Symposium 9: Fitness and evolution in a social environment: from theory to reality

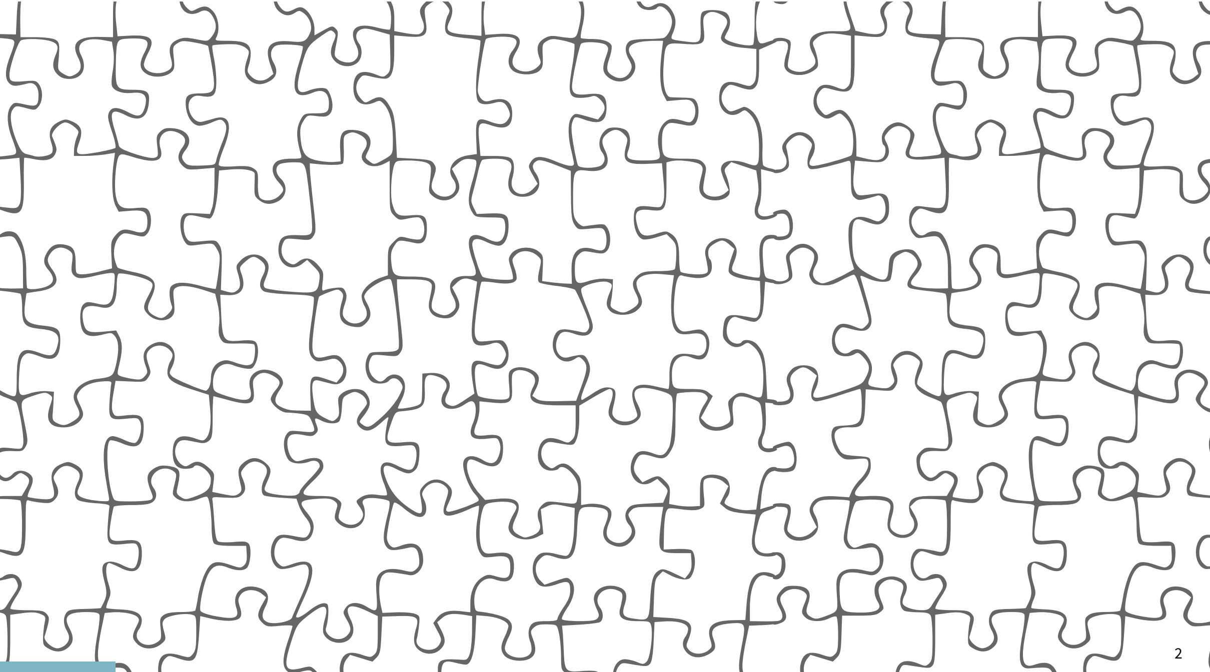
# Fidelity of parent-offspring transmission and the evolution of social behavior in subdivided populations.

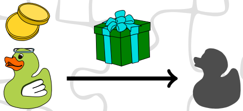

F. Débarre

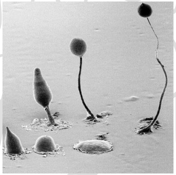
@flodebarre

CNRS

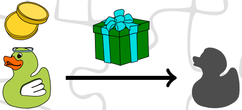
Centre de Recherches Interdisciplinaires en Biologie, Paris



