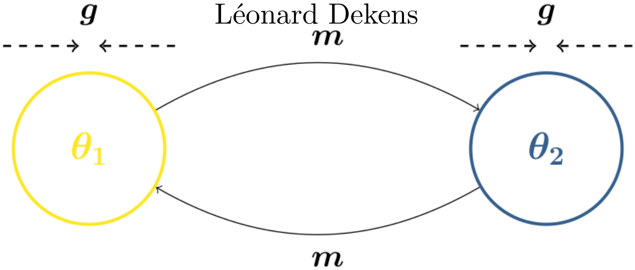
Illustration(s) of **constraints** induced by **sexual reproduction** in eco-evolutionary models with **spatial** structure and **polygenic** traits.

Léonard Dekens



Acknowledgments

((a)) Sepideh Mirrahimi*

((b)) Vincent Calvez †

((c)) Sarah Otto ‡

European Research Council
Established by the European Commission

Mitacs

*https://www.math.univ-toulouse.fr/ smirrahi/, credits: Vincent Moncorgé

†http://vcalvez.perso.math.cnrs.fr/

‡https://biodiversity.ubc.ca/people/faculty/sarah-otto

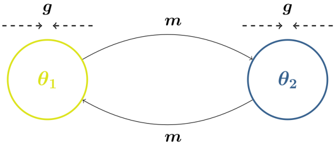
(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation

Continuous environment



Patchy environment

(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation

L loci

$$\sum_{k=1}^{L} \frac{\pm \boldsymbol{e}}{\sqrt{\boldsymbol{L}}} \quad \rightsquigarrow \quad \boldsymbol{z}$$

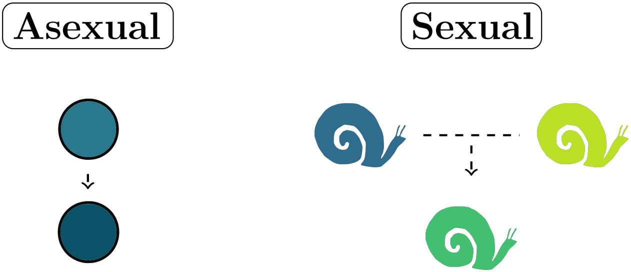
Quant. trait $\boldsymbol{z}$

(*i*) Spatial structure

(*ii*) Polygenic traits

(*iii*) Sexual reproduction

(*iv*) Constraint by segregation



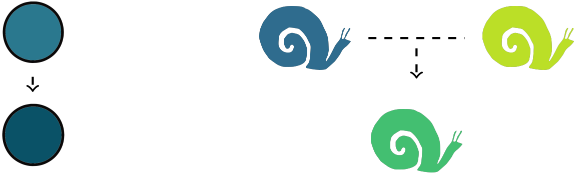
(*i*) Spatial structure

(*ii*) Polygenic traits

(*iii*) Sexual reproduction

(*iv*) Constraint by segregation

Asexual | **Sexual**



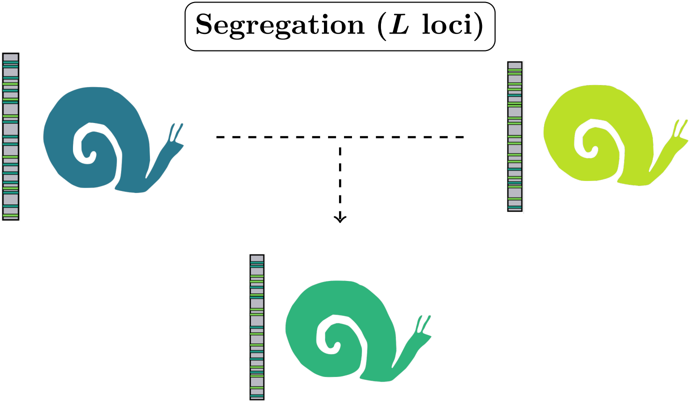
Linear, (non-)local | *Non-linear, non-local*

(*i*) Spatial structure

(*ii*) Polygenic traits

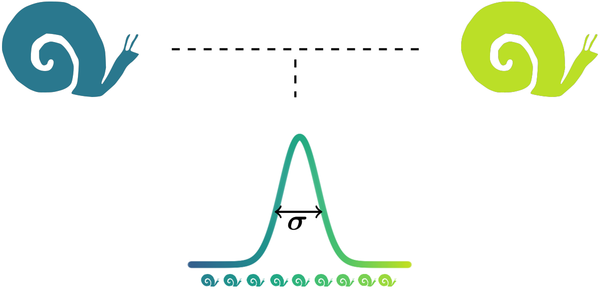
(*iii*) Sexual reproduction

(*iv*) Constraint by segregation



(*i*) Spatial structure
(*ii*) Polygenic traits
(*iii*) Sexual reproduction: example (Fisher (1919), Barton, Etheridge, and Véber (2017))
(*iv*) Constraint by segregation

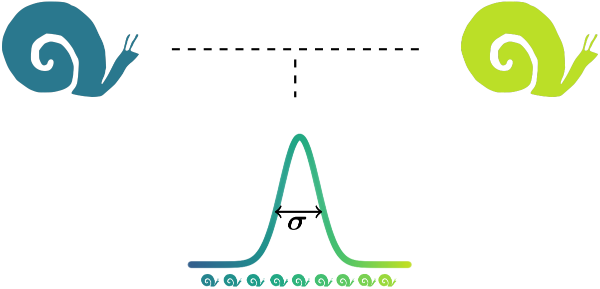
Infinitesimal model ($L \to \infty$)



$\boldsymbol{\sigma^2}$: parameter, constant across families

(i) Spatial structure
(ii) Polygenic traits
(iii) Sexual reproduction: example (Fisher (1919), Barton, Etheridge, and Véber (2017))
(iv) Constraint by segregation

Infinitesimal model ($L \to \infty$)



$\boldsymbol{\sigma^2} = \boldsymbol{e^2}/2$: parameter, constant across families

