An asymptotic preserving scheme for capturing concentrations in age-structured models arising in adaptive dynamics

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Overview

Outline

Darwinian Evolution

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Major principles:

- variation
- heredity
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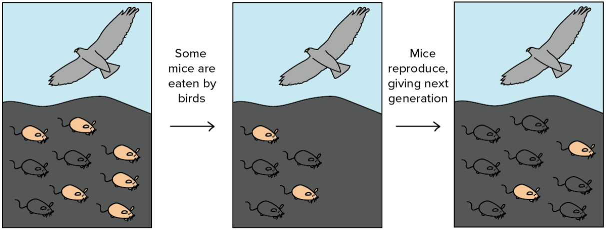

Figure: Natural selection.

Modelling of Natural Selection

Introduce

- x: a quantified phenotypical trait.
- $n(t,x)$: population density with a trait x at time t.
- $\rho(t)$: total size of population

$$\rho(t) = \int n(t,x)\,dx.$$

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$$\Downarrow$$

Adaptive population dynamics

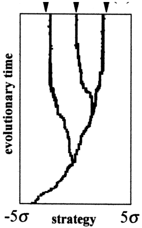

Figure: S. Geritz, E. Kisdi, G. Meszea and J. Metz (1998)

A Brief History

- Initially introduced in mathematical biology in the 90s: S. A. H. Geritz, E. Kisdi, G. Meszena, and J. A. J. Metz (1998).
- Widely theoretically studied: O. Diekmann, P.-E. Jabin, S. Mischler, and B. Perthame (2005), A. Calsina and S. Cuadrado (2007), L. Desvillettes, P.-E. Jabin, S. Mischler, and G. Raoul (2008)...
- Related models: competitive interactions, e.g. P.-E. Jabin and G. Raoul (2011), the chemostat, e.g. N. Champagnat, P.-E. Jabin, and G. Raoul (2010), ...
- Age-structured models have been widely used as well, e.g. L. Nunney (2013), and theoretically studied, e.g. V. C. Tran (2008), S. Méléard and V. C. Tran (2012), S. Nordmann, B. Perthame, and C. Taing (2018)...

Age-structured Population

Fecundity and survival differ with age.

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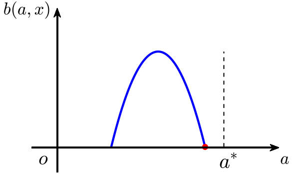

- $b(a,x)$: birth rate satisfying

$$0 < a^* := \inf\{\, a \,|\, b(a,x) = 0, \quad \forall x \geq 0\} < \infty.$$

- $d(a,x)$: death rate satisfying

$$\lim_{a\to\infty} d(a,x) = \infty.$$

An Model for Illustration

Assuming no death and considering only ageing and birth, then

$$n(t+s, a+s) = n(t, a), \quad \forall s \geq 0.$$

[1] Also called **McKendrick-Von Foerster Equation**: Introduced by **McKendrick** for epidemiology, and then re-discovered by **von Foerster** for the cell division cycle

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Boundary condition – new borns

$$n(t, 0) = \int b(a) n(t, a) \, da.$$

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The model without mutation

Including the death term and the trait x:

$$\begin{cases} \varepsilon\partial_t n_\varepsilon + \partial_a n_\varepsilon + d(a,x)n_\varepsilon = -\lambda_\varepsilon(t)n_\varepsilon, \\ n_\varepsilon(t,a=0,x) = \int_0^\infty b(a,x)n_\varepsilon\,da \end{cases}$$

where

- ε – long time evolution (two time scales),
- $\lambda_\varepsilon(t)$ – artificial normalization term such that $\rho(t) \equiv 1$.

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Completely decoupled system in x-direction.

Dirac Concentration

Samuel Nordmann, Benoit Perthame and Cecile Taing (2018) proved that under proper assumptions on $b(a,x)$, $d(a,x)$ and initial datas,

$$n(t,a,x) \rightharpoonup \delta(x-\bar{x}(t))N(a,\bar{x}(t)) \text{ as } \varepsilon \to 0 \quad (t \to \infty),$$

where $\bar{x}(t)$ is the fittest trait.

