Social evolution in structured populations

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Preamble: Structured populations

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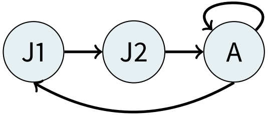
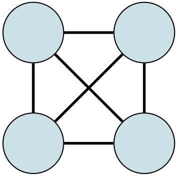
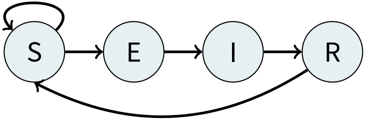
- Types of structures
  - Stage
  - Spatial
  - Types







Preamble: Structured populations

- Types of structures
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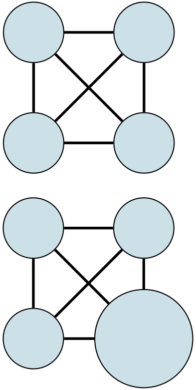
- Homogeneous / heterogeneous



Preamble: Structured populations

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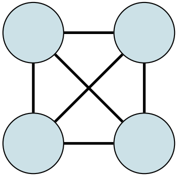

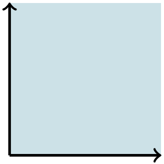

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- Demography / Evolution / Both (evo-demo)

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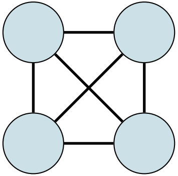

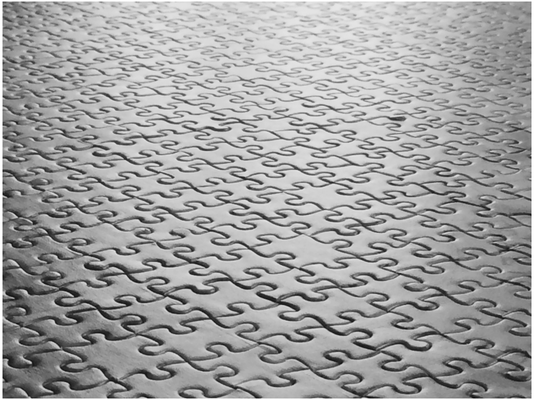

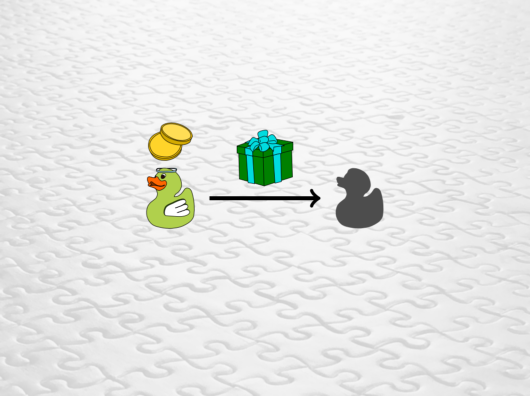

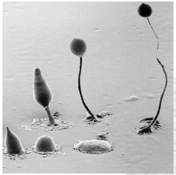

(c) Grimson & Blanton

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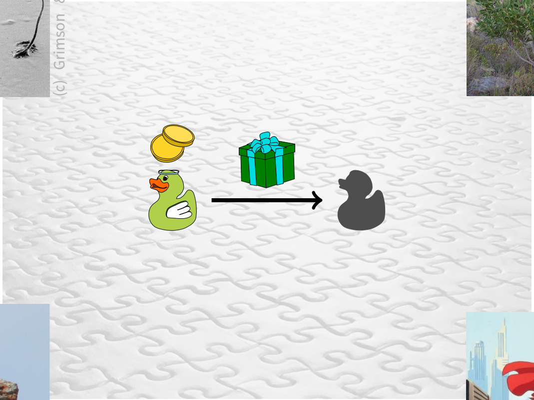
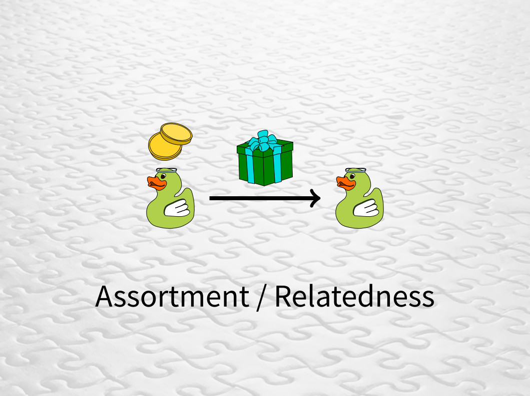
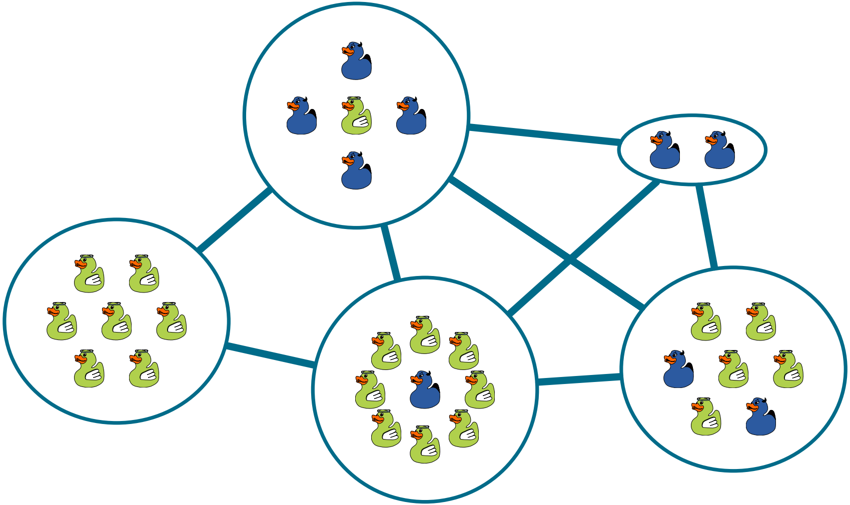


(c) FD

(c) picturesforcoloring.com


Assortment / Relatedness

Spatial structure, population viscosity and altruism



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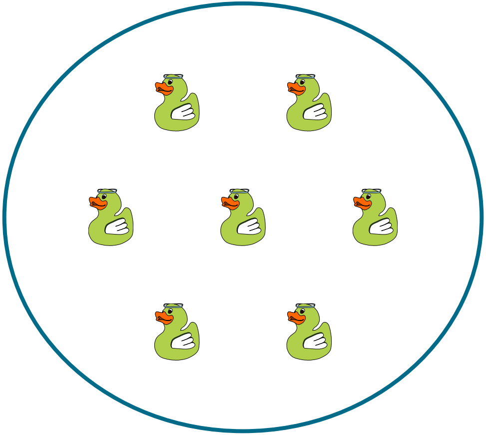

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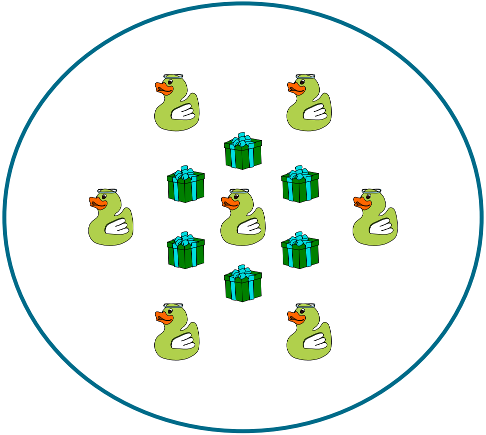

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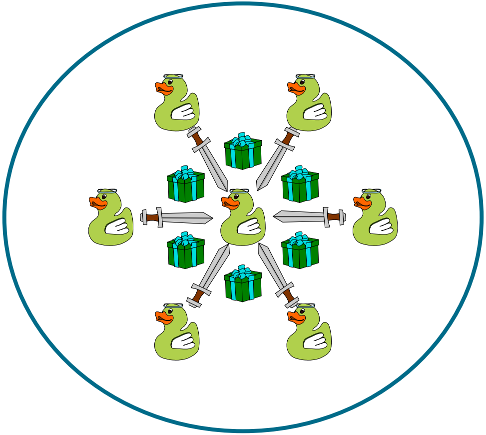

