Influence of sexual reproduction on evolutionary dynamics in a heterogeneous environment

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Aknowledgments

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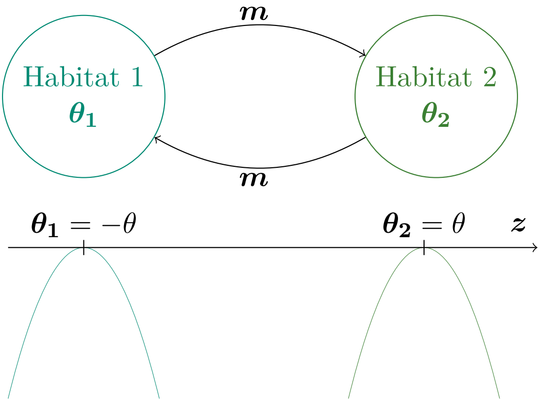
a. https ://www.math.univ-toulouse.fr/ smirrahi/, credits : Vincent Moncorgé
b. http ://vcalvez.perso.math.cnrs.fr/
c. https ://biodiversity.ubc.ca/people/faculty/sarah-otto

Outline

Quantitative trait under stabilizing selection in a heterogeneous (and symmetric) environment



Motivation

RONCE et KIRKPATRICK 2001 :

- moment-based quantitative model, unspecified mode of reproduction,
- local trait distributions assumed to be normal, with a fixed variance,
- numerical existence of bistable asymmetrical equilibria (source-sink).

MIRRAHIMI 2017 :

- mesoscopic model, asexual reproduction,
- possibility of bimodal distributions.
- single stable symmetrical equilibrium (either monomorphic or dimorphic).

Questions

(i) Could a model with an explicit term of sexual reproduction explain the discrepancy between these two studies ?

(ii) Could it shed some lights on the domain of validity of the Gaussian assumption on local trait distributions ?

Outline

Mesoscopic model in a symmetrical setting

$$\frac{\partial \boldsymbol{n_i}}{\partial \boldsymbol{t}} = \overbrace{\boldsymbol{r}_{\mathbf{max}}\,\boldsymbol{\mathcal{B}_\sigma}(\boldsymbol{n_i})}^{\text{reproduction}} - \left(\overbrace{\boldsymbol{s}\,(\boldsymbol{z} - \boldsymbol{\theta_i})^2}^{\text{selection}} + \overbrace{\boldsymbol{\kappa}\,\boldsymbol{\rho_i}}^{\text{competition}} \right) \boldsymbol{n_i} + \overbrace{\boldsymbol{m}\,(\boldsymbol{n_j} - \boldsymbol{n_i})}^{\text{migration}},$$

$\boldsymbol{n_i}(z)$: trait density of subpopulation i.
$\boldsymbol{\rho_i}$: size of subpopulation i.
$\boldsymbol{\mathcal{B}_\sigma}$: sexual reproduction operator.

The infinitesimal model Fisher 1919, Bulmer 1971, Lange 1978, Barton, Etheridge et Véber 2017

$$\mathcal{Z} | \{\mathcal{Z}_1 = \boldsymbol{z_1}, \mathcal{Z}_2 = \boldsymbol{z_2}\} \sim \frac{\boldsymbol{z_1} + \boldsymbol{z_2}}{2} + \mathcal{N}\left(0, \frac{\boldsymbol{\sigma}^2}{2}\right)$$

where $\frac{\boldsymbol{\sigma}^2}{2}$ is the variance within families, or segregational variance. We assume it to be constant and independent of the family.

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Infinitesimal model operator (Bouin et al. p. d., Calvez, Garnier et Patout 2019)

$$\boldsymbol{\mathcal{B}_\sigma}(\boldsymbol{n})(\boldsymbol{z}) = \frac{1}{\sqrt{\pi}\boldsymbol{\sigma}} \int_{\mathbb{R}^2} \exp\left[\frac{-(\boldsymbol{z} - \frac{\boldsymbol{z_1}+\boldsymbol{z_2}}{2})^2}{\boldsymbol{\sigma}^2}\right] \boldsymbol{n}(\boldsymbol{z_1}) \frac{\boldsymbol{n}(\boldsymbol{z_2})}{\boldsymbol{\rho}} d\boldsymbol{z_1} d\boldsymbol{z_2}.$$

