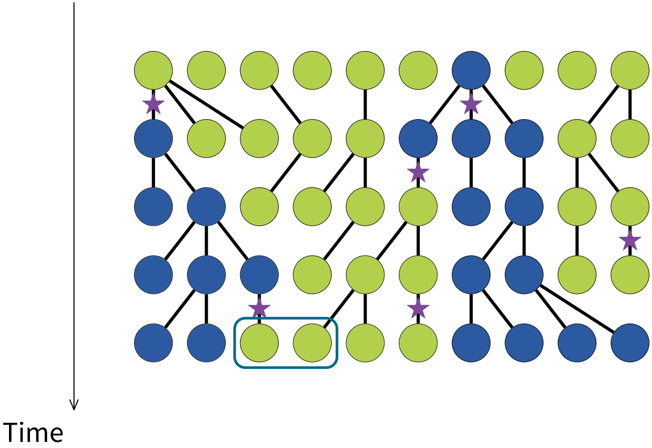


Genealogy, Identity by descent and Identity in state



Genealogy, Identity by descent and Identity in state



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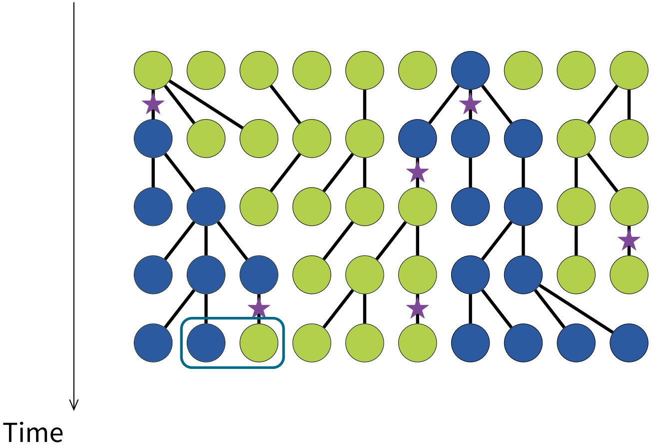
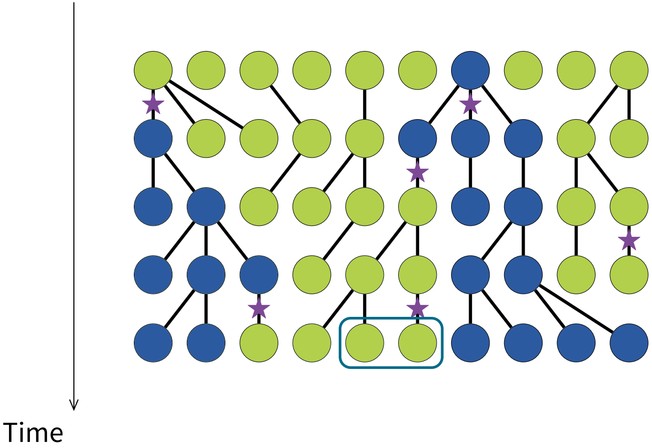
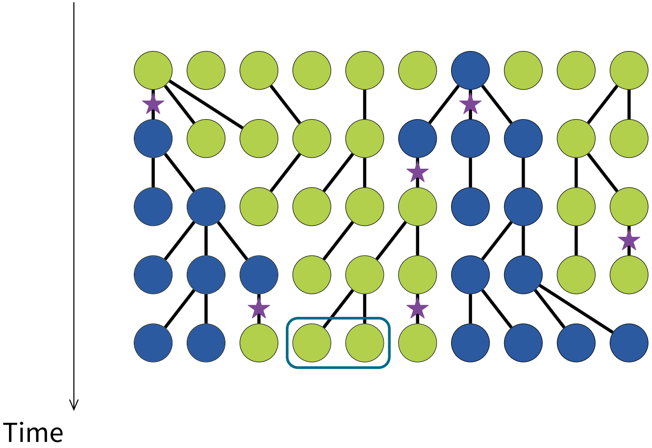