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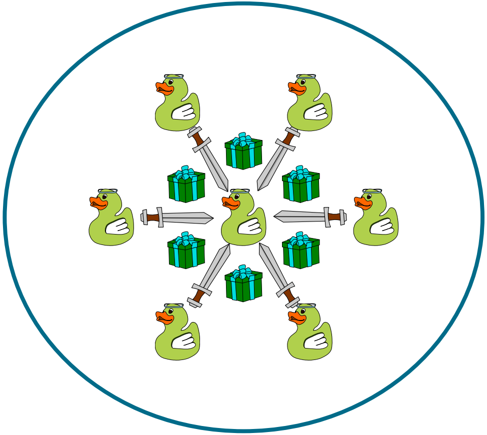


Evolutionary Ecology, 1992, **6**, 352–356

Altruism in viscous populations – an inclusive fitness model

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

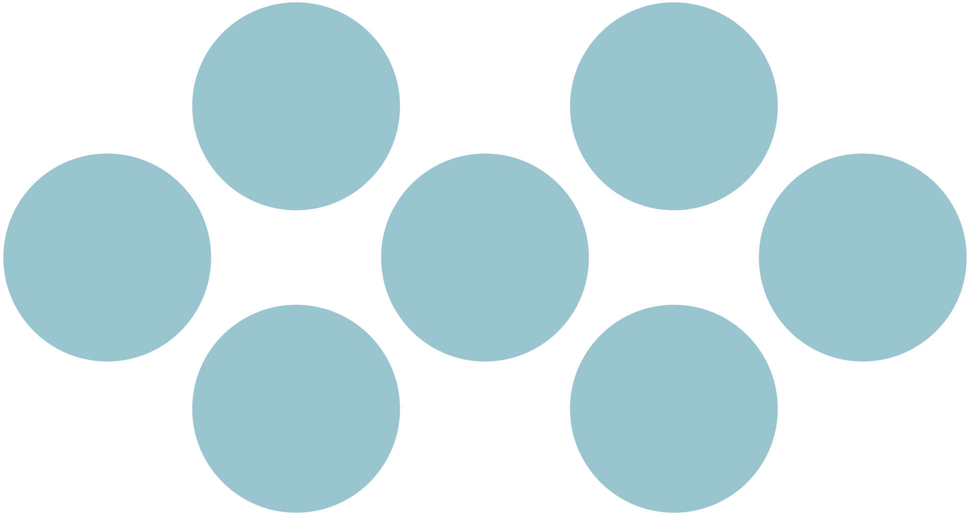
Summary

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

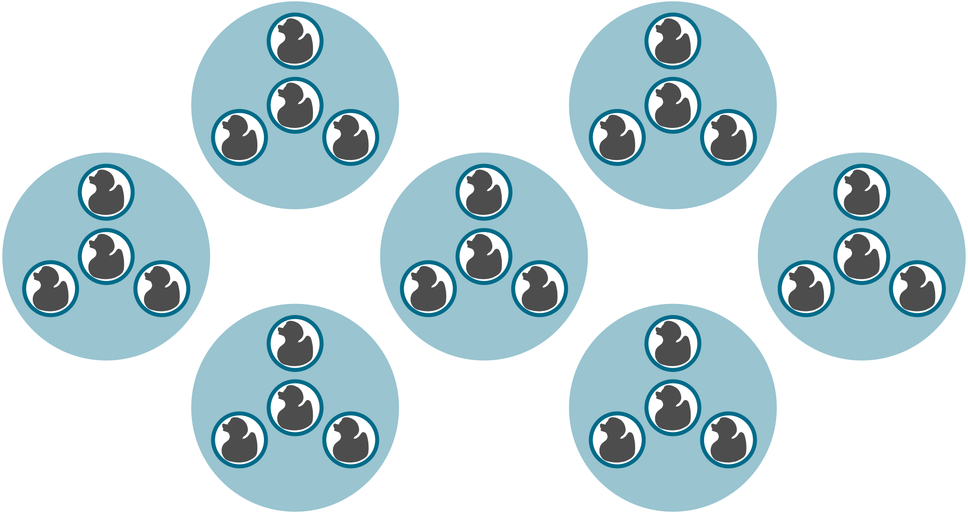
Subdivided population – Island model

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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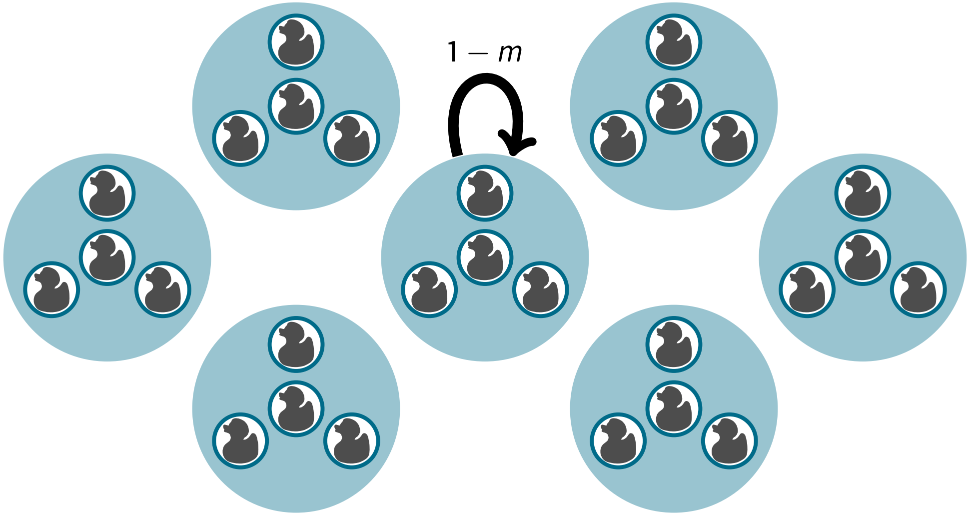

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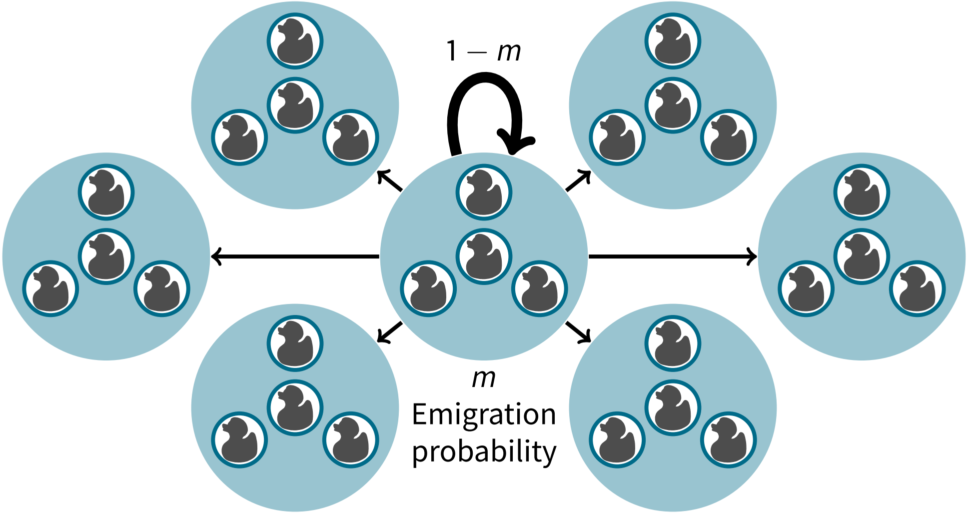

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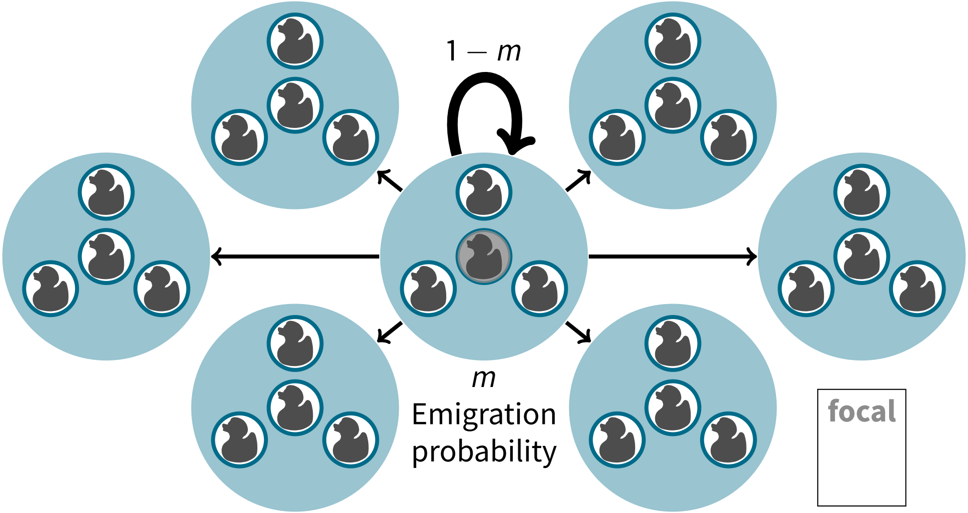