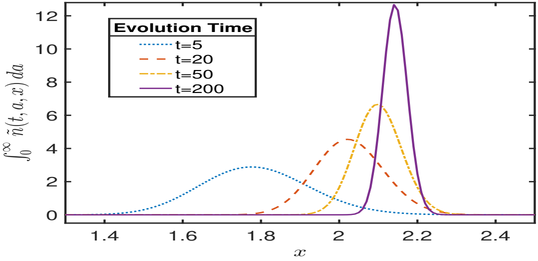

Figure: Sharper concentration as time progresses ($\varepsilon = 0.1$ fixed).

A Biological Point of View – Genetic Cancer

Trait x: the age beyond which the aggressiveness of the disease increases suddenly.

$$b(a,x) = (1-(a-2)^2)_+, \quad d(a,x) = 0.5a + 1000(a-x)_+.$$

See two movies ...

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Conclusion

The cancer mainly affects individuals beyond reproductive age, i.e. $a \geq a^*$(=3).

Outline

Main Idea

Numerical difficulty: ε-dependent mesh for capturing concentration.

WKB ansatz

Taking

$$n_\varepsilon(t,a,x) = e^{\frac{u_\varepsilon(t,x)}{\varepsilon}} q_\varepsilon(t,a,x),$$

we expect $u_\varepsilon(t,x)$ is easy to solve with

$$e^{\frac{u_\varepsilon(t,x)}{\varepsilon}} \rightharpoonup \delta(x-\bar{x}(t)),$$

while $q_\varepsilon(t,a,x)$ is fully regular.

Equations of q_ε and u_ε (I)

Substituting $n_\varepsilon(t,a,x) = e^{\frac{u_\varepsilon(t,x)}{\varepsilon}} q_\varepsilon(t,a,x)$,

$$\begin{cases} q_\varepsilon \partial_t u_\varepsilon + \varepsilon \partial_t q_\varepsilon + \partial_a q_\varepsilon + d(a,x) q_\varepsilon = -\lambda_\varepsilon(t) q_\varepsilon, \\ q_\varepsilon(t, a=0, x) = \int_0^{a^*} b(a,x) q_\varepsilon(t,a,x)\, da. \end{cases}$$

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Question: dynamics of q_ε and u_ε?

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\end{cases}
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Question: dynamics of q_ε and u_ε?

Key Idea: Associated eigenvalue problem needs to be considered.

Equations of q_ε and u_ε (II): Associated Spectral Problem

- Spectral Problem:

$$\begin{cases} \partial_a N(a,x) + d(a,x)N(a,x) = -\Lambda(x)N(a,x), \\ N(a=0,x) = \displaystyle\int_0^\infty b(a,x)N(a,x)\,da, \end{cases}$$

with $N > 0$, $\int_0^{+\infty} N(a,x)\,da = 1$ and $-\Lambda(x)$ being the leading eigenvalue.[2]

- Dual eigenvalue problem:

$$\begin{cases} -\partial_a \Phi(a,x) + d(a,x)\Phi(a,x) = -\Lambda(x)\Phi(a,x) + b(a,x)\Phi(0,x), \\ \displaystyle\int_0^{+\infty} \Phi(a,x)N(a,x)\,da = 1, \quad \text{with } \Phi > 0. \end{cases}$$

[2] Existence is from the Krein-Rutman theorem.

Equations of q_ε and u_ε (III)

$$\begin{cases} q_\varepsilon \partial_t u_\varepsilon + \varepsilon \partial_t q_\varepsilon + \partial_a q_\varepsilon + d(a,x) q_\varepsilon = -\Lambda(x) q_\varepsilon + (\Lambda(x) - \lambda_\varepsilon(t)) q_\varepsilon, \\ q_\varepsilon(t, a=0, x) = \int_0^{a^*} b(a,x) q_\varepsilon(t,a,x)\, da. \end{cases}$$

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As $\varepsilon \to 0^+$, we expect

$$q_\varepsilon(t,a,x) \to N(a,x),$$

which is regular.