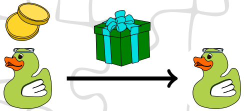

(c) Grimson & Blanton


(c) Wikimedia

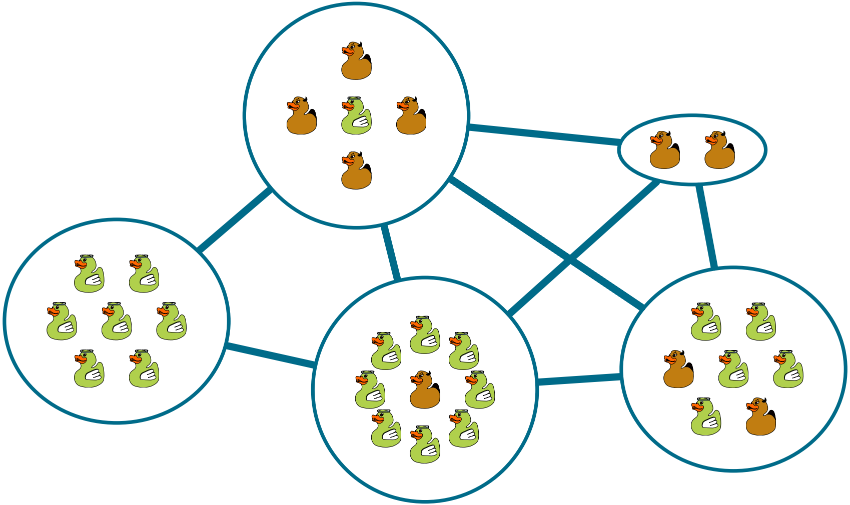



(c) FD

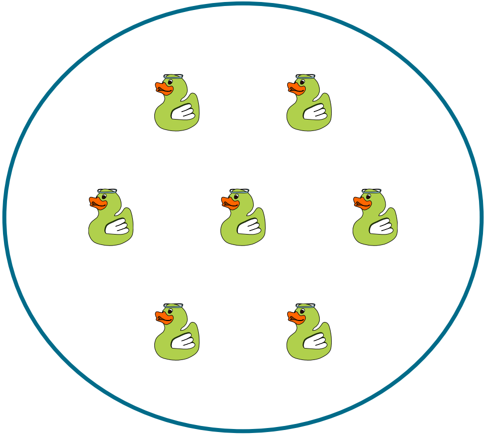

(c) picturesforcoloring.com



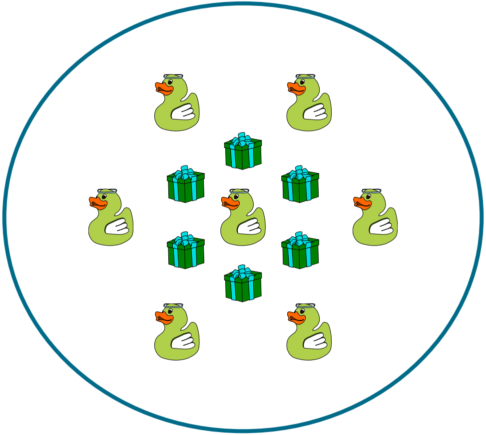
# Spatial structure and altruism



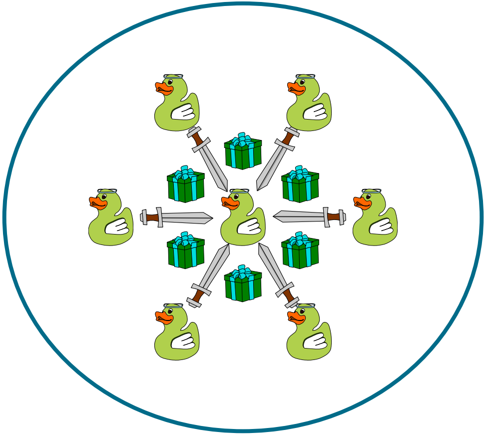
# Spatial structure and altruism



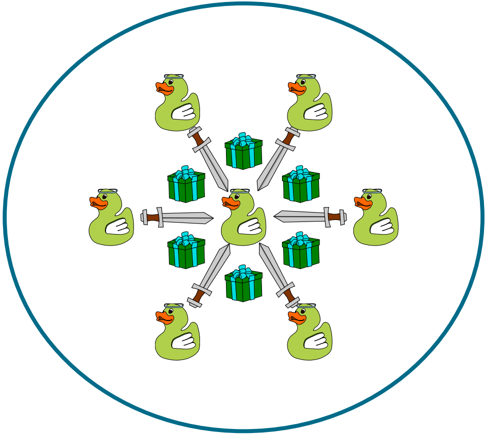
# Spatial structure and altruism

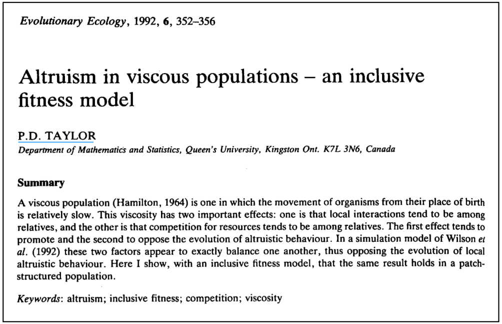


# Spatial structure and altruism



# Spatial structure and altruism





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

## Altruism in viscous populations – an inclusive fitness model

P.D. TAYLOR

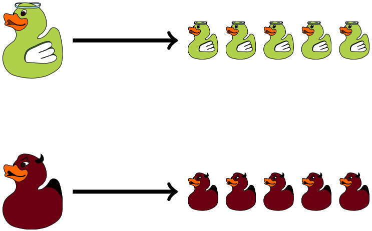
*Department of Mathematics and Statistics, Queen's University, Kingston Ont. K7L 3N6, Canada*

**Summary**

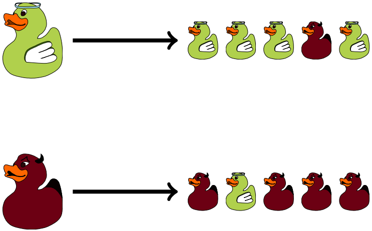
A viscous population (Hamilton, 1964) is one in which the movement of organisms from their place of birth is relatively slow. This viscosity has two important effects: one is that local interactions tend to be among relatives, and the other is that competition for resources tends to be among relatives. The first effect tends to promote and the second to oppose the evolution of altruistic behaviour. In a simulation model of Wilson *et al*. (1992) these two factors appear to exactly balance one another, thus opposing the evolution of local altruistic behaviour. Here I show, with an inclusive fitness model, that the same result holds in a patch-structured population.

*Keywords*: altruism; inclusive fitness; competition; viscosity

# A common feature of models



# A common feature of models

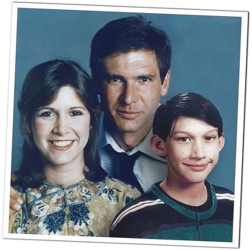


What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

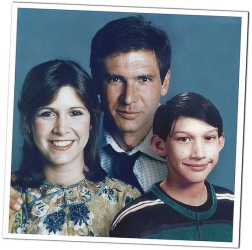
# Fidelity of parent-offspring transmission

## Causes of imperfect strategy transmission

- Mutation



# Fidelity of parent-offspring transmission



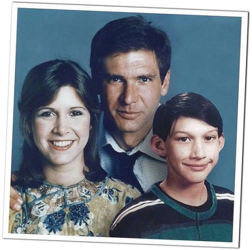
## Causes of imperfect strategy transmission

- Mutation
- Partial heritability

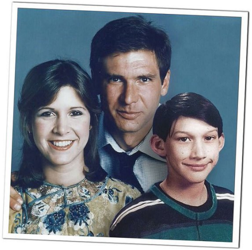
# Fidelity of parent-offspring transmission

## Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)



# Fidelity of parent-offspring transmission



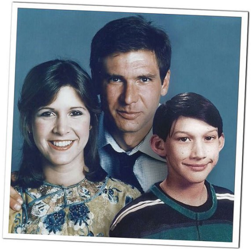
## Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

## In the model

Parent

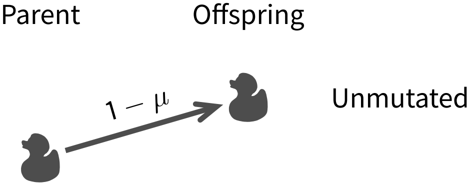
# Fidelity of parent-offspring transmission



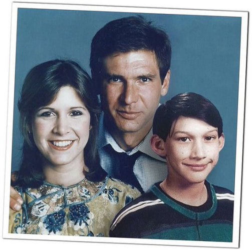
## Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

## In the model



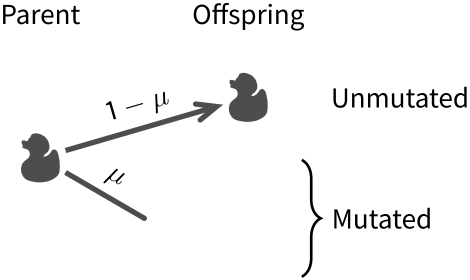
# Fidelity of parent-offspring transmission



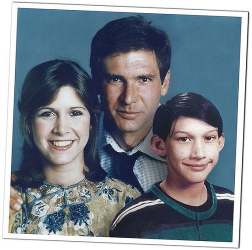
## Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

## In the model



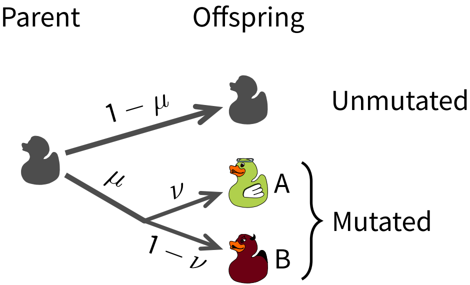
# Fidelity of parent-offspring transmission



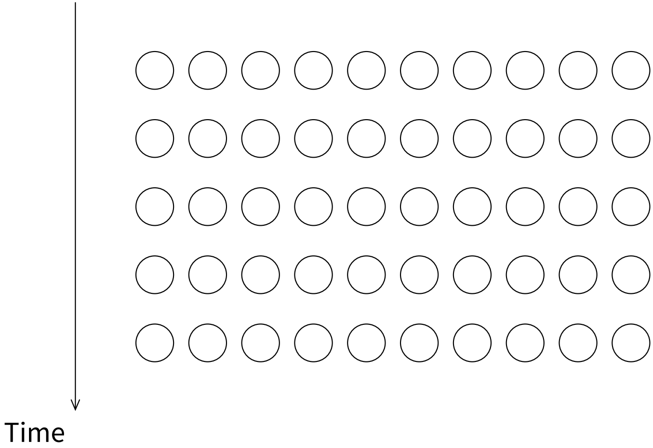
## Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

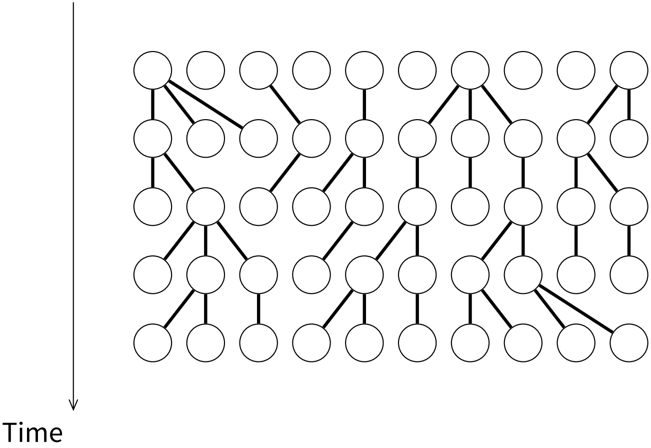
## In the model



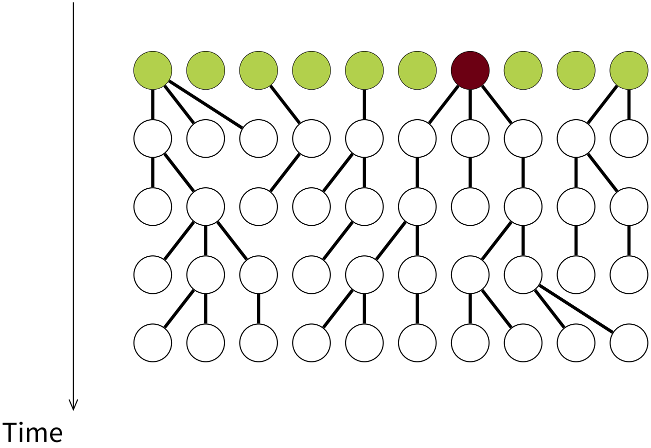
# Genealogy, Identity by descent and Identity in state



