Modèles mathématiques pour des écosystèmes complexes

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March 30, 2022

Outline

1. Optimisation of biofilm productivity,
   - Context,
   - Model,
   - Simulations,
   - Perspectives.

2. Contribution of (epi)genetic in periodic environment,
   - Context,
   - Model & Analysis,
   - Simulations,
   - Perspectives.

Phototrophic biofilm

Phototrophic?

Biofilm using light and inorganic carbon source to growth.

(a) Rotating microalgae biofilm device Hans C. Bernstein et al. 2014

Motivation:

Credible alternative for biofuels

Why?

- High production yield for lipids,
- Easy to harvest (just scalp),
- A wide variety of species,
- Can develop in sea and oceans,
- Combined with wastewater treatment?

Objective:

Quantify the influence of growing conditions and harvest on productivity.

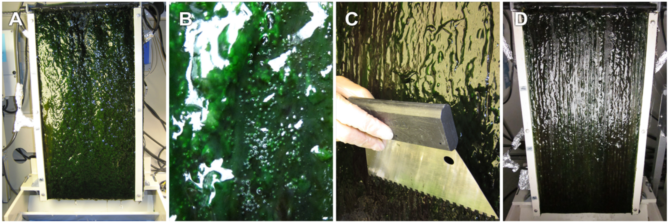


Fig. 2 The vertical phototrophic biofilm reactor (**a**), a close-up of the biofilm before harvesting (**b**), harvesting part of the biofilm with the adhesive comb (**c**), and the biofilm setup after harvesting (**d**)

Figure: Boelee et al. 2014

- Observation: Harvesting pattern impact biofilm productivity
- Question: What is the optimal harvesting strategy?
- Context:
  - Collaboration with biologist and experimentalist:
    - O. Bernard (Lov & Inria),
    - F. Lopes (CentraleSupélec),
    - A. Fanesi (CentraleSupélec),
  - M. Ribot (Institut Denis Poisson)

Theoretical framework for mixture theory

Mixture of $K \geqslant 1$ constituents: $\mathbf{C}_k$, each constituent is describe by:

- Its volume fraction: $\phi_k(t,x) := \lim_{\mathbb{V}\to 0} \frac{\text{volume of } \mathbf{C}_k \text{ in } \mathbb{V}}{\text{volume of } \mathbb{V}}$
- Its speed $V_k(t,x)$
- Its mass density ρ_k (assumed constant)

Fundamental properties:

- Total volume conservation: $\sum_{k=1}^{K} \phi_k = 1$
- Mass balance equation:

$$\underbrace{\partial_t(\phi_k\rho_k) + \nabla_x \cdot \Big(\phi_k\rho_k V_k\Big)}_{\text{transport}} = \underbrace{\nabla_x \cdot \Big(\mathrm{D}_k \nabla_x(\phi_k\rho_k)\Big)}_{\text{diffusion}} + \underbrace{\Gamma_k}_{\text{exchanges}}$$

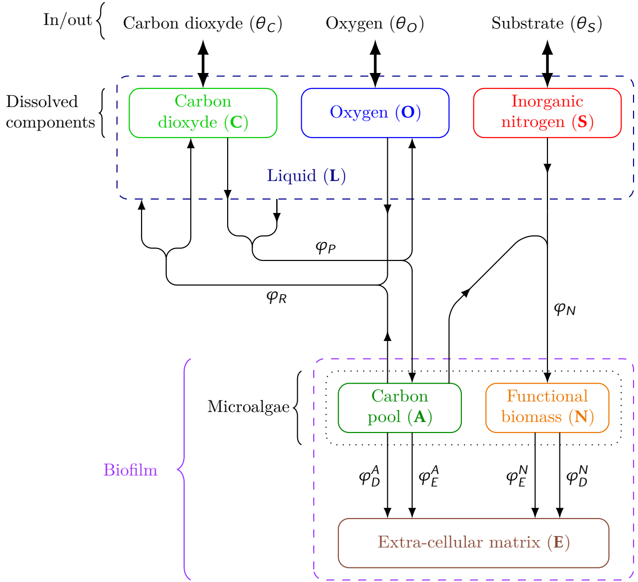
- Momentum conservation (Force balance equation):

$$\underbrace{\partial_t(\phi_k\rho_k V_k) + \nabla_x \cdot \Big(\phi_k\rho_k V_k \otimes V_k\Big)}_{\text{inertial terms}} = \underbrace{-\phi_k \nabla_x P}_{\text{pressure}} + \underbrace{\mathrm{F}_{\text{fric}} + \mathrm{F}_{\text{visc}} + \dots}_{\text{other forces}}$$

