Modèles d'adaptation de traits quantitatifs ; une approche asymptotique

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Objective of this lecture:

To introduce an asymptotic method to study adaptation of quantitative traits

Choice of the context:

Evolution of specialization in a two-habitat metapopulation model

Plan of the lecture

- Introduction
- Selection-mutation equilibria for asexual populations
- Selection-mutation-migration equilibria for asexual populations
- Some remarks on the case with sexual reproduction, the infinitesimal model (for more details: see the talk of L. Dekens)
- Transient dynamics (if we have time)

Introduction based on two articles using classical methods in quantitative genetics:

- Ronce and Kirkpatrick (2001) Evolution. *When sources become sinks: migration meltdown in heterogeneous habitats*.
- Débarre, Ronce and Gandon (2013) J. Evol. Biol. *Quantifying the effects of migration and mutation on adaptation and demography in spatially heterogeneous environments.*

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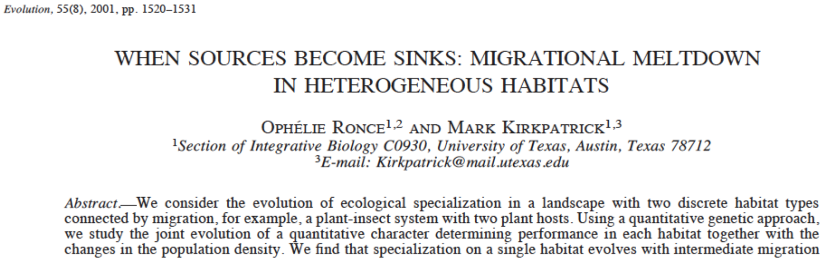
We then introduce an **asymptotic method** and show how it can be applied in the context of the model studied in these articles.

Ronce-Kirkpatrick study on the evolution of specialization



Evolution, 55(8), 2001, pp. 1520–1531

WHEN SOURCES BECOME SINKS: MIGRATIONAL MELTDOWN IN HETEROGENEOUS HABITATS

OPHÉLIE RONCE[1,2] AND MARK KIRKPATRICK[1,3]
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Abstract.—We consider the evolution of ecological specialization in a landscape with two discrete habitat types connected by migration, for example, a plant-insect system with two plant hosts. Using a quantitative genetic approach, we study the joint evolution of a quantitative character determining performance in each habitat together with the changes in the population density. We find that specialization on a single habitat evolves with intermediate migration

Work inspired by the rapid evolution of a metapopulation of the checkerspot butterfly, *Euphydryas editha*.

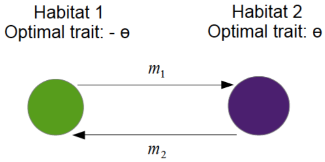
Rapid evolution of E. editha in western United States

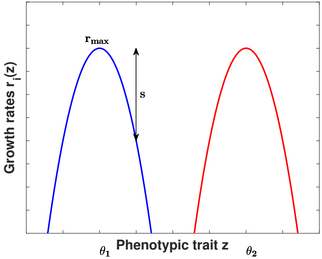
- Before 1989 : larvae of E. editha found on 2 habitats (clearings and outcrops) with 2 host plants. On
  Collinsia torreyi (in clearings): source populations
  Pedicularis semibarbata (in outcrops): pseudosink populations
- Early 1990s: accidental extinction of populations on Collinsia due to an unusual summer frost
- This led to a complete reversal in source-sink dynamics: since the disturbance, local populations have not regained the ability to use their former host, Collinsia.

Two stable equilibria: demographic disturbances may lead to rapid shifts in host use.

Is it possible to observe in mathematical models such bistable situations?

Ronce-Kirkpatrick quantitative genetics model





Fitness in habitat i ($i = 1, 2,\ z \in \mathbb{R}$):

$$w_i(z;\rho_i) = r_i(z) - \underbrace{\kappa\rho_i}_{\text{competition}} \qquad \rho_i\text{: total population size in habitat } i$$

$$r_i(z) = \underbrace{r_{\max}}_{\text{reproduction}} - \underbrace{s(z-\theta_i)^2}_{\text{selection}}, \qquad \theta_2 = -\theta_1 = \theta.$$

Migration rate from one habitat to other: $m_1 = m_2 = m$

How to characterize the phenotypic density?

Dynamics under Gaussian assumption

Hypothoseses:

- Genetic and phenotypic values are distributed normally within each population
- phenotypic variance σ_p^2 and genetic variance σ_g^2 are constant and identical in the two habitats ($\sigma_p^2 = \sigma_g^2 + \sigma_e^2$, σ_e^2: environ. variance)

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ρ_i: population size, $\overline{z}_i$: phenotypic mean

$$\begin{cases} \frac{d\rho_i}{dt} = \left[(r_{\max} - \kappa\rho_i) - s\sigma_p^2 - s\,(\overline{z}_i - \theta_i)^2\right]\rho_i + m\,(\rho_j - \rho_i). \\ \\ \frac{d\overline{z}_i}{dt} = \underbrace{2s\,\sigma_g^2\,(\theta_i - \overline{z}_i)}_{\text{response to selection (Lande 76)}} + m\,\frac{\rho_j}{\rho_i}\,(\overline{z}_j - \overline{z}_i) \end{cases}$$

Demographic loads:

