Wasserstein estimates and macroscopic limits in a model from ecology

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Collaborators

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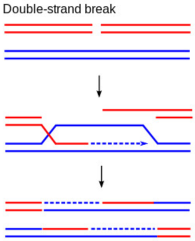
The Infinitesimal Model[1]



Genotype incoded in $u \in \{1, -1\}^N$ and

$$Z(u) := \frac{\sum_{i=1}^{N} u_i}{\sqrt{N}}$$

Infinitesimal model : If u and v give birth to w, the law of $Z(w)$ is a Gaussian distribution centered in $\frac{Z(u)+Z(v)}{2}$.

[1] R. Fisher, The correlations between relatives on the supposition of Mendelian inheritance. *Trans. R. Soc. Edin.* **52** (1918).

The Spatial Infinitesimal Model[2]

Dispersion

Selection

Competition

Reproduction

$$\partial_t n(t,x,y) = \Delta_x n(t,x,y) - \left(\gamma - 1 - \frac{A}{2} + \frac{1}{2}(y - y_{opt}(t,x))^2\right) n(t,x,y)$$

$$- n(t,x,y) \int n(t,x,z)\,dz$$

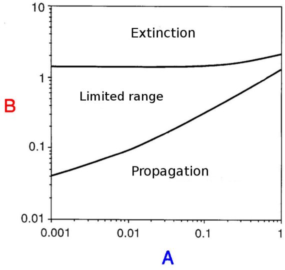
$$+ \gamma \int\int \Gamma_{A/2}\left(y - \frac{y_* + y'_*}{2}\right) \frac{n(t,x,y_*)n(t,x,y'_*)}{\int n(t,x,z)\,dz}\, dy_*\, dy'_*.$$

[2] S. Mirrahimi, G. Raoul, Population structured by a space variable and a phenotypical trait, *Theoretical Population Biology* **84**, 87–103 (2013).

The Kirkpatrick-Barton Model[3]

$N(t,x)$: population size
$Z(t,x)$: mean phenotypic trait

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \Big(1 - \frac{1}{2}(Z - y_{opt}(t,x))^2 - N\Big) N, \\ \\ \partial_t Z(t,x) - \Delta_x Z(t,x) = 2\frac{\partial_x N(t,x) \partial_x Z(t,x)}{N(t,x)} + A(y_{opt}(t,x) - Z(t,x)) \end{cases}$$



$y_{opt}(t,x) = Bx$, optimal trait

[3] Kirkpatrick, Barton, *American Naturalist* 1997.

Equations on moments

Let $N(t,x) = \int n(t,x,y)\,dy$ and $Z(t,x) = \int y\frac{n(t,x,y)}{N(t,x)}\,dy$. Then

$$\begin{cases} \partial_t N - \Delta_x N = \left[1 + \frac{1}{2}\left(A - \int (y-Z)^2 \frac{n}{N}\,dy\right) - \frac{1}{2}(Z - y_{opt})^2 - N\right] N, \\ \partial_t Z - \Delta_x Z = 2\frac{\partial_x N}{N}\partial_x Z + \frac{1}{2}(y_{opt} - Z)\int (y-Z)^2 \frac{n}{N}\,dy \\ \qquad\qquad - \int (y-Z)^3 \frac{n}{N}\,dy. \end{cases}$$

Note that $\gamma > 0$ does not appear.

Euristic moment closure[4]

If $\gamma > 0$ is large, the main term of the equation is

$$\partial_t n(t,x,y) \sim \gamma N(t,x)\left(\int\int \Gamma_{A/2}\left(y - \frac{y_* + y'_*}{2}\right) \frac{n(t,x,y_*)}{N(t,x)} \frac{n(t,x,y'_*)}{N(t,x)}\, dy_*\, dy'_* - \frac{n(t,x,y)}{N(t,x)} \right)$$

Then

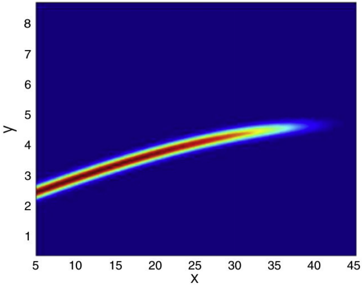
$$\int (y-Z)^2 \frac{n(t,x,y)}{N(t,x)}\, dy \to_{\gamma\to\infty} A,$$

