Link between stochastic individual-based evolutionary models and Hamilton-Jacobi equations

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Joint work with:
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How to characterize the evolutionary and demographic dynamics of phenotypically structured populations ?

Biological mechanisms:

- asexual reproduction
- heredity: transmission of ancestor traits to the offspring
- mutations: generate variability
- selection: individuals with better ability of survival and reproduction will spread through the population over time

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Our objective: Analytic approximations of the dynamics of large populations, but keep track of small subpopulations, take into account possible local extinctions

A stochastic birth-death-mutation-competition process

- **Large population:** the model is parametrized by an effective size parameter K, with $K \to +\infty$
- Size of the population: $\rho^K(t)$
- Individuals characterized by a quantitative trait : $x \in \mathbb{R}$

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An individual with trait x:

- gives birth to individual with the same trait at rate: $b(x)$
- gives birth to a mutant individual of trait y with rate

$$p(x)G_\varepsilon(x-y)dy = p(x)G((x-y)/\varepsilon)dy/\varepsilon,$$

ε^2: variance of mutations, $G \geq 0$, $\int G(y)dy = 1$,
$\int G(y)e^{y^2}dy \leq C$.

- dies with rate $d(x, \frac{1}{K}\rho^K(t))$
  d is increasing with respect to the 2nd variable (competition)

A stochastic birth-death-mutation-competition process

- The population is represented by the empirical measure

$$Z_t^K(dx) = \frac{1}{K} \sum_{i=1}^{\rho^K(t)} \delta_{X_i(t)}(dx)$$

- The initial condition Z_0^K: a poisson point measure with intensity

$$n_0^K(x)dx$$

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What is the dynamics of the population when the
effective size K is large and the mutational variance ε^2 is small?

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Scaling assumptions and notations

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A large population limit

Champagnat, Ferrière and Méléard 2008: As $K \to +\infty$ the empirical measure $Z_t^K(dx)$ converges in law to $n(t,x)dx$ solution to

$$\begin{cases} \partial_t n(t,x) = \underbrace{\int p(y) G_\varepsilon(y-x) n(t,y)dy - p(x)n(t,x)}_{\text{mutation}} \\ \qquad\qquad + \underbrace{n(t,x)R(x,\rho(t))}_{\text{selection \& competition}}, \\ \underbrace{\rho(t) = \int_{\mathbb{R}} n(t,y)dy}_{\text{Total size of the population}}, \qquad (t,x) \in \mathbb{R}^+ \times \mathbb{R}. \end{cases}$$

$$R(x,\rho) = b(x) + p(x) - d(x,\rho(t)).$$

$n(t,x)$: the density of individuals of trait x at time t

Continuum of alleles model (Kimura 1965)

Small mutational variance, long time; concentration

Accelerating time to observe the effect of small mutations:

$$\varepsilon \ll 1, \qquad t \to t/\varepsilon.$$

$$\begin{cases} \varepsilon \partial_t n_\varepsilon(t,x) & = \int p(y) G_\varepsilon(y-x) n_\varepsilon(t,y)dy - p(x) n_\varepsilon(t,x) \\ & \quad + n_\varepsilon(t,x) R(x, \rho_\varepsilon(t)) \\ \rho_\varepsilon(t) = \int_{\mathbb{R}} n_\varepsilon(t,y)dy, & \qquad (t,x) \in \mathbb{R}^+ \times \mathbb{R}. \end{cases}$$

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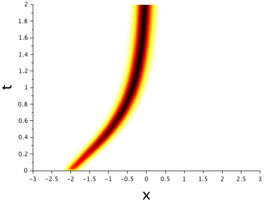
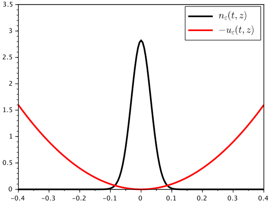
Concentration around an evolving dominant trait:
The colors represent the isolines of the phenotypic density.



How to characterize the phenotypic density ? The Hamilton-Jacobi approach

Hopf-Cole transformation :

$$n_\varepsilon(t,x) = \exp\left(\frac{u_\varepsilon(t,x)}{\varepsilon}\right).$$



We expect that

$$u_\varepsilon(t,x) \to u(t,x), \quad \text{as } \varepsilon \to 0.$$

Idea: to unfold the singularity of the phenotypic density (a very peaked distribution).