Genealogy, Identity by descent and Identity in state



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, $\delta = 0$),

Expected state of pairs of sites and identity by descent

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$$P_{ij}$$

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

Expected state of pairs of sites and identity by descent

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

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

Expected state
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= Probability that the two
individuals are altruists

Probability that the individuals at
sites i and j are identical by descent
(no mutation since
their common ancestor)

Expected state of pairs of sites and identity by descent

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

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

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

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

Probability that the individuals at sites i and j are identical by descent (no mutation since their common ancestor)

Expected state of pairs of sites and identity by descent

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

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

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

Probability that both sites
are occupied by an altruist

Probability that the individuals at sites
i and j are not identical by descent

Expected state of pairs of sites and identity by descent

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

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

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

Q_{in}, Q_{out}

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

$$
\begin{aligned}
\mathbb{E}[\overline{X}] = \boxed{\nu} + \delta\ \nu(1-\nu)\ \frac{1-\mu}{\mu}\ (1-Q_{\mathrm{out}})\ \times \\
\Bigg(-\mathrm{c} - (\mathrm{b}-\mathrm{c}) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d-1)} \right) \\
+ \frac{Q_{\mathrm{in}} - Q_{\mathrm{out}}}{1-Q_{\mathrm{out}}} \left[\ \mathrm{b} - (\mathrm{b}-\mathrm{c})\,(n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d-1)} \right) \right] \Bigg)
\end{aligned}
$$

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

Selection strength

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

Selection strength

Variance in the state of one site

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

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

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

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

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Variance in the state of one site

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

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

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

Selection strength

Variance in the state of one site

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

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

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

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

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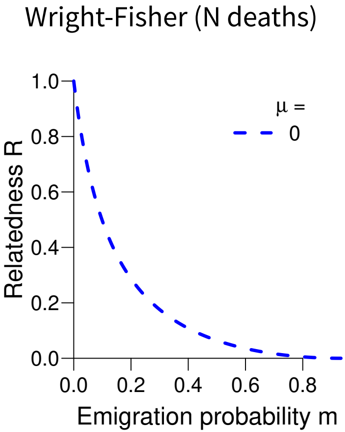
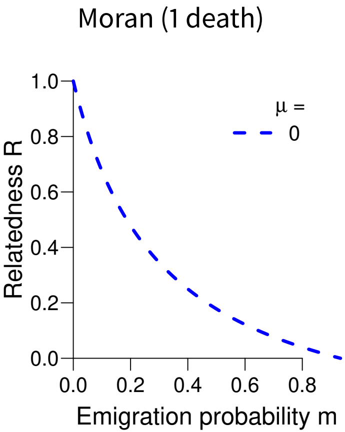
$$\left. + \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R} \left[\underbrace{\text{b} - (\text{b}-\text{c})\,(n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d - 1)} \right)}_{\mathcal{B}} \right] \right)$$

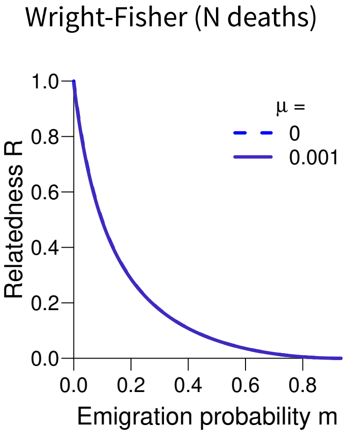
How does relatedness *R* change with the emigration probability *m*?