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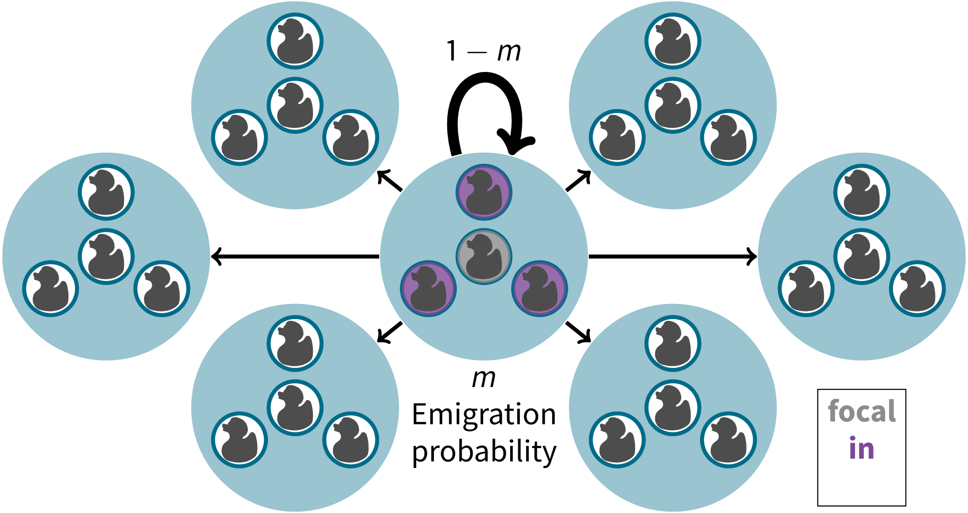

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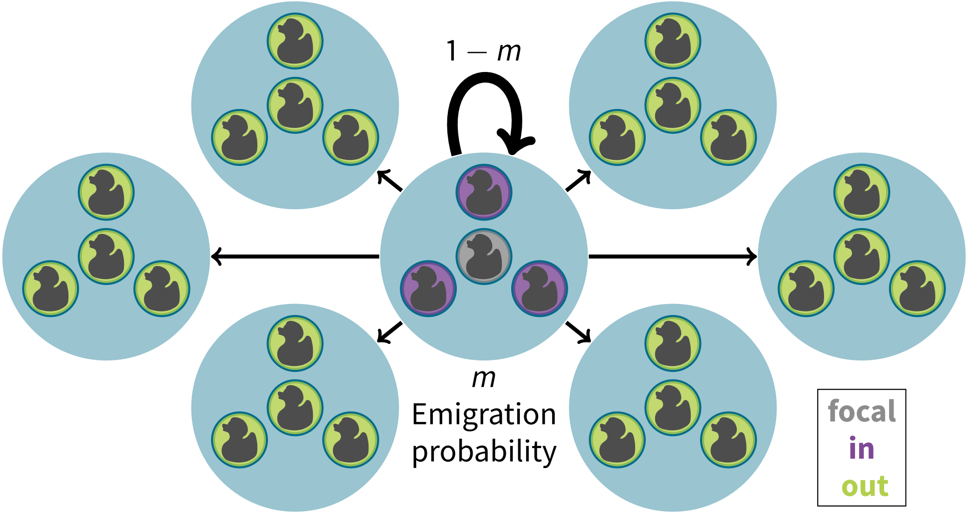

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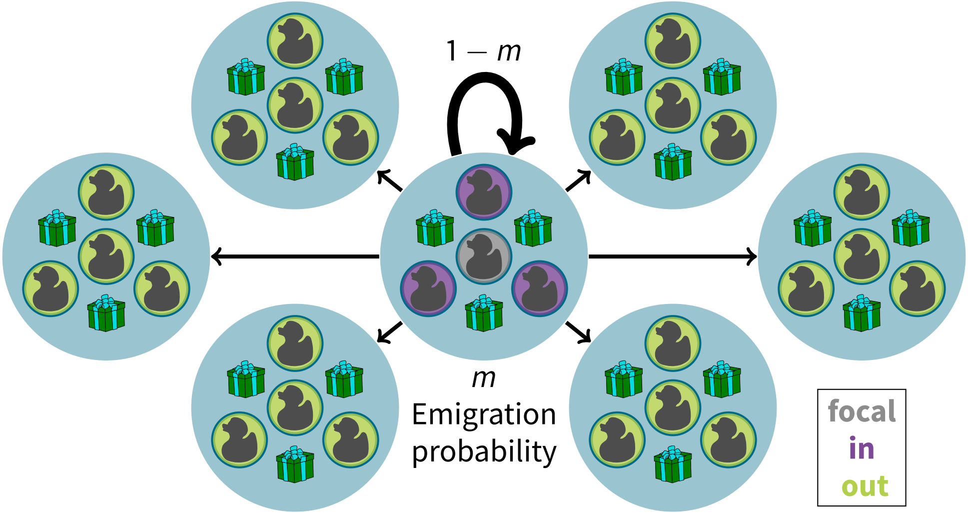

The choice of life-cycle matters

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

N & N

Moran Birth-Death

1 & 1

Moran Death-Birth

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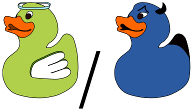

In homogeneously structured populations,
with effects of social interactions on **fecundity**.

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

A common feature of models

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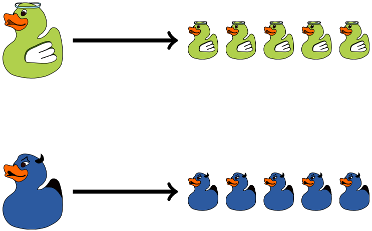

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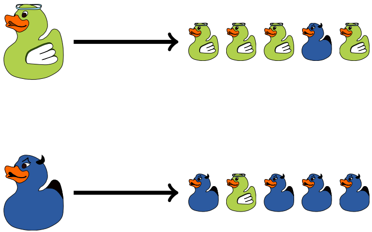

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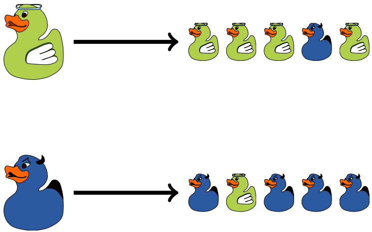
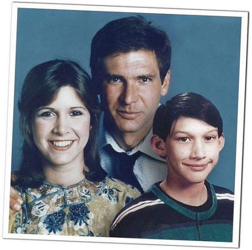


What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

Fidelity of parent-offspring transmission



Causes of imperfect strategy transmission

- Mutation

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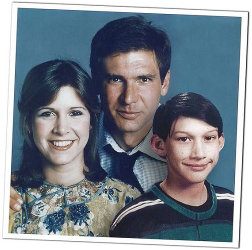

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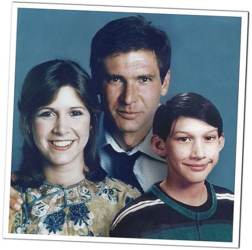

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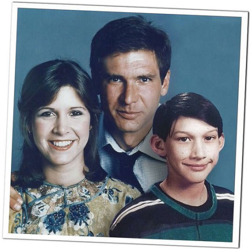

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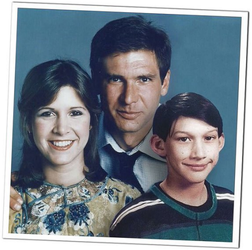
In the model

Parent

Fidelity of parent-offspring transmission



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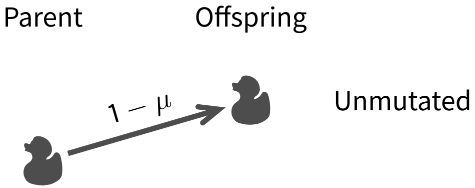