The asymptotic dynamics of the phenotypic density are derived by a Hamilton-Jacobi equation

Theorem [Perthame–Barles 2008, Barles–M.–Perthame 09']
As $\varepsilon \to 0$, $\rho_\varepsilon \to \rho$ and u_ε converges to u the viscosity solution to

$$\begin{cases} \frac{\partial}{\partial t} u = p(x) \int \left(e^{\partial_x u(t,x) \cdot y} - 1 \right) G(y) dy + R(x, \rho(t)) \\ \max_{x \in \mathbb{R}} u(t,x) = 0, \\ u(0,x) = u_0(x). \end{cases}$$

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The maximum points of u correspond to the dominant traits:

$$\text{as } \varepsilon \to 0 \quad n_\varepsilon \rightharpoonup n, \qquad \operatorname{supp} n(t,\cdot) \subset \{x \in \mathbb{R} | u(t,x) = 0\}$$

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Under regularity assumptions Lorz-M. Perthame 11':
Lande's equation

$$n(t,x) = \rho(t)\delta(x - \overline{x}(t)), \quad \dot{\overline{x}}(t) = \left(-\partial_{xx} u(t, \overline{x}(t))\right)^{-1} \partial_x R(\overline{x}(t), \rho(t)).$$

A repeated limit

The Hamilton-Jacobi equations are derived in two steps:

• **Individual based models → Integro-differential models**
in the limit of large populations (Fournier-Méléard 04', Champagnat-Ferrière-Méléard 08')

• **Integro-differential models → Hamilton-Jacobi equations**
In the limit of small mutational variance and long time (Dieckmann-Jabin-Mischler-Perthame 05', Perthame-Barles 08', Barles-M.-Perthame 09')

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Another limit: first small diffusion, next large population size
Tourniaire-Maillard-Raoul preprint 21'

These limits do not commute:

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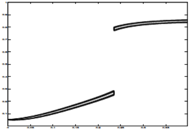
Another limit: first small diffusion, next large population size Tourniaire-Maillard-Raoul preprint 21'

These limits do not commute:

- It is hard to interpret the results of the Hamilton-Jacobi approach with regard to the initial individual based model
- Artefacts: fast evolutionary dynamics, artificial jumps in the phenotypic distribution

Artificial or relevant jumps of the dominant trait?

Emergence of a population from a possibly extinct subpopulation:



Discontinuity of the dominant trait:

Horizontal axis: time

Vertical axis: the dominant trait

Figure from Perthame-Barles 08'

Attempts to avoid the artefacts (artificial deterministic corrections):
Perthame-Gauduchon 10' M.-Barles-Perthame-Souganidis 12', Jabin 12'

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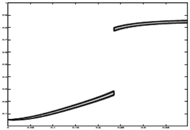
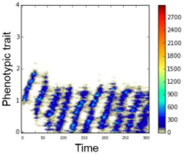


Attempts to avoid the artefacts (artificial deterministic corrections): Perthame-Gauduchon 10' M.-Barles-Perthame-Souganidis 12', Jabin 12'

But jumps also arise in stochastic simulations: emergence of a well-adapted trait from a small sub-population (model with horizontal gene transfer):

Stochastic individual based simulations from: Billiard-Collet-Ferrière-Méléard-Tran 18'



How to distinguish between relevant jumps and artefacts?

Motivating questions

- Can we derive the Hamilton-Jacobi equations directly from individual based models?
- How to take into account the extinction of subpopulations?
- How to distinguish between artefacts and real jumps of the phenotypic distribution?
- Can we identify the historical lineages of the individuals present in the population? (a by-product of our result) (Forien-Garnier-Patout 22': in a deterministic context)

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A stochastic birth-death-mutation process- new scaling

- **Large population:** the model is parametrized by an effective size parameter K, with $K \to +\infty$
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- **Large population:** the model is parametrized by an effective size parameter K, with $K \to +\infty$
- Individuals characterized by a quantitative trait : $x \in \mathbb{R}$,
- clonal birth at rate: $b(x)$
- **small mutation effects**, rate of mutation from x to y

$$p(x)G_\varepsilon(x-y)dy = p(x)G((x-y)/\varepsilon)dy/\varepsilon, \quad \varepsilon = 1/\log K.$$

$G \geq 0$, $\int G(y)dy = 1$, $\int G(y)e^{y^2}dy \leq C$

- death rate $d(x)$ (no competition)
- **we accelerate time:** $t \to t \log K$.