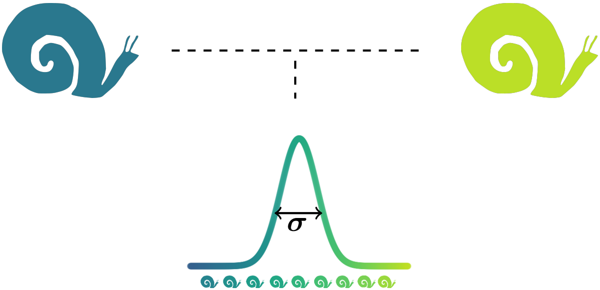
(*i*) Spatial structure

(*ii*) Polygenic traits

(*iii*) Sexual reproduction: example (Fisher (1919), Barton, Etheridge, and Véber (2017))

(*iv*) Constraint by segregation

Infinitesimal model ($L \to \infty$)



$$\mathcal{B}_{\sigma}[n](z) = \iint G_{0,\sigma^2}\left(z - \frac{z_1 + z_2}{2}\right) n(z_1) \frac{n(z_2)}{N} \, dz_1 \, dz_2$$

(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation : well-mixed populations $\boxed{\boldsymbol{\sigma^2_{\mathrm{pop}} \approx 2\sigma^2}}$

(*i*) Spatial structure

(*ii*) Polygenic traits

(*iii*) Sexual reproduction

(*iv*) Constraint by segregation : well-mixed populations $\boldsymbol{\sigma^2_{\mathrm{pop}} \approx 2\sigma^2}$

- ◇ $\boldsymbol{\mathcal{B}_\sigma}[G_{*,2\boldsymbol{\sigma}}] = G_{*,2\boldsymbol{\sigma}} \implies$ **Gaussian equilibria under random mating** (Bulmer 1980) :

$$\partial_t \boldsymbol{n}(t,z) = \boldsymbol{\mathcal{B}_\sigma}[\boldsymbol{n}] - \boldsymbol{n}.$$

(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation : well-mixed populations $\boldsymbol{\sigma^2_{\mathrm{pop}} \approx 2\sigma^2}$

- $\mathcal{B}_{\boldsymbol{\sigma}}[G_{*,2\boldsymbol{\sigma}}] = G_{*,2\boldsymbol{\sigma}} \implies$ **Gaussian equilibria under random mating** (Bulmer 1980)

- **Evolution of niche width** (sex vs asex, Roughgarden 1972), **weak selection** (Turelli and Barton (1994))

(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation : well-mixed populations $\boldsymbol{\sigma^2_{\text{pop}} \approx 2\sigma^2}$

- $\mathcal{B}_{\boldsymbol{\sigma}}[G_{*,2\boldsymbol{\sigma}}] = G_{*,2\boldsymbol{\sigma}} \implies$ **Gaussian equilibria under random mating** (Bulmer 1980)

- **Evolution of niche width** (sex vs asex, Roughgarden 1972), **weak selection** (Turelli and Barton (1994))

- **Contraction** properties (G. Raoul (2017)):

$$W_2\left(\mathcal{B}_{\boldsymbol{\sigma}}[\boldsymbol{n}], \mathcal{B}_{\boldsymbol{\sigma}}[\boldsymbol{m}]\right)^2 \leq \frac{1}{2} W_2\left(\boldsymbol{n}, \boldsymbol{m}\right)^2.$$

(i) Spatial structure

(ii) Polygenic traits

(iii) Sexual reproduction

(iv) Constraint by segregation : well-mixed populations $\boldsymbol{\sigma^2_{\mathrm{pop}} \approx 2\sigma^2}$

- $\boldsymbol{\mathcal{B}_\sigma}[G_{*,2\boldsymbol{\sigma}}] = G_{*,2\boldsymbol{\sigma}} \implies$ **Gaussian equilibria under random mating** (Bulmer 1980)
- **Evolution of niche width** (sex vs asex, Roughgarden 1972), **weak selection** (Turelli and Barton (1994))
- **Contraction** properties (G. Raoul (2017)):

$$W_2\left(\boldsymbol{\mathcal{B}_\sigma}[\boldsymbol{n}], \boldsymbol{\mathcal{B}_\sigma}[\boldsymbol{m}]\right)^2 \leq \frac{1}{2} W_2\left(\boldsymbol{n}, \boldsymbol{m}\right)^2 .$$

- **Perturbative analysis** in the regime of small variance $\boldsymbol{\sigma} \ll 1$ (V. Calvez, Garnier, and Patout (2019)). **Explicit math. constraint** on the distribution.

(i) Spatial structure

(ii) Polygenic traits

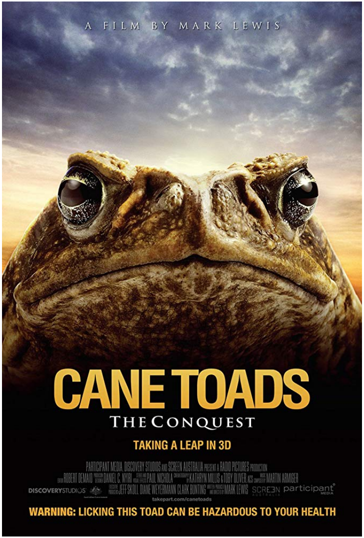
(iii) Sexual reproduction

(iv) Constraint by segregation : well-mixed populations $\boldsymbol{\sigma^2_{\text{pop}} \approx 2\sigma^2}$

Shape and influence of such constraint with spatial structure?