$s\sigma_p^2$: due to stabilizing selection act. on variance

$s(\overline{z}_i - \theta_i)^2$: due to the gap bet. mean and optimum (Lande-Shannon 96)

Ronce & Kirkpatrick analysis of equilibria

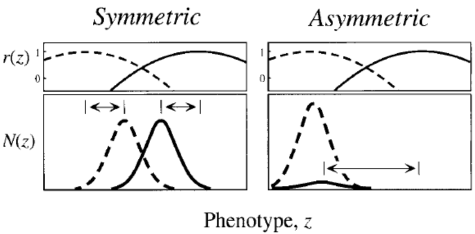

Figure from Ronce & Kirkpatrick 2001

- **Symmetric equilibrium:** equal maladptation and equal population sizes in both habitats (analytic derivation)
- **Asymmetric equilibria:** population adapted to one of the habitats, almost loss of use of the second habitat, existence for intermediate migration rates (equilibria obtained numerically)
- **Bistable asymmetric equilibria:** demographic disturbances can cause a switch from one equilibrium to another, triggering a switch in source-sink dynamics

The domain of the validity of this model?
The role of the mode of reproduction?

Derivation of the moment based model from a mesoscopic model :

$$\frac{\partial}{\partial t} n_i = \underbrace{r_{\max,i}\mathcal{B}(n_i)}_{\text{reproduction}}(z) - \Big(\underbrace{s(z-\theta_i)^2}_{\text{selection}} + \underbrace{\kappa\rho_i}_{\text{competition}}\Big) n_i + \underbrace{m(n_j - n_i)}_{\text{migration}}.$$

$n_i(z)$: the phenotypic density.

General reproduction operator $\mathcal{B}$ satisfying

$$\int \mathcal{B}(n)(z)dz = \int n(z)dz, \qquad \int z\mathcal{B}(n)(z)dz = \int zn(z)dz.$$

It may be sexual or asexual reproduction, with or without mutations.

Moments of the phenotypic distribution:

$$\rho_i(t) = \int n_i(t,z)dz, \quad \overline{z}_i(t) = \frac{1}{\rho_i(t)} \int z n_i(t,z)dz,$$

$$\sigma_i^2(t) = \frac{1}{\rho_i(t)} \int (z - \overline{z}(t))^2 n_i dz, \quad \psi_i(t) = \frac{1}{\rho_i(t)} \int (z - \overline{z}(t))^3 n_i dz.$$

Integrating the equations on n_i against 1 and z and combining them, we obtain

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

If Gaussian assumption with constant variance: $\sigma_i = \sigma$, $\psi_i = 0$.

$\Longrightarrow$ this is the Ronce-Kirkpatrick model.

When is the Gaussian assumption relevant?

R. & K. compared their results numerically with a genetic model:

Fisher's infinitesimal model (Fisher 1918):
Many independent alleles with small additive effects

$\Longrightarrow$ Good fit for weak selection or low habitat heterogeneity

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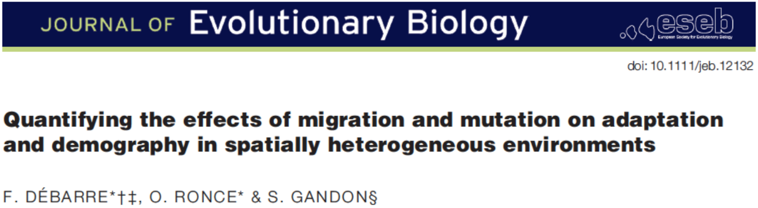
Fisher 1918, Barton, Etheridge & Veber 2017:
The above assumptions lead to Gaussian descendants:
The traits of descendants of known parents have approximately a normal distribution, centered at the average of the parental traits, and with a variance independent of the parental traits.

However, this does not mathematically justify the Gaussian assumption at the population level.

What can we say on the phenotypic distribution at the population level? (see the talk of L. Dekens)

The case of asexual populations



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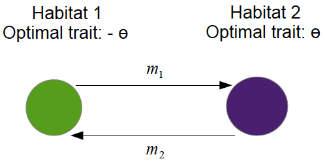
Quantifying the effects of migration and mutation on adaptation and demography in spatially heterogeneous environments

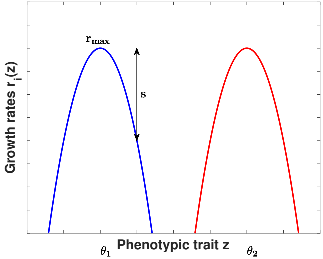
F. DÉBARRE*†‡, O. RONCE* & S. GANDON§

Model studied by Débarre, Ronce and Gandon, 2013



Habitat 1
Optimal trait: - ɵ

Habitat 2
Optimal trait: ɵ



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Migration rate from one habitat to other: $m_1 = m_2 = m$

Model with asexual reproduction

Continuum of alleles model:

(Kimura 1965, Champagnat, Ferrière & Méléard 2008)

$$\frac{\partial n_i(t,z)}{\partial t} \quad + \underbrace{n_i(t,z)\left(r_{\max} - s(z-\theta_i)^2 - \kappa\rho_i\right)}_{\text{growth}}$$

$$= \underbrace{U\Big(\int_{\mathbb{R}} n_i(t,z+y)K(y)dy - n_i(t,z)\Big)}_{\text{mutation}}$$

$$+ \underbrace{m(n_j(t,z) - n_i(t,z))}_{\text{migration}}.$$

K: PDF of $\mathcal{N}(0, 2V_m)$.

