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

F. Débarre

@flodebarre

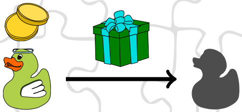
CNRS

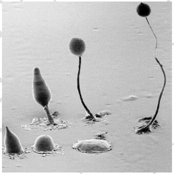
Centre de Recherches Interdisciplinaires en Biologie, Paris

Thematic semester on Mathematics Computer science and biology

CIMI Centre International de Mathématiques et d'Informatique TOULOUSE

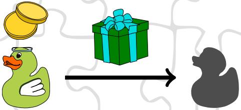
Ecology and evolutionary biology, deterministic and stochastic models





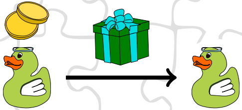
(c) Grimson & Blanton

(c) Wikimedia

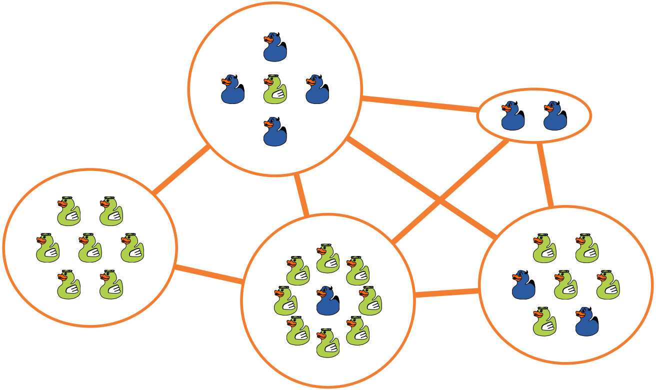


(c) FD

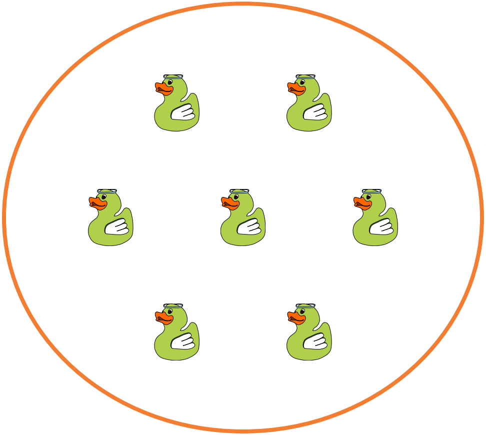
(c) ../Picturesforcoloring.com



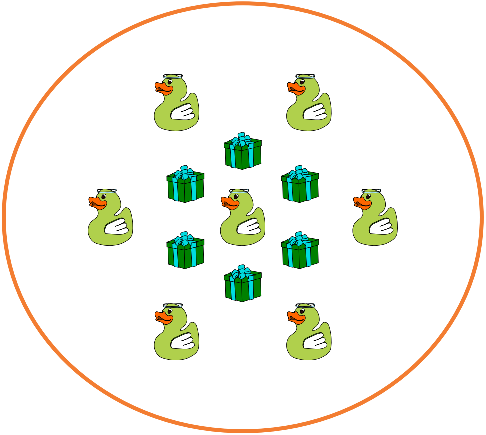
Spatial structure and altruism



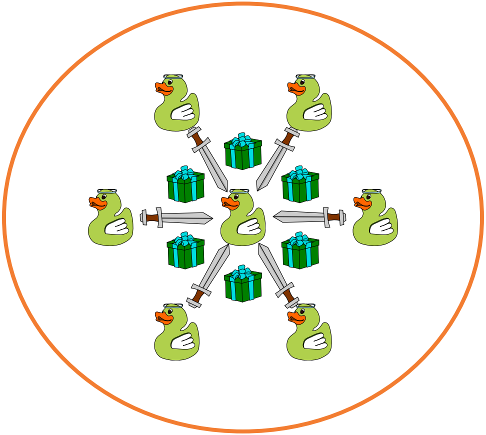
Spatial structure and altruism



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

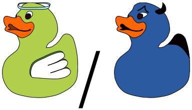
Summary

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

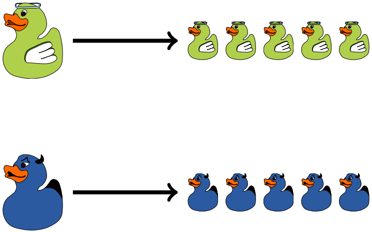
The choice of life-cycle matters

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

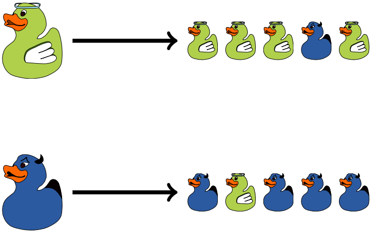
Wright-Fisher	Moran Birth-Death	Moran Death-Birth
		

Ohtsuki et al. (2006); Taylor, Day & Wild (2007); Taylor et al. (2010)

A common feature of models



A common feature of models

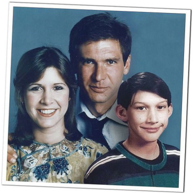


What is the effect of population viscosity on the evolution of altruism when parent-offspring strategy transmission is **imperfect**?

Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

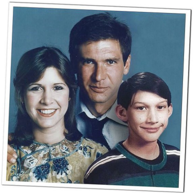
- Mutation



Fidelity of parent-offspring transmission

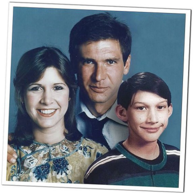
Causes of imperfect strategy transmission

- Mutation
- Partial heritability



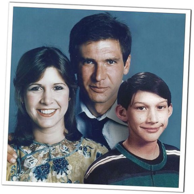
Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission



- Mutation
- Partial heritability
- Cultural transmission (vertical)

Fidelity of parent-offspring transmission



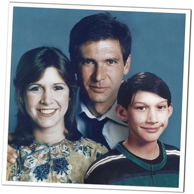
Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

In the model

Parent

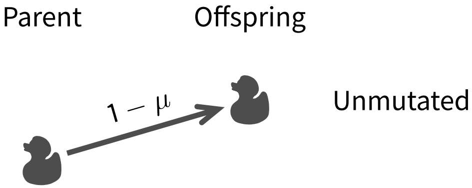
Fidelity of parent-offspring transmission



Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)

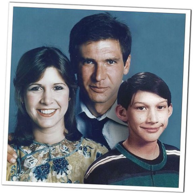
In the model



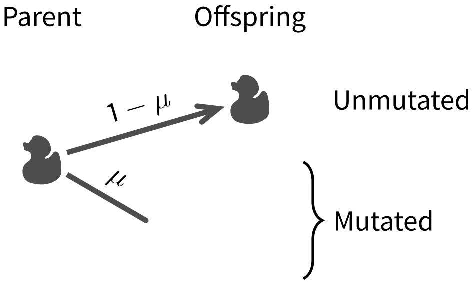
Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

- Mutation
- Partial heritability
- Cultural transmission (vertical)



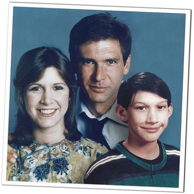
In the model



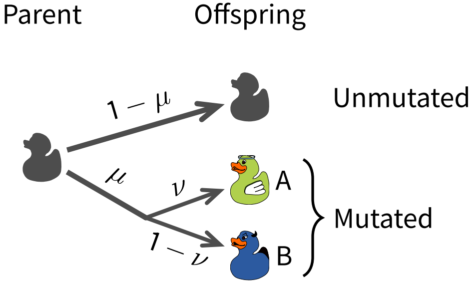
Fidelity of parent-offspring transmission

Causes of imperfect strategy transmission

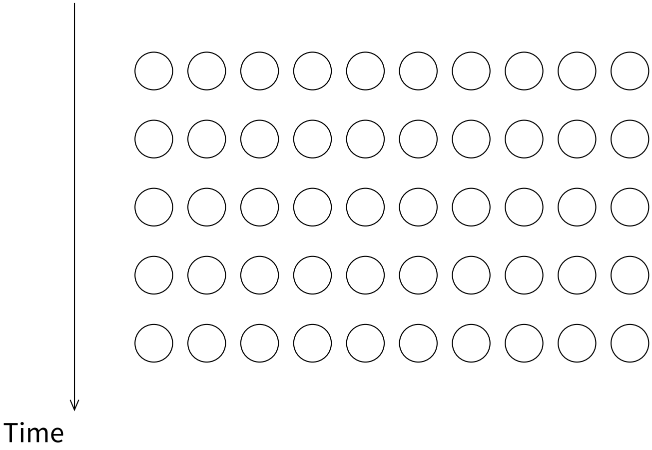
- Mutation
- Partial heritability
- Cultural transmission (vertical)



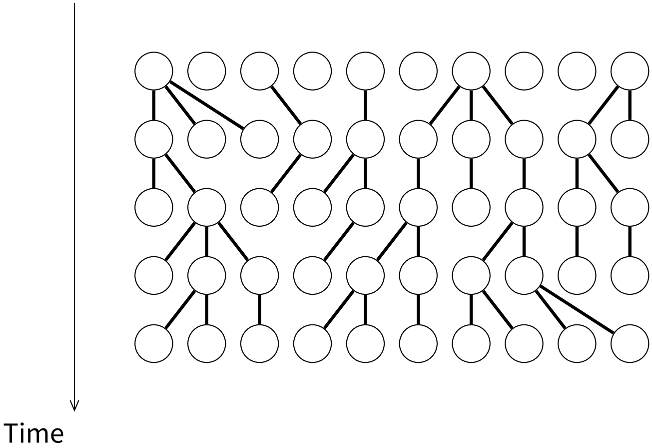
In the model



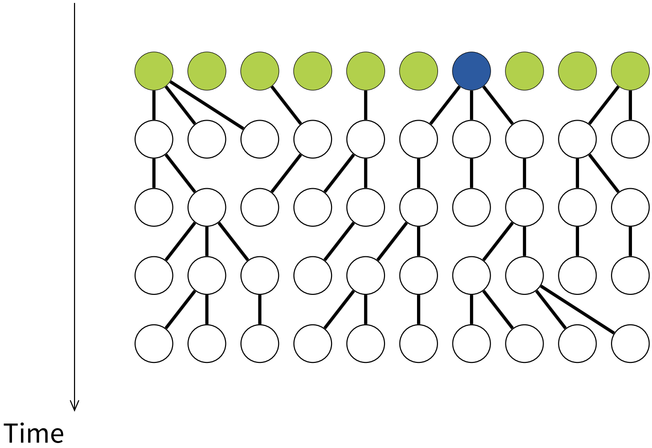
Genealogy, Identity by descent and Identity in state



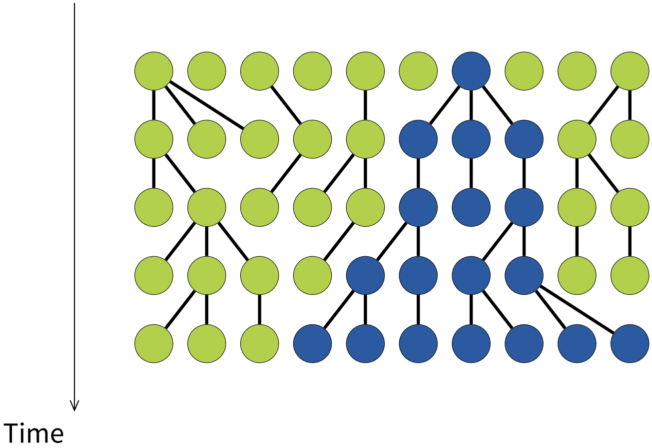
Genealogy, Identity by descent and Identity in state