Equations of q_ε and u_ε (IV)

- eq. of $u_\varepsilon(t,x)$:

$$\begin{cases} \partial_t u_\varepsilon = \Lambda(x) - \lambda_\varepsilon(t), \\ u_\varepsilon(t=0,x) = u_\varepsilon^0(x). \end{cases}$$

- eq. of $q_\varepsilon(t,a,x)$:

$$\begin{cases} \varepsilon \partial_t q_\varepsilon + \partial_a q_\varepsilon + d(a,x) q_\varepsilon = -\Lambda(x) q_\varepsilon, \\ q_\varepsilon(t, a=0, x) = \int_0^\infty b(a,x) q_\varepsilon(t,a,x)\, da, \\ q_\varepsilon(t=0,a,x) = q_\varepsilon^0(a,x). \end{cases}$$

Properties

Theorem (Maximum principle of q_ε)

$$0 < \underline{\gamma}(x)N(a,x) \leq q_\varepsilon(t,a,x) \leq \overline{\gamma}(x)N(a,x),$$

if it is true initially.

Theorem (Conservation law)

$$\int_0^{+\infty} q_\varepsilon(t,a,x)\Phi(a,x)\,da \equiv \int_0^{+\infty} q_\varepsilon^0(a,x)\Phi(a,x)\,da, \quad \forall x.$$

Theorem (Limiting equations)

$$\max_x u(t,x) = 0, \text{ and } q(t,a,x) = \rho^0(x)N(a,x),$$

where $\rho^0(x) := \int_0^{+\infty} q^0(a,x)\Phi(a,x)\,da$.

Finite Difference Discretization

Denote $\Lambda_k \approx \Lambda(x_k), N_{j,k} \approx N(a_j, x_k)$.
Discretized eigenproblem:

$$\begin{cases} \delta_a^- N_{j,k} + d(a_j, x_k) N_{j,k} = -\Lambda_k N_{j,k}, \\ N_{0,k} = \Delta a \displaystyle\sum_{j=1}^{K_a} b(a_j, x_k) N_{j,k}, \\ \Delta a \sum_{j=0}^{K_a} w_j^{(a)} N_{j,k} = 1. \end{cases}$$

where $-\Lambda_k$ is the leading eigenvalue such that $N_{j,k} > 0$. [3]

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Λ_k is the root of

$$1 = \Delta a \sum_{j=1}^{K_a} b(a_j, x_k) \prod_{s=1}^{j} \frac{1}{1 + \Delta a(d(a_s, x_k) + \Lambda_k)}.$$

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Finite Difference Discretization

Introducing

$$u_k^n \approx u_\varepsilon(t_n, x_k), q_{j,k}^n \approx q_\varepsilon(t_n, a_j, x_k),$$

- Scheme of $u_\varepsilon(t,x)$:

$$u_k^{n+1} = u_k^n + \Delta t(\Lambda_k - L^n),$$

  with L^n being the normalization parameter. [4]

- Scheme of $q_\varepsilon(t,a,x)$:

$$\begin{cases} \varepsilon \frac{q_{j,k}^{n+1} - q_{j,k}^n}{\Delta t} + \delta_a^- q_{j,k}^{n+1} + d(a_j, x_k) q_{j,k}^{n+1} = -\Lambda_k q_{j,k}^{n+1}, \\ q_{0,k}^{n+1} = \Delta a \sum_{j=1}^{K_a} b(a_j, x_k) q_{j,k}^{n+1}. \end{cases}$$

[4] It can be proved L^n is bounded indep. of ε.

Property

Theorem (Maximum principle)

$$0 < \underline{\gamma_k} N_{j,k} \leq q^n_{j,k} \leq \overline{\gamma_k} N_{j,k},$$

if it is true initially.