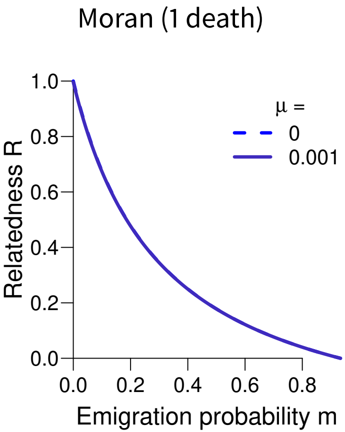




$$(n = 4, N_d = 15)$$

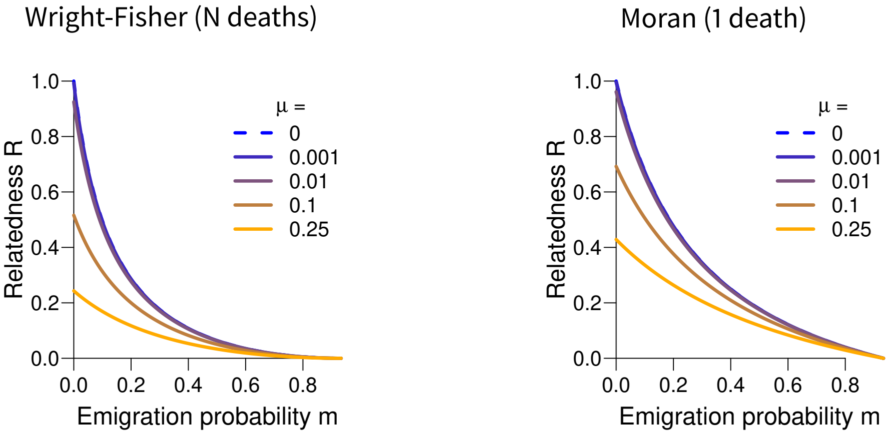
How does relatedness *R* change with the emigration probability *m*?





$(n = 4, N_d = 15)$

How does relatedness R change with the emigration probability m?



$(n = 4, N_d = 15)$

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

$$\mathbb{E}[\overline{X}] = \overbrace{\nu}^{\text{Mutation-drift equilibrium}} + \overbrace{\delta}^{\text{Selection strength}} \overbrace{\nu(1-\nu)}^{\text{Variance in the state of one site}} \frac{1-\mu}{\mu} \left(1 - Q_{\text{out}}\right) \times$$

$$\left(\underbrace{-\mathrm{c} - (\mathrm{b}-\mathrm{c}) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d - 1\right)} \right)}_{-\mathcal{C}} + \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R \searrow} \left[\underbrace{\mathrm{b} - (\mathrm{b}-\mathrm{c}) (n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d - 1\right)} \right)}_{\mathcal{B}} \right] \right)$$

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

Selection strength

Variance in the state of one site

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

$$\left(\underbrace{-\mathrm{c} - (\mathrm{b}-\mathrm{c}) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d - 1)} \right)}_{-\mathcal{C}} + \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R \searrow} \left[\underbrace{\mathrm{b} - (\mathrm{b}-\mathrm{c})\,(n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d-1)} \right)}_{\mathcal{B}} \right] \right)$$

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

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Variance in the state of one site

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

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

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

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

Expected frequency of altruists in the population

Equation for Moran Death-Birth and Wright-Fisher

Mutation-drift equilibrium

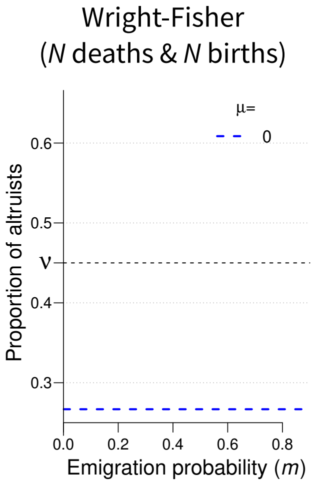
Selection strength

Variance in the state of one site $\searrow$

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

$$\left(\underbrace{-\mathrm{c} - (\mathrm{b}-\mathrm{c}) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d - 1)} \right)}_{-\mathcal{C} \nearrow} + \underbrace{\frac{Q_{\text{in}} - Q_{\text{out}}}{1 - Q_{\text{out}}}}_{R \searrow} \left[\underbrace{\mathrm{b} - (\mathrm{b}-\mathrm{c})\,(n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\,(N_d - 1)} \right)}_{\mathcal{B} \nearrow} \right] \right)$$