How to characterize the phenotypic densities n_i?

Equations on the moments

As previously, we can derive from the above equation:

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

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ρ_i: total population size, $\overline{z}_i$: phenotypic mean,

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The system is not closed, it depends on higher order moments.

Gaussian approximation? not a good approximation, when asexual reproduction (possibility of bimodal distribution)

The homogeneous case

Continuum of alleles model in a homogeneous habitat:

$$\begin{aligned}\frac{\partial n(t,z)}{\partial t} &= U\Big(\int_{\mathbb{R}} n(t,z+y)K(y)dy - n(t,z)\Big) \\ &+n(t,z)\big(r_{\max} - s(z-\theta)^2 - \kappa\rho\big).\end{aligned}$$

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Diffusive approximation of Kimura 1965:

$$\frac{\partial n(t,z)}{\partial t} = UV_m \frac{\partial^2}{\partial z^2} n(t,z) + n(t,z)\big(r_{\max} - s(z-\theta)^2 - \kappa\rho\big).$$

(Champagnat, Ferrière, Méléard 2008: rigorous derivation from an individual based model, under weak but frequent mutations)

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Gaussian equilibrium centered around the optimal trait:

$$\frac{r_{\max} - \sqrt{sUV_m}}{\kappa} f, \quad \text{with } f \text{ PDF of} \quad \mathcal{N}\Big(\theta, \frac{\sqrt{UV_m}}{\sqrt{s}}\Big).$$

The idea of D-R-G in the heterogeneous case; how to go beyond the Gaussian assumption?

The equilibrium of the heterogeneous model with diffusive approximation:

$$0 = UV_m n_i'' + n_i\big(r_{\max} - s(z-\theta_i)^2 - \kappa\rho_i\big) + m(n_j - n_i).$$

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When the mutational variance vanishes, one could expect to approach the adaptive dynamics framework:

Discrete phenotypic density at stable equilibrium corresponding to **evolutionary stable strategies** (ESS).

Idea of D-R-G: 1) Identify the ESS. 2) Provide an approximation of n_i, by considering Gaussian distributions around the ESS points.
$\Rightarrow$ approx. of the phenotypic density as a sum of Gaussian distributions

Two types of evolutionary stable strategies in this model

(we take $\theta_1 = -\theta_2 = \theta$):

- If $m \geq 2s\theta^2$:

  Monomorphic ESS: $z_* = 0$.

  Demographic equilibrium at ESS: $n_i^*(z) = \rho^* \delta(z)$.

- **If** $m < 2s\theta^2$:

  Dimorphic ESS: $z_I^* = -z_{II}^*$.

  Demographic equilibrium at ESS:
  $n_i^*(z) = \rho_{i,\mathrm{I}}^* \delta(z - z_{\mathrm{I}}^*) + \rho_{i,\mathrm{II}}^* \delta(z - z_{\mathrm{II}}^*)$.

Back to the model with mutational variance

D-R-G approximation of the phenotypic density at equilibrium:

Gaussian distributions around the ESS points.

- If monomorphic ESS ($m \geq 2s\theta$)

$$n_i(z) \approx \rho^* f_0, \quad \text{with } f_0 \text{ PDF of } \quad \mathcal{N}(0, V_{sm}).$$

- If dimorphic ESS ($m < 2s\theta$)

$$n_i(z) \approx \rho^*_{i,\mathrm{I}} f_{\mathrm{I}} + \rho^*_{i,\mathrm{II}} f_{\mathrm{II}},$$

with f_k PDF of $\mathcal{N}(z_k^*, V_{sm})$

and V_{sm} the variance at selection-mutation balance (homogeneous case):

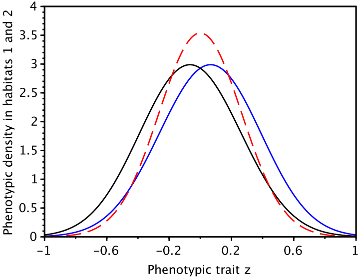
$$V_{sm} = \frac{\sqrt{UV_m}}{\sqrt{s}}.$$

Rather good qualitative approximation but not very precise

black line: numerical equil. in habitat 1

blue line: numerical equil. in habitat 2

dashed line: D-R-G approx. in both habitats



$$r_{\max} = 3, \quad s = 2, \quad \theta = 0.5, \quad m = 1.5, \quad \kappa = U = 1, \quad V_m = 0.01,$$

with these parameters the phenotypic density is unimodal in each habitat.

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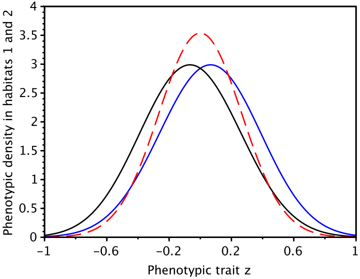

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with these parameters the phenotypic density is unimodal in each habitat.

- There is a shift between the phenotypic density of the habitats
- The migration seems to increase the variance around the peaks
- No mathematical justification of the approximation

Some general remarks on the two studies

- In both studies a priori assumptions are made on the phenotypical distribution
- The approximation are not always very satisfying (depending on the reproduction mode, or the parameters of the model)

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- In both studies a priori assumptions are made on the phenotypical distribution
- The approximation are not always very satisfying (depending on the reproduction mode, or the parameters of the model)

- Can we justify these assumptions mathematically ?
- Can we identify the domain of their validity ?
- Can we improve the precision of the approximations?