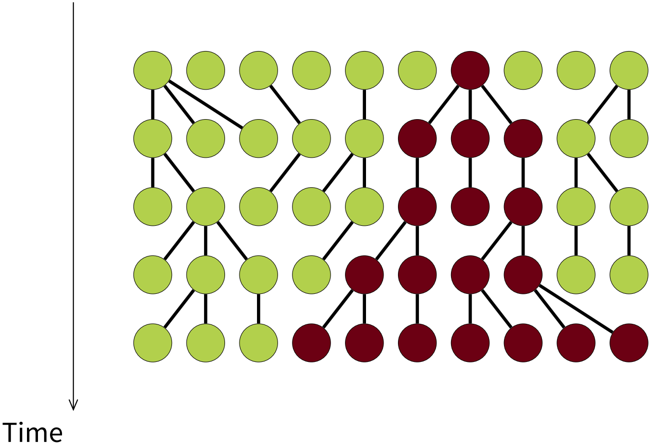
# Genealogy, Identity by descent and Identity in state



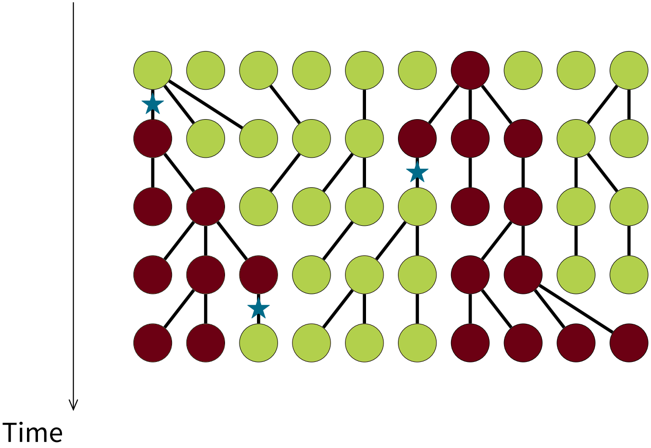
# Genealogy, Identity by descent and Identity in state



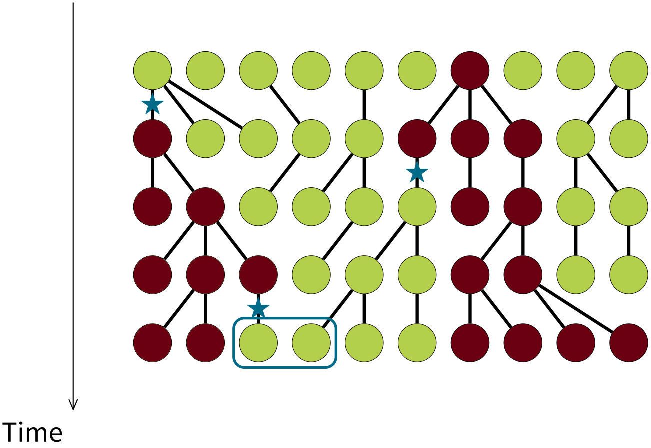
# Genealogy, Identity by descent and Identity in state



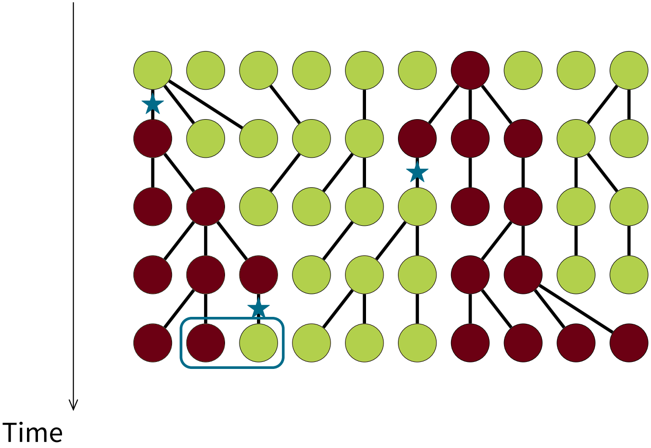
# Genealogy, Identity by descent and Identity in state



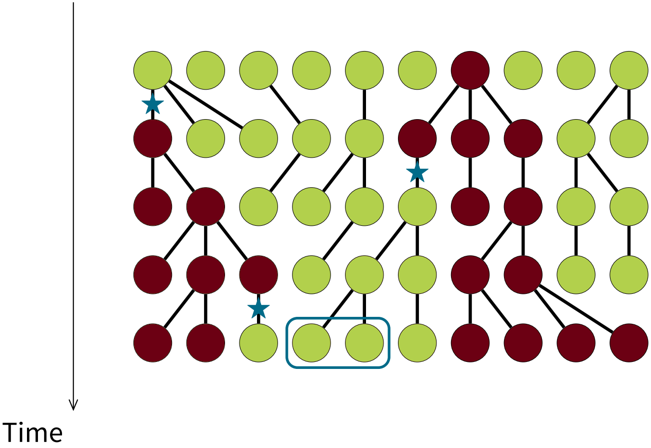
# Genealogy, Identity by descent and Identity in state



# 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)

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

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

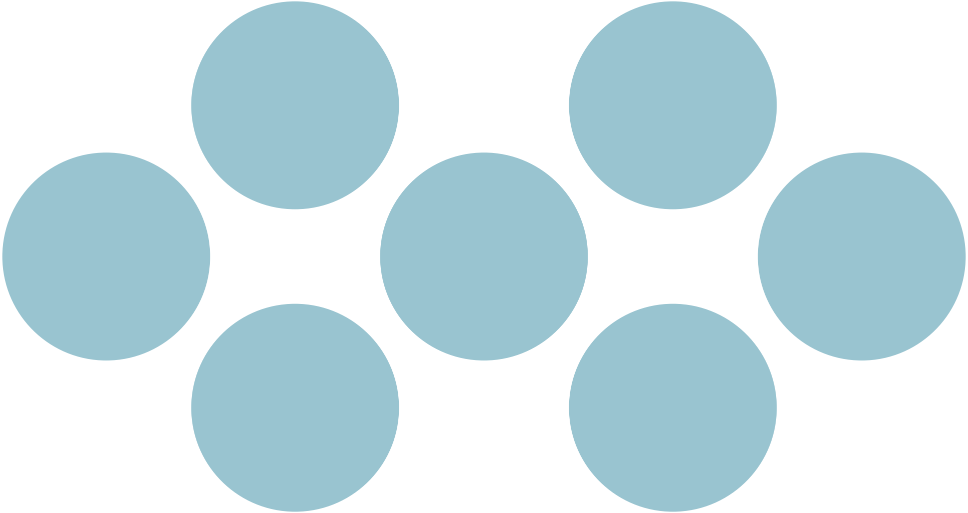
Probability that a mutant is an altruist = Probability that a given site is occupied by an altruist