Notations and assumptions

- V_t^K: the set of labels of individuals living at time t
- For $u \in V_t^K$, $(X_{s\wedge t}^{K,u})_{s\geq 0}$: the lineage of u, $X_{s\wedge t}^{K,u} \in \mathbb{D}([0,t],\mathbb{R})$
- Point measure-valued processes:

$$Z_t^K(dx) = \frac{1}{K}\sum_{u\in V_t^K} \delta_{X_t^{K,u}(dx)}, \qquad H_t^K(df) = \frac{1}{K}\sum_{u\in V_t^K} \delta_{X_{.\wedge t}^{K,u}(.\wedge t)}(df).$$

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- The initial condition Z_0^K: a poisson point measure with intensity

$$K^{\beta_0^K(x)}dx$$

β_0^K is a continuous function which converges locally uniformly to a Lipschitz-continuous function β_0, with

$$\beta_0(x) \leq \beta_1 - \beta_2|x|.$$

Subpopulations of size K^β: the Hopf-Cole transformation

If no mutation ($p(x) \equiv 0$), and discrete trait space : then the process $Z_x^K(t)$ is a one-dimensional branching process:

$$\mathbb{E}(Z_x^K(t)) = \mathbb{E}(Z_x^K(0))e^{(b(x)-d(x))t\log K} \sim K^{\beta_0(x)+(b(x)-d(x))t}.$$

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This motivates to introduce

$$\beta_x^K(t) = \frac{\log(Z_x^K(t))}{\log K}.$$

(Analogy with $u_\varepsilon(t,x) = \varepsilon \log(n_\varepsilon(t,x))$ in the deterministic case)

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(Champagnat-Méléard-M.-Tran 2023): supercritical case
$R(x) = b(x) + p(x) - d(x) > 0$ and no local extinction $\Rightarrow$
convergence to the standard Hamilton-Jacobi equation

Here: $R(x)$ may change sign and possible local extinctions $\Rightarrow$
a modified Hamilton-Jacobi equation, a different approach is needed

Notations

- Hamiltonian:

$$p(x)H(\alpha), \qquad H(\alpha) = \int_{\mathbb{R}} (e^{\alpha y} - 1)G(y)dy.$$

- Its Legendre transform (Lagrangian):

$$L(x, \beta) = \sup_{\alpha \in \mathbb{R}} (\alpha\beta - p(x)H(\alpha)).$$

- Rate function:

$$I_t(f) = \begin{cases} \int_0^t L(f_s, \dot{f}_s)ds & \text{if } f \in AC([0,t], \mathbb{R}) \\ +\infty & \text{otherwise.} \end{cases}$$

- Cost function: for $f \in C([0,t], \mathbb{R})$,

$$F_t(f) = \beta_0(f(0)) + \int_0^t R(f_s)ds - I_t(f).$$

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Main results

Define, for $A \subset AC([0,t],\mathbb{R})$

$$N_t^{K,A} = \langle H_t^K, 1_A \rangle$$

Theorem (Champagnat-Méléard-M.-Tran, preprint):
(i) $\forall\ t > 0$ and any closed set $A \subset AC([0,t],\mathbb{R})$: in probability

$$\limsup_{K\to+\infty} \frac{1}{\log K} \log N_t^{K,A} \leq \sup\{F_t(f); f \in A, \forall s \in [0,t],\ F_s(f) \geq -1\}.$$

(ii) $\forall\ t > 0$ and any open set $B \subset AC([0,t],\mathbb{R})$: almost surely

$$\liminf_{K\to+\infty} \frac{1}{\log K} \log N_t^{K,B} \geq \sup\{F_t(f); f \in B, \forall s \in [0,t],\ F_s(f) > -1\}.$$

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Let $f_0 \in AC[0,t]$, and A and B be small tubes around f_0.
Then, the inequalities above provide an estimate on the number of individuals whose historical lineages are approximately given by f_0.

Main results

Define

$$u_a(t,x) = \sup\{F_t(f) \mid f \in AC[0,t],\ f(t) = x,\ \forall s \in [0,t],\ F_s(f) \geq a\}.$$

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$$A_t^{x,\delta} = \{f \mid f(t) \in [x-\delta, x+\delta]\}, \qquad B_t^{x,\delta} = \{f \mid f(f) \in (x-\delta, x+\delta)\},$$

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Then

$$\lim_{a\downarrow -1} u_a(t,x) \leq \liminf_{\delta\to 0} \liminf_{K\to+\infty} \frac{\log N_t^{K,B_t^{x,\delta}}}{\log K}$$
$$\leq \limsup_{\delta\to 0} \limsup_{K\to+\infty} \frac{\log N_t^{K,A_t^{x,\delta}}}{\log K} \leq u_{-1}(t,x).$$