The objective of this lecture: to introduce an asymptotic method to study models in quantitative genetics

- No Gaussian a priori assumption
- Allows to recover some classical results and provides a mathematical justification for some previous approximations
- Improves the results when Gaussian assumption is not satisfying
- Well-developed for asexual reproduction
- Sexual reproduction, more recent, under development

History of the method

Asexual reproduction:

- Regime of small mutational variance
- Method based on Hamilton-Jacobi equations
- First suggested by Diekmann–Jabin–Mischler–Perthame (2005)
- First results: Barles–Perthame (2007-2008), Barles–M.–Perthame (2009)
- Then developed widely for more complex models (heterogeneous environment, interaction with resource,...)
- Towards more quantitative results: M.–Roquejoffre (2015-2016), M.–Gandon (2016-2020), PhD thesis of S. Figueroa (2016-2019)

My lecture will be mostly based on:

M. (2017) M3AS, and M.–Gandon (2020) Genetics.

History of the method

Sexual reproduction (infinitesimal model):

- Infinitesimal model, regime of small segregational variance
- First suggested in: Bouin–Bourgeron–Calvez–Cotto–Garnier–Lepoutre–Ronce (In progress).
- Homogeneous environment: PhD thesis of Florian Patout, Calvez–Garnier–Patout (2019).
- Heterogeneous two-habitat environment: PhD thesis of Léonard Dekens, in progress, (co-supervision with V. Calvez).

Section 2: The case of one habitat;

Selection-mutation equilibrium of an asexual population

Example 1: Quadratic growth rate

$$r_0(z) = r_{\max,0} - s_0(z - \theta_0)^2.$$

Considering such growth rate, our method leads to

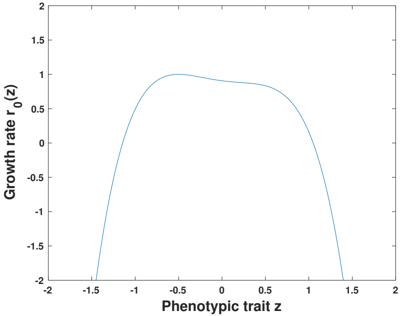
$$n_{\varepsilon,0}(z) \approx \rho^*_{\varepsilon,0} f_\varepsilon, \quad \text{with } f_\varepsilon \text{ PDF of } \mathcal{N}(\theta_0, \varepsilon\,\sigma^2),$$

$$\rho^*_{\varepsilon,0} \approx \frac{1}{\kappa_0}(r_{\max,0} - \varepsilon\sqrt{s_0}), \qquad \sigma^2 = \frac{1}{\sqrt{s_0}}.$$

In this case the Gaussian distribution is indeed an exact solution.

Non-quadratic and non-symmetric growth rate

$$r_0(z) = r_{\mathrm{max},0} - s(z-\theta_0)^2\left(a + (z+\theta_0)^2\right)$$



$$r_{\mathrm{max},0} = 1, \quad s = 0.84, \quad \theta = -0.5, \quad a = 0.2, \quad \varepsilon = 0.05.$$

Non-quadratic and non-symmetric growth rate

Using our method, we can compute

$$\rho_\varepsilon \approx \rho_0^* + \varepsilon K, \qquad n_\varepsilon(z) \approx \frac{1}{\sqrt{2\pi\varepsilon}} \exp\left(\frac{u_0(z) + \varepsilon v_0(z)}{\varepsilon}\right).$$

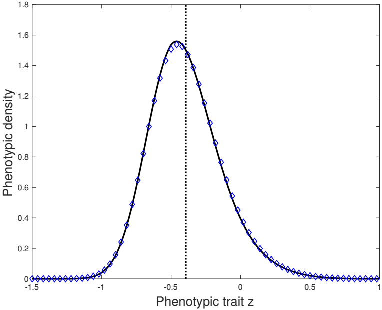
$$\rho_0^* = \frac{r_{\max,0}}{\kappa_0}, \qquad K = \sqrt{s\,(a + 4\theta_0^2)},$$

$$u_0(z) = -\Big|\int_{\theta_0}^{z} \sqrt{s(y-\theta_0)^2(a+(y+\theta_0)^2)}dy\Big|.$$

The next order term v_0 can also be computed explicitly.

The method captures well the skewness in the case of non-symmetric growth rate

Blue dots: the exact solution obtained from numerical computations.
Full black line: our approximation.
Vertical dotted line: phenotypic mean.



The selection-mutation equilibrium of the phenotypic density ($n_{\varepsilon,0}(z)$).

$$r_0(z) = 1 - s(z-\theta_0)^2\left(a + (z+\theta_0)^2\right)$$

$$s = 0.84, \quad \theta = -0.5, \quad a = 0.2, \quad \varepsilon = 0.05.$$

Analytic approximation of the moments of the phenotypic distribution at equilibrium

$$r_0(z) = r_{\max,0} - s(z-\theta_0)^2\left(a + (z+\theta_0)^2\right)$$

Phenotypic mean:

$$\mu_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int z n_{\varepsilon,0}(z)dz = \theta_0 - \frac{4\theta_0\varepsilon}{\sqrt{s}(a+4\theta_0^2)^{3/2}} + O(\varepsilon^2),$$