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

$Q_{\text{in}}$, $Q_{\text{out}}$

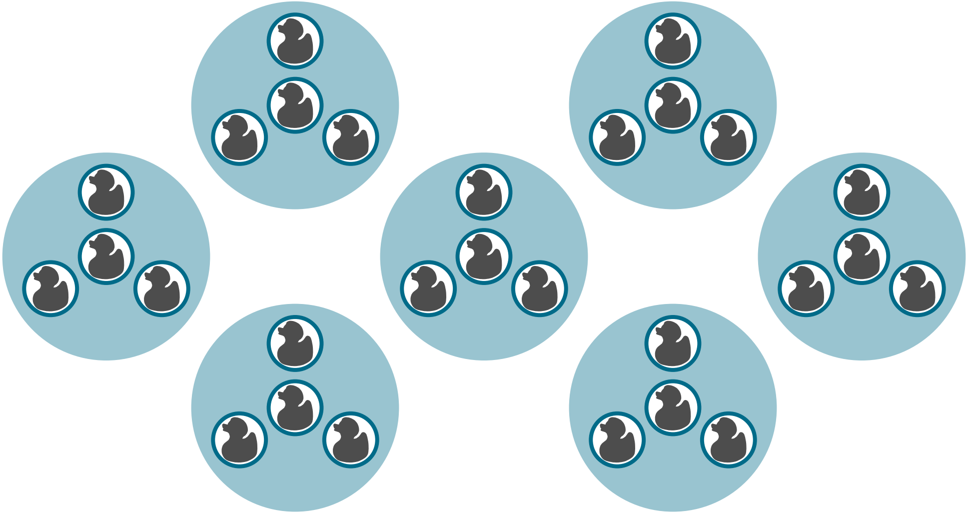
# Subdivided population – Island model

$N_d$ demes



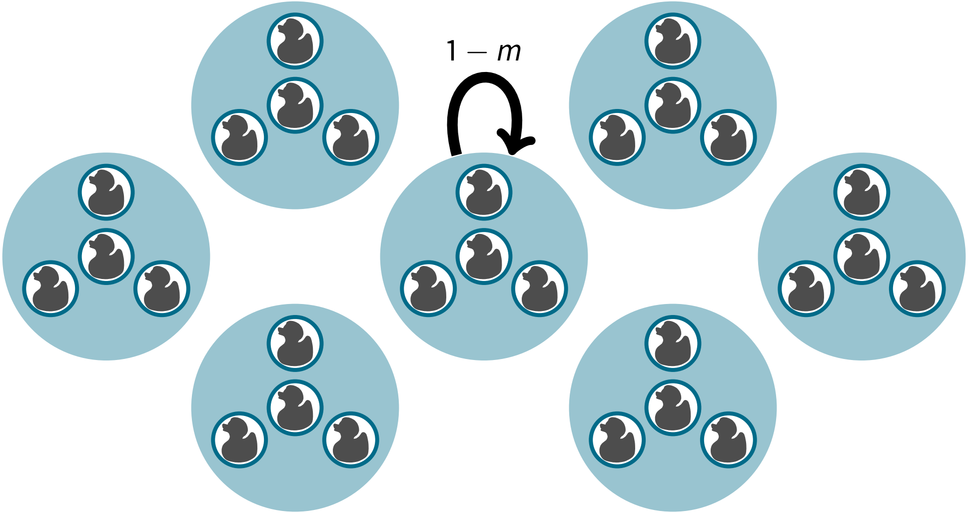
# Subdivided population – Island model

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



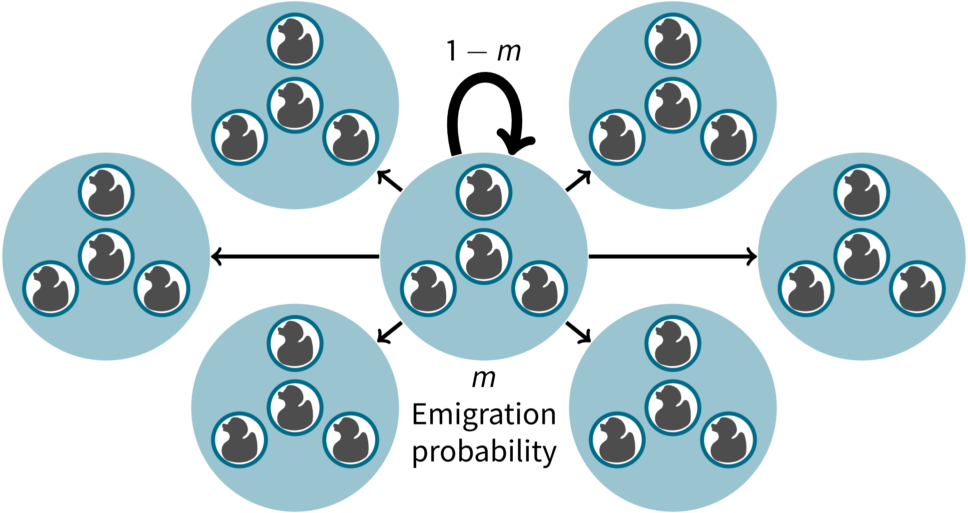
# Subdivided population – Island model

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



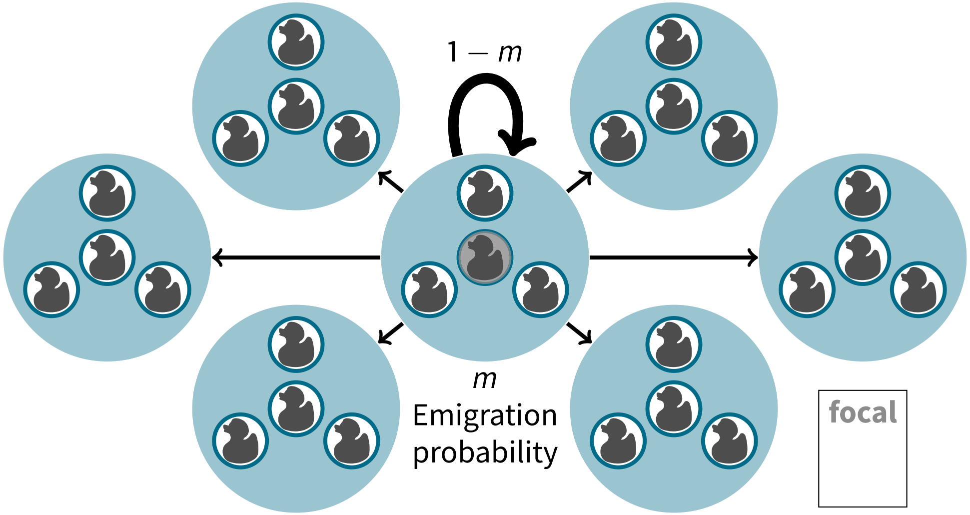
# Subdivided population – Island model

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



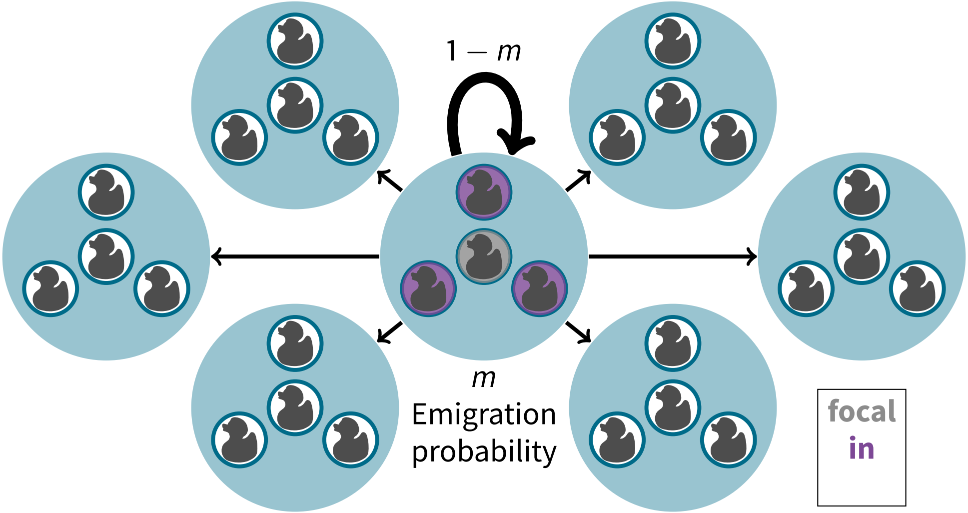
# Subdivided population – Island model

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



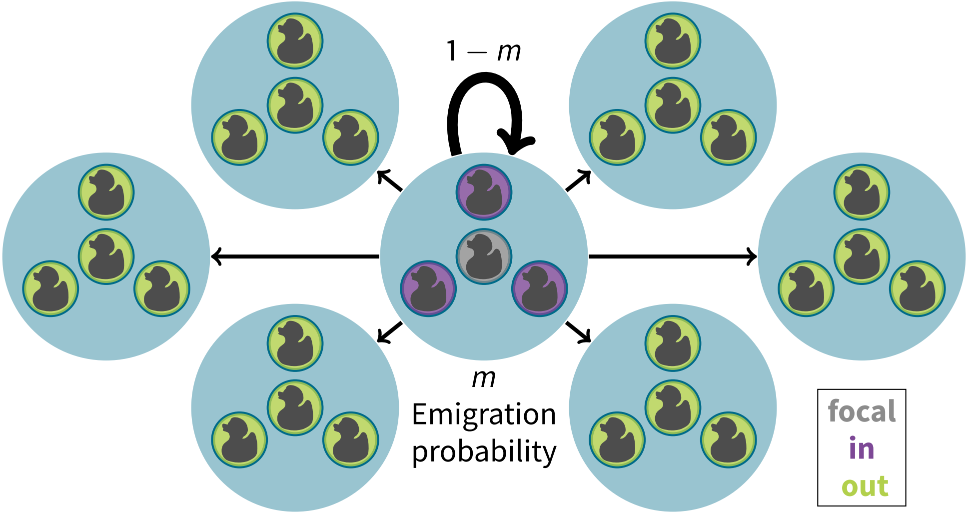
# Subdivided population – Island model

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



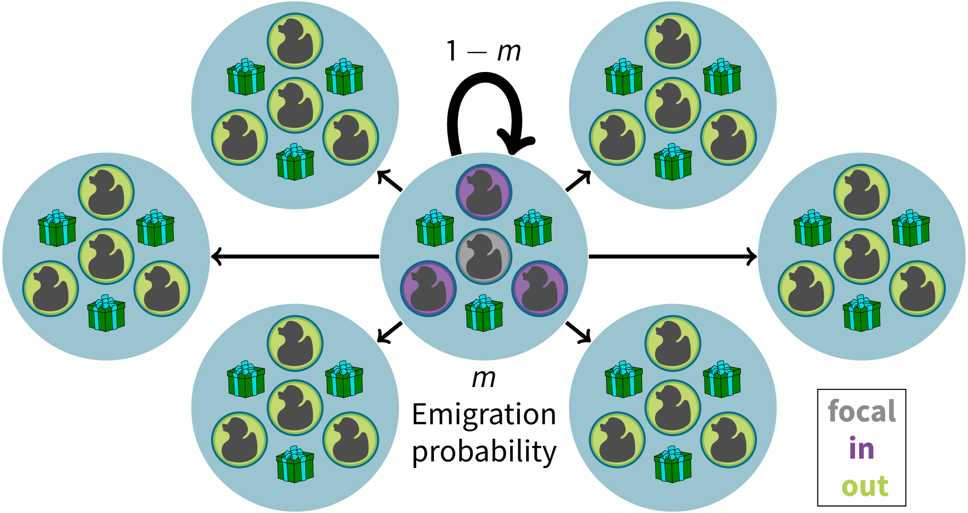
# Subdivided population – Island model

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



# Subdivided population – Island model

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



# Updating the population

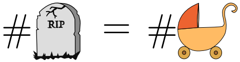
Constant population size ($N$), so between two time steps,

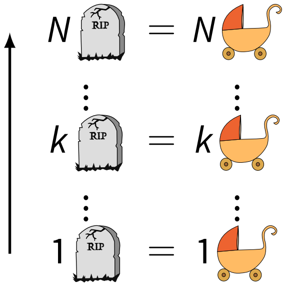
$\#$ 

$=$ $\#$ 

# Updating the population

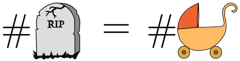
Constant population size ($N$), so between two time steps,

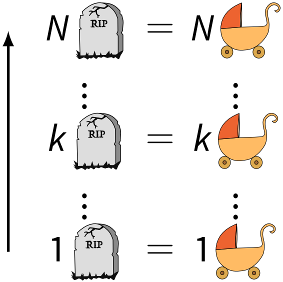


# Updating the population

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



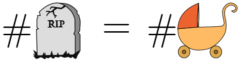



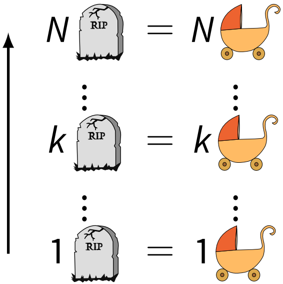

Wright-Fisher