Scenery

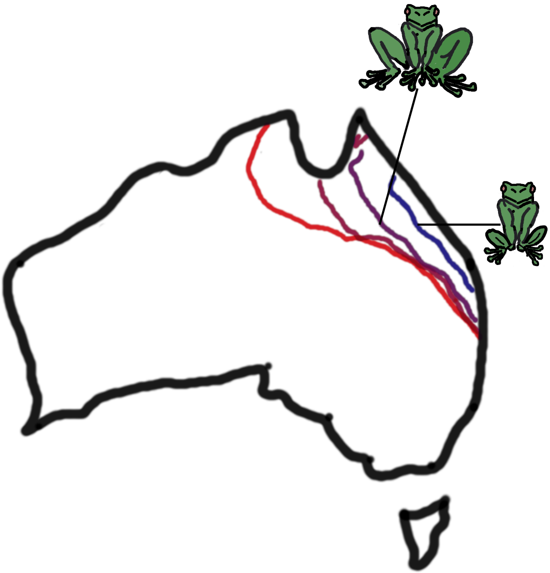
Scenery


A FILM BY MARK LEWIS
CANE TOADS
THE CONQUEST
TAKING A LEAP IN 3D
takepart.com/canetoads
WARNING: LICKING THIS TOAD CAN BE HAZARDOUS TO YOUR HEALTH

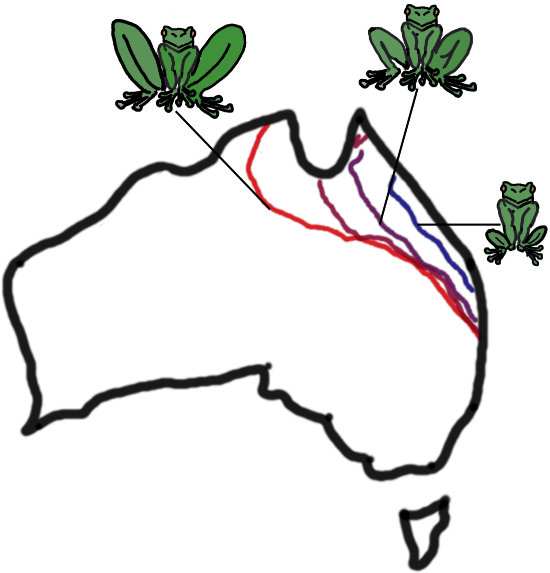
Scenery (Phillips et al. (2006), Urban et al. (2008))

Scenery (Phillips et al. (2006), Urban et al. (2008))

Scenery (Phillips et al. (2006), Urban et al. (2008))



Scenery (Phillips et al. (2006), Urban et al. (2008))



Cane-toads equation $(t > 0, \quad x \in \mathbb{R}, \quad z \in \mathbb{R})$

Reaction-diffusion with **diffusion coefficient under evolution**

$$\frac{\partial n}{\partial t}(t,x,\boldsymbol{z}) = \overbrace{\mathcal{B}[n(t,x,\cdot)](\boldsymbol{z})}^{\text{reproduction}} \quad \overbrace{-n(t,x,z)\int n\,dz'}^{\text{competition}} \quad + \overbrace{\boldsymbol{z}\,\Delta_x n(t,x,z)}^{\text{diffusion}}.$$

Reaction-diffusion with **diffusion coefficient under evolution**

$$\frac{\partial n}{\partial t}(t, x, z) = \overbrace{n + \sigma_M^2 \Delta_z n}^{\textbf{mutations}} \quad \overbrace{-n(t, x, z) \int n \, dz'}^{\text{competition}} \quad + \overbrace{z \, \Delta_x n(t, x, z)}^{\text{diffusion}} .$$

◇ **Asexual** reproduction[§] ⇝ **self-accelerating** front $\boxed{X(t) \propto t^{3/2}}$ [¶]

§(Prevost 2004, Champagnat and Méléard 2007)

¶(Bouin, C. Henderson, and Ryzhik 2017; Berestycki, Mouhot, and Raoul 2017; Calvez, Henderson, et al. 2022

Cane-toads equation $(t > 0, \quad x \in \mathbb{R}, \quad z \in \mathbb{R})$

Reaction-diffusion with **diffusion coefficient under evolution**

$$\frac{\partial n}{\partial t}(t,x,z) = \overbrace{n(t,x,z)}^{\text{growth}} \quad \overbrace{-n(t,x,z)\int n\,dz'}^{\text{competition}} \quad + \quad \overbrace{\mathbf{1}\Delta_x n(t,x,z)}^{\textbf{constant}\text{ diffusion}} \quad .$$

- **Asexual** reproduction[§] $\rightsquigarrow$ **self-accelerating** front $\boxed{X(t) \propto t^{3/2}}$ [¶]
- Constant diffusion (FKPP) $\rightsquigarrow$ front at **constant speed** $\boxed{X(t) \propto t}$

[§](Prevost 2004, Champagnat and Méléard 2007)

[¶](Bouin, C. Henderson, and Ryzhik 2017; Berestycki, Mouhot, and Raoul 2017; Calvez, Henderson, et al. 2022

Cane-toads equation $(t > 0, \quad x \in \mathbb{R}, \quad z \in \mathbb{R})$

Reaction-diffusion with **diffusion coefficient under evolution**

$$\frac{\partial n}{\partial t}(t,x,z) = \boxed{\overbrace{\mathcal{B}_\sigma[n(t,x,\cdot)](z)}^{\textbf{Inf. model}}} \quad \overbrace{-n(t,x,z)\int n\,dz'}^{\text{competition}} \quad + \overbrace{z\,\Delta_x n(t,x,z)}^{\text{diffusion}}.$$

- **Asexual** reproduction[§] $\rightsquigarrow$ **self-accelerating** front $\boxed{X(t) \propto t^{3/2}}$ [¶]
- And for **sexually reproducing** toads? (with infinitesimal model)

[§] (Prevost 2004, Champagnat and Méléard 2007)

[¶] (Bouin, C. Henderson, and Ryzhik 2017; Berestycki, Mouhot, and Raoul 2017; Calvez, Henderson, et al. 2022

- **Front position** $\boxed{X(t) = y_c t^{5/4}}$, $\quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}$.

Conjecture about long time asymptotics ([D. and Lavigne (2021)])

- **Front position** $\boxed{X(t) = y_c t^{5/4}}$, $\quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}$.