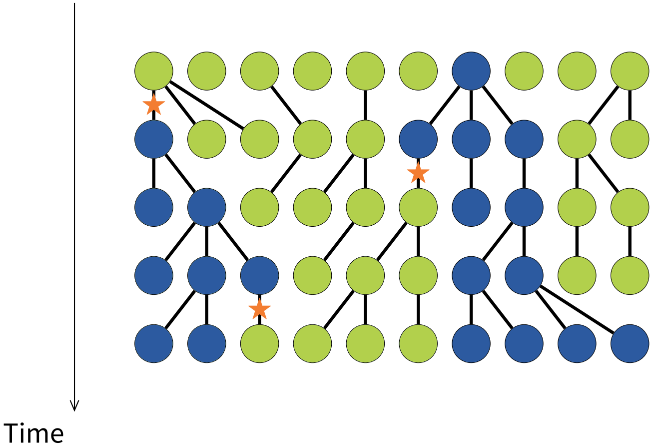
Genealogy, Identity by descent and Identity in state



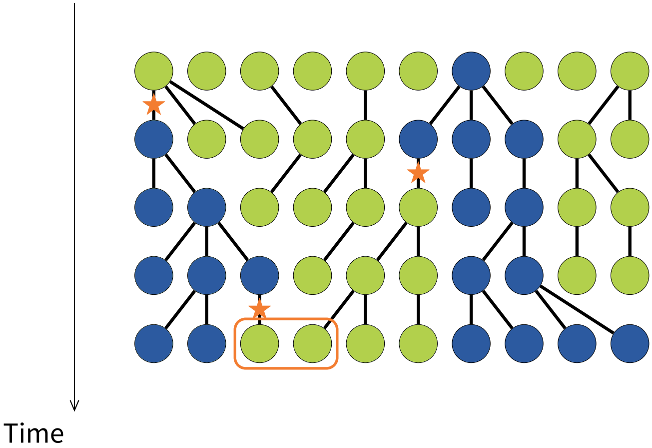
Genealogy, Identity by descent and Identity in state



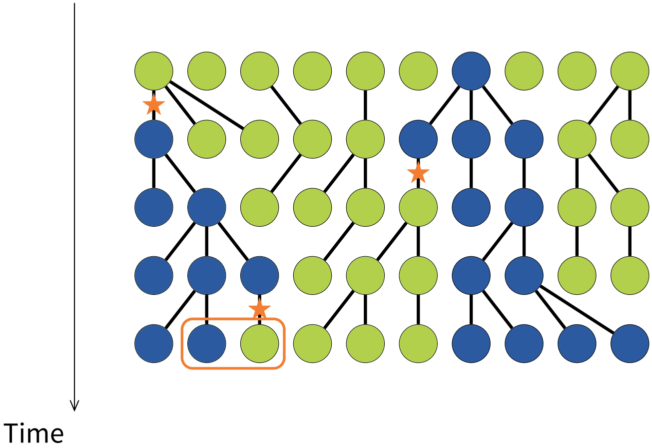
Genealogy, Identity by descent and Identity in state



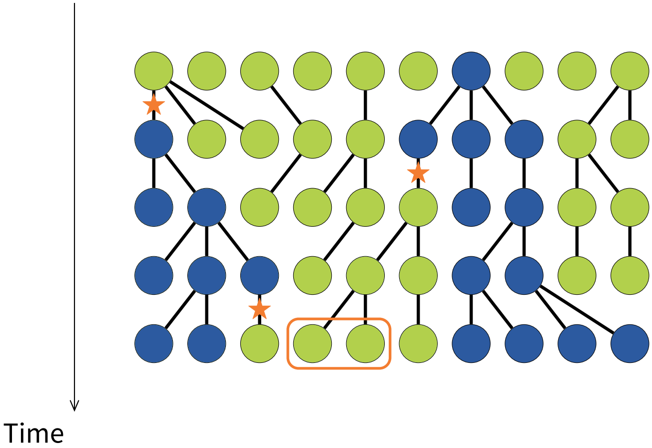
Genealogy, Identity by descent and Identity in state



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, $\delta = 0$),

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

P_{ij}: Expected state of the i, j pair = Probability that the two individuals are altruists

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

Q_{ij}: 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 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 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_{in}, Q_{out}

Population structures

Population of fixed size N

Taylor, Day, Wild (2007)

Population structures

Population of fixed size N

Dispersal graph

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

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

Taylor, Day, Wild (2007)

Population structures

Population of fixed size N

Dispersal graph

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

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

Interaction graph

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

(any)

Taylor, Day, Wild (2007)

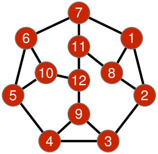
Population structures

Population of fixed size N

Dispersal graph

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

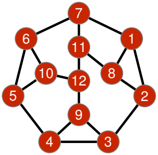
$$\sum_{i=1}^N d_{ij} = \sum_{j=1}^N d_{ji} = 1.$$



Interaction graph

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

(any)



Evolutionary graph theory

Taylor, Day, Wild (2007)

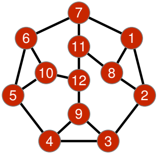
Population structures

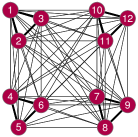
Population of fixed size N

Dispersal graph

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

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

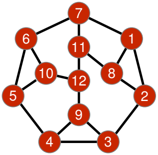


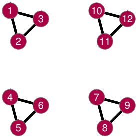


Interaction graph

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

(any)





Evolutionary graph theory

Subdivided populations

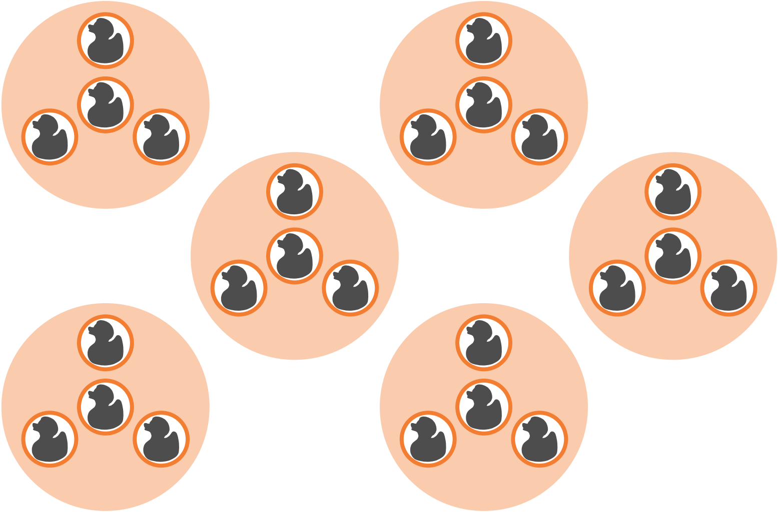
Taylor, Day, Wild (2007)