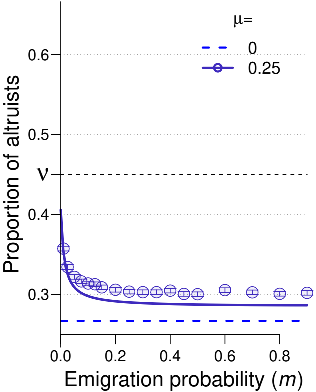
Effect of the emigration probability m on the expected proportion of altruists



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

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

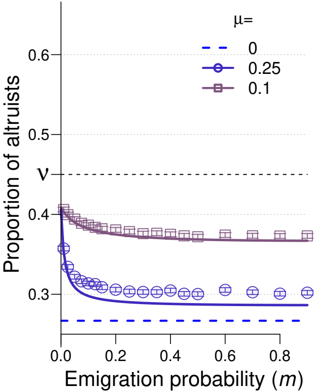
Wright-Fisher
(N deaths & N births)



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

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

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



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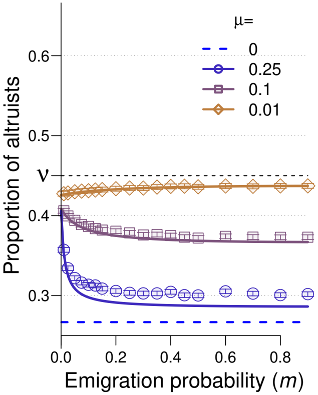

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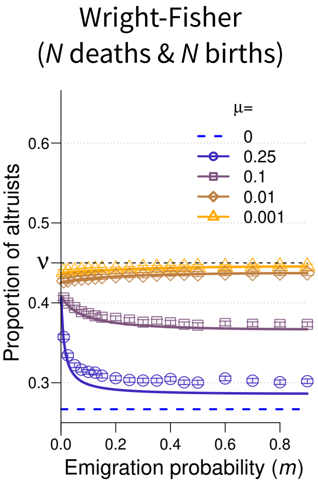

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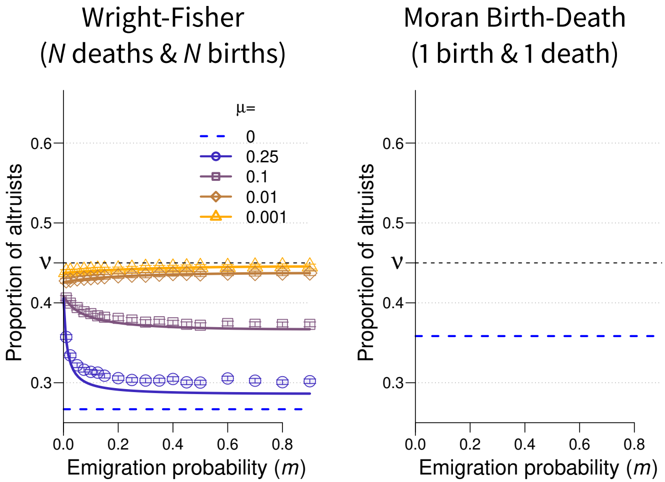
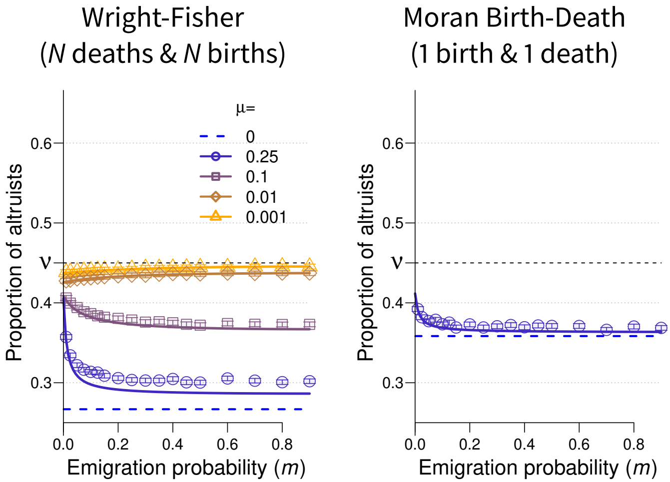