- **Behind** $(x \leq X(t))$: mean dispersal trait

$$\boxed{\bar{z}^b(x) = \sigma^{4/5} 6^{1/5} x^{2/5}} \rightsquigarrow \textbf{stationary}$$

- **Front position** $\boxed{X(t) = y_c t^{5/4}}$, $\quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}$.
- **Behind** $(x \leq X(t))$: stationary trait distribution for $|z - \bar{z}^b(x)| \leq \delta \bar{z}^b(x)$:

$$\boxed{n(t,x,z) = G_{\bar{z}^b(x), \boldsymbol{2\sigma^2}}(z)} \times \left[1 + \underset{\delta \to 0}{\mathcal{O}}(\delta) + \underset{t \to \infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right],$$

Conjecture about long time asymptotics ([D. and Lavigne (2021)])

- **Front position** $\boxed{X(t) = y_c t^{5/4}}, \quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}.$

- **Behind** $(x \leq X(t))$: stationary trait distribution for $|z - \bar{z}^b(x)| \leq \delta \bar{z}^b(x)$:

$$\boxed{n(t,x,z) = G_{\bar{z}^b(x),\mathbf{2\sigma^2}}(z)} \times \left[1 + \underset{\delta\to 0}{\mathcal{O}}(\delta) + \underset{t\to\infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right],$$

- **Ahead** $(x \geq X(t))$: mean dispersal trait

$$\boxed{\bar{z}^a(t,x) = \left(3\sigma^2 \frac{x^2}{2t}\right)^{1/3}}.$$

Conjecture about long time asymptotics ([D. and Lavigne (2021)])

- **Front position** $\boxed{X(t) = y_c t^{5/4}}$, $\quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}$.

- **Behind** $(x \leq X(t))$: stationary trait distribution for $|z - \bar{z}^b(x)| \leq \delta \bar{z}^b(x)$:

$$\boxed{n(t,x,z) = G_{\bar{z}^b(x), \boldsymbol{2\sigma^2}}(z)} \times \left[1 + \underset{\delta \to 0}{\mathcal{O}}(\delta) + \underset{t\to\infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right],$$

- **Ahead** $(x \geq X(t))$: distribution for $|z - \bar{z}^a(t,x)| \leq \delta \bar{z}^a(x)$:

$$\boxed{n(t,x,z) = e^{-c\left(t, \frac{x}{X(t)}\right)} \times G_{\bar{z}^a(t,x), \boldsymbol{2\sigma^2}}(z)}$$

$$\times \left[1 + \underset{\delta\to 0}{\mathcal{O}} + \left(\delta + \delta^2 \left[\frac{x}{t^{5/4}}\right]^{8/3}\right) + \underset{t\to\infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right].$$

Conjecture about long time asymptotics ([D. and Lavigne (2021)])

- **Front position** $\boxed{X(t) = y_c \boldsymbol{t^{5/4}} \ll \boldsymbol{t^{3/2}}}$, $\quad y_c = 4\left(\frac{\sigma}{3}\right)^{1/2}$.

- **Behind** $(x \le X(t))$: stationary trait distribution for $|z - \bar{z}^b(x)| \le \delta \bar{z}^b(x)$:

$$\boxed{n(t,x,z) = G_{\bar{z}^b(x), \boldsymbol{2\sigma^2}}(z)} \times \left[1 + \underset{\delta \to 0}{\mathcal{O}}(\delta) + \underset{t\to\infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right],$$

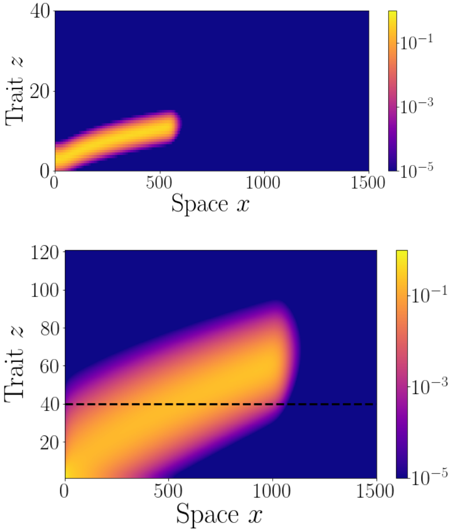
- **Ahead** $(x \ge X(t))$: distribution for $|z - \bar{z}^a(t,x)| \le \delta \bar{z}^a(x)$:

$$\boxed{n(t,x,z) = e^{-c\left(t, \frac{x}{X(t)}\right)} \times G_{\bar{z}^a(t,x), \boldsymbol{2\sigma^2}}(z)}$$

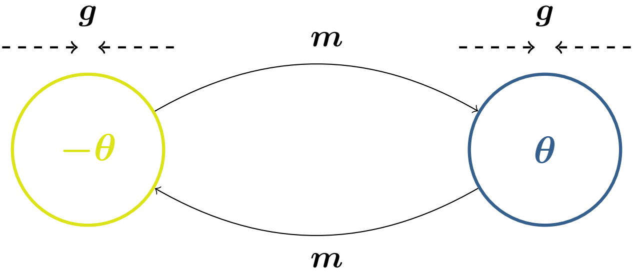
$$\times \left[1 + \underset{\delta\to 0}{\mathcal{O}} + \left(\delta + \delta^2 \left[\frac{x}{t^{5/4}}\right]^{8/3}\right) + \underset{t\to\infty}{\mathcal{O}}\left(\frac{1}{t}\right)\right].$$

Constrained by segregation $\Longrightarrow$ **slower** than asexual

Sex vs asex ($\sigma^2 = \sigma_M^2, t = 100$)