Theorem (Conservation law)

$$\Delta a \sum_{j=1}^{K_a} q^n_{j,k} \phi_{j-1,k} \equiv \Delta a \sum_{j=1}^{K_a} q^0_{j,k} \phi_{j-1,k}.$$

Theorem (Asymptotic preserving)

$$\max_k u_k^{n+1} = 0, \text{ and } q^n_{j,k} = \rho^0_k N_{j,k},$$

where $\rho^0_k = \Delta a \sum_{j=1}^{K_a} q^0_{j,k} \phi_{j-1,k}$.

Proof of Maximal Principle

Theorem (Maximum principle)

$$0 < \underline{\gamma_k} N_{j,k} \le q_{j,k}^n \le \overline{\gamma_k} N_{j,k},$$

if it is true initially.

Proof:

- The discrete **general relative entropy**

$$\sum_{j=1}^{K_a} \phi_{j-1,k} N_{j,k} H\left(\frac{q_{j,k}^{n+1}}{N_{j,k}}\right) \le \sum_{j=1}^{K_a} \phi_{j-1,k} N_{j,k} H\left(\frac{q_{j,k}^{n}}{N_{j,k}}\right).$$

  where $H(\cdot)$ is an arbitrary convex function.
- Upper bound: Taking $H(u) = (u - \overline{\gamma_k})_+^2$.

Capture Concentration with a Coarse Mesh

Reconstruction:

$$N_{\mathrm{f}} = Q_{\mathrm{f}} e^{\frac{u_{\mathrm{f}}}{\varepsilon}},$$

where Q_{f} and u_{f} are the interpolated numerical solutions on a fine mesh.

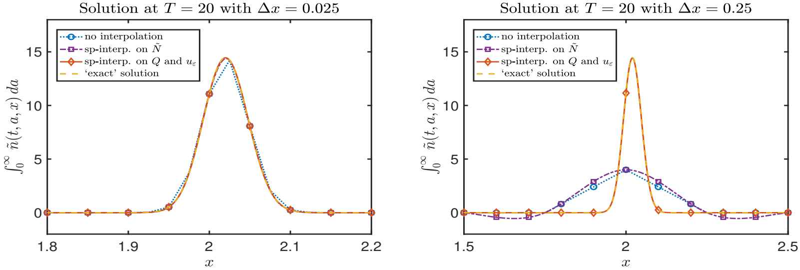
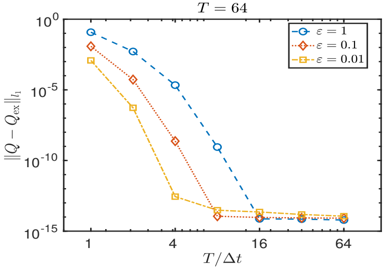


Figure: Comparison of $\int_0^\infty n(t,a,x)\,da$ with the 'exact' one. Here $\varepsilon = 0.01$ and $\Delta x = 0.025$ (left) or 0.25 (right).

Numerical Test: Temporal Convergence



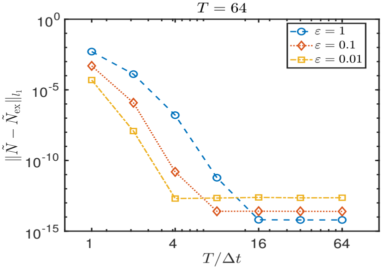


Figure: Temporal convergence in l_1-norm.

Outline

The model with mutation

$$\begin{cases} \varepsilon \partial_t n_\varepsilon + \partial_a n_\varepsilon + d(a,x) n_\varepsilon = -\lambda_\varepsilon(t) n_\varepsilon, \\ n_\varepsilon(t, a=0, x) = (1-m) \displaystyle\int_0^\infty b(a,x) n_\varepsilon \, da \\ \qquad\qquad + \dfrac{m}{\varepsilon} \displaystyle\int_0^\infty \int_0^\infty b(a,y) M\left(\dfrac{x-y}{\varepsilon}\right) n_\varepsilon(t,a,y) da dy, \end{cases}$$

where

- $0 \le m \le 1$: the proportion of birth with mutations,
- $\frac{1}{\varepsilon} M(\frac{x-y}{\varepsilon})$: probability density to change from the inherited trait x to trait y.

Model with Mutation

- No Dirac mass in the mutation case.
- Concentration be more obvious as $\varepsilon \to 0$, $m \to 0$.