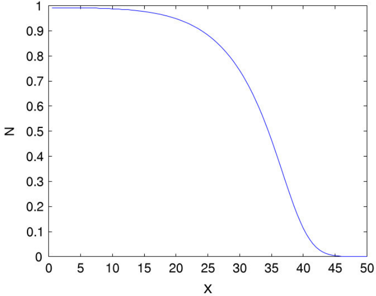
$$\int (y-Z)^3 \frac{n(t,x,y)}{N(t,x)}\, dy \to_{\gamma\to\infty} 0,$$

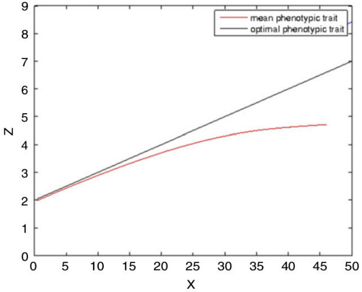
and we recover the Kirkpatrick-Barton model.

[4] Mirrahimi, R., *Theoretical Population Biology* 2013.

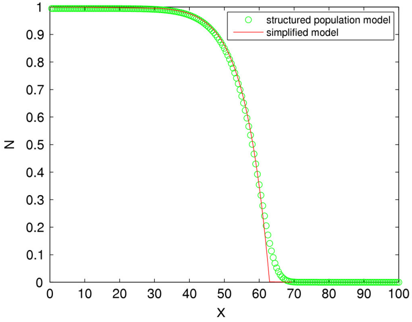
Simulation results

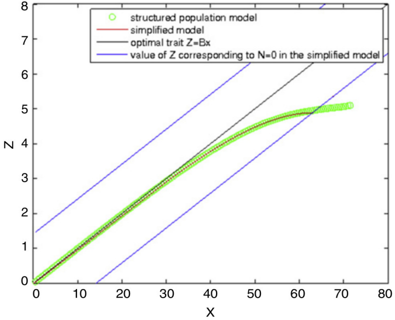






Simulation results





Tanaka-type inequality[5]

For $\tilde{n} \in \mathcal{P}_2(\mathbb{R})$ (proba. measure s.t. $\int y^2 d\tilde{n}(y) < \infty$), let

$$T(\tilde{n})(y) := \int \int \Gamma_{A/2}\left(y - \frac{y_* + y_*'}{2}\right) \tilde{n}(y_*)\tilde{n}(y_*')\, dy_*\, dy_*'.$$

Theorem

Let $\tilde{n}, \tilde{m} \in \mathcal{P}_2(\mathbb{R})$ such that $\int y\, d\tilde{n}(y) = \int y\, d\tilde{m}(y)$. Then

$$W_2(T(\tilde{n}), T(\tilde{m})) \leq \frac{1}{\sqrt{2}} W_2(\tilde{n}, \tilde{m}).$$

Maxwellians: $T(\Gamma_A(\cdot + Z)) = \Gamma_A(\cdot + Z)$, for any $Z \in \mathbb{R}$.

[5] H. Tanaka, Probabilistic treatment of the Boltzmann equation of Maxwellian molecules. *Probabability Theory and Related Fields* **46** , 67–105 (1978).

Equation on the normalized population

Let

$$\tilde{n}(t,x,y) = \frac{n(t,x,y)}{\int n(t,x,y')\,dy'}.$$

$\tilde{n}$ satisfies

$$\begin{aligned}
&\partial_t \tilde{n}(t,x,y) - \Delta_x \tilde{n}(t,x,y) \\
&\quad = 2\frac{\nabla_x N(t,x)}{N(t,x)} \cdot \nabla_x \tilde{n}(t,x,y) + \gamma \left(T(\tilde{n}(t,x,\cdot)) - \tilde{n}(t,x,y)\right) \\
&\qquad + \frac{1}{2}\tilde{n}(t,x,y)\left(\int (z - y_{opt}(t,x))^2 \tilde{n}(t,x,z)\,dz - (y - y_{opt}(t,x))^2\right).
\end{aligned}$$

Step 1: a bound on $\|Z\|_{L^\infty}$ implies a bound on $\|V\|_{L^\infty}$

Let $V(t,x) = \int y^4 \tilde{n}(t,x,y)\,dy$ satisfies

$$\partial_t V - \Delta_x V = 2\frac{\nabla_x N}{N} \cdot \nabla_x V + \frac{1}{2}\int \left(V - y^4\right)\left(y - y_{opt}\right)^2 \tilde{n}(t,x,y)\,dy$$
$$+\gamma\left(\int y^4\, T(\tilde{n})(y)\,dy - V\right).$$