Moran process

# Updating the population

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




Wright-Fisher

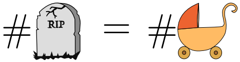
Moran process

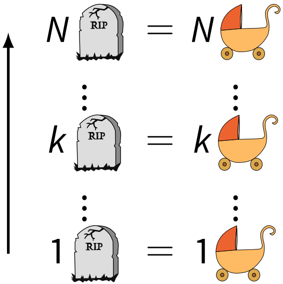
## Life-cycle

Offspring production

# Updating the population

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




Wright-Fisher

Moran process

## Life-cycle

Offspring production

Offspring dispersal

# Updating the population

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

$\#$ 

$=$ $\#$ 

$N$ 

$=$ $N$  Wright-Fisher

$\vdots$ $\vdots$

$k$ 

$=$ $k$ 

$\vdots$ $\vdots$

$1$ 

$=$ $1$  Moran process

## Life-cycle

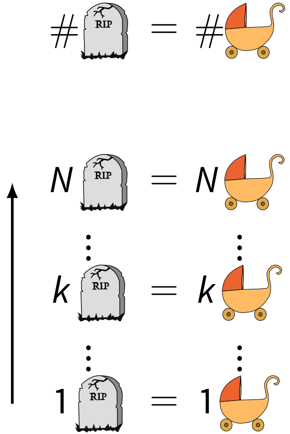
Offspring production

Offspring dispersal

$k$ parents die

# Updating the population

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




Wright-Fisher

Moran process

## Life-cycle

Offspring production

Offspring dispersal

$k$ parents die

Establishment of $k$ offspring

# Updating the population

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

$\#$  $=$ $\#$ 

$N$  $=$ $N$  Wright-Fisher

$\vdots$

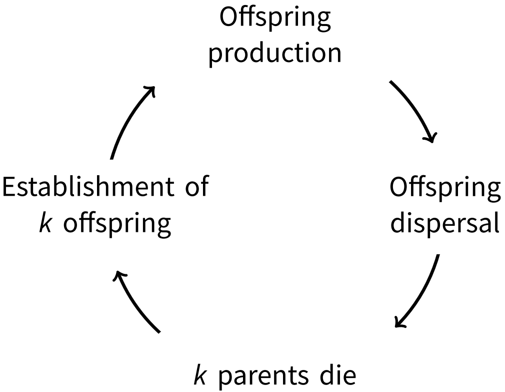
$k$  $=$ $k$ 

$\vdots$

$1$  $=$ $1$  Moran process

## Life-cycle

"Death-Birth" updating



# Population

$X_i(t) = 1$ if site $i$ occupied by  at time $t$ $(1 \leq i \leq N)$

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

# Population

$X_i(t) = \begin{cases} 1 \\ 0 \end{cases}$

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

We are interested in $\mathbb{E}[\overline{X}]$,
the expected ($\mathbb{E}$) proportion ($\overline{X}$) of altruists in the population.