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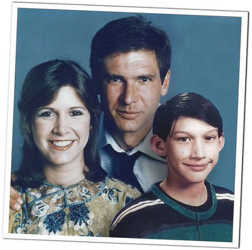

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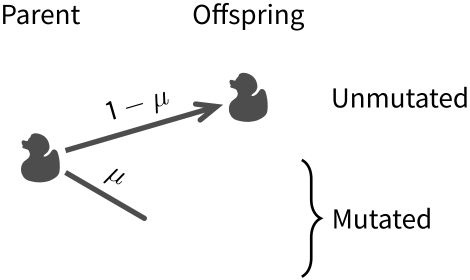

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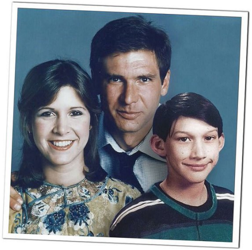

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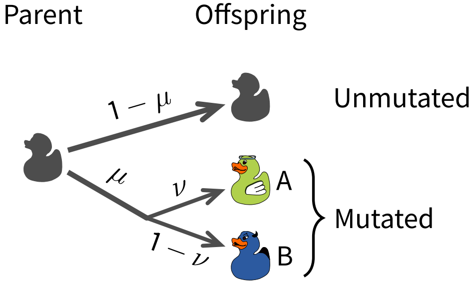

Notation

$\mathbf{X}(t)$; $X_i(t) =$

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

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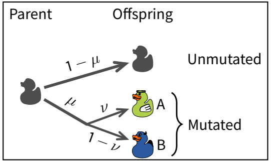

$$\mathbb{E}[Y_i] \qquad = (1-\mu)X_i + \mu\nu \times 1 + \mu(1-\nu) \times 0.$$

Expected trait of the offspring of individual i

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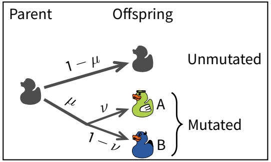

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Proportion of altruists in the population:

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

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,

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Proportion of altruists among the other deme-mates

The cost is only paid by altruists

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

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

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

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

- We obtain

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

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)

Calculations (3)

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

- So

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

Rousset & Billiard (2000)

Calculations (3)

- In a subdivided population,

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- Then further decompose with partial derivatives:

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

Rousset & Billiard (2000)

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

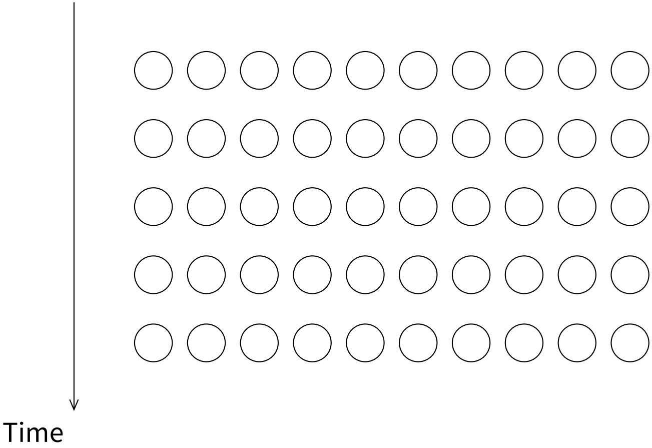
$$\delta \mu B^* \frac{\partial \mathbb{E}[\overline{X}]}{\partial \delta} = \frac{\delta}{N} \sum_{i=1}^{N} \left(\underbrace{\frac{\partial W_i}{\partial \phi_i}}_{-\mathcal{C}} + \underbrace{(n-1)\frac{\partial W_i}{\partial \phi_{\text{in}}}}_{\mathcal{B}} \underbrace{\frac{P_{\text{in}} - P_{\text{out}}}{P_{ii}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

- Then further decompose with partial derivatives:

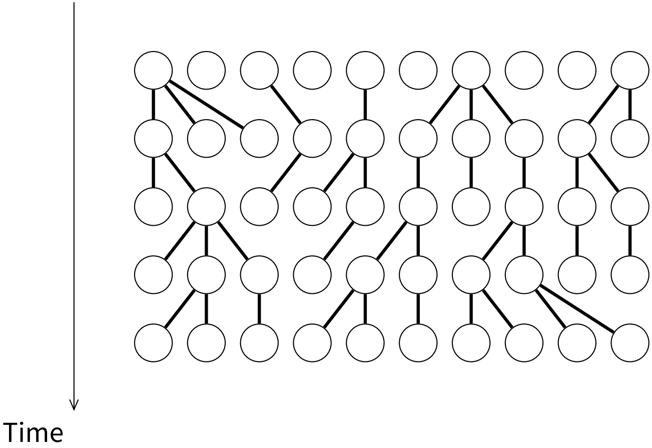
$$\frac{\partial W_i}{\partial \phi_k} = \sum_{\ell=1}^{N} \frac{\partial W_i}{\partial f_\ell} \frac{\partial f_\ell}{\partial \phi_k} \quad \text{and} \quad \frac{\partial f_\ell}{\partial \phi_\ell} = -\text{c}; \quad \frac{\partial f_\ell}{\partial \phi_{\text{in}}} = \frac{\text{b}}{n-1}; \quad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

Rousset & Billiard (2000)

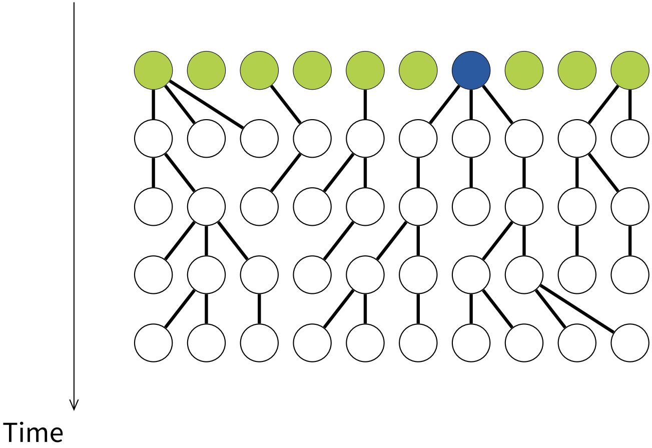
Genealogy, Identity by descent and Identity in state



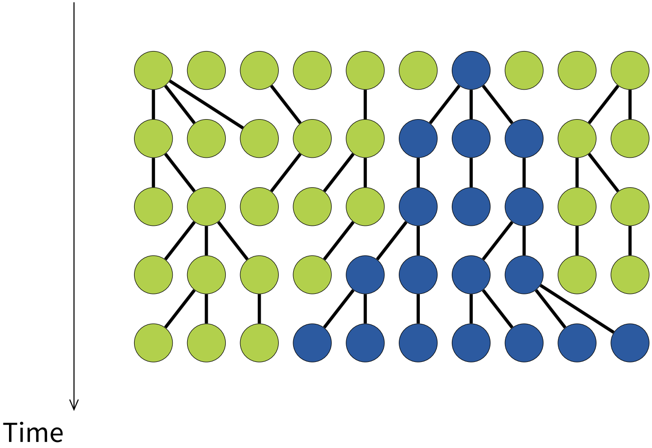
Genealogy, Identity by descent and Identity in state



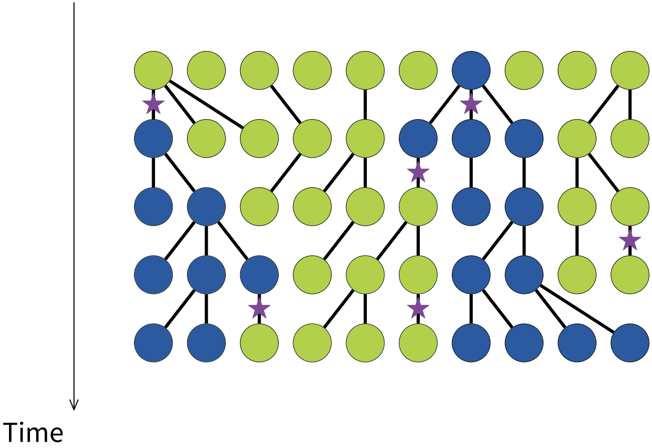
Genealogy, Identity by descent and Identity in state