Subdivided population – Island model

N_d demes

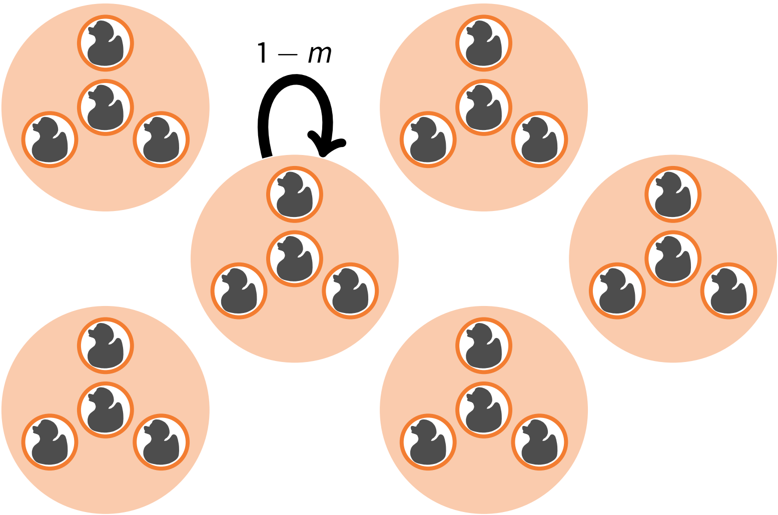
Subdivided population – Island model

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



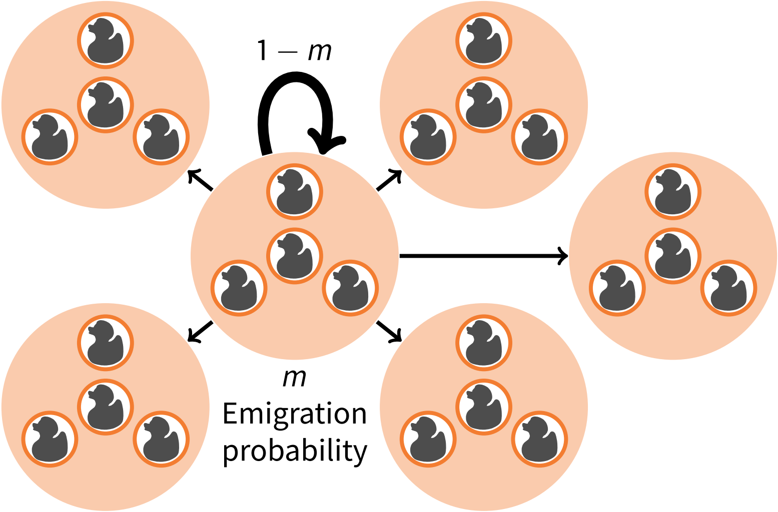
Subdivided population – Island model

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



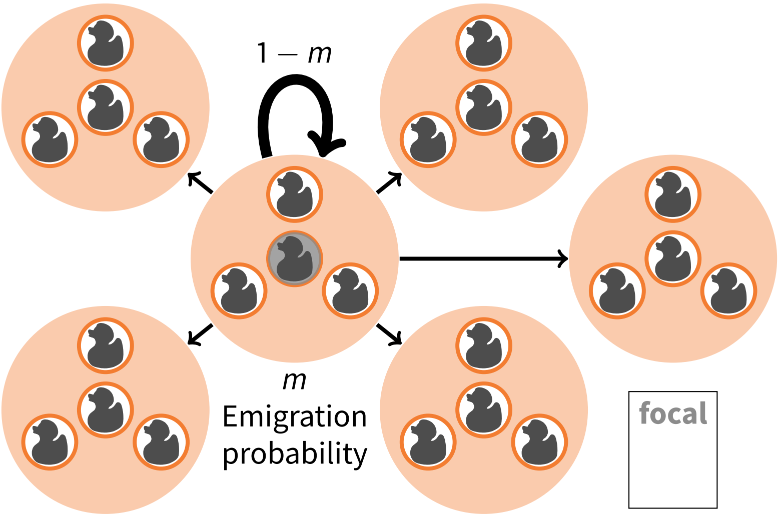
Subdivided population – Island model

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



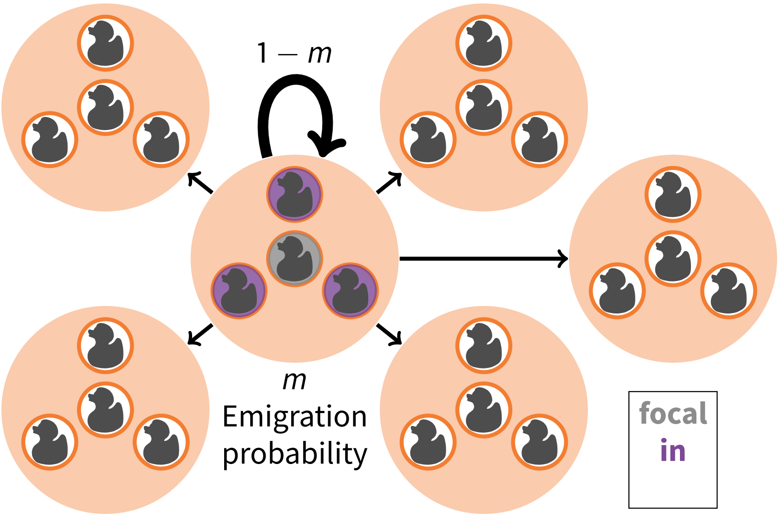
Subdivided population – Island model

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



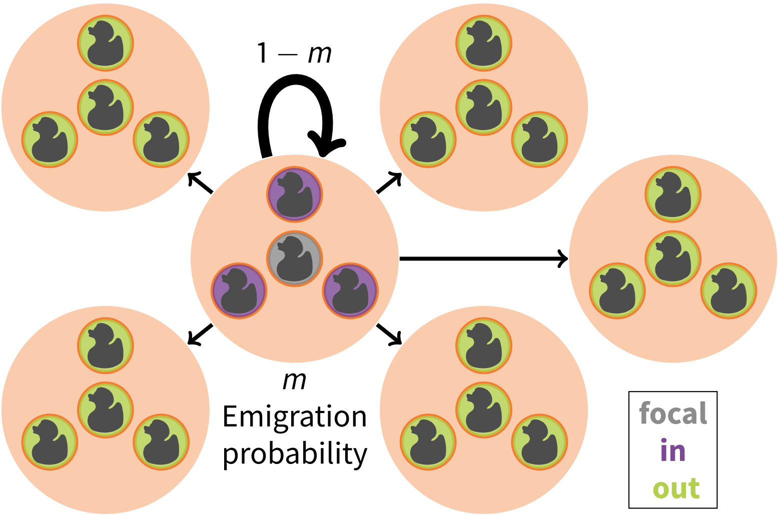
Subdivided population – Island model

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



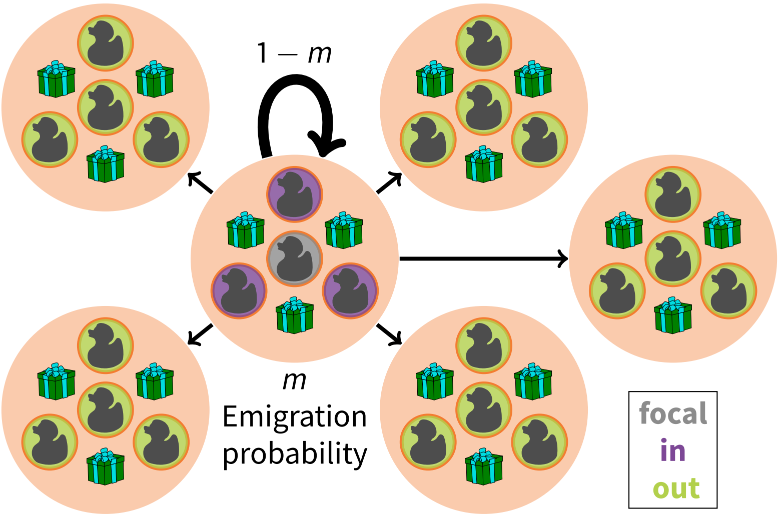
Subdivided population – Island model

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,

\#  = # 