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Then

$$\begin{aligned}\lim_{a\downarrow -1} u_a(t,x) &\leq \liminf_{\delta\to 0}\liminf_{K\to+\infty} \frac{\log N_t^{K,B_t^{x,\delta}}}{\log K} \\ &\leq \limsup_{\delta\to 0}\limsup_{K\to+\infty} \frac{\log N_t^{K,A_t^{x,\delta}}}{\log K} \leq u_{-1}(t,x).\end{aligned}$$

which leads, up to small modification of the initial condition, to

$$\lim_{\delta\to 0}\lim_{K\to+\infty} \frac{\log N_t^{K,B_t^{x,\delta}}}{\log K} = u_{-1}(t,x).$$

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Define

$$\Omega_{-1} = \{(t,x) \in \mathbb{R}^+ \times \mathbb{R} \,|\, u_{-1}(t,x) > -1\}.$$

Theorem (Champagnat-Méléard-M.-Tran, preprint): u_{-1} is the unique locally Lipschitz-continuous and bounded above viscosity solution to

$$\begin{cases} \partial_t u_{-1}(t,x) = p(x)H(\partial_x u_{-1}(t,x)) + R(x) & (t,x) \in \Omega_{-1} \\ u_{-1}(t,x) = -1 & (t,x) \in \partial\Omega_{-1},\ t > 0 \\ u_{-1}(t,x) = -\infty & (t,x) \in \mathbb{R} \setminus \overline{\Omega}_{-1} \\ u_{-1}(0,x) = \beta_0(x) & \text{for all } x \text{ s. t. } \beta_0(x) > -1. \end{cases}$$

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- This can be written as a free boundary problem on (u_{-1}, Ω_{-1}) where u_{-1} satisfies both Dirichlet and state constraint boundary conditions (M.-Barles-Perthame-Souganidis 2012).

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- No constraint in the limit problem, since no competition term.

Some ingredients of the proof

Proof inspired by:

M.-Barles-Perthame-Souganidis 2012,

Berestycki-Brunet-Harris-Harris-Roberts 2015, Mallein 2015

Some ingredients of the proof

Upper bound: to prove, for any closed set $A \in \mathbb{D}[0,t]$, in probability

$$\limsup_{K \to +\infty} \frac{\log N_t^{K,A}}{\log K} \leq \sup \{ F_t(f)\,;\, f \in A,\, \forall s \in [0,t]\; F_s(f) \geq -1 \}.$$

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- Feynman-Kac formula and large deviation estimate:

$$\limsup_{K\to+\infty} \frac{\log \mathbb{E}[N_t^{K,A}]}{\log K} \leq F_t(A) := \sup\left\{F_t(f)\,;\; f\in A\right\}.$$

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Some ingredients of the proof

- Then, for $\delta > 0$,

$$\mathbb{P}\big(N_t^{K,A} \geq K^{F_t(A)+\delta}\big) \leq \frac{\mathbb{E}(N_t^{K,A})}{K^{F_t(A)+\delta}} \qquad \Rightarrow$$

Hence for K large,

$$\mathbb{P}\big(N_t^{K,A} \geq K^{F_t(A)+\delta}\big) \leq K^{-\delta/2} \Rightarrow \mathbb{P}\big(\frac{\log N_t^{K,A}}{\log K} \geq F_t(A) + \delta\big) \underset{K\to\infty}{\longrightarrow} 0$$

$$\Rightarrow \quad \text{in probability} \quad \frac{\log N_t^{K,A}}{\log K} \leq F_t(A).$$

Some ingredients of the proof

- Then, for $\delta > 0$,

$$\mathbb{P}\big(N_t^{K,A} \geq K^{F_t(A)+\delta}\big) \leq \frac{\mathbb{E}(N_t^{K,A})}{K^{F_t(A)+\delta}} \qquad \Rightarrow$$

Hence for K large,

$$\mathbb{P}\big(N_t^{K,A} \geq K^{F_t(A)+\delta}\big) \leq K^{-\delta/2} \Rightarrow \mathbb{P}\Big(\frac{\log N_t^{K,A}}{\log K} \geq F_t(A) + \delta\Big) \underset{K\to\infty}{\longrightarrow} 0$$

$$\Rightarrow \quad \text{in probability} \quad \frac{\log N_t^{K,A}}{\log K} \leq F_t(A).$$

- If $F_t(A) < -1$, since $KN_t^{K,A}$ has integer values, we obtain $\mathbb{P}\big(\frac{\log N_t^{K,A}}{\log K} > -\infty\big) \underset{K\to\infty}{\longrightarrow} 0$.