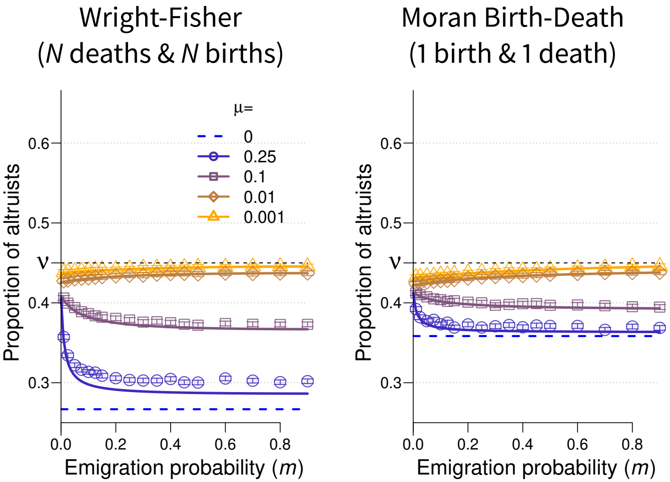
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



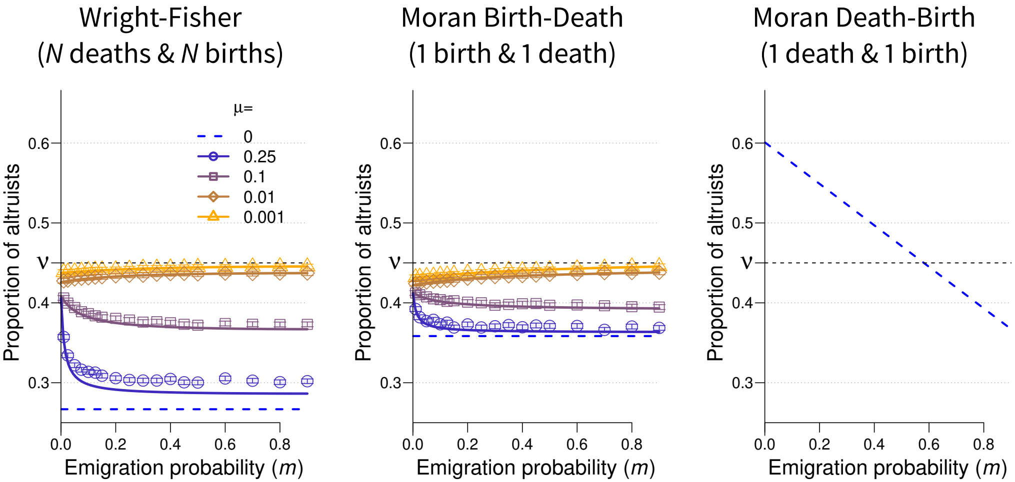
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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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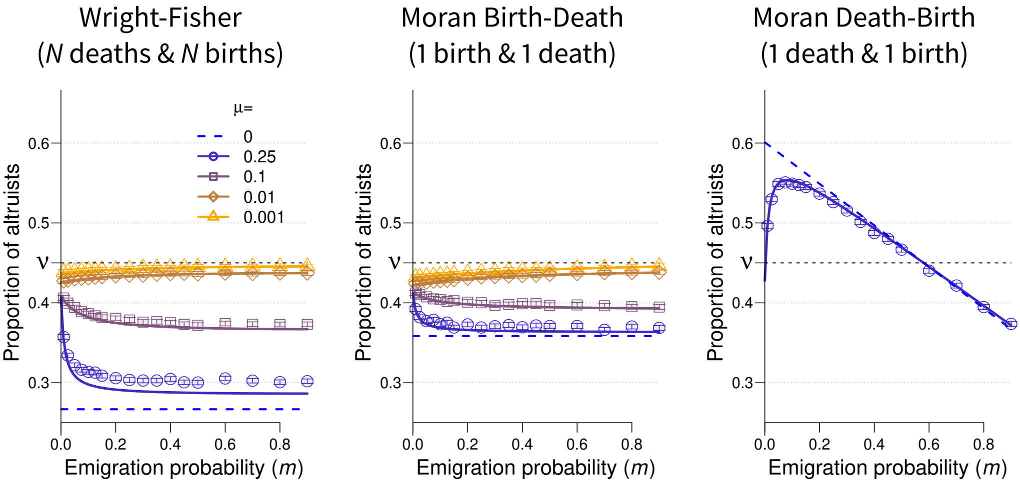