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We can compute that :

$$\int_{\mathbb{R}} \boldsymbol{\mathcal{B}_{\sigma}}(\boldsymbol{n})(\boldsymbol{z})\, d\boldsymbol{z} = \boldsymbol{\rho}, \quad \int_{\mathbb{R}} \boldsymbol{z}\, \boldsymbol{\mathcal{B}_{\sigma}}(\boldsymbol{n})(\boldsymbol{z})\, d\boldsymbol{z} = \int_{\mathbb{R}} \boldsymbol{z}\, \boldsymbol{n}(\boldsymbol{z})\, d\boldsymbol{z} = \overline{\boldsymbol{z}}.$$

System of moments deduced from the mesoscopic model

From the properties of $\boldsymbol{\mathcal{B}_\sigma}$, we get the following system :

$$\begin{cases} \frac{d\boldsymbol{\rho_i}}{dt} = \boldsymbol{\rho_i}\left[\boldsymbol{r_{\max}} - \boldsymbol{\kappa\rho_i} - \boldsymbol{s}\ \left((\overline{\boldsymbol{z}}_i - \boldsymbol{\theta}_i)^2 + \boldsymbol{s}\,\boldsymbol{\sigma_i}^2\right)\right] + \boldsymbol{m}(\boldsymbol{\rho_j} - \boldsymbol{\rho_i}), \\ \\ \frac{d\overline{\boldsymbol{z}}_i}{dt} = -2\,\boldsymbol{\sigma_i}^2\boldsymbol{s}\ \left((\overline{\boldsymbol{z}}_i - \boldsymbol{\theta_i}) + \boldsymbol{\psi}_i\right) + \boldsymbol{m}\,\frac{\boldsymbol{\rho_j}}{\boldsymbol{\rho_i}}(\overline{\boldsymbol{z}}_j - \overline{\boldsymbol{z}}_i) \\ \\ \frac{d\boldsymbol{\sigma_i}}{dt} = \ldots \end{cases}$$

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From the properties of $\boldsymbol{\mathcal{B}_\sigma}$, we get the following system :

$$\begin{cases} \frac{d\rho_i}{dt} = \rho_i \left[r_{\max} - \kappa \rho_i - s \left((\overline{z}_i - \theta_i)^2 + s\, \sigma_i^2 \right) \right] + m(\rho_j - \rho_i), \\ \frac{d\overline{z}_i}{dt} = -2\, \sigma_i^2 s \left((\overline{z}_i - \theta_i) + \psi_i \right) + m\, \frac{\rho_j}{\rho_i} (\overline{z}_j - \overline{z}_i). \end{cases}$$

Idea

In regime of small variance, we can asymptotically close this system of moments.

Small variance regime* : $\varepsilon^2 := \frac{\sigma^2}{\theta^2} \ll 1$

. * (Diekmann et al. 2005, Perthame et Barles 2008, Desvillettes et al. 2008, Mirrahimi 2017, Bouin et al. p. d., Calvez, Garnier et Patout 2019)

Small variance regime : $\varepsilon^2 := \frac{\sigma^2}{\theta^2} \ll 1$

Rescaling

$$z := \frac{\boldsymbol{z}}{\boldsymbol{\theta}}, \quad n_{i,\varepsilon}(z) := \boldsymbol{n_i(z)},$$

$$\mathcal{B}_\varepsilon(n_{i,\varepsilon})(z) = \frac{1}{\sqrt{\pi}\varepsilon} \int_{\mathbb{R}^2} \exp\left[\frac{-(z - \frac{z_1+z_2}{2})^2}{\varepsilon^2}\right] n_{\varepsilon,i}(z_1) \frac{n_{\varepsilon,i}(z_2)}{\rho_i} dz_1 dz_2.$$

Small variance regime : $\varepsilon^2 := \frac{\sigma^2}{\theta^2} \ll 1$

Hopf-Cole transform :

$$n_{\varepsilon,i}(z) = \frac{1}{\sqrt{2\pi}\varepsilon} \exp\left(\frac{u_{\varepsilon,i}}{\varepsilon^2}\right) \quad = \frac{1}{\sqrt{2\pi}\varepsilon} \exp\left(\frac{u_{0,i} + \varepsilon^2 v_{\varepsilon,i}}{\varepsilon^2}\right).$$

