

Emergence of homogamy in a two-loci stochastic population model

Manon Costa

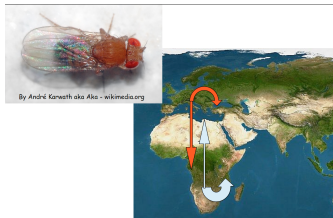
Institut de Mathématiques de Toulouse

joint work Camille Coron, Fabien Laroche, Hélène Leman et Charline Smadi.

Motivation

Homogamy is a mating pattern in which individuals with similar phenotypes reproduce more frequently than expected under random uniform mating.

How does such mechanism arise in a randomly mating population?



Motivation

Eco-Evolutionary framework : take into account the underlying environment :

- Varying size populations
- Interactions with other individuals (competition for resource)
- Adaptive dynamics : Metz and al 1996, Bolker and Pacala 1997,...
- In the context of stochastic individual based models : Fournier and Méléard 2004, Champagnat 2006,...

Uniformly mating population

Genotypes

- A or a

Ecological parameters

- b mating rate
- d intrinsic death rate
- c competitive pressure.
- $K \in \mathbb{N}$ rescales the competition \approx carrying capacity.

Random mating

- Initially, individuals mate uniformly
- Every individual, at rate b , chooses independently a mate uniformly
- Mendelian inheritance $A \times a \rightarrow 1/2\delta_A + 1/2\delta_a$

Birth rate

$$b_\alpha(N) = b \left(N_\alpha \frac{N_\alpha + N_{\bar{\alpha}}/2}{N_\alpha + N_{\bar{\alpha}}} + N_{\bar{\alpha}} \frac{0 \cdot N_{\bar{\alpha}} + N_\alpha/2}{N_\alpha + N_{\bar{\alpha}}} \right) = bN_\alpha,$$

Death rate

$$d_\alpha(N) = \left(d + \frac{c}{K}(N_A + N_a) \right) N_\alpha, \quad \alpha \in \{A, a\}.$$

Dimorphic population with random mating

When population size of order K , rescaled population process $(N_A + N_a)/K$ evolves as a **competitive Lotka-Volterra equation** (Ethier and Kurtz 1986) :

$$\begin{cases} \dot{z}_A = (b - d - c(z_A + z_a))z_A \\ \dot{z}_a = (b - d - c(z_A + z_a))z_a \end{cases}$$

Positive equilibrium if $b > d$

$$b - d - c(z_A + z_a) = 0 \iff z_A + z_a = \bar{z} = \frac{b - d}{c}$$

$$\frac{\dot{z}_A}{z_A + z_a} = 0 \Rightarrow \text{infinity of equilibria, any allele proportions}$$

Mutation impacting the mate choice

- When random mating : allele p ; new mutant : allele P
- On a chromosome different from the chromosome coding for a/A
- **Benefit** : higher birth rate with individuals of the same type (a/A) :

$$b(1 + \beta_1), \quad (\beta_1 \geq 0)$$

- **Cost** : smaller birth rate with individuals of the other type (a/A) :

$$b(1 - \beta_2) \quad (0 \leq \beta_2 < 1)$$

Assortative mating : preference for individuals of the same type

Birth rate

Possible couples to generate Ap (first parent **choosing** and second parent **chosen**)

$$\begin{array}{lll}
 (1) & Ap \times Ap & (1/2) Ap \times ap & (1/2) ap \times Ap \\
 (1/2) & Ap \times AP & (1/4) ap \times AP & (1/4) Ap \times aP \\
 (1/2) & AP \times Ap & (1/4) AP \times ap & (1/4) aP \times Ap
 \end{array}$$

Assortative birth rate

$$\begin{aligned}
 b_{Ap}(N) = & \frac{b}{N_A + N_a} \left[1N_{Ap}N_{Ap} + \frac{1}{2}N_{Ap}N_{ap} + \frac{1}{2}N_{ap}N_{Ap} + \frac{1}{2}N_{Ap}N_{AP} \right. \\
 & \left. + \frac{1}{4}N_{ap}N_{AP} + \frac{1}{4}N_{Ap}N_{aP} \right] \\
 & + \frac{(1 + \beta_1)b}{N_A + N_a} \left[\frac{1}{2}N_{AP}N_{Ap} \right] + \frac{(1 - \beta_2)b}{N_A + N_a} \left[\frac{1}{4}N_{AP}N_{ap} + \frac{1}{4}N_{aP}N_{Ap} \right].
 \end{aligned}$$