Proposition

Let $\kappa > 0$. There exist $\bar{\gamma} > 0$ and $C_\kappa > 0$ such that for any $\gamma > \bar{\gamma}$, the following statement holds: If $\|Z\|_{L^\infty([0,\tau)\times\mathbb{T}^d)} \le \kappa$, then

$$\forall (t,x) \in [0,\tau) \times \mathbb{T}^d, \quad V(t,x) = \int |y|^4 \tilde{n}(t,x,y)\,dy \le C_\kappa.$$

Step 2: a bound on $\|Z\|_{L^\infty}$ implies regularity of Z ($x \in \mathbb{T}^d$)

$$\begin{cases} \partial_t N - \Delta_x N = \left(1 + \frac{A}{2} - N\right) N - \frac{N}{2} \int (y - y_{opt})^2 \tilde{n}(y)\, dy \\ \partial_t Z - \Delta_x Z = 2 \frac{\nabla_x N}{N} \cdot \nabla_x Z - \frac{1}{2} \int (y - Z)(y - y_{opt})^2 \tilde{n}(y)\, dy. \end{cases}$$

Then, for $s, t \geq \delta > 0$,

$$\frac{|Z(s,z) - Z(t,x)|}{|s-t|^\theta + |x-z|^\theta} \leq C, \quad \frac{|N(s,z) - N(t,x)|}{|s-t|^\theta + |x-z|^\theta} \leq C,$$

for some $\theta \in (0,1)$ and $C > 0$.

Step 3: Contraction from the Tanaka inequality

Assume we have a bound on $\|Z\|_{L^\infty}$.

$$\partial_t \tilde{n}(t,x,y) - \Delta_x \tilde{n}(t,x,y)$$
$$= 2\frac{\nabla_x N(t,x)}{N(t,x)} \cdot \nabla_x \tilde{n}(t,x,y) + \gamma \left(T(\tilde{n}(t,x,\cdot)) - \tilde{n}(t,x,y) \right)$$
$$+ \frac{1}{2}\tilde{n}(t,x,y) \left(\int (z - y_{opt}(t,x))^2 \tilde{n}(t,x,z)\, dz - (y - y_{opt}(t,x))^2 \right).$$

For $t \geq \delta > 0$ and $\gamma > 0$ large enough, as long as $\|Z(t,\cdot)\|_{L^\infty} \leq C$,

$$\max_{x \in \mathbb{T}^d} W_2 \left(\tilde{n}(t,x,\cdot), \Gamma_A(\cdot - Z(t,x)) \right) \leq \frac{C}{\gamma^\theta},$$

for some $\theta \in [0,1]$.

$$
\begin{aligned}
\tilde{n}(t,x,y) = {} & e^{-\gamma t} \int \tilde{n}(0,z,y)\phi_{0,z,y}(t,x)\,dz \\
& + \frac{1}{2}\int_0^t e^{-\gamma(t-s)} \int \phi_{s,z,y}(t,x)\tilde{n}(s,z,y) \\
& \qquad \left(\int (w - y_{opt}(s,z))^2\,\tilde{n}(s,z,w)\,dw\right)\,dz\,ds \\
& + \gamma \int_0^t e^{-\gamma(t-s)} \int \phi_{s,z,y}(t,x)\,T(\tilde{n}(s,z,\cdot))(y)\,dz\,ds.
\end{aligned}
$$

$$
\begin{cases}
\partial_t \phi_{s,z,y}(t,x) - \Delta_x \phi_{s,z,y}(t,x) \\
\qquad = \frac{\nabla_x N(t,x)}{N(t,x)} \cdot \nabla_x \phi_{s,z,y}(t,x) - \frac{1}{2}(y - y_{opt}(t,x))^2 \phi_{s,z,y}(t,x), \\
\phi_{s,z,y}(s,x) = \delta_z(x),\ x \in \mathbb{T}^d.
\end{cases}
$$

Step 4: Estimate on $\|Z\|_{L^\infty}$

$$\partial_t Z - \Delta_x Z = 2\frac{\nabla_x N}{N} \cdot \nabla_x Z - A(Z(t,x) - y_{opt}(t,x))$$
$$+ \int (y - Z(t,x))\,(y - y_{opt}(t,x))^2\,(\Gamma_A(y - Z(t,x)) - \tilde{n}(t,x,y))\; dy.$$