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We compute, for $z \in \mathbb{R}$:

$$\frac{\mathcal{B}_\varepsilon(n_{i,\varepsilon})(z)}{n_{i,\varepsilon}(z)} = \frac{1}{\sqrt{\pi}\varepsilon} \int_{\mathbb{R}^2} \frac{\exp\left[\frac{u_{0,i}(z_1)+u_{0,i}(z_2)-\left(z-\frac{z_1+z_2}{2}\right)^2-u_{0,i}(z)}{\varepsilon^2}\right]}{\int_{\mathbb{R}} \exp\left[\frac{u_{0,i}(z')}{\varepsilon^2} + v_{\varepsilon,i}(z')\, dz'\right]} \times \exp\left[v_{i,\varepsilon}(z_1) + v_{i,\varepsilon}(z_2) - v_{i,\varepsilon}(z)\right] dz_1\, dz_2.$$

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We need $u_{0,i}$ to be a non-positive function such that :

$$\forall z \in \mathbb{R}, \max_{(z_1,z_2)} \left[u_{0,i}(z_1) + u_{0,i}(z_2) - \left(z - \frac{z_1+z_2}{2}\right)^2 - u_{0,i}(z)\right] = 0.$$

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From Bouin et al. p. d.,

$$u_{0,i}(z) = -\frac{(z - z_i^*)^2}{2}$$

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We need $u_{0,i}$ to be a non-positive function such that :

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From Bouin et al. p. d.,

$$u_{0,i}(z) = -\frac{(z-z_i^*)^2}{2}$$

and $n_{i,\varepsilon}$ is Gaussian at first order, of mean z_i^* and variance ε^2.

Moments approximation when $\varepsilon^2 \ll 1$

As the local trait distributions are normal at the first order, we get :

$$\sigma_{i,\varepsilon}^2 = \varepsilon^2 + \mathcal{O}(\varepsilon^4), \quad \psi_{i,\varepsilon} = \mathcal{O}(\varepsilon^4),$$

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which leads to :

$$\begin{cases} \frac{d\boldsymbol{\rho_i}}{dt} = \boldsymbol{\rho_i}\left[\boldsymbol{r_{\max}} - \boldsymbol{\kappa}\boldsymbol{\rho_i} - \boldsymbol{s}\left((\overline{\boldsymbol{z}}_i - \boldsymbol{\theta}_i)^2 + \boldsymbol{\sigma}^2\right)\right] + \boldsymbol{m}(\boldsymbol{\rho_j} - \boldsymbol{\rho_i}) + \mathcal{O}\left(\frac{\boldsymbol{\sigma}^4}{\boldsymbol{\theta}^4}\right), \\ \frac{d\overline{\boldsymbol{z}}_i}{dt} = -2\boldsymbol{\sigma}^2\boldsymbol{s}\left(\overline{\boldsymbol{z}}_i - \boldsymbol{\theta}_i\right) + \boldsymbol{m}\frac{\boldsymbol{\rho_j}}{\boldsymbol{\rho_i}}(\overline{\boldsymbol{z}}_j - \overline{\boldsymbol{z}}_i) + \mathcal{O}\left(\frac{\boldsymbol{\sigma}^4}{\boldsymbol{\theta}^4}\right). \end{cases}$$

Conclusion

In the regime of small variance, this model is equivalent to Ronce et Kirkpatrick 2001.

Numerical comparison with RONCE et KIRKPATRICK 2001's model, in a small variance $(\varepsilon^2 = 2.5 \cdot 10^{-3})$ [d]

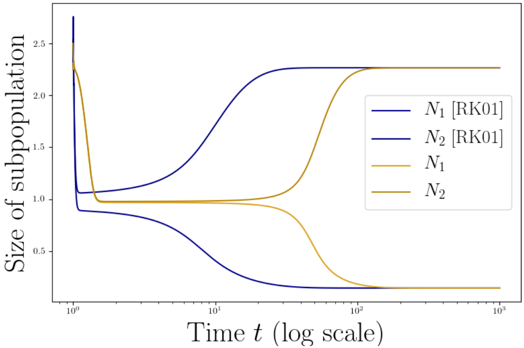

FIGURE – Dynamics of the sizes of subpopulations

d. (other parameter values taken from RONCE et KIRKPATRICK 2001, fig.1)

Numerical comparison with RONCE et KIRKPATRICK 2001's model, in a small variance $(\varepsilon^2 = 2.5 \cdot 10^{-3})$ d