Assortative birth rate

$$b_{Ap}(\mathbf{N}) = bN_{Ap} + \frac{b}{N} \left[\frac{\beta_1}{2} N_{AP} N_{Ap} - \beta_2 \left(\frac{1}{4} N_{AP} N_{ap} + \frac{1}{4} N_{aP} N_{Ap} \right) \right] \\ - \frac{b}{2N} [N_{aP} N_{Ap} - N_{AP} N_{ap}].$$

$$b_{AP}(\mathbf{N}) = bN_{AP} + \frac{b}{N} \left[\beta_1 N_{AP} \left(N_{AP} + \frac{1}{2} N_{Ap} \right) \right. \\ \left. - \beta_2 \left(N_{AP} \left(n_{aP} + \frac{1}{4} N_{ap} \right) + \frac{1}{4} N_{aP} N_{Ap} \right) \right] \\ + \frac{b}{2N} [N_{aP} N_{Ap} - N_{AP} N_{ap}].$$

Death rates

When the population is in state $\mathbf{N} = (N_{AP}, N_{aP}, N_{Ap}, N_{ap})$
the total death rate of i individuals ($i \in \{AP, aP, Ap, ap\}$) :

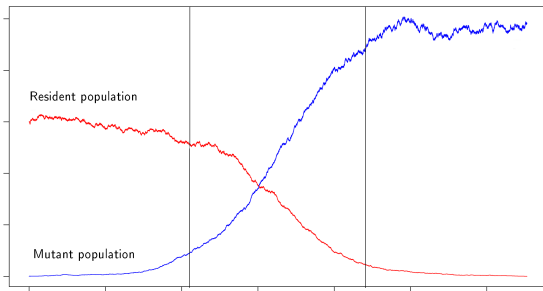
$$N_i \left(d + \frac{c}{K} (N_{AP} + N_{aP} + N_{Ap} + N_{ap}) \right).$$

Questions

- Under which conditions may the mutant P invade?
- What is the invasion probability?
- What is the final state of the population?
- What is the invasion time scale?

Dynamics

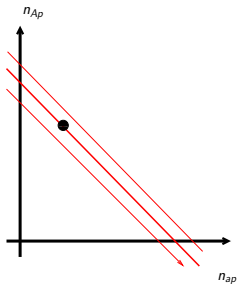
- 1- Invasion phase
- 2- Comparison with a deterministic limit
- 3- Extinction



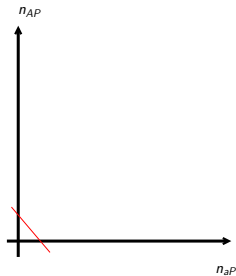
Invasion phase

First idea to study the beginning of the invasion process

- Consider that as long as the mutant population size is small ($\ll K$) it has a small impact on the resident individuals
- Freeze the resident population size and allele proportions
- Compare the mutant population to a bitye branching process.



Resident population



Mutant population

Mathematical issues

- Proportions in the resident population **not an hyperbolic equilibrium**
- No large deviation results to ensure that they stay almost constant during an exponential time
- Proportions in the resident population very dependent on the P -population size

⇒ p and P – populations have to be studied together

Step 1 : control of the resident population size

- Coupling of the p -population size with two logistic processes with close birth and death rates as long as the P -population size is smaller than εK
- Classical large deviation results to ensure that the total p -population size stays close to $(b - d)K/c$ during an exponential time
- Invasion time of order $\log K$

Step 2 : Control of the proportions in the resident population

- As long as

$$0 < N_P < \varepsilon^\xi K \quad \text{and} \quad \left| \frac{N_P}{K} - \frac{b-d}{c} \right| < \varepsilon,$$

the proportions in the resident population stay close to their initial value :

$$\left| \frac{N_{Ap}}{N_P} - \frac{N_{Ap}(0)}{N_P(0)} \right| \leq (\mathcal{B}\varepsilon)^{1/4}$$

- Idea of the proof : amounts to control

$$\frac{1}{K} \mathbb{E} \left[\int_0^{\tau_\varepsilon} N_P(s) ds \right] \leq C\varepsilon^\xi.$$

Achieved by finding a function such that

$$\int_0^t N_P \leq \int_0^t \mathcal{L}f(N_{Ap}, N_{ap}, N_{AP}, N_{aP}) = f(\mathbf{N}(t)) - f(\mathbf{N}(0)) + \text{Mart}$$