Proposition

There exist $\bar{\gamma} > 0$ and $\theta \in (0,1)$ such that for any $\gamma > \bar{\gamma}$, there exists a solution $n \in L^\infty(\mathbb{R}_+ \times \mathbb{T}^d, L^1((1+|y|^4)\,dy))$ of the SIM with initial condition n^0 such that

$$\|Z\|_{L^\infty(\mathbb{R}_+\times\mathbb{T}^d)} \leq \|Z(0,\cdot)\|_{L^\infty(\mathbb{T}^d)} + \|y_{opt}\|_{L^\infty(\mathbb{R}_+\times\mathbb{T}^d)} + 1.$$

Result

$$n(t,x,y) \sim_{\gamma \gg 1} N(t,x)\Gamma_A(y - Z(t,x)).$$

If $\gamma > 0$ is large enough, the SIM solutions are global, and

$$\max_{(t,x)\in[1/\gamma^\theta,\infty)\times\mathbb{T}^d} W_2\left(\frac{n(t,x,\cdot)}{N(t,x)}, \Gamma_A(\cdot - 2Z(t,x))\right) \leq \frac{C}{\gamma^\theta},$$

where (N,Z) is an approximate solution of the KBM:

$$\begin{cases} \partial_t N - \Delta_x N = \Big(1 - \frac{1}{2}(Z - y_{opt})^2 - N + \mathcal{O}\left(\frac{1}{\gamma^\theta}\right)\Big)N, \\ \partial_t Z - \Delta_x Z - 2\frac{\nabla_x N}{N}\cdot\nabla_x Z = A\Big(y_{opt} - Z\Big) + \mathcal{O}\left(\frac{1}{\gamma^\theta}\right). \end{cases}$$

Finally, the solutions of this approximate KBM converge to solutions of the KBM when $\gamma \gg 1$.

Application of this macroscopic limit to a specific biological problem.

Effect of pollen dispersal on a species submitted to climate change[6]

[6] R. Aguilee, G. Raoul, F. Rousset, O. Ronce, Pollen dispersal slows geographical range shift and accelerates ecological niche shift under climate change, *Proceedings of the National Academy of Sciences of the United States of America* **113**(39), 5741-5748 (2016).

Model

We consider a tree population $n(t,x,y)$, and the pollen population $p(t,x,y)$:

$$\partial_t n(t,x,y) = \Delta_x n(t,x,y) - \left(\gamma - 1 - \frac{A}{2} + \frac{1}{2}(y - y_{opt}(t,x))^2\right) n(t,x,y)$$
$$- n(t,x,y) \int n(t,x,z)\, dz$$
$$+ \gamma \int\int \Gamma_{A/2}\left(y - \frac{y_* + y_*'}{2}\right) \frac{n(t,x,y_*) p(t,x,y_*')}{\int n(t,x,z)\, dz}\, dy_*\, dy_*',$$

with $0 = n(t,x,y) - p(t,x,y) + \frac{\sigma_p^2}{2}\Delta_x p(t,x,y)$.

The macroscopic model

When $\gamma \gg 1$, the population satisfies

$$n(t,x,y) \sim N(t,x)\Gamma_A(y - Z(t,x)),$$

where

$$\begin{cases} \partial_t N(t,x) - \Delta_x N(t,x) = \Big(1 - \frac{1}{2}(Z - y_{opt}(t,x))^2 - N\Big)N, \\ \\ \partial_t Z(t,x) - \frac{1}{1-\gamma}\Delta_x Z(t,x) = \frac{2}{1-\gamma}\frac{\partial_x N(t,x)\partial_x Z(t,x)}{N(t,x)} \\ \\ \qquad\qquad\qquad\qquad\qquad\qquad + A(y_{opt}(t,x) - Z(t,x)). \end{cases}$$

Optimal pollen dispersal

The optimal critical speed is obtained for $g_{opt} = \frac{2}{3} - \frac{1}{A}\left(|B|\sqrt{2} - \frac{4}{3}\right)$. It is then best to:

- disperse pollen a lot when $|B| < \frac{4-A}{3\sqrt{2}}$,
- not disperse pollen when $|B| > \frac{\sqrt{2}}{3}(2+A)$,
- disperse at an intermediate rate for an intermediate gradient of the optimal phenotypic trait B.