Phenotypic variance:

$$\sigma^2_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int (z-\mu_{\varepsilon,0})^2 n_{\varepsilon,0}(z)dz = \frac{\varepsilon}{\sqrt{s(a+4\theta_0^2)}} + O(\varepsilon^2),$$

Third central moment:

$$\psi_{\varepsilon,0} = \frac{1}{\rho_{\varepsilon,0}} \int (z-\mu_{\varepsilon,0})^3 n_{\varepsilon,0}(z)dz = -\frac{4\theta_0\varepsilon^2}{s(a+4\theta_0^2)^2} + O(\varepsilon^3).$$

Approximation of the moments of the phenotypic distribution

	Exact value	***First approximation***	***Second approximation***
Phenotypic Mean	-0.391	-0.394	-0.416
Phenotypic variance	0.068	0.067	0.05
Third central moment	0.009	0.009	0.004

$$r_0(z) = 1 - s(z-\theta_0)^2\left(a + (z+\theta_0)^2\right)$$

$$s = 0.84, \quad \theta = -0.5, \quad a = 0.2, \quad \varepsilon = 0.05.$$

In what range of parameters the approximation holds?

$$-UV_m n_0(z) = n_0(z)\big(r_0(z) - \rho_0\big),$$

We saw that a change of variables can bring the equation to

$$-\varepsilon^2 n_{\varepsilon,0}(z) = n_\varepsilon(z)\big(1 - \mu(z) - \rho_{\varepsilon,0}\big),$$

$$\min_z \mu(z) = 0, \quad -\frac{1}{2}\mu''(z_0) = 1.$$

with

$$\varepsilon = \frac{\sqrt{UV_m s_0}}{r_{\max}}.$$

U: mutation rate, V_m: variance of mutations,

s_0: selection pressure, $r_{\max}$: maximal growth rate.

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In our simulations;

$$\mu(z) = 0.84(z+0.5)^2\big(0.2 + (z-0.5)^2\big).$$

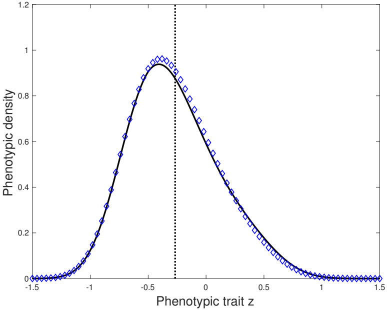
Extinction for $\varepsilon \gtrapprox 1$.

For which values of ε the approximation works well?

Blue dots: the exact solution obtained from numerical computations.

Full black line: our approximation.

Vertical dotted line: phenotypic mean.



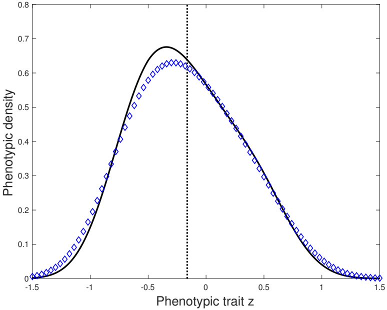
The selection-mutation equilibrium of the phenotypic density ($n_{\varepsilon,0}(z)$).

$$r_0(z) = 1 - 0.84\,(z+0.5)^2\big(0.2 + (z-0.5)^2\big)$$

$$\varepsilon = 0.1.$$

For which values of ε the approximation works well?

Blue dots: the exact solution obtained from numerical computations.
Full black line: our approximation.
Vertical dotted line: phenotypic mean.



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$$r_0(z) = 1 - 0.84\,(z+0.5)^2\big(0.2+(z-0.5)^2\big)$$

$$\varepsilon = 0.15.$$

For which values of ε the approximation works well?

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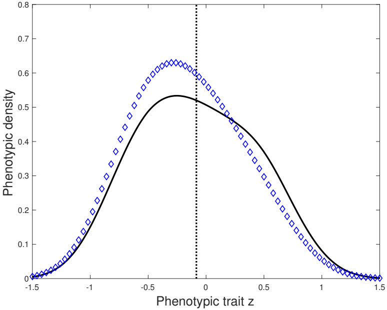
Vertical dotted line: phenotypic mean.



The selection-mutation equilibrium of the phenotypic density ($n_{\varepsilon,0}(z)$).

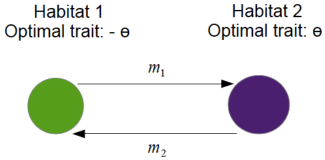
$$r_0(z) = 1 - 0.84\,(z+0.5)^2\left(0.2+(z-0.5)^2\right)$$

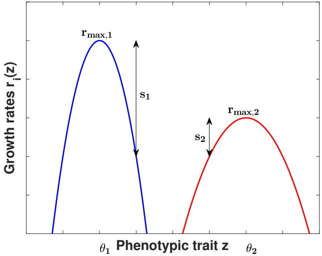
$$\varepsilon = 0.2.$$

Section 3: The case of two habitats;

Selection-mutation-migration equilibrium of an asexual population

Our two-habitat model





Fitness in habitat i ($i = 1, 2,\ z \in \mathbb{R}$):

$$w_i(z;\rho_i) = r_i(z) - \underbrace{\kappa_i\rho_i}_{\text{competition}}$$

ρ_i: total population size in habitat i

$$r_i(z) = \underbrace{r_{\max,i}}_{\text{reproduction}} - \underbrace{s_i(z-\theta_i)^2}_{\text{selection}}, \qquad \theta_2 = -\theta_1 = \theta.$$

Migration rate from habitat i: m_i

Adaptive dynamics for the two-habitat model

How to define **Effective fitness**?
(e.g. Meszéna, Czibula and Geritz 97)

Resident population: $(\widetilde{n}_1(z), \widetilde{n}_2(z))$
total population sizes: $(\widetilde{\rho}_1 = \int_{\mathbb{R}} \widetilde{n}_1(y)dy, \widetilde{\rho}_2 = \int_{\mathbb{R}} \widetilde{n}_2(y)dy)$.