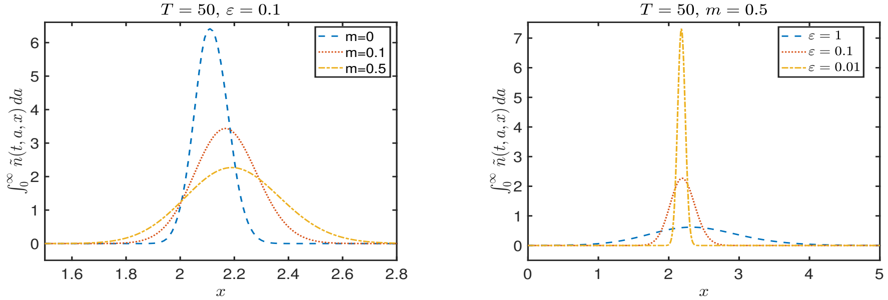


Figure: Illustration of the mutation effect parameterized via ε and m.

Design a scheme that works for all $\varepsilon > 0$.

WKB ansatz

Taking the same ansatz

$$n_\varepsilon(t,a,x) = e^{\frac{u_\varepsilon(t,x)}{\varepsilon}} q_\varepsilon(t,a,x),$$

and introducing $z = (x-y)/\varepsilon$, we get

$$\begin{cases} q_\varepsilon \partial_t u_\varepsilon + \varepsilon\partial_t q_\varepsilon + \partial_a q_\varepsilon + d(a,x) q_\varepsilon = -\lambda_\varepsilon(t) q_\varepsilon, \\ q_\varepsilon(t, a=0, x) = (1-m)\displaystyle\int_0^\infty b(a,x) q_\varepsilon(t,a,x)\, da \\ \qquad\qquad + \text{mutation part}, \end{cases}$$

where the mutation part is

$$m \int_{-\infty}^{\infty} \left(\int_0^\infty b(a, x-\varepsilon z) q_\varepsilon(t,a,x-\varepsilon z)\, da \right) M(z)\, e^{\frac{u_\varepsilon(t,x-\varepsilon z) - u_\varepsilon(t,x)}{\varepsilon}}\, dz.$$

Associated Eigenvalue Problem

By formally taking $\varepsilon \to 0$, we have

$$q_\varepsilon(t, a = 0, x) = (1 - m + m\bar{\eta}[\partial_x u_\varepsilon]) \int_0^\infty b(a, x) q_\varepsilon(t, a, x)\, da,$$

with

$$\bar{\eta}[\partial_x u_\varepsilon] := \int_{-\infty}^{\infty} M(z)\, e^{-z\partial_x u_\varepsilon(t,x)}\, dz.$$

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Associated Eigenvalue Problem

$$\begin{cases} \partial_a N(a,x,\eta) + d(a,x) N(a,x,\eta) = -\Lambda(x,\eta) N(a,x,\eta), \\ N(a=0,x,\eta) = (1 - m + m\eta) \displaystyle\int_0^\infty b(a,x) N(a,x,\eta)\, da. \end{cases}$$

Dynamics of q_ε and u_ε

- Dynamics of u_ε—Hamilton-Jacobi equation

$$\partial_t u_\varepsilon(t,x) = \Lambda(x, \bar{\eta}[\partial_x u_\varepsilon]) - \lambda_\varepsilon(t).$$

- Dynamics of q_ε

$$\begin{cases} \varepsilon \partial_t q_\varepsilon + \partial_a q_\varepsilon + d(a,x) q_\varepsilon = -\Lambda(x, \bar{\eta}[\partial_x u_\varepsilon]) q_\varepsilon, \\ q_\varepsilon(t, a=0, x) = (1-m) \int_0^\infty b(a,x) q_\varepsilon(t,a,x)\, da + \text{mutation part.} \end{cases}$$

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Formally it can be showed that the limiting equation as $\varepsilon \to 0$ is the associated eigenvalue problem.