# Social interactions

Social interactions affect fecundity

In a deme with $k$:

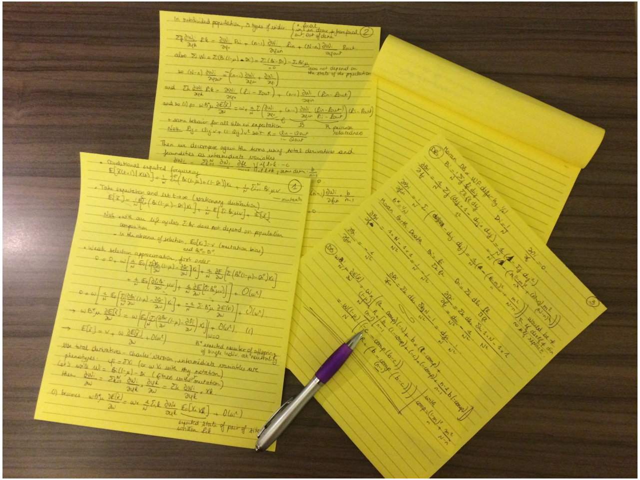
$$f = 1 + \omega\left(b\,\frac{k-1}{n-1} - c\right),$$

$$f = 1 + \omega\left(b\,\frac{k}{n-1}\right).$$

Selection is weak

$$\omega \ll 1.$$

# “Field site”



# Expected frequency of altruists in the population

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

## Expected frequency of altruists in the population

Mutation-drift equilibrium

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

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~

Variance in the state of one site

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

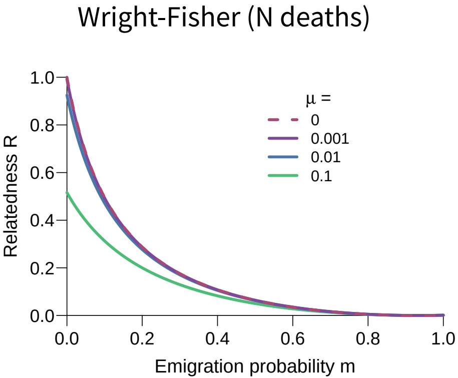
~~Population variance~~
Variance in the state of one site

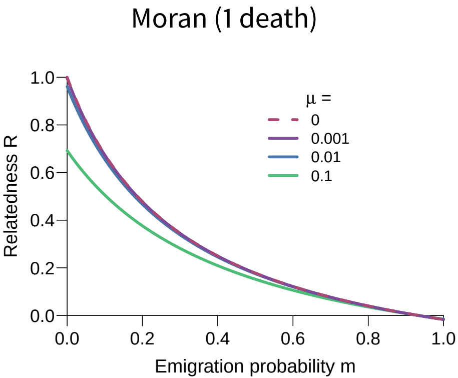
$$\mathbb{E}[\overline{X}] = \nu + \delta\, \nu(1-\nu)\, \frac{1-\mu}{\mu}\, (1 - Q_{\text{out}}) \times$$

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

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

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




$(n = 4, N_d = 15)$

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site

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

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

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

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

# Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~
Variance in the state of one site $\searrow$

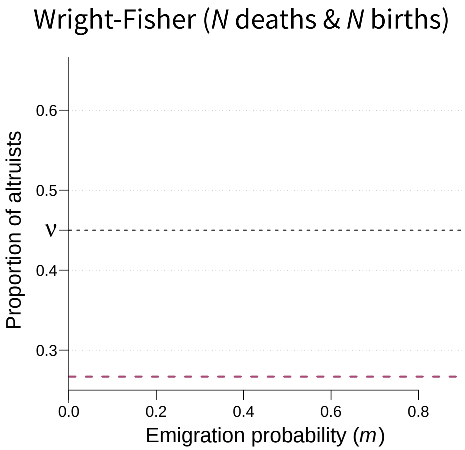
$$\mathbb{E}[\overline{X}] = \nu + \delta\, \nu(1-\nu)\, \frac{1-\mu}{\mu}\, (1-Q_{\text{out}}) \times$$

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

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

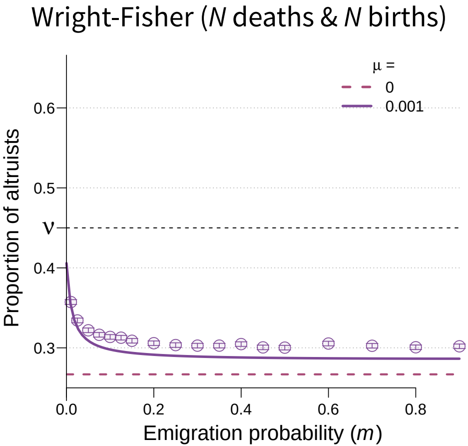
$R \searrow$ $\qquad$ $\mathcal{B} \nearrow$

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




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

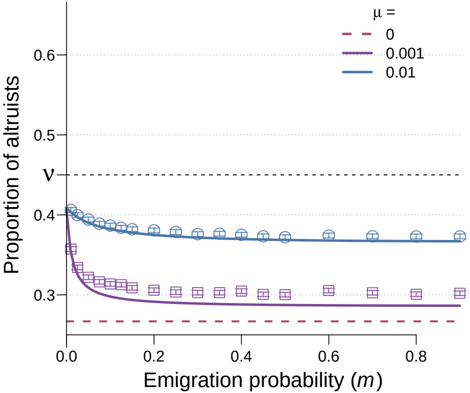
# Effect of the emigration probability $m$ on the expected proportion of altruists




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

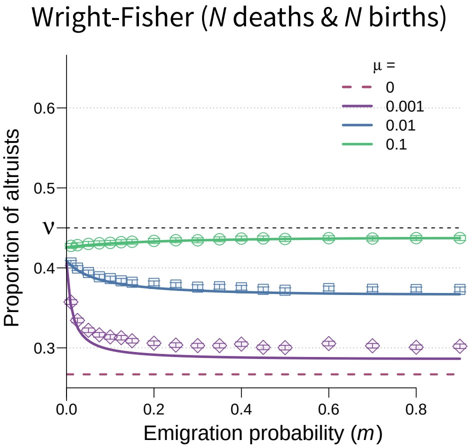
# Effect of the emigration probability *m* on the expected proportion of altruists

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




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

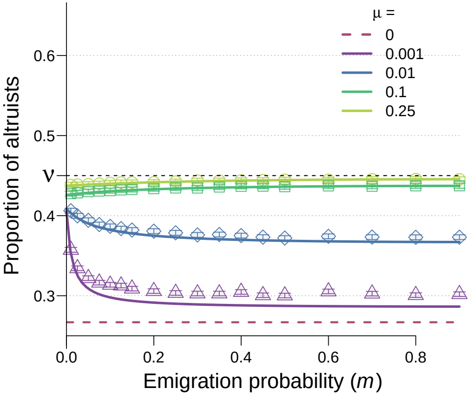
# Effect of the emigration probability *m* on the expected proportion of altruists