The effective fitness $W(z; \widetilde{\rho}_1, \widetilde{\rho}_2)$, associated with z in the resident population $(\widetilde{n}_1(z), \widetilde{n}_2(z))$, is **the principal eigenvalue** of:

$$\mathcal{A}(z; \widetilde{\rho}_1, \widetilde{\rho}_2) = \begin{pmatrix} w_1(z; \widetilde{\rho}_1) - m_1 & m_2 \\ m_1 & w_2(z; \widetilde{\rho}_2) - m_2 \end{pmatrix},$$

$$w_i(z, \widetilde{\rho}_i) = r_{\max,i} - s_i(z - \theta_i)^2 - \kappa_i \widetilde{\rho}_i.$$

Adaptive dynamics framework–Demographic equilibria

Consider

$$\Omega = \{z_1, \cdots, z_m\}.$$

The **demographic equilibrium** corresponding to Ω is given by

$$\widetilde{n}_i(z) = \sum_{j=1}^{m} \alpha_{j,i}\delta(z - z_j), \qquad \widetilde{\rho}_i = \sum_{j=1}^{m} \alpha_{j,i}, \qquad i = 1, 2,$$

such that

$$\mathcal{A}(z; \widetilde{\rho}_1, \widetilde{\rho}_2) \begin{pmatrix} \widetilde{n}_1 \\ \widetilde{n}_2 \end{pmatrix} = 0,$$

Adaptive dynamics framework–Evolutionary equilibria

Evolutionary stable strategies (ESS):

$\Omega^* = \{z_1^*, \cdots, z_m^*\}$ is called an evolutionary stable strategy if

$$W(z, \rho_1^*, \rho_2^*) = 0, \quad \text{for } z \in \Omega^* \text{ and,} \quad W(z, \rho_1^*, \rho_2^*) < 0, \quad \text{for } z \notin \Omega^*,$$

ρ_1^*, ρ_2^*: total population sizes corresponding to the demographic equilibrium associated with the set Ω^*.

The adaptive dynamics framework: identification of the ESS

Theorem: [M., M3AS 2017]

There exists a **unique ESS**.

(i) The ESS is **dimorphic** if and only if

$$\frac{m_1 m_2}{4 s_1 s_2 \theta^4} < 1,$$

$$C_1 < \alpha_2 r_{\max,2} - \alpha_1 r_{\max,1},$$

$$C_2 < \beta_1 r_{\max,1} - \beta_2 r_{\max,2}.$$

with C_i, α_i and β_i constants depending on $m_1, m_2, s_1, s_2, \kappa_1, \kappa_2, \theta$ which can be determined explicitly.

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$$z^{D*} := \sqrt{\theta^2 - \frac{m_1 m_2}{4\theta^2 s_1 s_2}}.$$

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(ii) If the above conditions are not satisfied then the ESS is **monomorphic**.

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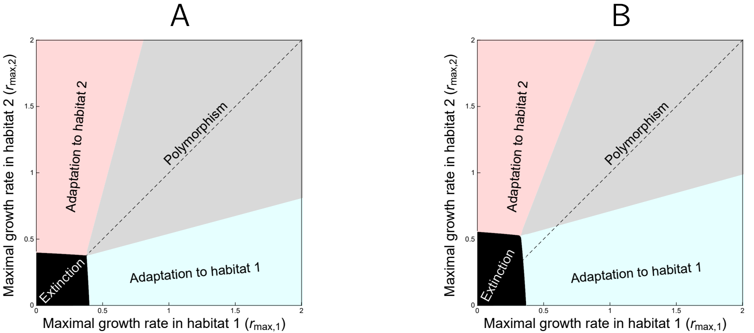
(ii) If the above conditions are not satisfied then the ESS is **monomorphic**.

For **symmetric habitats**, the ESS is given by $\{z^{M*} = 0\}$.

Maintenance of polymorphism and non-symmetric adaptation as a function of the maximal growth rates $r_{max,i}$



(A) a symmetric situation:

$$m_1 = m_2 = 0.5, \quad s_1 = s_2 = 2, \quad \kappa_1 = \kappa_2 = 1, \quad \theta = 0.5.$$

(B) a non-symmetric situation:

$$m_1 = 0.5, \quad m_2 = 0.7, \quad s_1 = s_2 = 2, \quad \kappa_1 = \kappa_2 = 1, \quad \theta = 0.5.$$