The Implicit Scheme

Scheme of u_ε – monotone

$$\begin{cases} u_k^{n+1} = u_k^n + \Delta t(\Lambda_k(\eta_k^{n+1}) - L^n), \\ \eta_k^{n+1} = \Delta z \sum_{l=0}^{K_z} \left(M_{(-l)} e^{z_l \delta_x^+ u_k^{n+1}} + M_l e^{-z_l \delta_x^- u_k^{n+1}} \right). \end{cases}$$

Scheme of q_ε

$$\begin{cases} \varepsilon \frac{q_{j,k}^{n+1} - q_{j,k}^n}{\Delta t} + \delta_a^- q_{j,k}^{n+1} + d(a_j, x_k) q_{j,k}^{n+1} = -\Lambda_k(\eta_k^{n+1}) q_{j,k}^{n+1}, \\ q_{0,k}^{n+1} = (1-m)\Delta a \sum_{j=1}^{K_a} b(a_j, x_k) q_{j,k}^{n+1} + \\ \qquad m\Delta z \sum_{l=-K_z}^{K_z} \left[\Delta a \sum_{j=1}^{K_a} b(a_j, x_k - \varepsilon z_l) q_{j,k-\tilde{\varepsilon} l}^{n+1} \right] M_l e^{\frac{u_{k-\tilde{\varepsilon} l}^{n+1} - u_k^{n+1}}{\varepsilon}}, \end{cases}$$

where $\tilde{\varepsilon} = \varepsilon \Delta z / \Delta x$. When $\tilde{\varepsilon} < 1$, we have

$$\frac{u_{k-\tilde{\varepsilon} l}^{n+1} - u_k^{n+1}}{\varepsilon} = \begin{cases} -z_l \delta_x^+ u_k^{n+1}, & l \le 0, \\ -z_l \delta_x^- u_k^{n+1}, & l > 0. \end{cases}$$

Computation of $\Lambda_k(\eta_k^{n+1})$

Noticing

$$\delta_x^+ u_k^{n+1} = \delta_x^+ (u_k^n + \Delta t \Lambda_k(\eta_k^{n+1})),$$

we only need to compute $\Lambda_k(\eta_k^{n+1})$ from the equations

$$1 = (1 - m + m\eta_k^{n+1})\Delta a \sum_{j=1}^{K_a} b(a_j, x_k) \prod_{s=1}^{j} \frac{1}{1 + \Delta a(d(a_s, x_k) + \Lambda_k)},$$

where

$$\eta_k^{n+1} = \Delta z \sum_{l=0}^{K_z} \left(M_{(-l)} e^{z_l \delta_x^+ (u_k^n + \Delta t \Lambda_k)} + M_l e^{-z_l \delta_x^- (u_k^n + \Delta t \Lambda_k)} \right).$$

The above system has a unique solution.

Numerical Test: Reconstruction from a Coarse Mesh

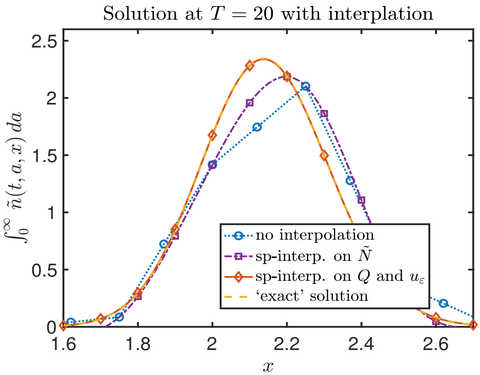

Figure: Comparison of $\int_0^\infty n(t,a,x)\,da$ with the 'exact' one. Here $\varepsilon = 0.1$, $m = 0.5$ and $\Delta x = 0.25$.

Conclusion

Conclusion

- With the WKB ansatz, an implicit asymptotic preserving scheme is designed for the age-structured model.
- Nice numerical properties are rigorously proved in the case without mutation.
- An easy-to-implement generalization is made for the case with mutation.

Reference

"An asymptotic preserving scheme for capturing concentrations in structured PDEs arising in evolution theory" (*with Luis Almeida and Benoit Perthame*), *submitted.*