Step 3 : comparison of the P mutant population with a bi-type branching process

- Once we know that the size and proportions vary slightly during the invasion, we can compare the p mutant population with a bi-type branching process
 - ▶ If supercritical, positive probability of invasion,
 - ▶ if subcritical, no invasion
- Also give the invasion time scaling if supercritical ($\log K/\lambda$, where λ maximal eigenvalue of the mean matrix of the branching process)

How to compute the approximation

Assume $(N_{AP}, N_{ap}) = K \frac{b-d}{c} (\rho_A, 1 - \rho_A)$ and $N_P \simeq \varepsilon$:

$$\begin{aligned}
 b_{AP}(\mathbf{N}) = & bN_{AP} \left[1 + \frac{\beta_1}{N} \left(N_{AP} + \frac{1}{2} N_{Ap} \right) - \frac{\beta_2}{N} \left(n_{aP} + \frac{1}{4} N_{ap} \right) - \frac{N_{ap}}{2N} \right] \\
 & + bN_{aP} \frac{(2 - \beta_2)}{4N} N_{Ap}
 \end{aligned}$$

How to compute the approximation

Assume $(N_{Ap}, N_{ap}) = K \frac{b-d}{c} (\rho_A, 1 - \rho_A)$ and $N_P \simeq \varepsilon$:

$$\begin{aligned}
 b_{AP}(\mathbf{N}) &= bN_{AP} \left[1 + \frac{\beta_1}{N} \left(N_{AP} + \frac{1}{2} N_{Ap} \right) - \frac{\beta_2}{N} \left(n_{aP} + \frac{1}{4} N_{ap} \right) - \frac{N_{ap}}{2N} \right] \\
 &\quad + bN_{aP} \frac{(2 - \beta_2)}{4N} N_{Ap} \\
 &\simeq bN_{AP} \left[1 + \beta_1 \frac{\rho_A}{2} - \beta_2 \frac{1 - \rho_A}{4} - \frac{1 - \rho_A}{2} \right] \\
 &\quad + bN_{aP} \frac{(2 - \beta_2)}{4} \rho_A
 \end{aligned}$$

How to compute the approximation

Assume $(N_{AP}, N_{ap}) = K \frac{b-d}{c} (\rho_A, 1 - \rho_A)$ and $N_P \simeq \varepsilon$:

$$\begin{aligned}
 b_{AP}(\mathbf{N}) &= bN_{AP} \left[1 + \frac{\beta_1}{N} \left(N_{AP} + \frac{1}{2} N_{Ap} \right) - \frac{\beta_2}{N} \left(n_{aP} + \frac{1}{4} N_{ap} \right) - \frac{N_{ap}}{2N} \right] \\
 &\quad + bN_{aP} \frac{(2 - \beta_2)}{4N} N_{Ap} \\
 &\simeq bN_{AP} \left[1 + \beta_1 \frac{\rho_A}{2} - \beta_2 \frac{1 - \rho_A}{4} - \frac{1 - \rho_A}{2} \right] \\
 &\quad + bN_{aP} \frac{(2 - \beta_2)}{4} \rho_A
 \end{aligned}$$

$$d_{AP}(\mathbf{N}) = N_{AP} \left(d + \frac{c}{K} N \right) \simeq b$$

Mutant population of size εK

Comparison of the mutant population with supercritical branching process

Infinitesimal generator :

$$\frac{b}{2} \begin{pmatrix} \rho_A(1 + \beta_1) - \frac{\beta_2}{2}(1 - \rho_A) - 1 & (1 - \rho_A) \left(1 - \frac{\beta_2}{2}\right) \\ \rho_A \left(1 - \frac{\beta_2}{2}\right) & (1 - \rho_A)(1 + \beta_1) - \frac{\beta_2}{2}\rho_A - 1 \end{pmatrix},$$

Kesten-Sigmund Theorem

If $\pi = (\pi_A, \pi_a)$ is the normalized left eigenvector associated to the maximal eigenvalue

\Rightarrow the proportions of A and a in the mutant population close to π when the mutant population reaches a size of order K .