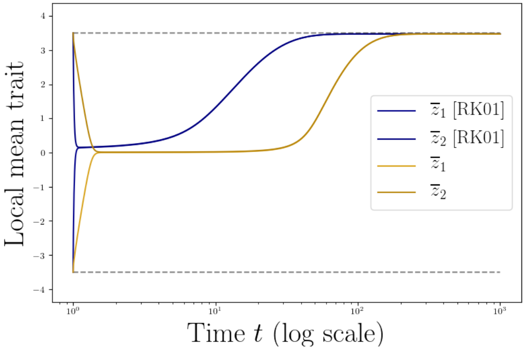

FIGURE – Dynamics of the local means trait

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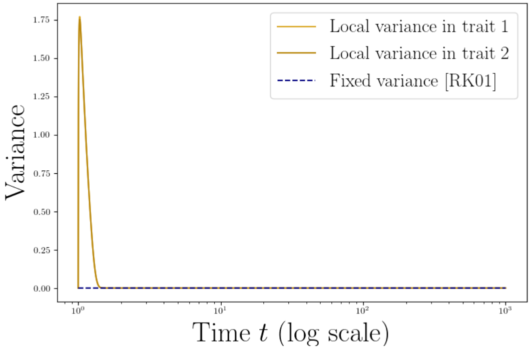

FIGURE – Dynamics of the local variances in trait

d. (other parameter values taken from RONCE et KIRKPATRICK 2001, fig.1)

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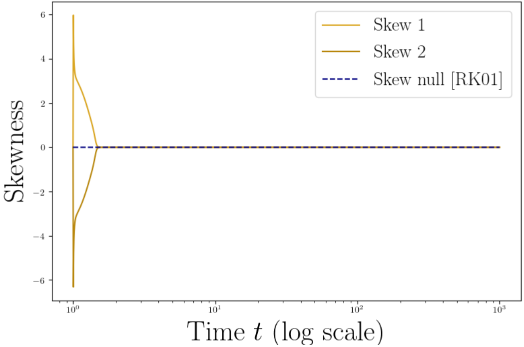

Figure – Dynamics of the local skews

d. (other parameter values taken from Ronce et Kirkpatrick 2001, fig.1)

Outline

Scaling to get a dimensionless system and scaling time

$$t := \varepsilon^2 \boldsymbol{r_{\max} t}, \quad s := \frac{\boldsymbol{s\,\theta}^2}{\boldsymbol{r_{\max}}}, \quad m := \frac{\boldsymbol{m}}{\boldsymbol{r_{\max}}}, \quad n_{i,\varepsilon}(t,z) := \frac{\boldsymbol{\kappa}}{\boldsymbol{r_{\max}}}\boldsymbol{n_i(t,z)}.$$

$$\boldsymbol{r_{\max}} \rightsquigarrow 1, \quad \boldsymbol{\kappa} \rightsquigarrow 1, \quad \boldsymbol{\theta_i} \rightsquigarrow (-1)^i.$$

$$(S_\varepsilon): \begin{cases} \varepsilon^2 \frac{d\rho_{\varepsilon,i}}{dt} = \rho_{\varepsilon,i}\left[1 - \rho_{\varepsilon,i} - s\left((\overline{z}_{\varepsilon,i} - (-1)^i)^2 + \varepsilon^2\right)\right] + m\big(\rho_{\varepsilon,j} - \rho_{\varepsilon,i}\big) \\ \qquad + \mathcal{O}(\varepsilon^4), \\ \varepsilon^2 \frac{d\overline{z}_{\varepsilon,i}}{dt} = 2\,\varepsilon^2\, s\left((-1)^i - \overline{z}_{\varepsilon,i}\right) + m\,\frac{\rho_{\varepsilon,j}}{\rho_{\varepsilon,i}}(\overline{z}_{\varepsilon,j} - \overline{z}_{\varepsilon,i}) + \mathcal{O}(\varepsilon^4). \end{cases}$$

Two different time scales : ecology and evolution.

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Two different time scales : ecology and evolution.