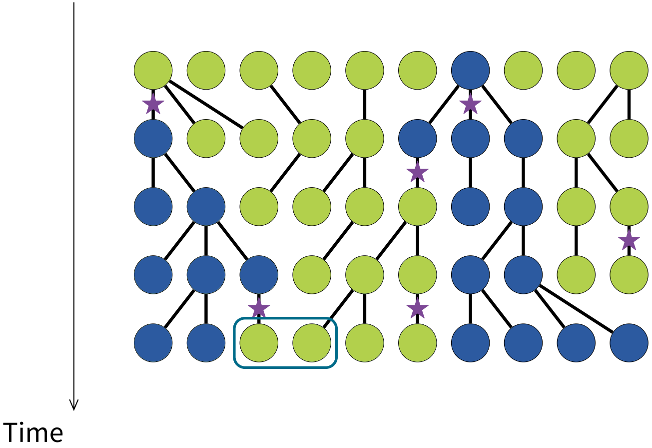
Genealogy, Identity by descent and Identity in state



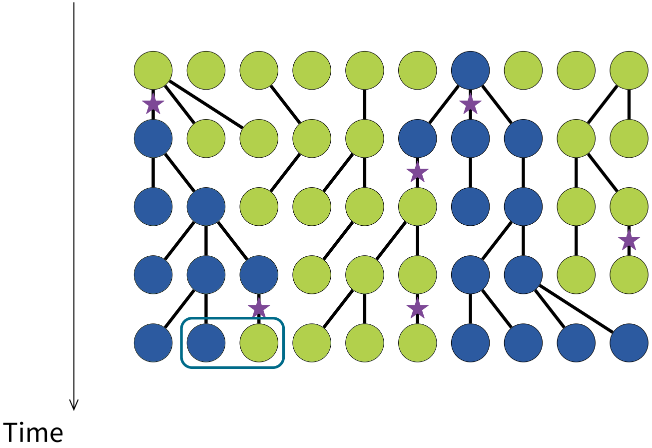
Genealogy, Identity by descent and Identity in state



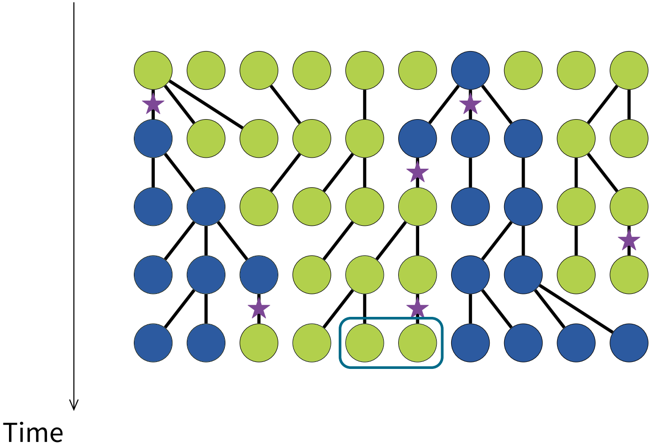
Genealogy, Identity by descent and Identity in state



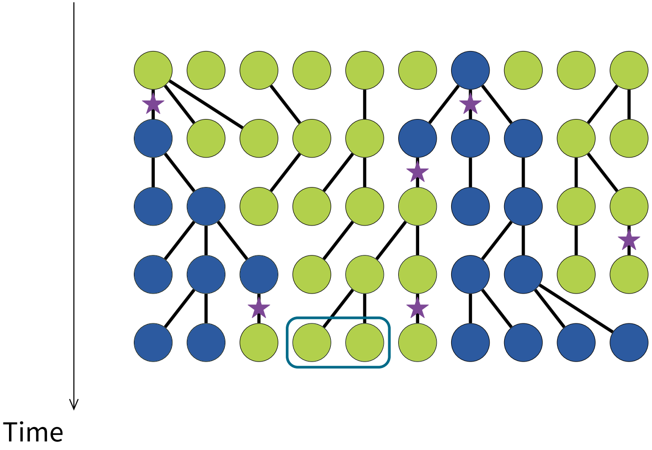
Genealogy, Identity by descent and Identity in state



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

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

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
of the i, j pair
= 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)

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

Probability that both sites are occupied by an altruist

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

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

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

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

Expected frequency of altruists in the population

Mutation-drift
equilibrium

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

Expected frequency of altruists in the population

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

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

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

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

Expected frequency of altruists in the population

$$
\begin{aligned}
\mathbb{E}[\overline{X}] = {} & \overbrace{\nu}^{\text{Mutation-drift equilibrium}} + \overbrace{\delta}^{\text{Selection strength}} \; \overbrace{\nu(1-\nu)}^{\text{Variance in the state of one site}} \frac{1-\mu}{\mu} \left(1 - Q_{\mathrm{out}}\right) \times \\
& \left(\boxed{-\mathrm{c} - (\mathrm{b}-\mathrm{c}) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d - 1\right)} \right)} \; -\mathcal{C} \right. \\
& \left. + \frac{Q_{\mathrm{in}} - Q_{\mathrm{out}}}{1 - Q_{\mathrm{out}}} \left[\underbrace{\mathrm{b} - (\mathrm{b}-\mathrm{c})\,(n-1) \left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d - 1\right)} \right)}_{\mathcal{B}} \right] \right)
\end{aligned}
$$

Expected frequency of altruists in the population

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

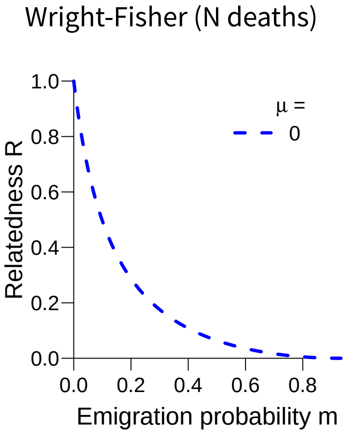
$$
\left(\underbrace{-\mathrm{c} - (\mathrm{b}-\mathrm{c})\left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d-1\right)}\right)}_{-\mathcal{C}} + \underbrace{\frac{Q_{\text{in}}-Q_{\text{out}}}{1-Q_{\text{out}}}}_{R} \left[\underbrace{\mathrm{b} - (\mathrm{b}-\mathrm{c})\,(n-1)\left(\frac{(1-m)^2}{n} + \frac{m^2}{n\left(N_d-1\right)}\right)}_{\mathcal{B}}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

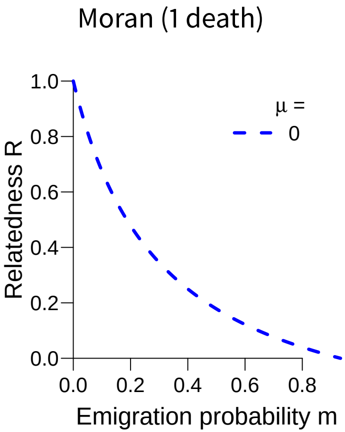
Expected frequency of altruists in the population

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

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

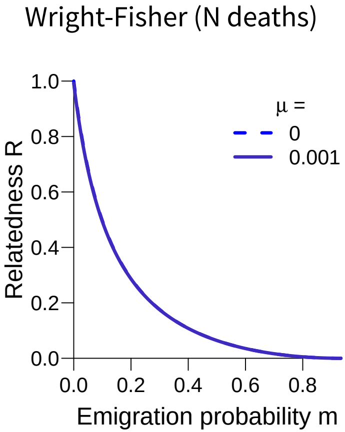
How does relatedness R change with the emigration probability m?