Advantages:

- Mesoscale
- Physical constraints included
- Different properties for each $\mathbf{C}_k$
- Interfaces without free boundary

Schematic representation of the system



Mixture framework – Mass balance

- Total volume conservation: $A+N+E+L=1$

- Mass conservation: Transport

$$\text{Microalgae}\left\{\begin{array}{ll}\text{Carbon pool:} & \partial_t A+\nabla_x\cdot(A\boldsymbol{V_M})=\Gamma_A/\rho\\ \text{Functional biomass:} & \partial_t N+\nabla_x\cdot(N\boldsymbol{V_M})=\Gamma_N/\rho\\ \text{Extracellular matrix:} & \partial_t E+\nabla_x\cdot(E\boldsymbol{V_E})=\Gamma_E/\rho\\ \text{Liquid:} & \partial_t L+\nabla_x\cdot(L\boldsymbol{V_L})=\Gamma_L/\rho\end{array}\right.$$

- Pseudo incompressibility: Mass transfers ⇒ Pressure

$$\nabla_x\cdot\Big((A+N)\boldsymbol{V_M}+E\boldsymbol{V_E}+L\boldsymbol{V_L}\Big)=\frac{1}{\rho}\Big(\Gamma_A+\Gamma_N+\Gamma_E+\Gamma_L\Big)$$

- Dissolved components: Transport by the liquid & Diffusion

$$\theta=\left\{\begin{array}{ll}S & \text{Substrate}\\ C & \text{Carbon dioxide}\\ O & \text{Oxygen}\end{array}\right.\quad \partial_t(\theta\boldsymbol{L})+\nabla_x\cdot(\theta\boldsymbol{L}\boldsymbol{V_L})=\underbrace{\nabla_x\cdot\Big(\mathcal{D}_\theta\boldsymbol{L}\nabla_x\theta\Big)}_{\text{diffusion}}+\frac{\Gamma_\theta}{\boldsymbol{\rho_L}}.$$

Mixture framework – Force balance

- Biological phases: $\phi = A + N,\ E$

$$\partial_t\left(\phi\rho_\phi V_\phi\right) + \nabla_x\cdot\left(\phi_\phi\rho_\phi V_\phi\otimes V_\phi\right) = -\underbrace{\phi\nabla_x P}_{\text{Pressure}} + \underbrace{\nabla_x\left(\gamma_\phi\phi\right)}_{\text{Elastic}} + \underbrace{\sum_{\ell\neq\phi} m_{\ell,\phi}\left(V_\phi - V_\ell\right)}_{\text{Friction}} + \underbrace{\Gamma_\phi V_\phi}_{\text{Exch.}}$$

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- Hypothesis: Conservation of total momentum supply

Mixture framework – Force balance

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- Hypothesis: Conservation of total momentum supply
- Liquid phase:

$$\partial_t(L\rho_L V_L) + \nabla_x \cdot (L\rho_L V_L \otimes V_L) = - \underbrace{L\nabla_x P}_{\text{Pressure}} - \underbrace{\sum_{\phi\neq L} m_{k,L}\left(V_L - V_\phi\right)}_{\text{Friction}} - \underbrace{\sum_{\phi\neq L}\Gamma_\phi V_\phi}_{\text{Exch.}}$$

Source terms modelling

- Construction of source terms:
  1. Identify a biological mechanism

$$6CO_2 \quad + \quad 6H_2O \xrightarrow{\text{photosynthesis}} C_6H_{12}O_6 \quad + \quad 6O_2$$