N  = N 

⋮

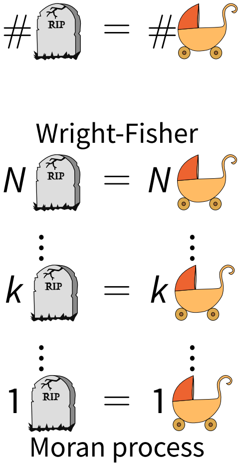
k  = k 

⋮

1  = 1 

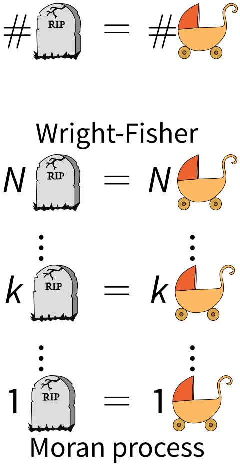
Updating the population

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



Updating the population

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

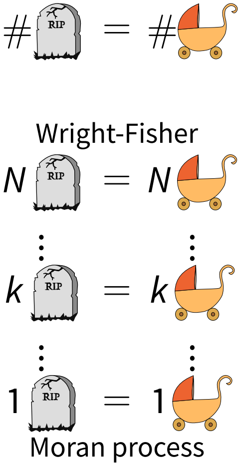


Life-cycle

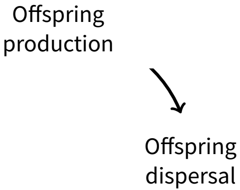
Offspring production

Updating the population

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

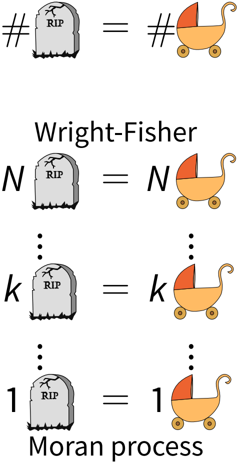


Life-cycle

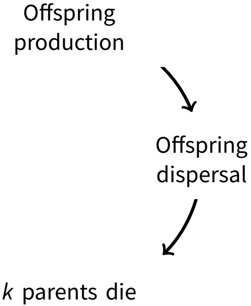


Updating the population

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

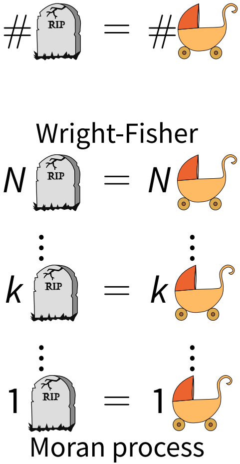


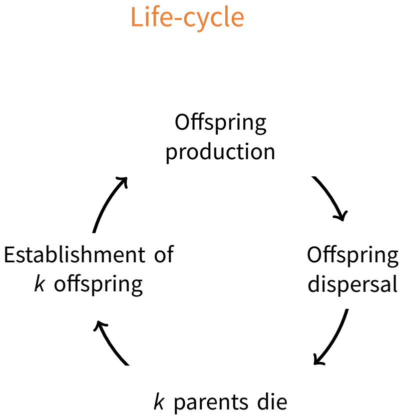
Life-cycle



Updating the population

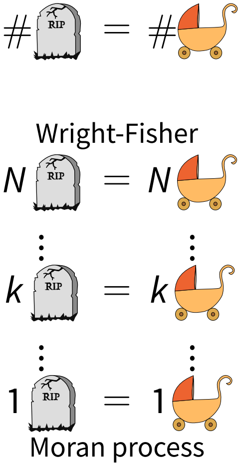
Constant population size (N), so between two time steps,