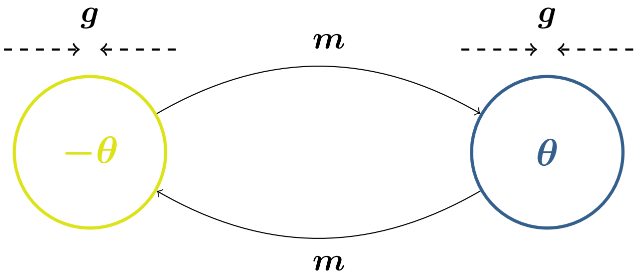


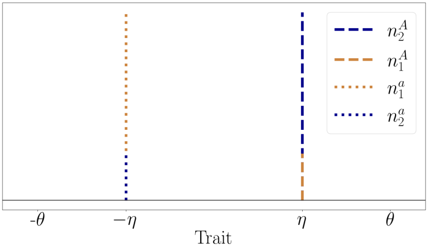
Scenery: patchy environment



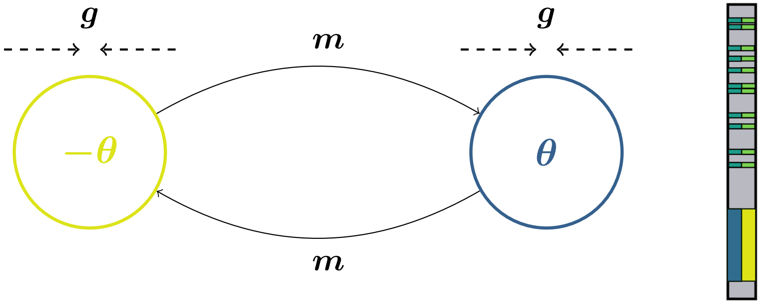
Quantitative trait

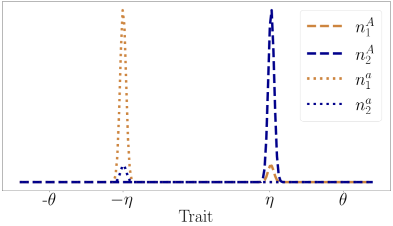
One-locus haploid model: stable dimorphism





Major locus with small quantitative background[‖]: stability?



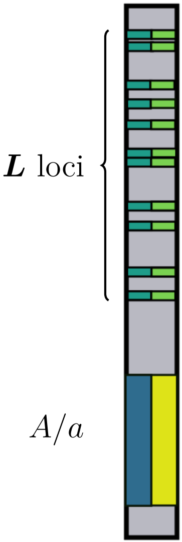


[‖] Orr (2001)

Major locus with small quantitative background[‖]: stability?

[‖] Orr (2001)

Quantitative trait with hybrid genetic architecture**

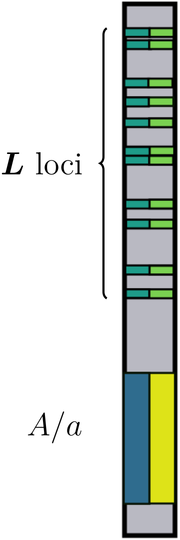


Hybrid trait

$$\overbrace{\pm\boldsymbol{\eta}}^{\text{major effect}} \quad + \quad \overbrace{\sum_{k=1}^{\boldsymbol{L}} \pm\frac{\boldsymbol{e}}{\sqrt{\boldsymbol{L}}}}^{\text{quant. background } \boldsymbol{z}}$$

**haploid, unlinked loci, no mutations

Quantitative trait with hybrid genetic architecture**



Hybrid trait

major effect: $\overbrace{\pm \boldsymbol{\eta}}$ + quant. background $\boldsymbol{z}$: $\overbrace{\sum_{k=1}^{\boldsymbol{L}} \pm \frac{\boldsymbol{e}}{\sqrt{\boldsymbol{L}}}}$

$$\underbrace{\pm \boldsymbol{\eta}}_{\text{major effect}} + \underbrace{\sum_{k=1}^{\boldsymbol{L}} \pm \frac{\boldsymbol{e}}{\sqrt{\boldsymbol{L}}}}_{\text{quant. background } \boldsymbol{z}}$$

Asymptotics: $\varepsilon = \frac{\boldsymbol{e}}{\boldsymbol{\eta}} \ll 1$

**haploid, unlinked loci, no mutations

PDE model

Dynamics of the 4 local $(i, j = 1, 2)$ allelic (A/a) trait densities

$$\frac{\partial n_i^A}{\partial t}(z) = \overbrace{\mathcal{B}_\sigma^A[n_i^A, n_i^a]}^{\text{reproduction}} - \left(\overbrace{g\,(z + \eta - \theta_i)^2}^{\text{selection}} + \overbrace{N_i}^{\text{compet.}} \right) n_i^A + \overbrace{m\left(n_j^A - n_i^A\right)}^{\text{migration}},$$

$$\frac{\partial n_i^a}{\partial t}(z) = \overbrace{\mathcal{B}_\sigma^a[n_i^A, n_i^a]}^{\text{reproduction}} - \left(\overbrace{g\,(z - \eta - \theta_i)^2}^{\text{selection}} + \overbrace{N_i}^{\text{compet.}} \right) n_i^a + \overbrace{m\left(n_j^a - n_i^a\right)}^{\text{migration}}.$$

PDE model

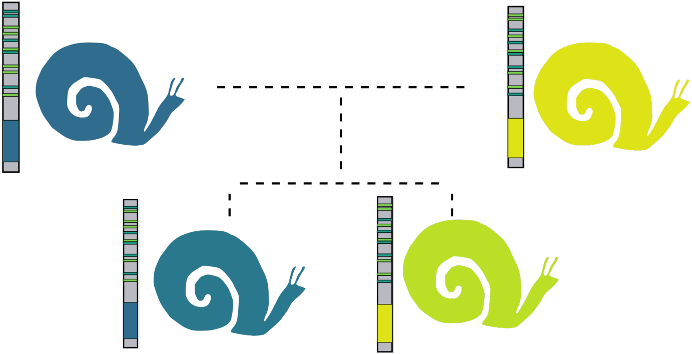
Dynamics of the 4 local $(i, j = 1, 2)$ allelic (A/a) trait densities

$$\frac{\partial \boldsymbol{n_i^A}}{\partial \boldsymbol{t}}(\boldsymbol{z}) = \overbrace{\boldsymbol{\mathcal{B}_\sigma^A}[\boldsymbol{n_i^A}, \boldsymbol{n_i^a}]}^{\text{reproduction}} - \left(\overbrace{\boldsymbol{g}\,(\boldsymbol{z} + \boldsymbol{\eta} - \boldsymbol{\theta_i})^2}^{\text{selection}} + \overbrace{\boldsymbol{N_i}}^{\text{compet.}} \right) \boldsymbol{n_i^A} + \overbrace{\boldsymbol{m}\left(\boldsymbol{n_j^A} - \boldsymbol{n_i^A}\right)}^{\text{migration}},$$