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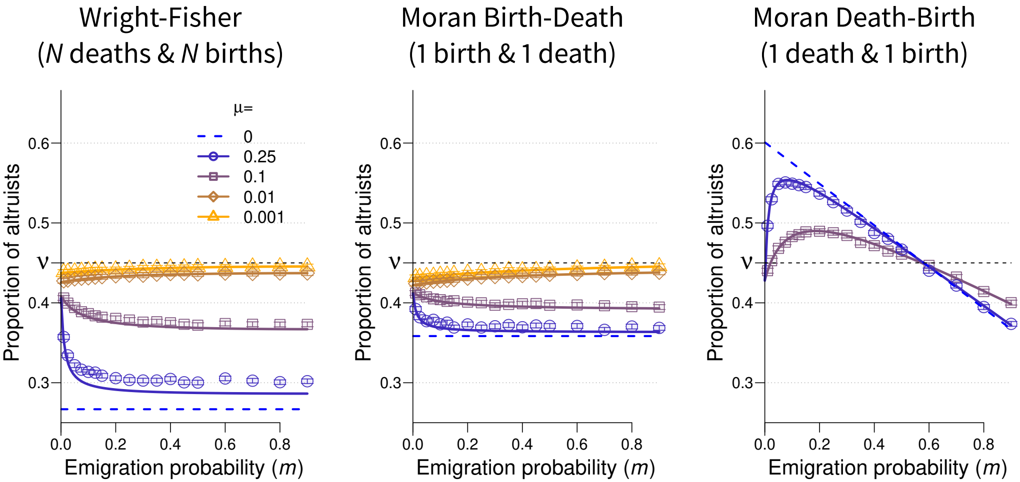