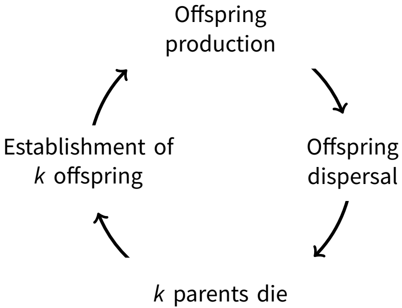
Updating the population

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



Life-cycle

"Death-Birth" updating



Population

$$X_i(t) = \begin{cases} 1 & \text{if site } i \text{ occupied by [duck 1] at time } t \ (1 \leq i \leq N) \\ 0 & \text{if site } i \text{ occupied by [duck 2] at time } t \ (1 \leq i \leq N) \end{cases}$$

Population

$X_i(t) =$

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

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

Social interactions

Phenotype

$$\phi_i = \delta X_i.$$

Social interactions affect fecundity

In a deme with k :

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

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

Social interactions

Phenotype

$$\phi_i = \delta X_i.$$

Social interactions affect fecundity


In a deme with k :

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

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

Selection is weak

$$\delta \ll 1.$$

Calculations

Notation

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

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

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.

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

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

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.

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

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

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

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

Calculations (2)

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

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

which we rewrite as

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

Calculations (2)

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

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

  which we rewrite as

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

- Using partial derivatives: phenotypes

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

Calculations (2)

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

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

  which we rewrite as

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

- Using partial derivatives: phenotypes

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

- We obtain

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

Calculations (3)

- In a subdivided population,

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

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

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

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:

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

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

Rousset & Billiard (2000)

Expected frequency of altruists in the population

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~

Variance in the state of one site

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

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

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

$\mathcal{B}$

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

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

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

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

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

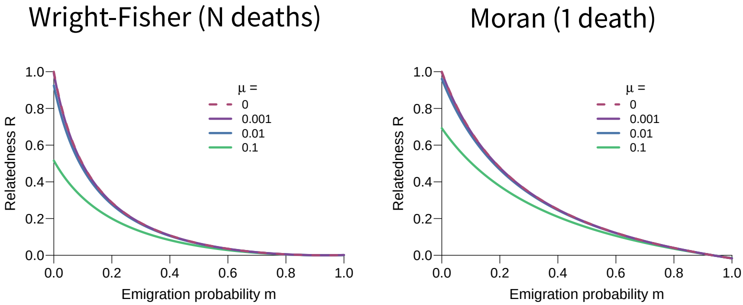
$$\left(-c - (b-c)\left(\frac{(1-m)^2}{n} + \frac{m^2}{n(N_d - 1)}\right) \quad -\mathcal{C} \right.$$

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

R $\quad$ $\mathcal{B}$

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

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

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

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

R ↘ $\mathcal{B}$

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~

Variance in the state of one site

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

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

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

R ↘ $\qquad \mathcal{B}$

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~

Variance in the state of one site

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

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

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

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

Expected frequency of altruists in the population

Mutation-drift equilibrium

Selection strength

~~Population variance~~

Variance in the state of one site ↘

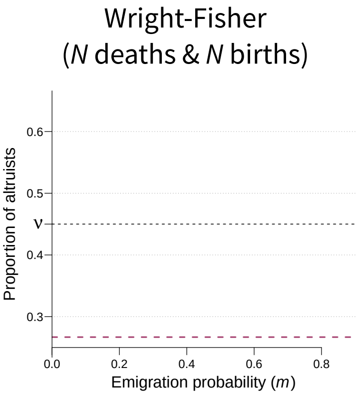
$$\mathbb{E}[\bar{X}] = \nu + \delta\, \nu(1-\nu)\, \frac{1-\mu}{\mu}\, (1 - Q_{out}) \times$$

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

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

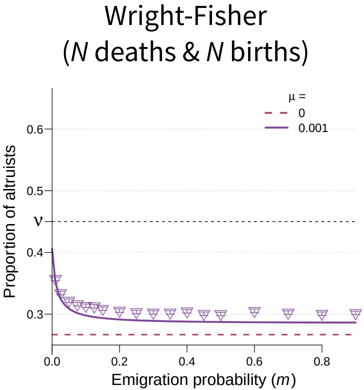
R ↘ $\qquad \mathcal{B}$ ↗

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



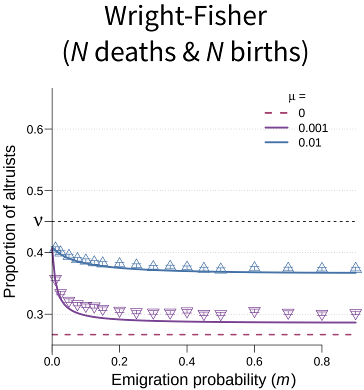
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



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

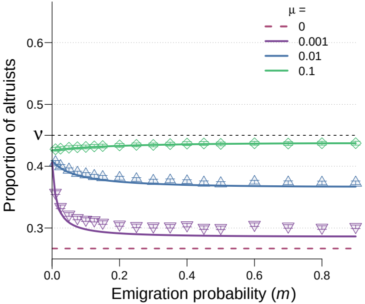
Effect of the emigration probability *m* on the expected proportion of altruists