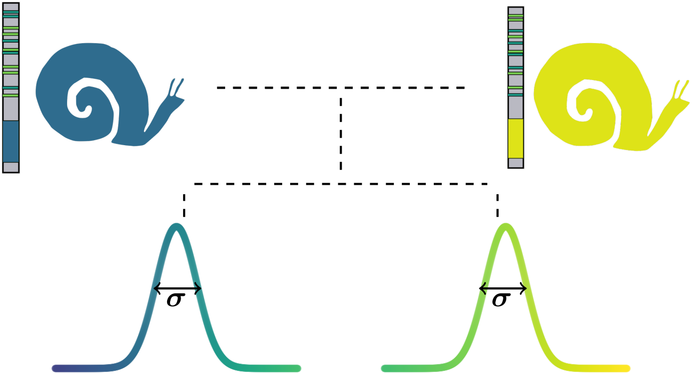
$$\frac{\partial \boldsymbol{n_i^a}}{\partial \boldsymbol{t}}(\boldsymbol{z}) = \overbrace{\boldsymbol{\mathcal{B}_\sigma^a}[\boldsymbol{n_i^A}, \boldsymbol{n_i^a}]}^{\text{reproduction}} - \left(\overbrace{\boldsymbol{g}\,(\boldsymbol{z} - \boldsymbol{\eta} - \boldsymbol{\theta_i})^2}^{\text{selection}} + \overbrace{\boldsymbol{N_i}}^{\text{compet.}} \right) \boldsymbol{n_i^a} + \overbrace{\boldsymbol{m}\left(\boldsymbol{n_j^a} - \boldsymbol{n_i^a}\right)}^{\text{migration}}.$$

Reproduction operators $\boldsymbol{\mathcal{B}_\sigma^a}$, $\boldsymbol{\mathcal{B}_\sigma^A}$?

Genes and trait's inheritance

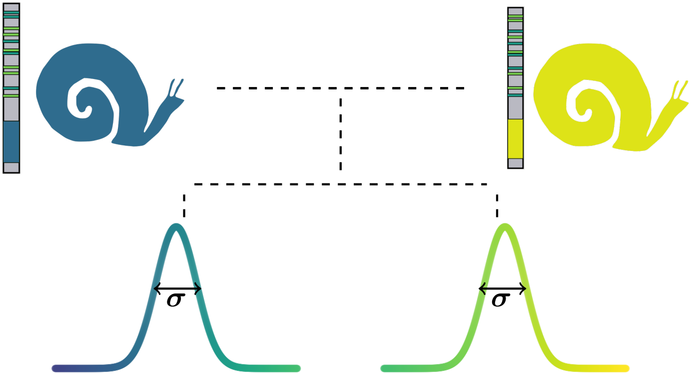


Genes and trait's inheritance



$\boldsymbol{\sigma^2}$: **segregational variance**,
parameter, constant across families

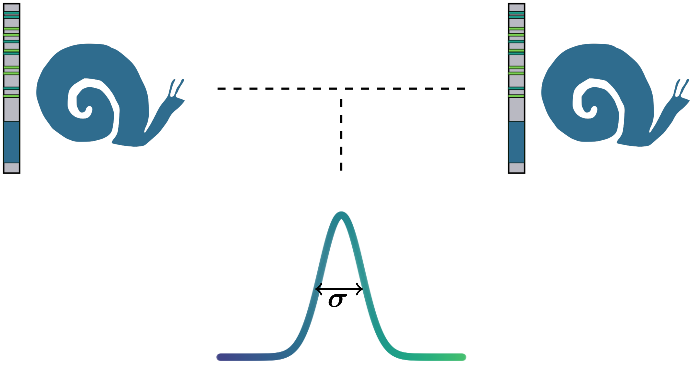
Genes and trait's inheritance



$$\mathcal{B}^{a}_{\sigma}[n^{A}, n^{a}](z) = \iint_{\mathbb{R}^2} G_{0,\sigma^2}\left[z - \frac{z_1 + z_2}{2}\right] n^{a}(z_1) \frac{n^{a}(z_2) + n^{A}(z_2)}{N}\, dz_1 dz_2.$$

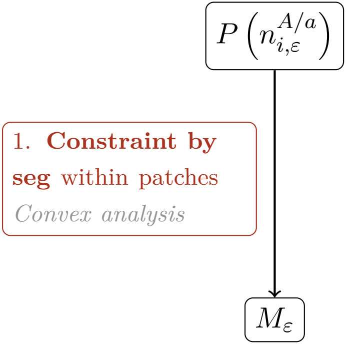
Genes and trait's inheritance

If fixation of one allele in the population and loss of the other $\rightsquigarrow$ previous operator

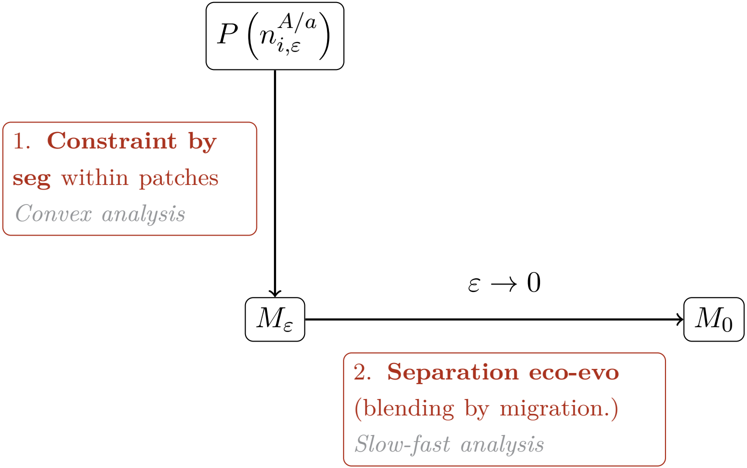


$$\mathcal{B}^{a}_{\sigma}[n^A, n^a](z) = \iint_{\mathbb{R}^2} G_{0,\sigma^2}\left[z - \frac{z_1 + z_2}{2}\right] n^a(z_1) \frac{n^a(z_2) + n^A(z_2)}{N} \, dz_1 dz_2.$$