$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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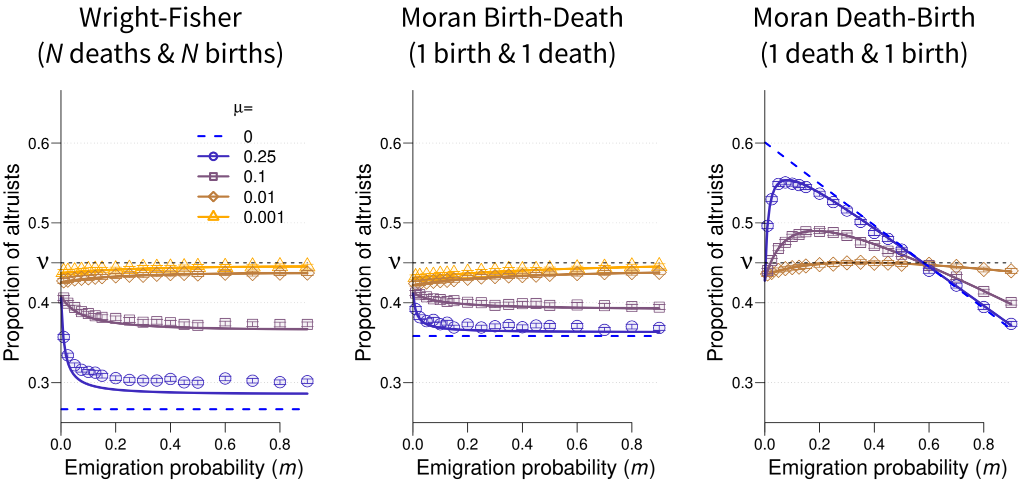
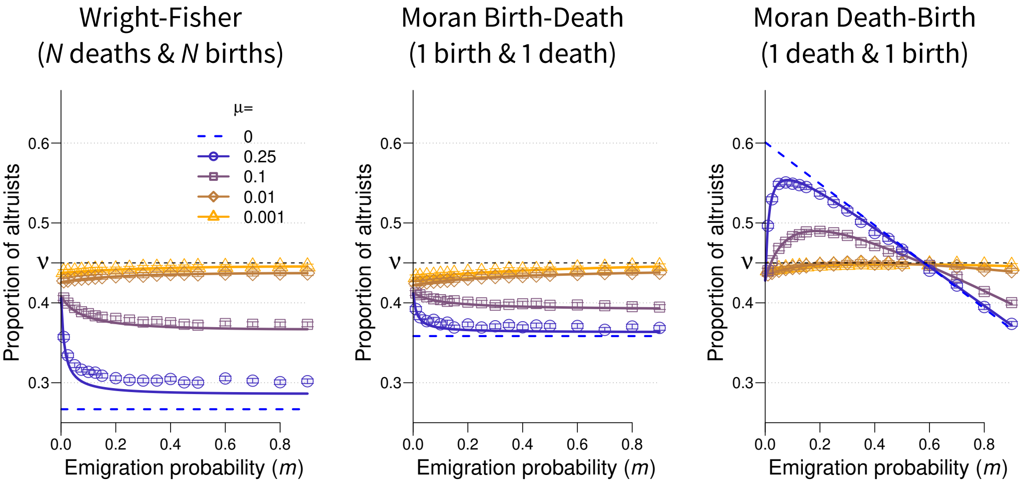


$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



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

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

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

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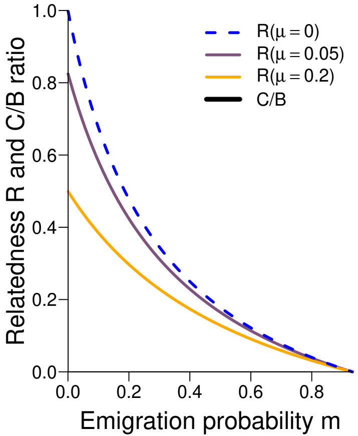
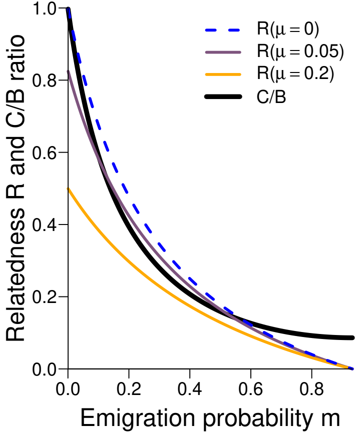


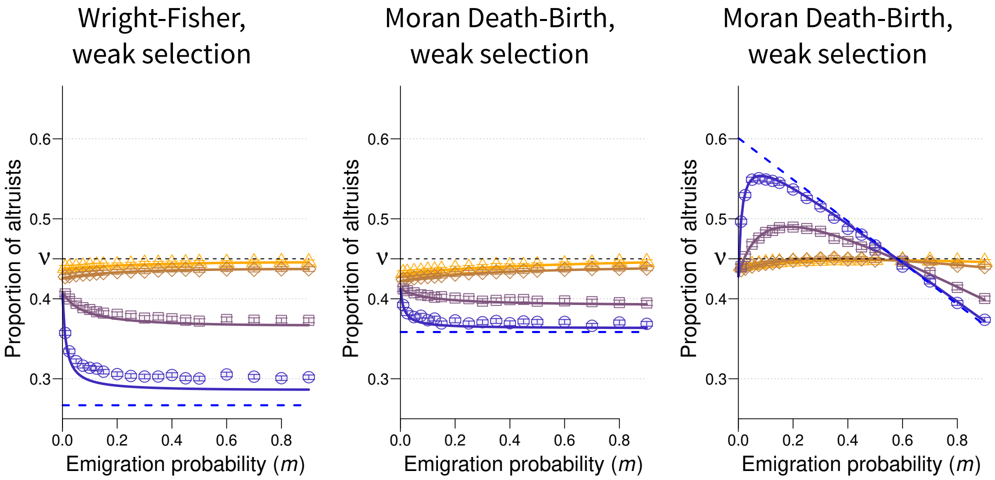
How to explain this result? (Moran Death-Birth)