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2. Translate in term of considered components

$$\eta_C \underbrace{\text{Inorganic carbon}}_{\mathbf{C}} + \eta_L \underbrace{\text{Liquid}}_{\mathbf{L}} \xrightarrow[\psi_P]{\text{Reaction rate}} \underbrace{\text{Carbon pool}}_{\mathbf{A}} + \eta_O \underbrace{\text{Oxygen}}_{\mathbf{O}}$$

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3. Express the information in the source terms:

$$\Gamma_C = -\eta_C \psi_P + \dots \qquad \Gamma_A = \psi_P + \dots$$
$$\Gamma_L = -\eta_L \psi_P + \dots \qquad \Gamma_O = \eta_O \psi_P + \dots$$

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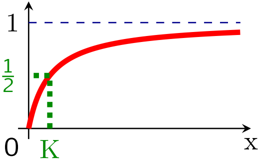
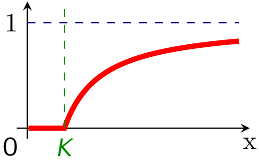
- Considered mechanisms:
  1. Photosynthesis
  2. Respiration
  3. Functional biomass synthesis
  4. Extra-cellular matrix excretion
  5. Mortality

Reaction rates modelling: ψ

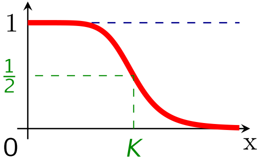
$$\psi := \prod_{i \geqslant 0} f_i(\phi) \qquad \begin{cases} f_i & \text{elementary functions} \\ \phi & \text{volume or mass fraction} \end{cases}$$



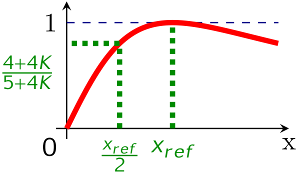
(a) Monod's law $f(x) = \frac{x}{K+x}$



(b) Droop's law $f(x) = \max\left\{0, 1 - \frac{K}{x}\right\}$



(c) Sigmoidal law $f(x) = \frac{1}{1+(x/K)^{\alpha}}$



(d) Haldane's law $f(x) = \frac{2(1+K)\tilde{x}}{\tilde{x}^2+2K\tilde{x}+1}$, $\tilde{x} = x/x_{ref}$

Reaction rates modelling

- Highly nonlinear reaction rates:
  Example:

$$\psi_P = \mu_P \rho_M N \frac{C}{\mathcal{K}_C + C} \frac{(1+K_L)L}{\mathcal{K}_L + L} \frac{2(1+\mathcal{K}_I)\hat{I}}{\hat{I}^2 + 2\mathcal{K}_I \hat{I} + 1} \frac{\max\left\{0, 1 - \frac{Q_{min}}{\min\{Q, Q_{max}\}}\right\}}{Q_{max} - Q_{min}} \frac{1}{1 + \left(\frac{O}{\mathcal{K}_O}\right)^{\alpha}},$$

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  - Received light intensity:

$$\hat{I}(z) = \frac{I_0}{I_{opt}} \exp\left(- \int_z^H \tau_L L + \tau_M (A + N + E) d\xi \right)$$

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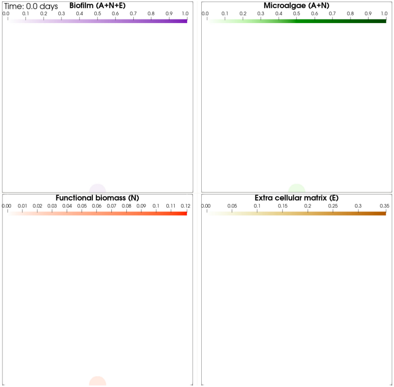
  - Functional biomass quota: $Q = \frac{N}{N+A}$.