Invasion with positive probability

From the branching approximation, we deduce that invasion has a positive probability $(1 - q_A/1 - q_a)$ if and only if

$$\beta_1 > \beta_2 \quad \text{or} \quad \rho_A(1 - \rho_A) < \frac{\beta_1(\beta_2 + 2)}{2(\beta_1 + \beta_2)(\beta_1 + 2)}.$$

Two conditions may foster the invasion

- Advantage of the homogamous reproduction has to be larger than cost
- Small initial allelic diversity

Invasion probability

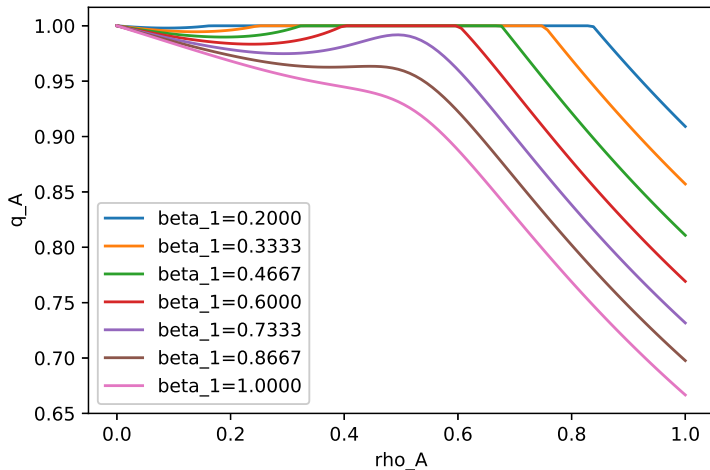
Invasion probability If first mutant of type α , $1 - q_\alpha$ where (q_A, q_a) smallest solution of

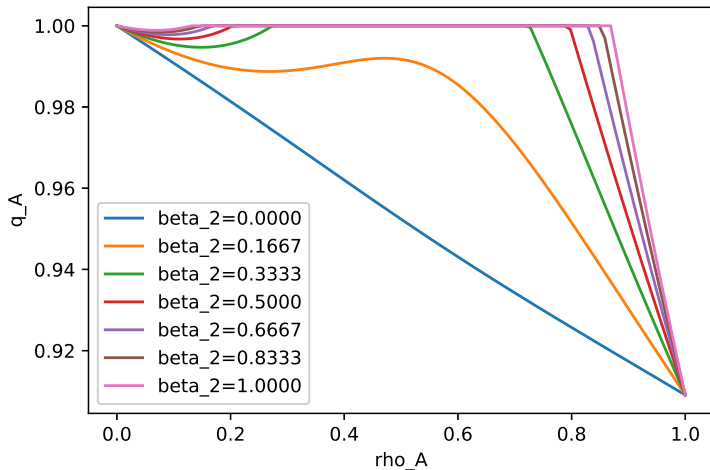
$$(1 - q_A) + \frac{1}{2} \left[1 + \rho_A(1 + \beta_1) - \frac{\beta_2}{2}(1 - \rho_A) \right] q_A(1 - q_A) + \frac{1 - \rho_A}{2} \left[1 - \frac{\beta_2}{2} \right] q_A(q_a - 1) = 0$$

$$(1 - q_a) + \frac{1}{2} \left[1 + (1 - \rho_A)(1 + \beta_1) - \frac{\beta_2}{2}\rho_A \right] q_a(1 - q_a) + \frac{\rho_A}{2} \left[1 - \frac{\beta_2}{2} \right] q_a(q_A - 1) = 0.$$

A special case If $\rho_A = 1$ (only A individuals), $q_A = 2/(2 + \beta_1)$

$$q_a = \frac{1}{2 - \beta_2} \left(\frac{6 - \beta_1\beta_2 + 4\beta_1 - \beta_2}{2 + \beta_1} - \sqrt{\left(\frac{6 - \beta_1\beta_2 + 4\beta_1 - \beta_2}{2 + \beta_1} \right)^2 - 4(2 - \beta_2)} \right).$$

q_A , for $\beta_2 = 0.7$ 

q_A , for $\beta_1 = 0.2$ 

Mean field phase

4-dimensional dynamical system Once p - and P -populations of order K , we can compare the evolution of the system to this of a dynamical system (Ethier and Kurtz 1986)

$$\left\{ \begin{array}{l} \dot{z}_{\alpha P} = bz_{\alpha P} + \frac{b}{z} \left[\beta_1 z_{\alpha P} \left(z_{\alpha P} + \frac{z_{\alpha p}}{2} \right) - \beta_2 \left(z_{\alpha P} \left(z_{\bar{\alpha} P} + \frac{z_{\bar{\alpha} p}}{4} \right) + z_{\alpha p} \frac{z_{\bar{\alpha} P}}{4} \right) \right] \\ \quad + \frac{b}{2z} (z_{\bar{\alpha} P} z_{\alpha p} - z_{\alpha P} z_{\bar{\alpha} p}) - (d + cz) z_{\alpha P} \\ \dot{z}_{\alpha p} = bz_{\alpha p} + \frac{b}{z} \left[\beta_1 z_{\alpha p} \frac{z_{\alpha P}}{2} - \beta_2 \left(z_{\alpha p} \frac{z_{\bar{\alpha} P}}{4} + z_{\alpha P} \frac{z_{\bar{\alpha} p}}{4} \right) \right] \\ \quad - \frac{b}{2z} (z_{\bar{\alpha} P} z_{\alpha p} - z_{\alpha P} z_{\bar{\alpha} p}) - (d + cz) z_{\alpha p} \end{array} \right.$$