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

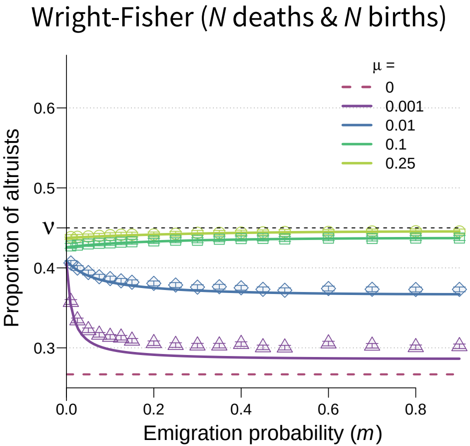
# Effect of the emigration probability *m* on the expected proportion of altruists

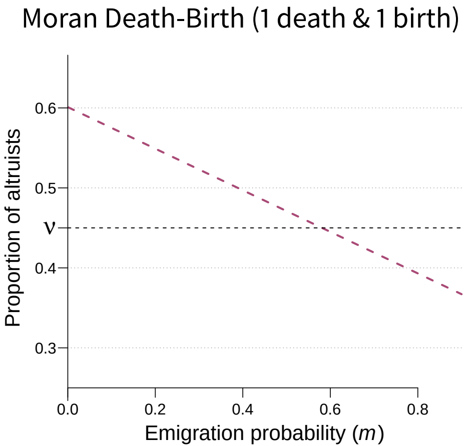
Wright-Fisher (*N* deaths & *N* births)




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

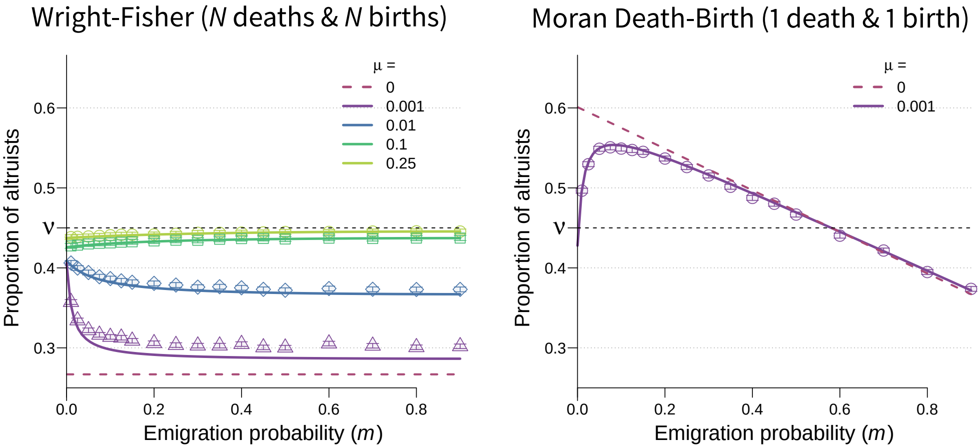
# Effect of the emigration probability *m* on the expected proportion of altruists



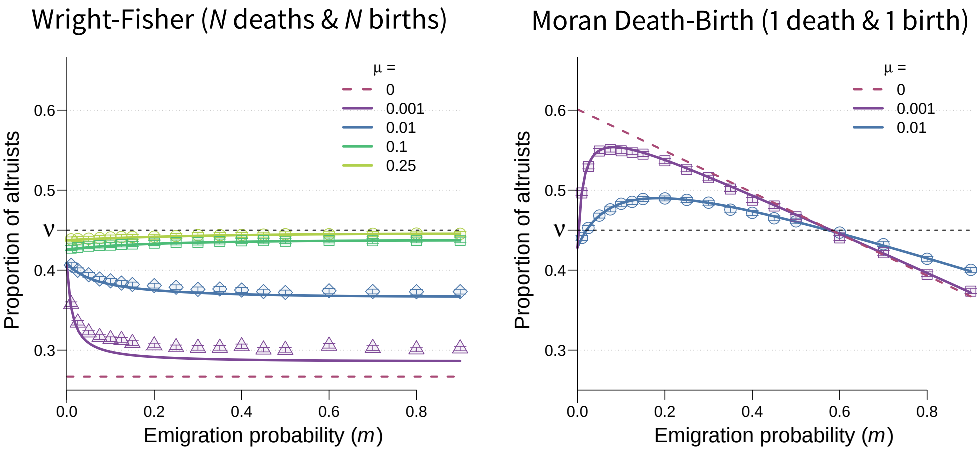

$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



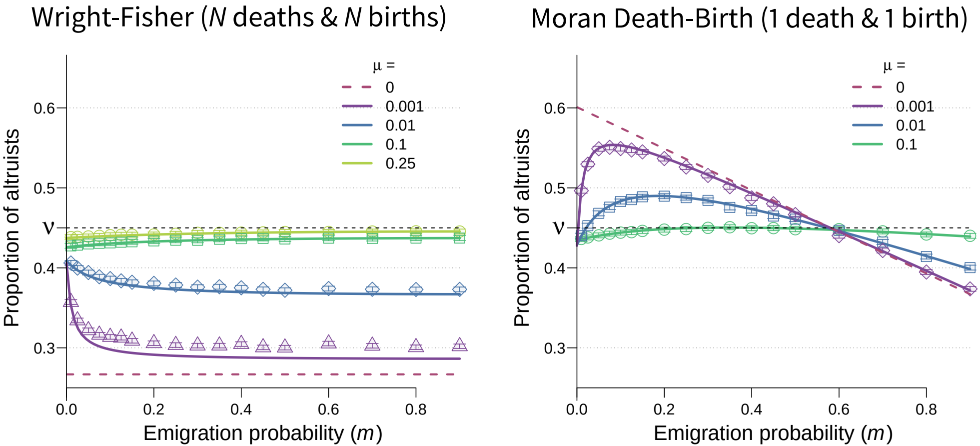

$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



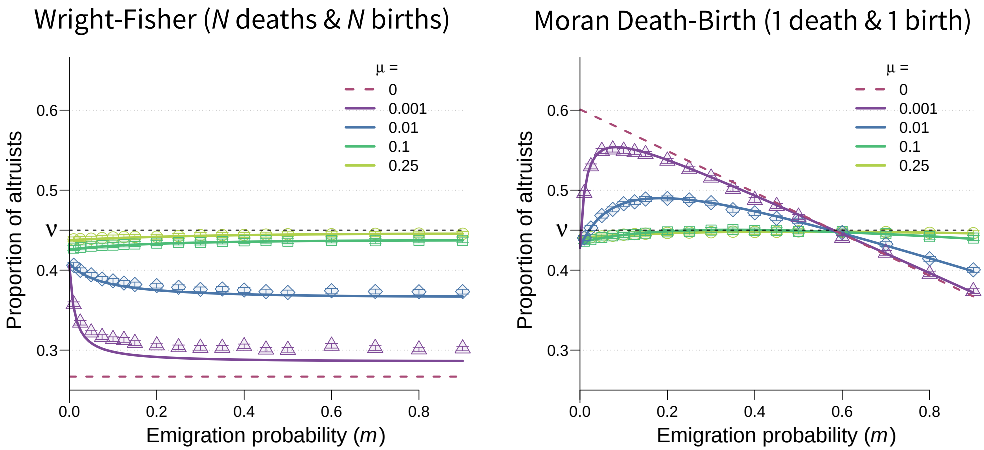

$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

# 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




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

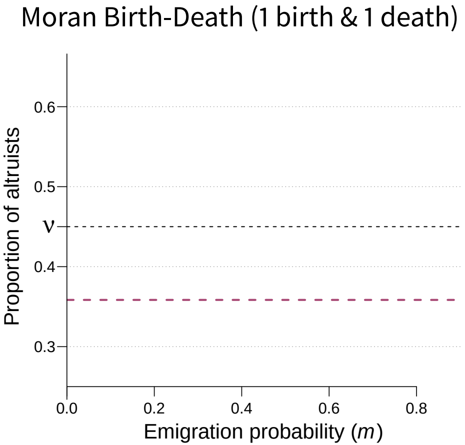
# Is the result robust?