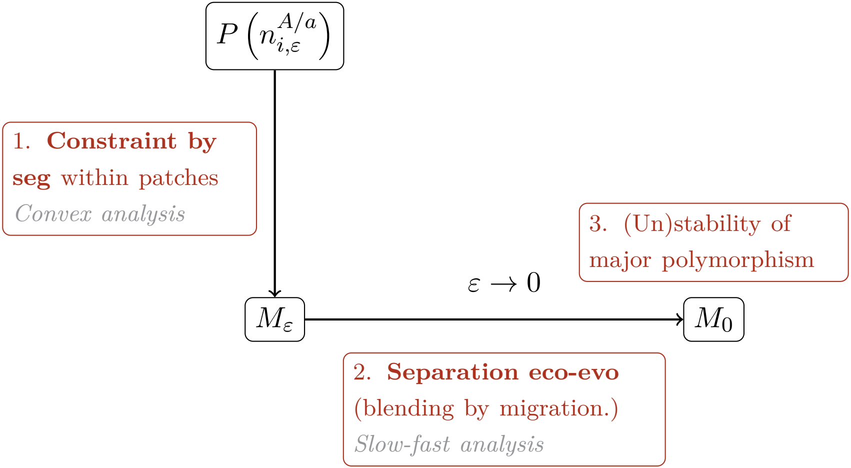
Strategy ([D., Otto and Calvez (2022)])



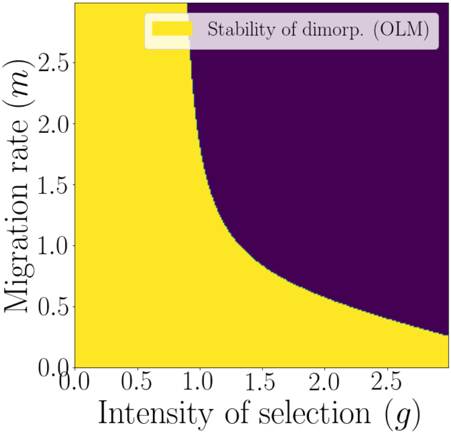
Strategy ([D., Otto and Calvez (2022)])

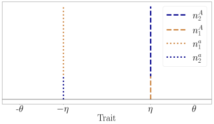


Strategy ([D., Otto and Calvez (2022)])

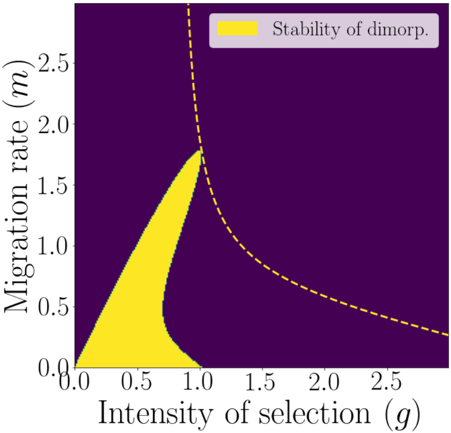


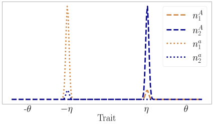
Stability of major dimorphism (Gulliver alone)



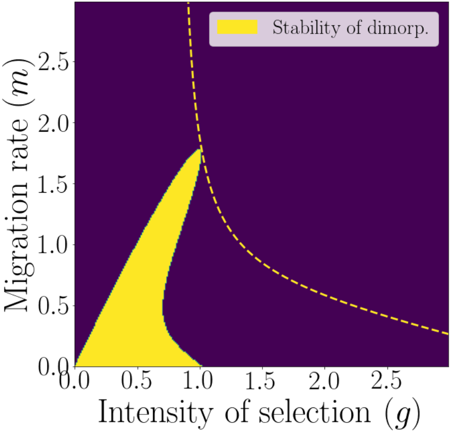


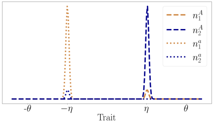
Stability of major dimorphism (Gulliver against the Lilliputians)





Stability of major dimorphism (Gulliver against the Lilliputians)





Constrained by segregation $\implies$ **loss** of major dimorp.

Perspectives

- **Invasions and sexual reproduction**: stochastic approach (demographic fluctuations, imbreeding depression...)

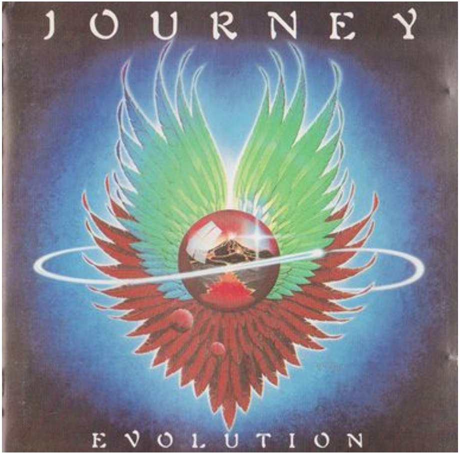
Perspectives

- **Invasions and sexual reproduction**: stochastic approach (demographic fluctuations, imbreeding depression...)
- **Hybrid genetic architecture**: mutation kernel on major locus.