Monomorphism in the small variance regime

$$\varepsilon^2 \frac{d\left(\overline{z}_{\varepsilon,1} - \overline{z}_{\varepsilon,2}\right)}{dt} = \underbrace{-\, m \left[\frac{\rho_{\varepsilon,1}}{\rho_{\varepsilon,2}} + \frac{\rho_{\varepsilon,2}}{\rho_{\varepsilon,1}}\right]}_{\leq -2\,m} \left(\overline{z}_{\varepsilon,1} - \overline{z}_{\varepsilon,2}\right) + \mathcal{O}(\varepsilon^2).$$

- ◇ Due to the mixing effect of **migration**, $\overline{z}_{\varepsilon,1}$ and $\overline{z}_{\varepsilon,1}$ relax **quickly** towards the same dominant trait z^*.
- ◇ z^* moves according to **slow dynamics** (driven by the **selection** term), which justifies the scaling of time.

Fast-slow analysis result *

Proposition

The solutions $(\rho_{\varepsilon,1}, \rho_{\varepsilon,2}, \overline{z}_{\varepsilon,1}, \overline{z}_{\varepsilon,2})$ *of* (S_ε) *converge uniformly over finite time towards a solution* $(\rho_1, \rho_2, z^*, z^*)$ *of the unperturbed system* (S_0) *when* ε *vanishes (depending on initial conditions) :*

$$(S_0) : \begin{cases} \rho_1 \left[1 - \rho_1 - s\,(z^* + 1)^2 - m\right] + m\,\rho_2 = 0, \\ \rho_2 \left[1 - \rho_2 - s\,(z^* - 1)^2 - m\right] + m\,\rho_1 = 0, \\ \frac{dz^*}{dt} = 2\,s\left(\frac{\frac{\rho_2}{\rho_1} - \frac{\rho_1}{\rho_2}}{\frac{\rho_2}{\rho_1} + \frac{\rho_1}{\rho_2}} - z^*\right), \end{cases}$$

The first two equations define the slow manifold ($\subset \left(\mathbb{R}_+^*\right)^2 \times \mathbb{R}$) constituted by the fast equilibria. The slow variable's dynamics (last ODE) happen on that manifold.

. * the proof relies on arguments from Levin et Levinson 1954

Fast-slow analysis result *

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The solutions $(\rho_{\varepsilon,1}, \rho_{\varepsilon,2}, \overline{z}_{\varepsilon,1}, \overline{z}_{\varepsilon,2})$ *of* (S_ε) *converge uniformly over finite time towards a solution* $(\rho_1, \rho_2, z^*, z^*)$ *of the unperturbed system* (S_0) *when* ε *vanishes (depending on initial conditions) :*

$$(S_0) : \begin{cases} \rho_1 \left[1 - \rho_1 - s\,(z^* + 1)^2 - m\right] \rho_1 + m\,\rho_2 = 0, \\ \rho_2 \left[1 - \rho_2 - s\,(z^* - 1)^2 - m\right] + m\,\rho_1 = 0, \\ \frac{dz^*}{dt} = 2\,s\,\left(\frac{\frac{\rho_2}{\rho_1} - \frac{\rho_1}{\rho_2}}{\frac{\rho_2}{\rho_1} + \frac{\rho_1}{\rho_2}} - z^*\right), \end{cases}$$

(S_0) has a reduced complexity in comparison to (S_ε). (and this result does not depend on the selection functions !)

. * the proof relies on arguments from LEVIN et LEVINSON 1954

Outline

Using the symmetries of the system to solve for equilibria

$$(S_0): \begin{cases} \rho_1 \left[1 - \rho_1 - s\,(z^* + 1)^2 - m\right] + m\,\rho_2 = 0, \\ \rho_2 \left[1 - \rho_2 - s\,(z^* - 1)^2 - m\right] + m\,\rho_1 = 0, \\ \frac{dz^*}{dt} = 2\,s\,\left(\frac{\frac{\rho_2}{\rho_1} - \frac{\rho_1}{\rho_2}}{\frac{\rho_2}{\rho_1} + \frac{\rho_1}{\rho_2}} - z^*\right), \end{cases}$$

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Invariant :

$$(\rho_1, \rho_2, z^*) \mapsto (\rho_2, \rho_1, -z^*).$$

Using the symmetries of the system to solve for equilibria

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Invariant :

$$(\rho_1, \rho_2, z^*) \mapsto (\rho_2, \rho_1, -z^*).$$

Algebraically :

$$\exists \mathcal{P} \in \mathbb{R}_3[X], \quad \mathcal{P}\left(\frac{\rho_2}{\rho_1} + \frac{\rho_1}{\rho_2}\right) = 0.$$