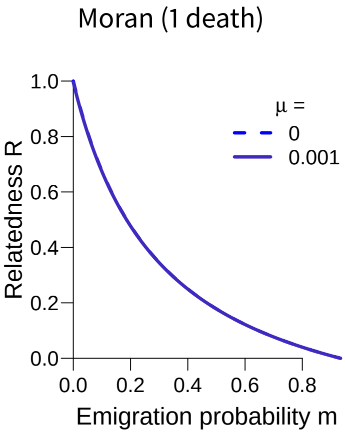




$(n = 4, N_d = 15)$

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

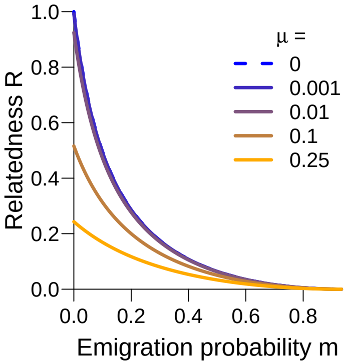




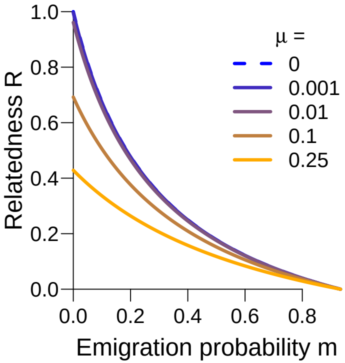
$(n = 4, N_d = 15)$

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

Wright-Fisher (N deaths)



Moran (1 death)



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

Expected frequency of altruists in the population

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

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

Expected frequency of altruists in the population

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

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

Variance in the state of one site $\searrow$

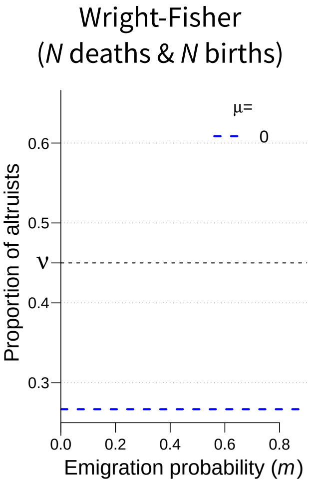
$$\mathbb{E}[\overline{X}] = \nu + \delta\, \nu(1-\nu)\, \frac{1-\mu}{\mu} \left(1 - Q_{\text{out}}\right) \times$$

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

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

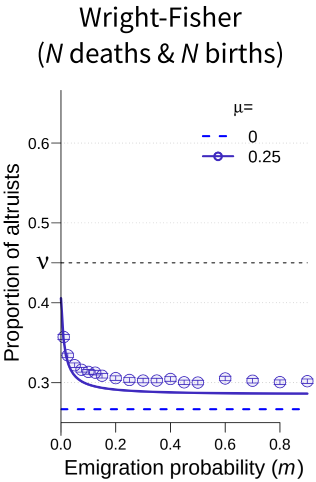
$R \searrow \qquad \mathcal{B} \nearrow$

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



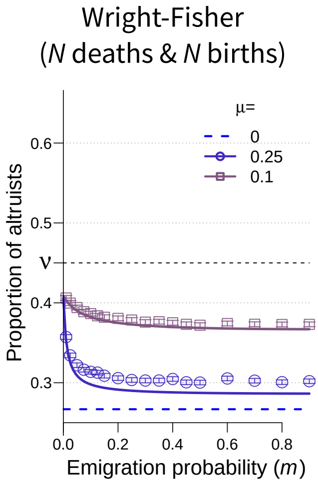
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



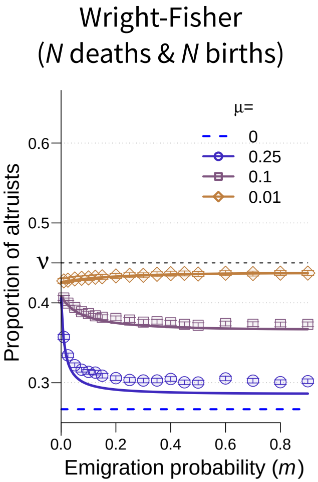
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

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



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

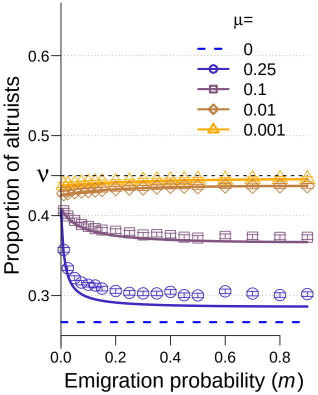
Effect of the emigration probability m on the expected proportion of altruists



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

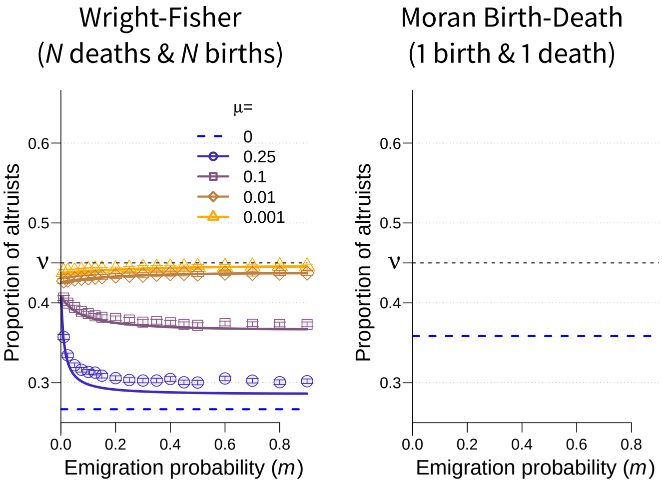
Effect of the emigration probability m on the expected proportion of altruists

Wright-Fisher
(N deaths & N births)



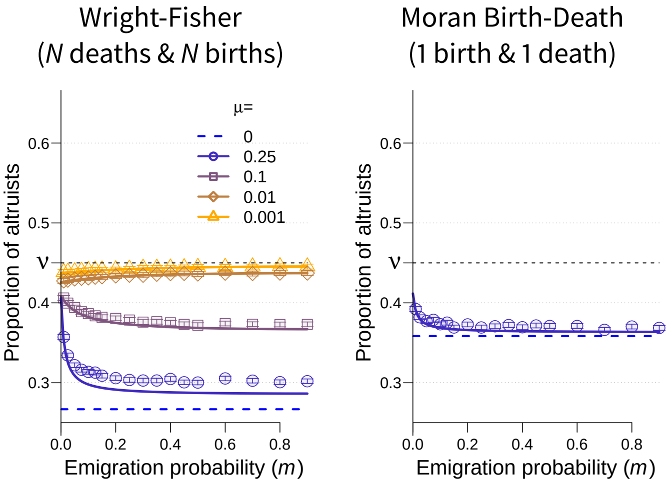
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



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

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



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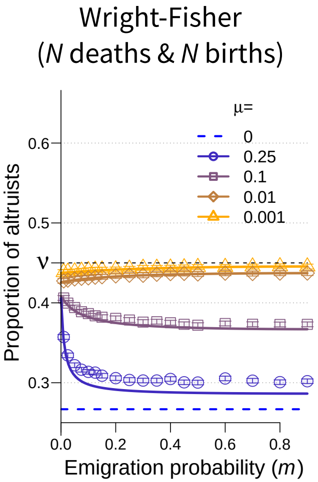

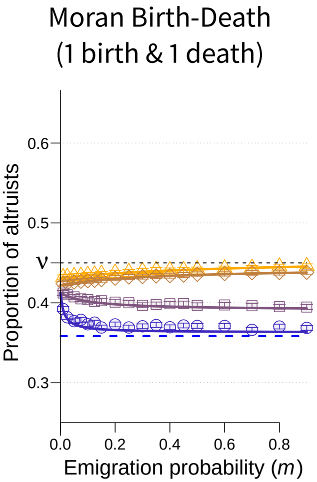

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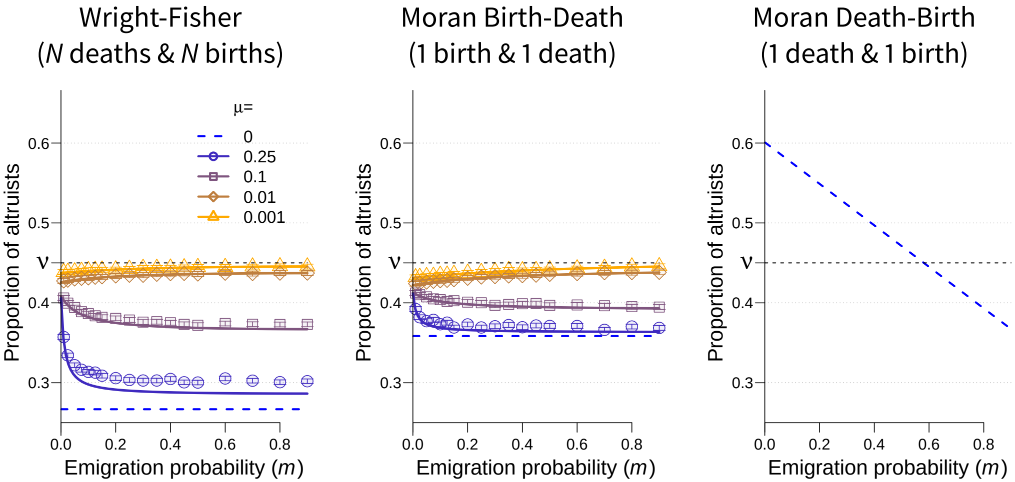