- Coupled mass balances:

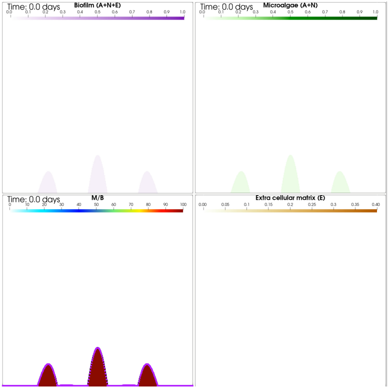
$$\partial_t A + \nabla_x \cdot (A V_M) = \frac{1}{\rho_M}\left(\psi_P - \psi_R - \eta_N^A \psi_N - \psi_E^A - \psi_D^A\right)$$

$$\partial_t (CL) + \nabla_x \cdot (C L V_L) - \nabla_x \cdot (\mathcal{D}_C L \nabla_x C) = \frac{1}{\rho_L}\left(\eta_R^C \psi_R - \eta_P^C \psi_P\right),$$

2D numerical simulations

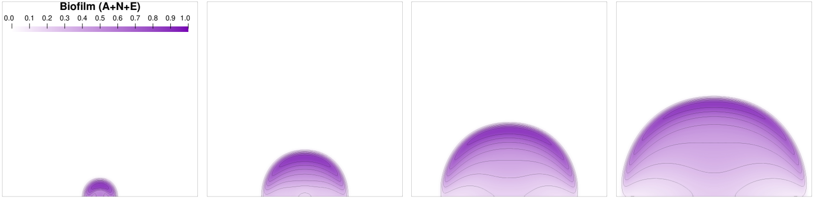


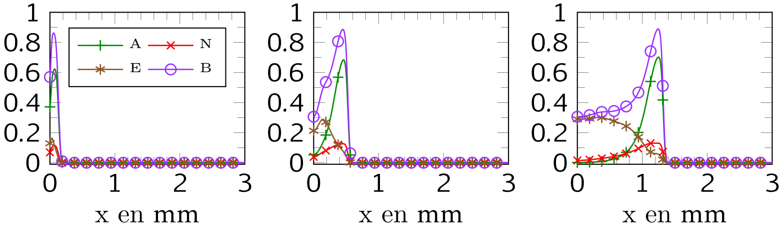
(a) Single spot colonie



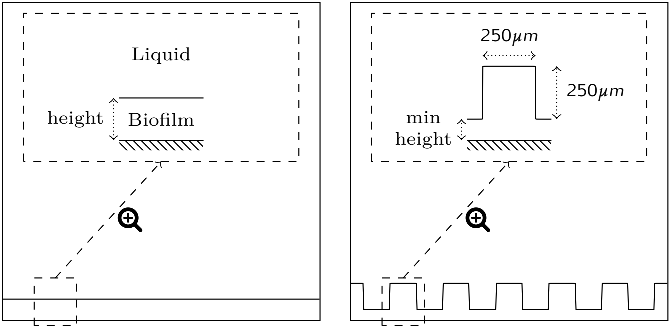
(b) Three spots colonie

1D versus 2D numerical simulations





Harvest policy: Battlement versus uniform



(a) Uniform harvesting (b) Battlement harvesting

Example: Battlement harvesting video.

Harvest policy: Impact of height and frequency?

Objective

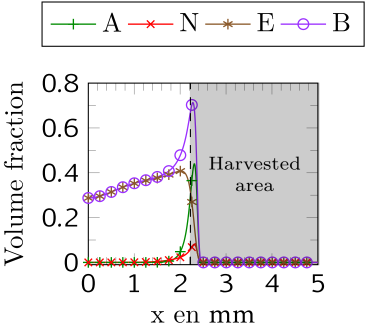
Quantify the impact of harvesting parameters on productivity.

Limitation

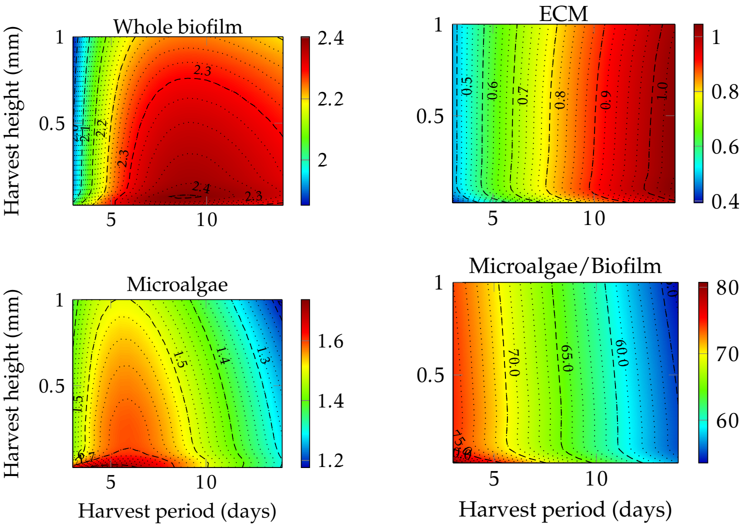
2D numerical simulation of ~ 50 days takes aboute two weeks on 2.40GHz Xeon.