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

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

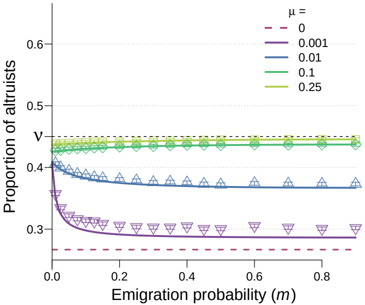
Wright-Fisher
(*N* deaths & *N* births)



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

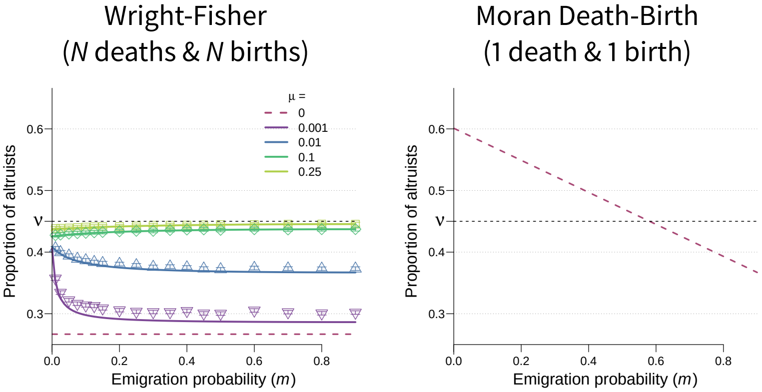
Effect of the emigration probability *m* on the expected proportion of altruists

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



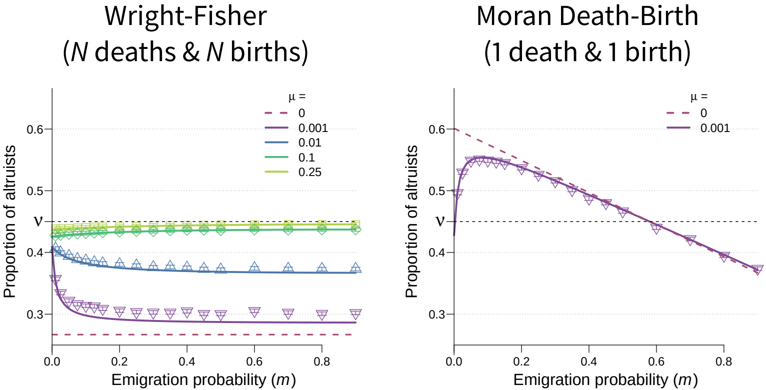
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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



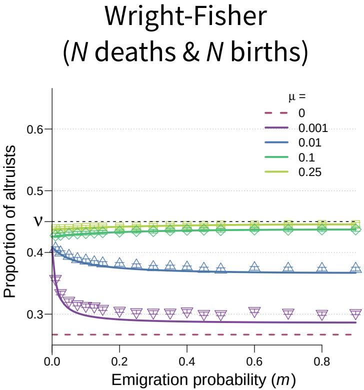
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

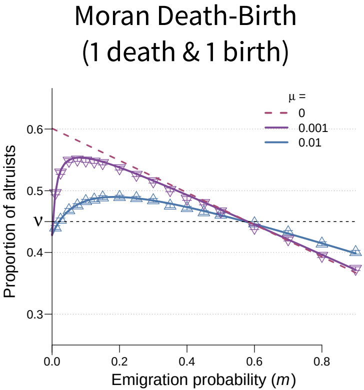
Effect of the emigration probability *m* on the expected proportion of altruists



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

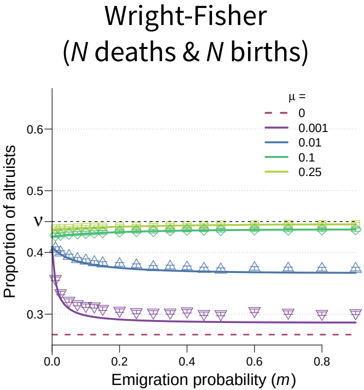
Effect of the emigration probability *m* on the expected proportion of altruists

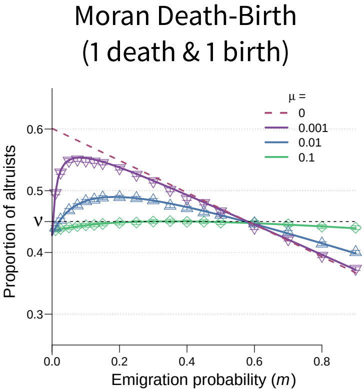




$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

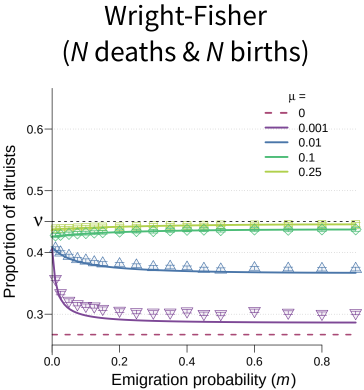
Effect of the emigration probability *m* on the expected proportion of altruists

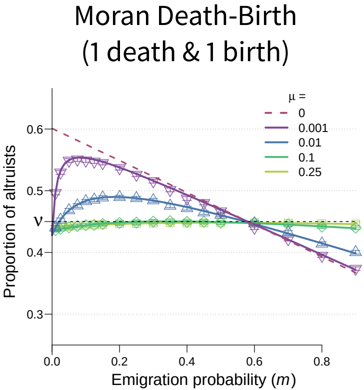




$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

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





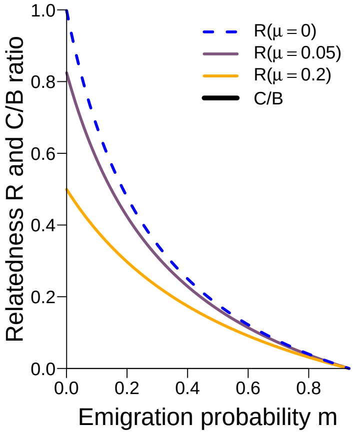
$$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$$