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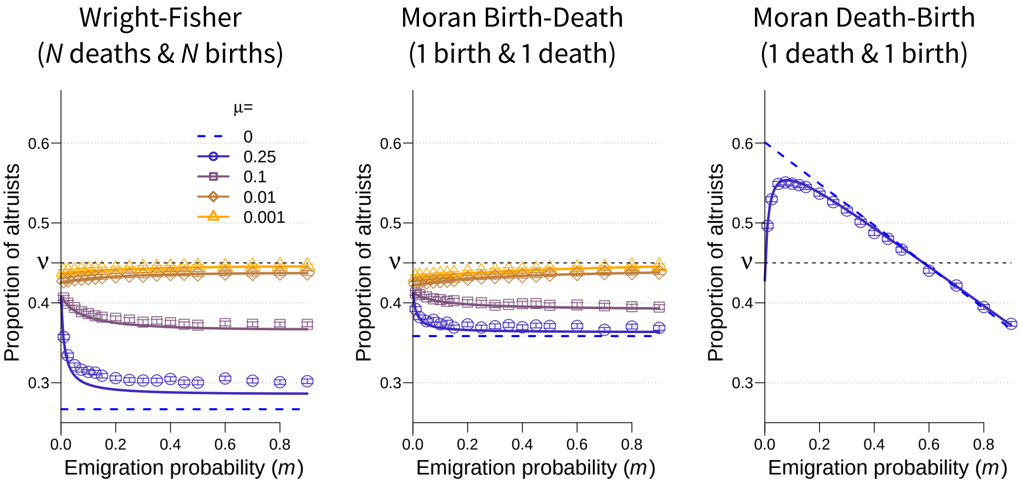

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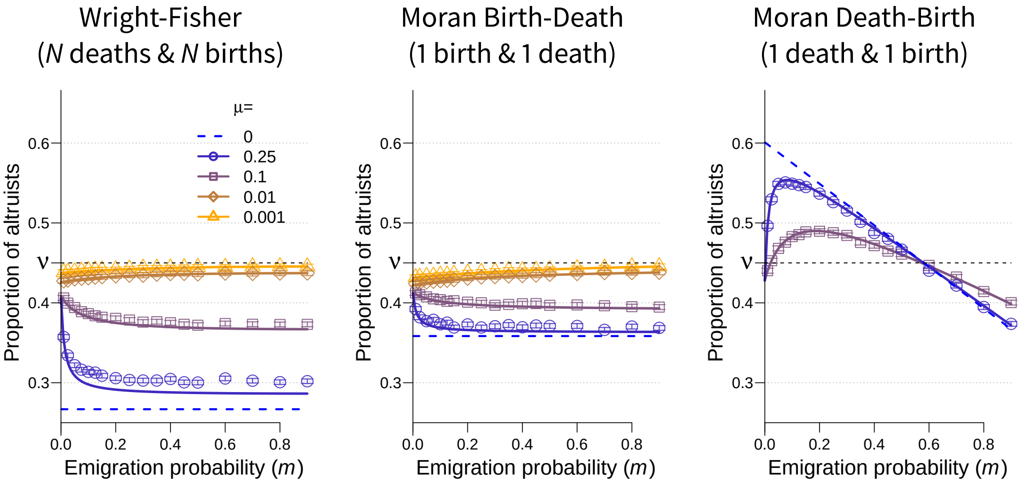

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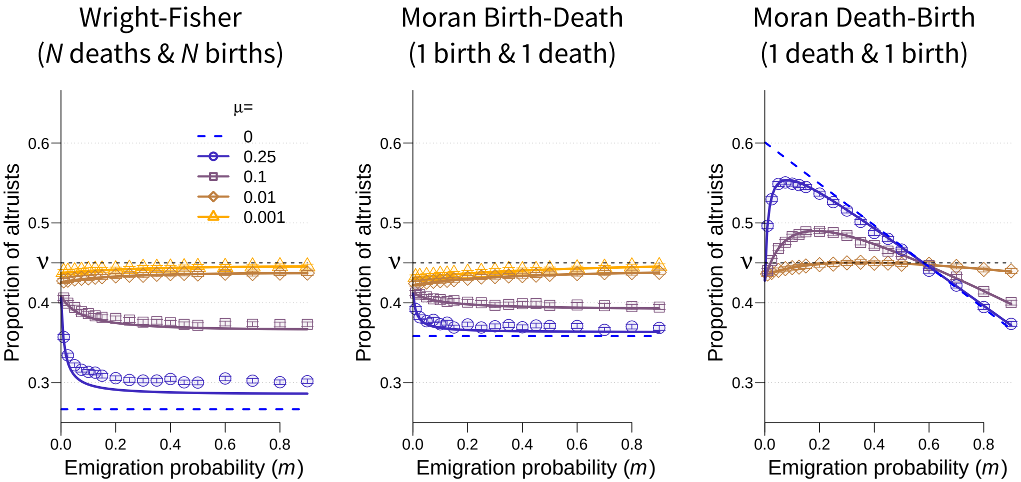

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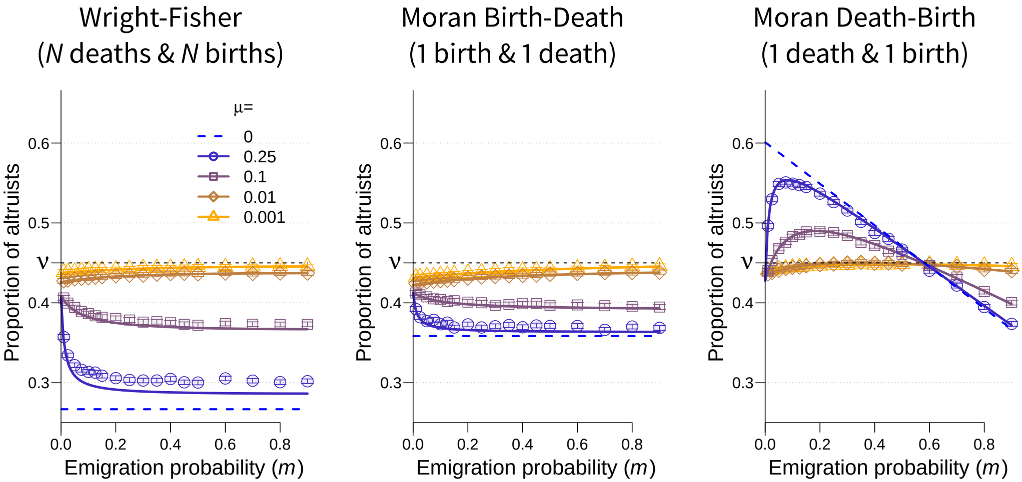

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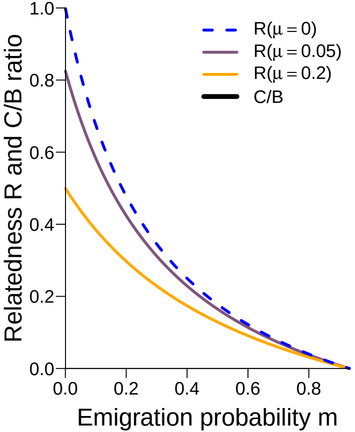