# Another life-cycle

Moran Birth-Death (1 birth & 1 death)

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

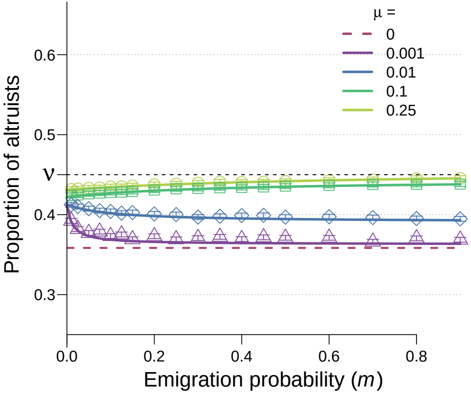
# Another life-cycle




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

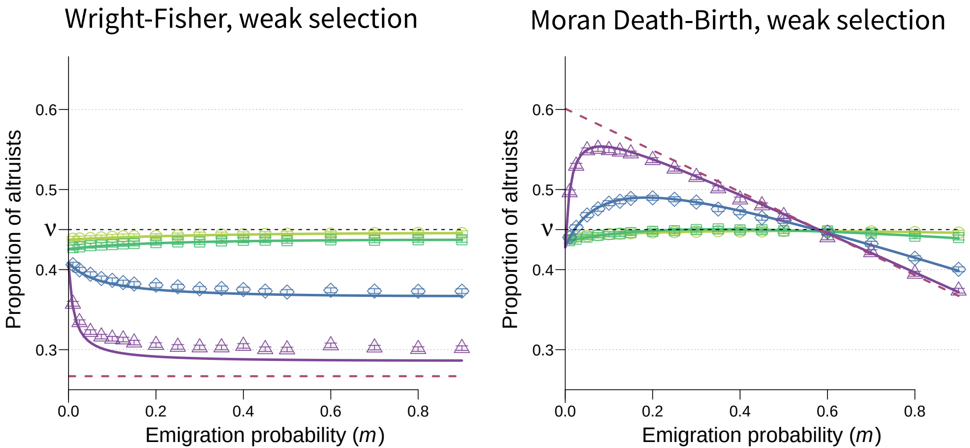
# Another life-cycle

Moran Birth-Death (1 birth & 1 death)



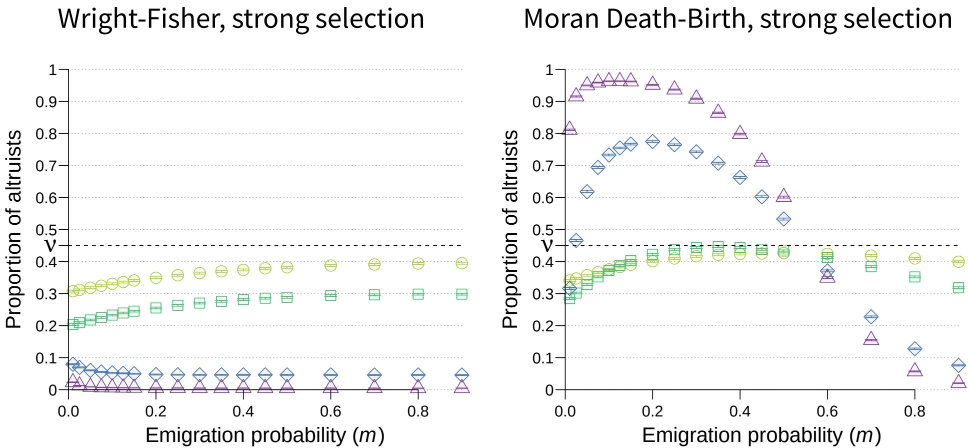

$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

# Strong selection




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

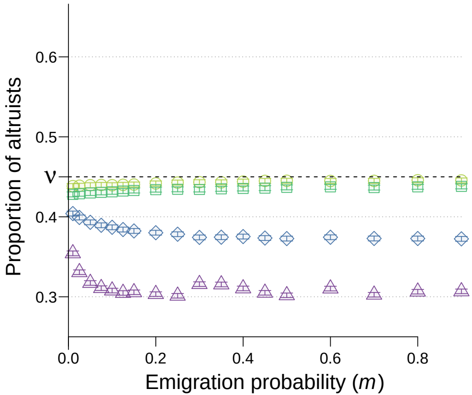
# Strong selection



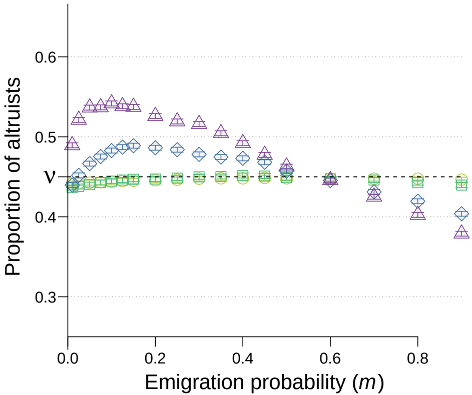

$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.1)$$

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

Wright-Fisher




Moran Death-Birth




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

## Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)

## Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- $\mathbb{E}[\overline{X}] > \nu \Leftrightarrow \mathcal{B}\, R > \mathcal{C} \Leftrightarrow b\, \kappa > c$.

# Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- $\mathbb{E}[\overline{X}] > \nu \Leftrightarrow \mathcal{B}\, R > \mathcal{C} \Leftrightarrow b\, \kappa > c$.
- In subdivided populations, $\mathbb{E}[\overline{X}]$ can increase with the emigration probability $m$ when strategy transmission is imperfect ($\mu > 0$).

# Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- $\mathbb{E}[\overline{X}] > \nu \Leftrightarrow \mathcal{B}\,R > \mathcal{C} \Leftrightarrow b\,\kappa > c$.
- In subdivided populations, $\mathbb{E}[\overline{X}]$ can increase with the emigration probability $m$ when strategy transmission is imperfect ($\mu > 0$).
- This result seems to hold under stronger selection and in heterogeneous populations.

# Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- $\mathbb{E}[\overline{X}] > \nu \Leftrightarrow \mathcal{B}\, R > \mathcal{C} \Leftrightarrow b\, \kappa > c$.
- In subdivided populations, $\mathbb{E}[\overline{X}]$ can increase with the emigration probability $m$ when strategy transmission is imperfect ($\mu > 0$).
- This result seems to hold under stronger selection and in heterogeneous populations.

## Take-Home Messages

- Under weak selection, it is possible to compute the expected frequency of social individuals, for any life-cycle, any regular population structure, any mutation probability. (Débarre 2017 JTB)
- $\mathbb{E}[\overline{X}] > \nu \Leftrightarrow \mathcal{B}\, R > \mathcal{C} \Leftrightarrow b\, \kappa > c$.
- In subdivided populations, $\mathbb{E}[\overline{X}]$ can increase with the emigration probability $m$ when strategy transmission is imperfect ($\mu > 0$).
- This result seems to hold under stronger selection and in heterogeneous populations.

---


## Funding & Thanks

ANR-14-ACHN-0003-01

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


and thank you for your attention!