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



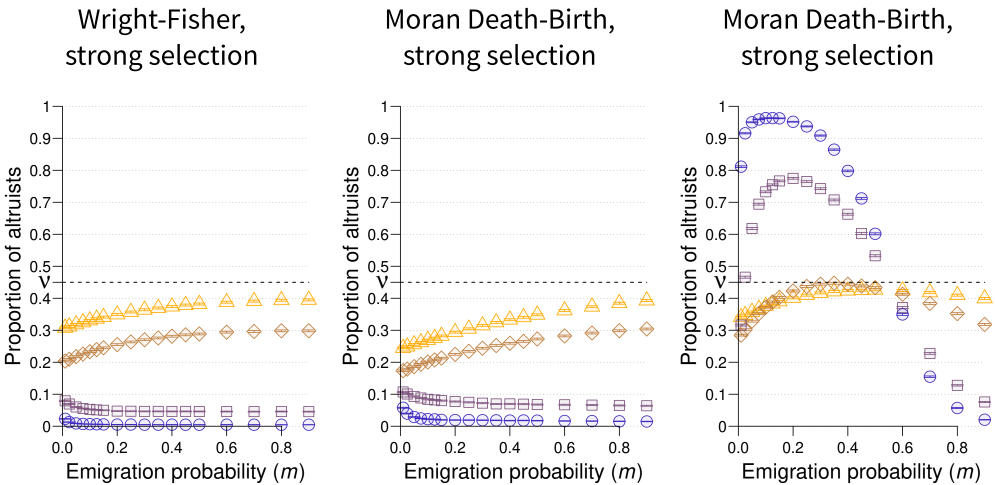
Is the result robust?

Strong selection



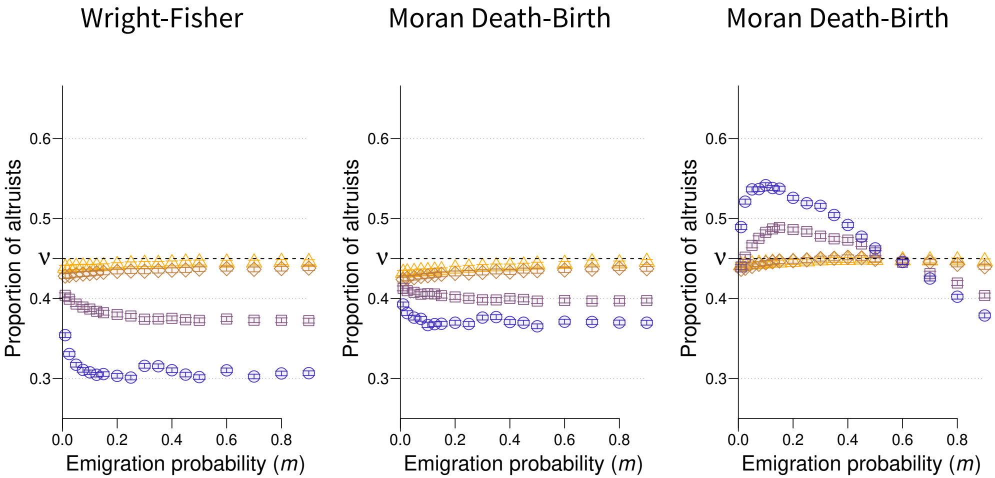
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

Strong selection



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

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



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

Political implications

Take-Home Messages

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