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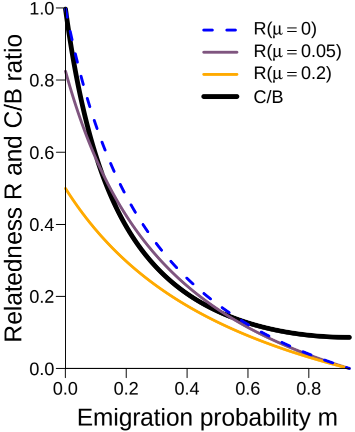
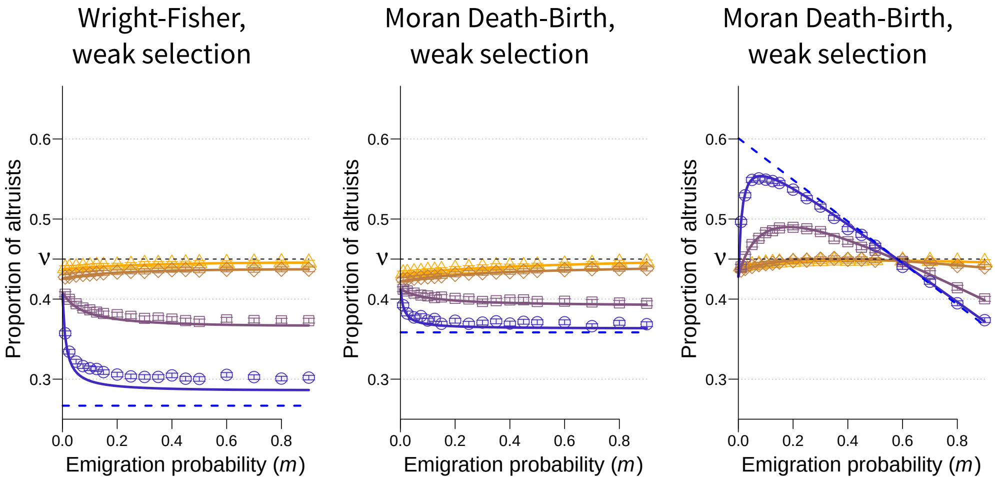


Is the result robust?

Strong selection



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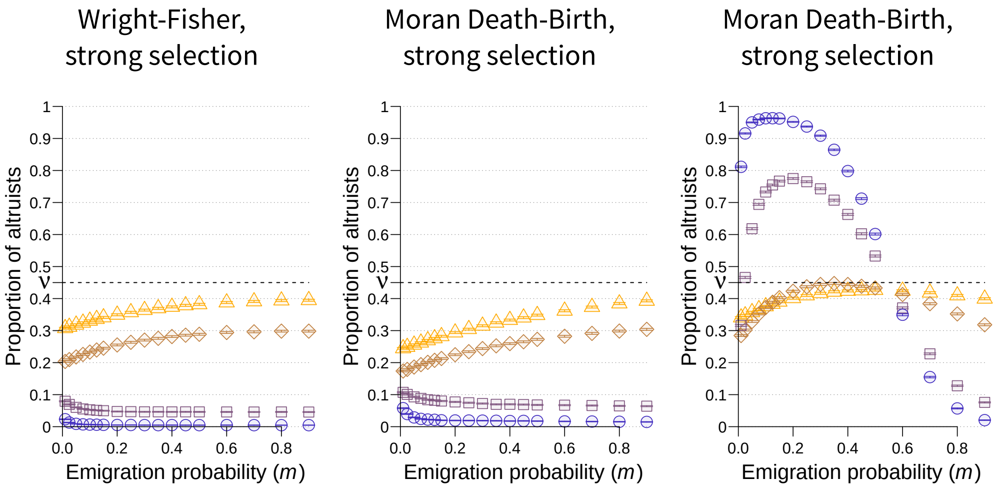

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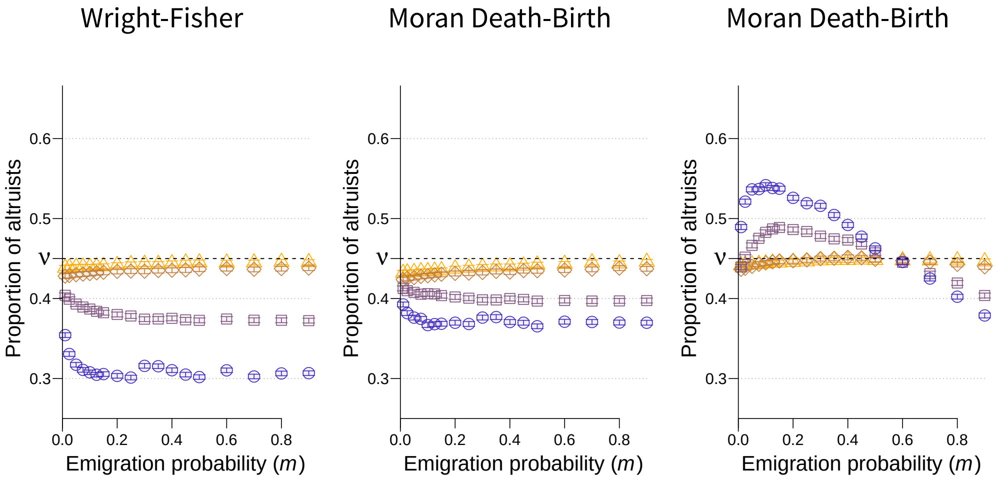
Heterogeneous deme sizes ($\bar{n} = 4$ as before, but $2 \leq n \leq 5$)



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Political implications

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PLoS one

A Test of Evolutionary Policing Theory with Data from Human Societies

Rolf Kümmerli[1,2]*

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Abstract

In social groups where relatedness among interacting individuals is low, cooperation can often only be maintained through mechanisms that repress competition among group members. Repression-of-competition mechanisms, such as policing and punishment, seem to be of particular importance in human societies, where cooperative interactions often occur among unrelated individuals. In line with this view, economic games have shown that the ability to punish defectors enforces cooperation among humans. Here, I examine a real-world example of a repression-of-competition system, the police institutions common to modern human societies. Specifically, I test evolutionary policing theory by comparing data on policing effort, per capita crime rate, and similarity (used as a proxy for genetic relatedness) among citizens across the 26 cantons of Switzerland. This comparison revealed full support for all three predictions of evolutionary policing theory. First, when controlling for policing efforts, crime rate correlated negatively with the similarity among citizens. This is in line with the prediction that high similarity results in higher levels of cooperative self-restraint (i.e. lower crime rates) because it aligns the interests of individuals. Second, policing effort correlated negatively with the similarity among citizens, supporting the prediction that more policing is required to enforce cooperation in low-similarity societies, where individuals' interests diverge most. Third, increased policing efforts were associated with reductions in crime rates, indicating that policing indeed enforces cooperation. These analyses strongly indicate that humans respond to cues of their social environment and adjust cheating and policing behaviour as predicted by evolutionary policing theory.

Citation: Kümmerli R (2011) A Test of Evolutionary Policing Theory with Data from Human Societies. PLoS ONE 6(9): e24350. doi:10.1371/journal.pone.0024350

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A Test of Evolutionary Policing Theory with Data from

For the per capita crime rate, I considered crimes that violated the main code of law (i.e. the 'Schweizerische Strafgesetzbuch', StGB) and divided the number of registered crimes by the number of citizens. The StGB covers all types of crimes, except crimes related to drug abuse/dealing and violation of traffic rules (i.e. 82% of all crimes reported in Switzerland in 2009 fall under the StGB). For the policing effort, I divided the amount of tax money invested into policing by the number of citizens. To obtain a proxy for relatedness, I calculated a similarity index (s) as follows. I first defined dissimilarity (d) among citizens as $d = w\log(c) + f$, where $\log(c)$ is the natural logarithm of the number of citizens, f is the proportion of foreigners, and w is a scaling factor such that both addends are weighted equally. I then calculated $s = 1\text{-}d/d_{max}$, where d_{max} represents the highest dissimilarity value observed among all cantons. Consequently, s ranges between zero and one, whereby s=0 for the canton with d_{max}.

...witzerland, 2 Department of

...maintained through ...s, such as policing ...ctions often occur ...o punish defectors enforces cooperation among humans. Here, I examine a real-world example of a repression-of-competition system, the police institutions common to modern human societies. Specifically, I test evolutionary policing theory by comparing data on policing effort, per capita crime rate, and similarity (used as a proxy for genetic relatedness) among citizens across the 26 cantons of Switzerla... when controlling fo... the prediction that... the interests of indi... prediction that mo... diverge most. Thir... indeed enforces co... adjust cheating and policing behaviour as predicted by evolutionary policing theory.

The first finding, showing that crime rates were lower in societies with high similarity indexes, suggests that similarity among citizens can be considered analogous to genetic relatedness as used in Hamilton's rule. Specifically, it seems that high similarity, analogous to high genetic relatedness, aligns the interest of individuals in a group and thereby promotes cooperative self-restraint even in the absence of policing. There are at least two explanations why this might be.

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and thank you for your attention!