Some ingredients of the proof

Lower bound (in probability): to prove, for any open set $B \in \mathbb{D}[0,t]$, almost surely,

$$\liminf_{K\to+\infty} \frac{\log N_t^{K,B}}{\log K} \geq \sup\{F_t(f)\,;\, f \in B,\ \forall s \in [0,t]\ F_s(f) > -1\}.$$

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• It is enough to prove, for all $f \in B$ s.t. $\forall s \leq t$, $F_s(f) > -1$, almost surely, for sufficiently small $\varepsilon > 0$,

$$\liminf_{K\to+\infty} \frac{1}{\log K} \log N_t^{K,B_\varepsilon(f)} \geq F_t(f).$$

• We first prove that this inequality holds with a positive probability. To obtain the almost sure lower bound, we next use the branching property by dividing the initial population into several groups.

Some ingredients of the proof

- Feynman-Kac formula and large deviation estimate:

$$\liminf_{K\to+\infty} \frac{\log \mathbb{E}[N_t^{K,B_\varepsilon(f)}]}{\log K} \geq F_t(B_\varepsilon(f)) := \sup\{F_t(f)\,;\ f \in B_\varepsilon(f)\}.$$

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- For all $f \in B$ s.t. $\forall s \leq t$, $F_s(f) > -1$ and $\forall\ \delta > 0$, $\varepsilon > 0$ small enough and K large enough:

$$\mathbb{E}\big[\big(N_t^{K,B_\varepsilon(f)}\big)^2\big] \leq \mathbb{E}^2\big[N_t^{K,\varepsilon,f}\big] \times K^\delta.$$

Perspectives

- Taking into account a competition term: $R(x) \mapsto R(x, \rho(t))$

- Dispersion models : Fisher-KPP type model with local competition (with J. Olayé and P. Maillard)

- Well-posedness of the free boundary Hamilton-Jacobi formulation

- Identifying the correction due to the free boundary in biological examples

Thank you for your attention !

A Feynman-Kac formula for $\mathbb{E}(N_t^{K,A})$

An auxiliary pure jump process $(X_t^K)_{t\in\mathbb{R}^+}$ with generator

$$\mathcal{A}^K\varphi(x) = p(x)\int_{\mathbb{R}} \Big[\varphi\big(x+\frac{y}{\log K}\big)-\varphi(x)\Big]G(y)dy.$$

- **Feynman-Kac Formula**: For all $t>0$, and $A\in\mathbb{D}[0,t]$

$$\mathbb{E}(N_t^{K,A}) = \int_{\mathbb{R}} K^{\beta_0(x)}\mathbb{E}_x\Big[K^{\int_0^t R(X^K_{s\log K})ds}\mathbb{1}_{(X^K_{s\log K})_{s\in[0,t]}\in A}\Big]dx$$

This can be extended to

$$\mathbb{E}_x(\langle H^K_{t\log K},\Phi\rangle) = \mathbb{E}_x\Big(K^{\int_0^t R(X_{s\log K})ds}\Phi(X^K_{s\log K}, s\in[0,t])\Big).$$

- $\mu^K_{x,T}$: the law of $(X^K_{t\log K})_K, t\in[0,T])$, given $X_0^K = x$.

Large deviation principle for $(\mu^K_{x,T})_{K\geq 1}$

For $(t,x) \in \mathbb{R}^+ \times \mathbb{R}$, we define for all $\mathbb{D}([0,t],\mathbb{R})$,

$$I_{t,x}(\varphi) = \begin{cases} I_t(\varphi) & \text{if } \varphi(0) = x \\ 0 & \text{otherwise.} \end{cases}$$

Theorem:
(i) For all $T > 0$, the family of laws $(\mu^K_{x,T})_{K\geq 1}$ satisfies a large deviation principle on $\mathcal{D}[0,T]$ with rate $1/\log K$ and good rate function $I_{T,x}$.

(ii) For all $T > 0$, the family of measures $(\mu^K_{x,T})_{K,x}$ is exponentially tight, uniformly on compact sets:
for $M < +\infty$, there exists a compact subset A of $\mathbb{D}[0,T]$ such that

$$\limsup_{K\to+\infty} \sup_{x\in B \text{ compact}} \frac{1}{\log K} \log \mu^K_{x,T}(A^c) \leq -M.$$

Control of the second moment

$$\mathbb{E}\left[\left(N_t^{K,\varepsilon,f}\right)^2\right] = \mathbb{E}\left(\left(\sum_{v \in V^K_{t\log K}} \mathbb{1}_{B_\varepsilon(f)}\left(X^{K,v}_{s\log K}, s \leq t\right)\right)^2\right)$$

We decompose $\left(N_t^{K,\varepsilon,f}\right)^2$ in three terms :

- the square terms
- the terms where the individuals have a common ancestor in $[0, t)$
- the ones where the two individuals have no common ancestor in $[0, t)$.