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

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

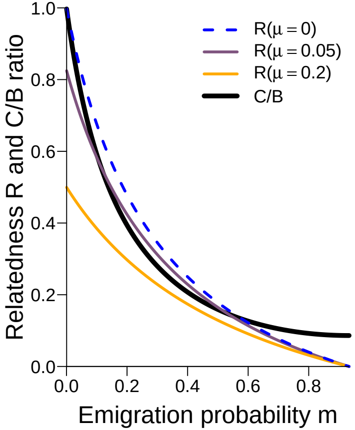
How to explain this result? (Moran Death-Birth)

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



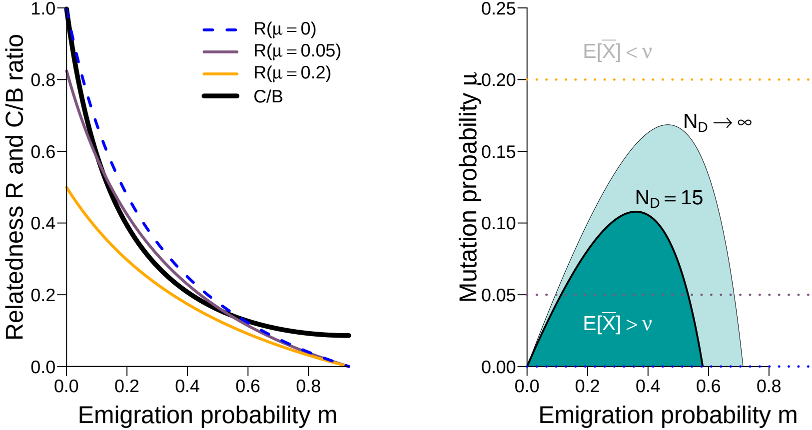
How to explain this result? (Moran Death-Birth)

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



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

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



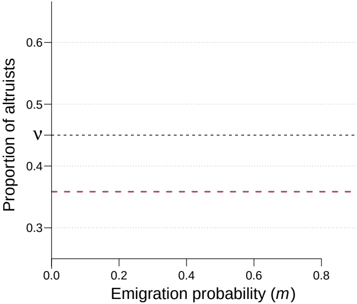
Is the result robust?

Moran Birth-Death
(1 birth & 1 death)

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

Another life-cycle

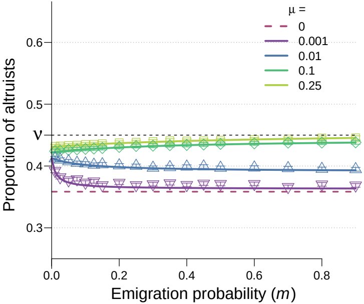
Moran Birth-Death
(1 birth & 1 death)



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

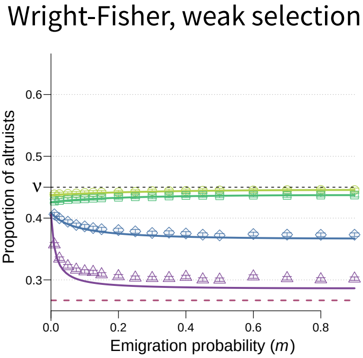
Another life-cycle

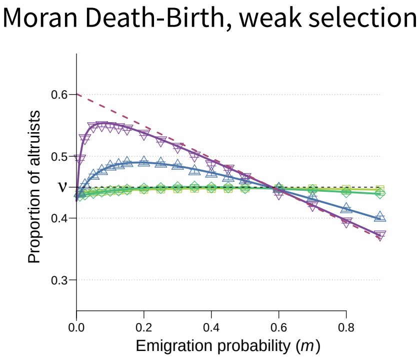
Moran Birth-Death
(1 birth & 1 death)



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

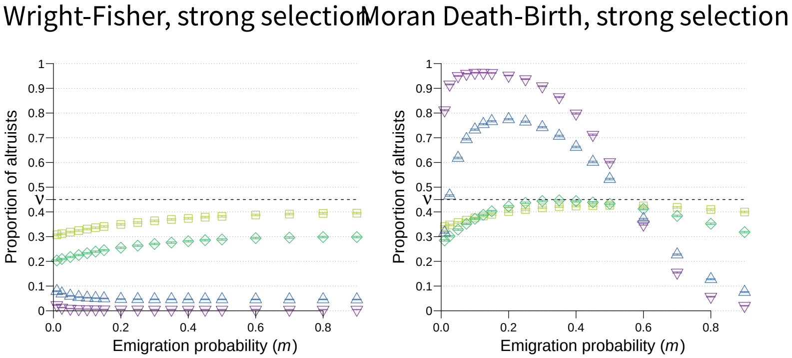
Strong selection





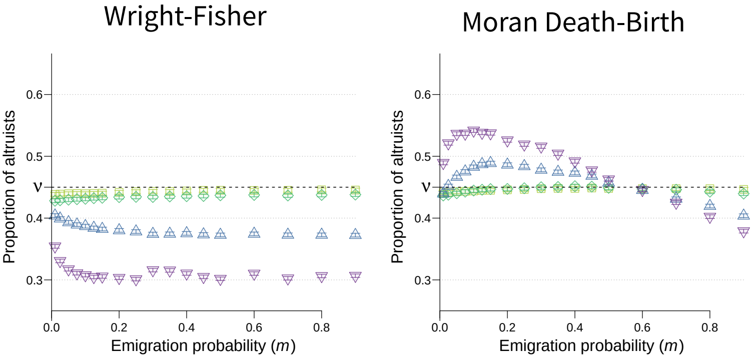
$(b = 15, c = 1, n = 4, N_d = 15, \delta = 0.005)$

Strong selection



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

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



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

Political implications

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

Take-Home Messages

- 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. (D., 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. (D., 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. (D., 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 ($\mu > 0$). (D., *in review.*)

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. (D., 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 ($\mu > 0$). (D., *in review.*)
- 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. (D., 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 ($\mu > 0$). (D., *in review.*)
- This result seems to hold under stronger selection and in heterogeneous populations.

Funding & Thanks

ANR-14-ACHN-0003-01

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

Ch. Mullon,
S. Lion

and thank you
for your attention!