More frequent mutations: selection-mutation-migration equilibrium

Our objective is to characterize the solution to the following equation:

$$\begin{cases} 0 = \underbrace{\varepsilon^2 n''_{\varepsilon,1}(z)}_{\text{mutation}} + \underbrace{n_{\varepsilon,1}(z)\left(r_1(z) - \kappa_1 \rho_{\varepsilon,1}\right)}_{\text{clonal reproduction and death}} + \underbrace{m_2 n_{\varepsilon,2}(z) - m_1 n_{\varepsilon,1}(z)}_{\text{migration}}, \\ 0 = \varepsilon^2 n''_{\varepsilon,2}(z) + n_{\varepsilon,2}(z)\left(r_2(z) - \kappa_2 \rho_{\varepsilon,2}\right) + m_1 n_{\varepsilon,1}(z) - m_2 n_{\varepsilon,2}(z). \end{cases}$$

$$\varepsilon^2 = UV_m, \qquad r_i(z) = \underbrace{r_{\max,i}}_{\text{reproduction}} - \underbrace{s(z-\theta_i)^2}_{\text{selection}}.$$

A symmetric case study

$$m_1 = m_2 = m, \quad \kappa_1 = \kappa_2 = \kappa, \quad s_1 = s_2 = s, \quad r_{\max,1} = r_{\max,2} = r_{\max}.$$

Condition for dimorphic ESS: $m < 2s\theta^2$.

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$$m_1 = m_2 = m, \quad \kappa_1 = \kappa_2 = \kappa, \quad s_1 = s_2 = s, \quad r_{\max,1} = r_{\max,2} = r_{\max}.$$

Condition for dimorphic ESS: $m < 2s\theta^2$.

Some analytic results when $m > 2s\theta^2$ (monomorphic ESS):

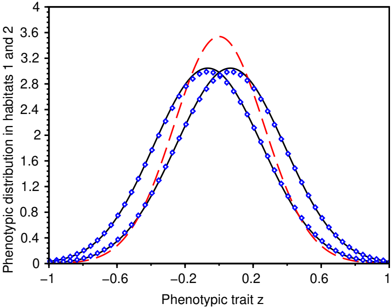
A gap between the phenotypic means:

$$\mu_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}} \int z n_{\varepsilon,i}(z) dz = \pm \frac{\varepsilon \sqrt{s}\theta}{m\sqrt{1 - 2s\theta^2/m}} + O(\varepsilon^2).$$

Increases of the variance due to the heterogeneity:

$$\sigma^2_{\varepsilon,i} = \frac{1}{\rho_{\varepsilon,i}} \int (z - \mu_{\varepsilon,i})^2 n_{\varepsilon,i}(z) dz = \frac{\varepsilon}{\sqrt{s}\sqrt{1 - 2s\theta^2/m}} + O(\varepsilon^2).$$

Symmetric habitats with monomorphic ESS



$$m = 1.5, \quad r_{\max} = 3,$$

$$s = 2, \quad \theta = 0.5,$$

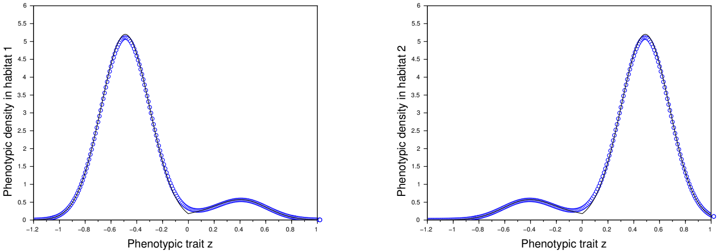
$$\kappa = 1, \quad \varepsilon = 0.1.$$

Blue dots: the phenotypic densities obtained from the numerical resolution of the equation

Full black line: our approximation of the phenotypic density

Red dashed line: the approximation of Débarre-Ronce-Gandon 2013

Symmetric habitats with dimorphic ESS

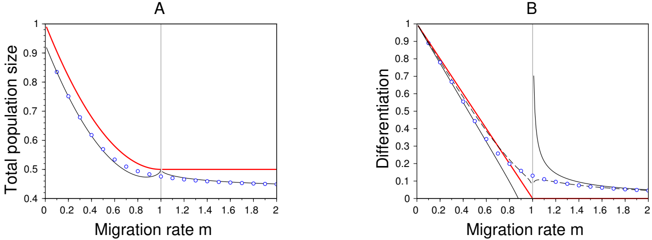


$$m = 0.2, \quad r_{\max} = 3, \quad s = 2, \quad \theta = 0.5, \quad \kappa = 1, \quad \varepsilon = 0.1.$$

Blue dots: the phenotypic densities obtained from the numerical resolution of the equation

Full black line: our approximation of the phenotypic density

Effects of migration in a symmetric scenario on the moments of the phenotypic density

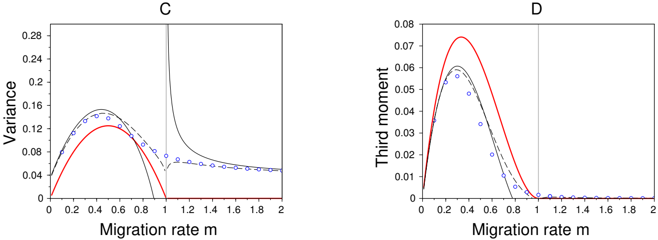


Differentiation: $\mu_{\varepsilon,2} - \mu_{\varepsilon,1}$

Dots: the numerical resolution of the problem
Red line: the adaptive dynamics scenario ($\varepsilon = 0$)
Dashed black line: our *first approximation*
Full black line: our *second approximation*
Vertical gray line: threshold for dimorphic ESS

$$r_{\max} = 1, \quad s = 2, \quad \theta = 0.5, \quad \kappa = 1, \quad \varepsilon = 0.05.$$