Results : equilibrium analysis

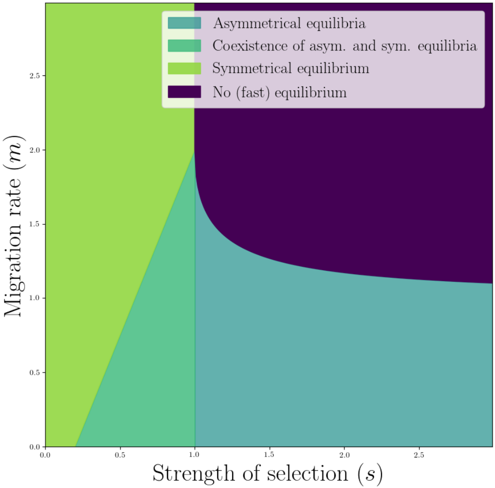
- If $s < 1$, there exists a unique symmetrical equilibrium :

$$z^* = 0, \quad \rho_1 = \rho_2 = 1 - s.$$

- If $[1 + 2m < 5\,s] \wedge \left[m^2 > 4\,s\,(m-1)\right]$, then **there exists additionally a unique mirrored couple of asymmetrical equilibria**.

- Elsewhere, no (fast) equilibrium exists.

Results : equilibrium analysis (same with colors)



Stability

When $1 + 2m > s$, the slow manifold can be globally parametrized by z^* (slow variable) :

$$(S_0) \rightsquigarrow \begin{cases} \frac{\rho_2}{\rho_1} = \phi(z^*) \\ \\ \frac{dz^*}{dt} = f(z^*) := 2\,s\,\left(\frac{\phi(z^*)-\phi(z^*)^{-1}}{\phi(z^*)+\phi(z^*)^{-1}} - z^*\right). \end{cases}$$

- **Both asymmetrical equilibria are locally stable** upon existence.

- The symmetrical equilibrium is locally stable if and only if the asymmetrical equilibria do not exist.

Stability

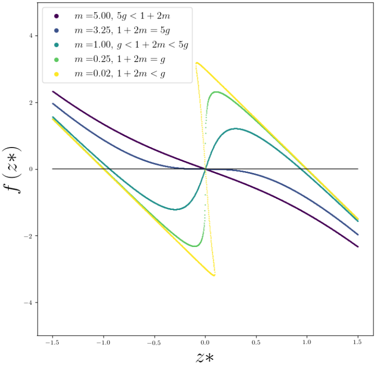
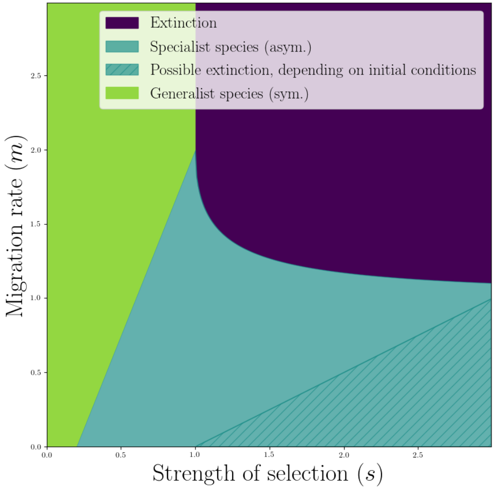
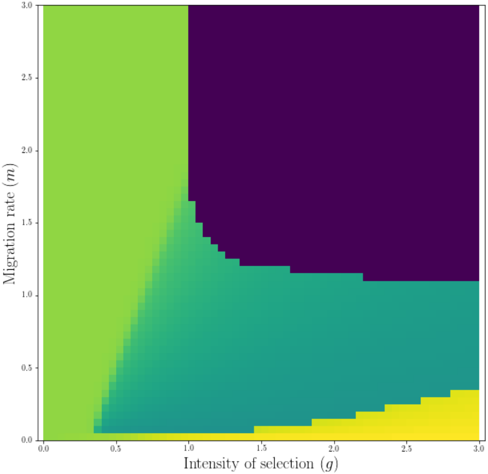


FIGURE – Stability reading ($s = 1.5, m \in \{0.02,\ 0.25,\ 1,\ 3.25,\ 5\}$)

Summary of the stationary states of the model



Numerical summary of the outcomes ($\varepsilon^2 = 2.5 \cdot 10^{-3}$)



Conclusion

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- Other frameworks with sexual reproduction ?

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