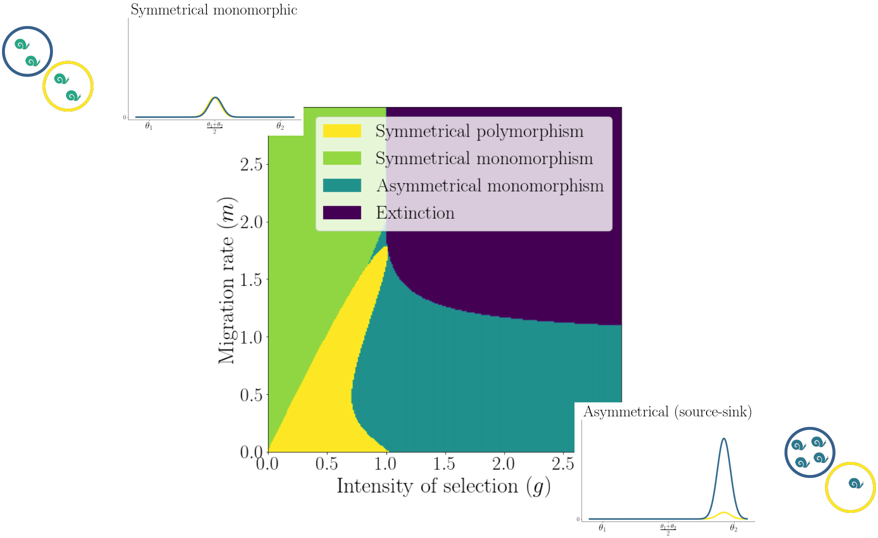
Perspectives

- **Invasions and sexual reproduction**: stochastic approach (demographic fluctuations, imbreeding depression...)
- **Hybrid genetic architecture**: mutation kernel on major locus.
- **Other gene-traits associations with sex**: quantitative alleles (Collet, Méléard, and Metz (2013), D. and Mirrahimi, (2022))

Thank you!



Full analytical outcomes ([D., 2022])



Small variance methodology

Introduced by Diekmann et al. (2005) for quantitative genetics models[††][‡‡] :

Diversity from reproduction $\ll$ Selection pressure

$\rightsquigarrow$ **Concentration** on the fittest traits.

$\rightsquigarrow$ Unfold Dirac singularities: $u_\varepsilon := \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$.

[††] Geometric optics for reaction-diffusion (Freidlin 1986; Evans and Souganidis 1989)

[‡‡] Asexual: *constrained Hamilton-Jacobi* (Perthame and Barles 2008; Barles, Mirrahimi, and Perthame 2009; Lorz, Mirrahimi, and Perthame 2011; Mirrahimi 2017)

Sexual: *Finite-difference term* (V. Calvez, Garnier, and Patout 2019; Patout 2020)

Small variance methodology

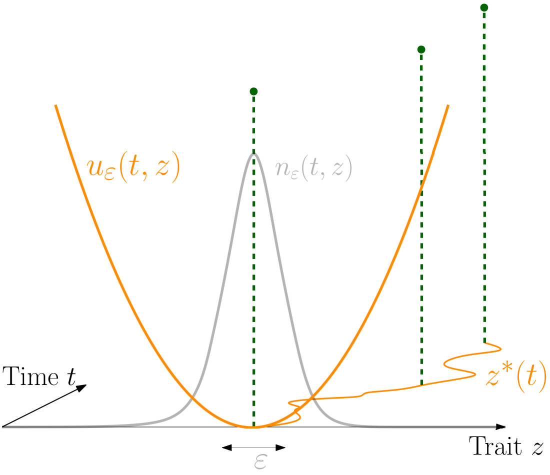


Figure: Transform: $n_\varepsilon = \frac{1}{\varepsilon}\,\exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right)$.

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$0 < \int_{\mathbb{R}} n_\varepsilon(z)dz = \int_{\mathbb{R}} \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right) dz < +\infty$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space

$$\varepsilon^2 \partial_t n_\varepsilon(t,z) = \overbrace{\mathcal{B}_\varepsilon(n_\varepsilon)(t,z)}^{\text{reproduction}} - \overbrace{N_\varepsilon(t) n_\varepsilon(t,z)}^{\text{compet.}} - \overbrace{m(z) n_\varepsilon(t,z)}^{\text{selection}}.$$

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space

$$\varepsilon^2 \partial_t \log\left(n_\varepsilon\right)(t,z) = \overbrace{\frac{\mathcal{B}_\varepsilon(n_\varepsilon)(t,z)}{n_\varepsilon(t,z)}}^{\varepsilon \ll 1?} - N_\varepsilon(t) - m(z).$$

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space and infinitesimal model

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

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space and infinitesimal model

$$\frac{\mathcal{B}_\varepsilon(n_\varepsilon)(z)}{n_\varepsilon(z)} = \int_{\mathbb{R}^2} \frac{\exp\left[\frac{u_0(z_1)+u_0(z_2)-\left(z-\frac{z_1+z_2}{2}\right)^2-u_0(z)}{\varepsilon^2} + \mathcal{O}(1)\right]}{\sqrt{\pi}\varepsilon \int_{\mathbb{R}} \exp\left[-\frac{u_0(z')}{\varepsilon^2} + \mathcal{O}(1)\right] dz'} dz_1 dz_2.$$

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space and infinitesimal model

$$\forall z \in \mathbb{R}, \max_{(z_1,z_2)} \left[u_0(z_1) + u_0(z_2) - \left(z - \frac{z_1 + z_2}{2} \right)^2 - u_0(z) \right] = 0.$$

An example in homogeneous space, no major effects: constraint on $u_\varepsilon = \varepsilon^2 \log(\varepsilon\, n_\varepsilon)$ (V. Calvez, Garnier, and Patout 2019)

(i) If u_ε is smooth, then (Taylor expansions)

$$n_\varepsilon(z) = \frac{1}{\varepsilon} \exp\left(-\frac{u_\varepsilon(z)}{\varepsilon^2}\right) \quad = \frac{1}{\varepsilon} \exp\left(-\frac{u_0(z) + \varepsilon^2\, v^\varepsilon(z)}{\varepsilon^2}\right)$$

$\rightsquigarrow$ u_0 is non-negative and cancels on a non-empty null set.

(ii) Homogeneous space and infinitesimal model

$$\forall z \in \mathbb{R},\ \max_{(z_1, z_2)} \left[u_0(z_1) + u_0(z_2) - \left(z - \frac{z_1 + z_2}{2}\right)^2 - u_0(z) \right] = 0.$$

Convex analysis (E. Bouin et al. n.d.):

$$\boxed{\exists z^* \in \mathbb{R}, \quad \forall z \in \mathbb{R}, \quad u_0(z) = \frac{(z - z^*)^2}{2}},$$

and n_ε is Gaussian at first order, of mean z^* and variance ε^2.