$$\alpha \in \{a, A\}.$$

Convergence of the dynamical system

Theorem

Assume that the initial condition \mathbf{z} satisfies $z_{AP} \geq z_{aP}$ and $z_{Ap} \geq z_{ap}$ and moreover that

$$\beta_1 > \beta_2 \quad \text{or} \quad \frac{z_{ap}(0) z_{Ap}(0)}{z_p(0) z_p(0)} < \frac{\beta_1(\beta_2 + 2)}{2(\beta_1 + \beta_2)(\beta_1 + 2)}.$$

then the solution $\mathbf{z}(t)$ converges as $t \rightarrow \infty$ toward

$$z_{AP}^* = \frac{(1 + \beta_1)b - d}{c} \quad \text{and} \quad z_{aP}^* = z_{Ap}^* = z_{ap}^* = 0$$

Idea of the proof

- If $\exists t_0$, $(z_{AP} - z_{aP})(z_{Ap} - z_{ap})(t_0) > 0$, holds true for any $t \geq t_0$
- Let us introduce $D = z_A z_a / (z_A + z_a)^2$. Then

$$\dot{D} \leq -D \frac{\beta_1 b}{z^2} (z_{AP} - z_{aP})(z_{Ap} - z_{ap})$$

D positive, decreasing, thus converges to a limit point such that $\dot{D} = 0$

- Among the possible limits, we prove that only one is possible :

$$(z_{Ap}, z_{ap}, z_{AP}, z_{aP}) = \left(0, 0, \frac{(1 + \beta_1)b - d}{c}, 0 \right).$$

Extinction phase

Combining previous steps, with the Markov property we can assume that

$$(Z_{Ap}, Z_{ap}, Z_{AP}, Z_{aP}) \in [0, \eta]^2 \times \left[\frac{(1 + \beta_1)b - d}{c} \pm \eta \right] \times [0, \eta]$$

- Coupling with a subcritical birth and death process. Time to reach 0 for the p -population size :

$$\frac{2}{b\beta_1} \log K.$$

Summary of the results

Initial condition $(N_{\alpha P}(0), N_{\bar{\alpha}P}(0)) = (1, 0), \quad \alpha \in \mathfrak{A}$

$$\left(Z_{Ap}^K(0), Z_{ap}^K(0) \right) \xrightarrow{K \rightarrow \infty} \left(\rho_A \frac{b-d}{c}, (1-\rho_A) \frac{b-d}{c} \right), \quad \rho_A > 1/2$$

Stopping times

$T_0^P = \inf\{t \geq 0, N_{AP}(t) + N_{aP}(t) = 0\}$ **extinction of mutant**

$T_{S_\mu} = \inf\{t \geq 0, \mathbf{N}(t) \in S_\mu\}$ **invasion of mutant**

where

$$S_\mu = \left\{ (Z_{AP}, Z_{aP}, Z_{Ap}, Z_{ap}) \in \left[\frac{(1+\beta_1)b-d}{c} \pm \mu \right] \times \{0\}^3 \right\}$$

Summary of the results

Theorem

Assume furthermore that $\lambda \neq 0$.

Then there exists a Bernoulli random variable B with parameter $1 - q_\alpha$, such that for any $0 < \mu < (b(1 + \beta_1) - d)/c$:

$$\lim_{K \rightarrow \infty} \left(\frac{T_{S_\mu} \wedge T_0^P}{\ln K}, \mathbf{1}_{\{T_{S_\mu} < T_0^P\}} \right) = B \times \left(\frac{1}{b\tilde{\lambda}(\rho_A, \beta_1, \beta_2)} + \frac{2}{b\beta_1}, 1 \right),$$

where the convergence holds in probability.

Future work

- Recombinations
- Dimorphic populations and dominance?
- Applications to mosquitoes

Future work

- Recombinations
- Dimorphic populations and dominance?
- Applications to mosquitoes

Thank you for your attention !