Effects of migration in a symmetric scenario on the moments of the phenotypic density



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A source and sink case study

$$m_1 > 0, \qquad m_2 = 0.$$

Obvious evolutionary outcome **in habitat 1**:

$$n_{\varepsilon,1} = \rho_{\varepsilon,1} f_\varepsilon,$$

$$\rho_{\varepsilon,1} = \frac{r_{\mathrm{max},1} - m_1 - \varepsilon\sqrt{s_1}}{\kappa_1}, \quad f_\varepsilon \text{ the PDF of } \mathcal{N}(-\theta, \frac{\varepsilon}{\sqrt{s_1}}).$$

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In habitat 2: adaptive dynamics outcome:
Maladapted monomorphic ESS: $\{-\theta\}$, if

$$\frac{4 s_2 \theta^2 r_{\max,2}}{\kappa_2} \leq \frac{m_1 (r_{\max,1} - m_1)}{\kappa_1}.$$

Otherwise, dimorphic ESS: $\{-\theta, \theta\}$.

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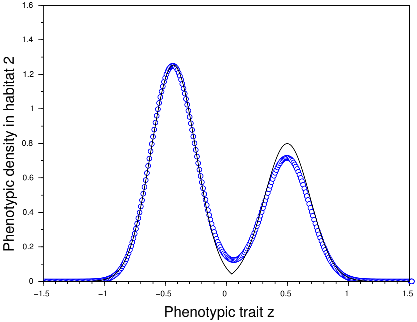
Otherwise, dimorphic ESS: $\{-\theta, \theta\}$.
The **selection-mutation-migration equilibrium** can also be characterized by our method.

The phenotypic density in the sink may be bimodal

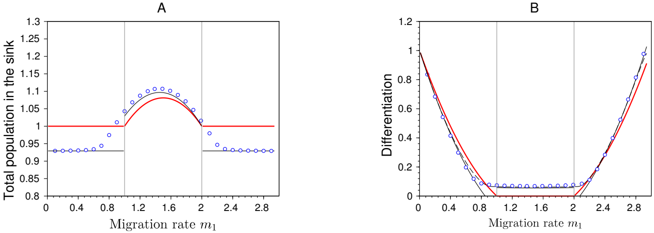


$$r_{\max,1} = 3, \quad r_{\max,2} = 1, \quad s_1 = 3, \quad s_2 = 2,$$

$$\theta = 0.5, \quad \kappa_1 = \kappa_2 = 1, \quad m_1 = 0.4, \quad m_2 = 0, \quad \varepsilon = 0.05.$$

Non-monotonic effect of the migration on the adaptation

Intermediate migration rates have a beneficial effect on the demography but prevent local adaptation in the sink.



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Going back to the previous works with symmetric habitats

What our method brings with respect to the work of D-R-G (2013):

- It provides a mathematical justification of the link between the quantitative genetics equilibria and the ESS
- It provides better approximations of the peaks and the moments of the phenotypic distributions
- No Gaussian assumption

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- It provides better approximations of the peaks and the moments of the phenotypic distributions
- No Gaussian assumption

Ronce and Kirkpatrick (2001):

In their work:

- The reproduction mode not specified
- Based on the Gaussian assumption
- Possibility of two non-symmetric stable equilibria

In our work:

- Asexual mode of reproduction
- Possibility of bimodal distributions (far from Gaussian)
- Only one symmetric stable equilibrium

How about the sexual mode of reproduction? Possibility of bistable equilibria?

$$\frac{\partial}{\partial t} n_i(z) = \underbrace{r_{\max,i}\mathcal{B}(n_i)}_{\text{reproduction}}(z) - \Big(\underbrace{s(z-\theta_i)^2}_{\text{selection}} + \underbrace{\kappa\rho_i}_{\text{competition}}\Big) n_i + \underbrace{m(n_j - n_i)}_{\text{migration}}. \tag{1}$$

The **infinitesimal model** for the reproduction term:
(assuming many independent alleles with small effects)

$$\mathcal{B}(n)(z) = \iint_{\mathbb{R}^2} G_\sigma\left(z - \frac{z_1+z_2}{2}\right) n(z_1) \left(\frac{n(z_2)}{\int_{\mathbb{R}} n(z_2')\,dz_2'}\right) dz_1\,dz_2.$$

G_σ the PDF of $\mathcal{N}(0, \frac{\sigma^2}{2})$.

Regime of small segregational variance

Small segregational variance compared to the heterogeneity:

$$\frac{\sigma}{\theta} = \varepsilon << 1.$$

An adapted **Hopf-Cole transformation**:

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

We expect that

$$u_{\varepsilon,i}(z) = -\frac{1}{2}(z - \overline{z})^2 + \varepsilon^2 v_i(z) + o(\varepsilon^2).$$

$\Longrightarrow$ the phenotypic distributions are well approximated by Gaussian distributions
(Homogeneous case: Calvez-Garnier-Patout 2019)

Regime of small segregational variance

Dekens, preprint (cf. his talk):

- When ε is small, (1) is equivalent with the macroscopic model of R-K 2001.
- A consequence of small segregational variance regime: monomorphism. The phenotypic distributions in the two habitats have almost the same modes.
- Analytic identification of asymptotic equilibria: possibility of asymmetric bistable equilibria observed numerically in R-K 2001.

Thank you for your attention.