Methodology

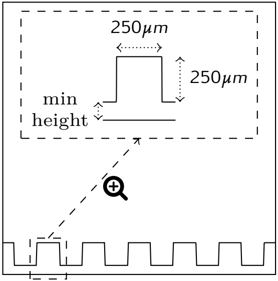
Investigate the impact of harvest height and frequency with 1D numerical simulation (about ~ 1h for 90 days).



Harvest policy: Impact of height and frequency



Harvest policy: Impact of scraping pattern

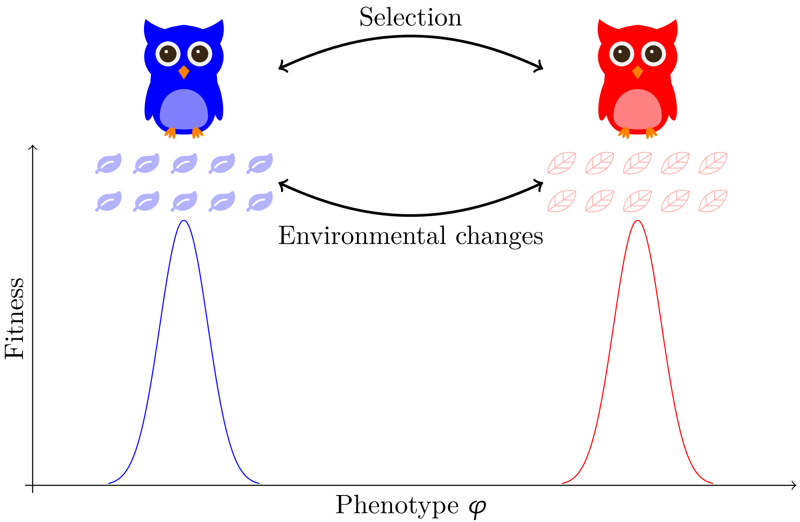


Battlement harvest shape:

- significantly increases productivity,
- modifies components productivity.

Period	(days)	4	6.5	9
Min height	(μm)	100	100	75
A	(%)	10.33	9.98	1.90
M	(%)	8.87	8.97	1.77
E	(%)	-19.77	-2.44	10.58
B	(%)	-1.31	4.92	4.90

Evolution: process of mutation and selection



General context

- Observation: Heredity is not just genetics
- Debate: What is the contribution of non-genetic heredity to evolution?
- Difficulties:
  - Non-genetic inheritance is multiple and heterogeneous, eg. methylation ≠ culture,
  - It is complex to formalize and analyze (≠ genetic),
  - Evolution theory is based on population genetic whereas others mode of heredity is unclear and under debate.

Approach from E. Rajon & S. Charlat, 2018

Philosophy

Idea: Expand the concept of mutation rate to epimutation rate,

Epigenetic: Heritable phenotype changes that do not involve alterations in the DNA sequence,

Advantages:

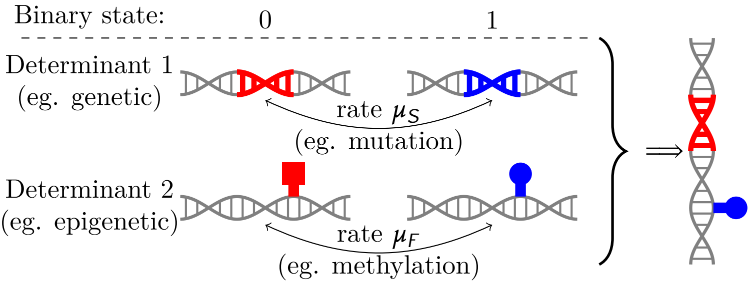
- Provides a comparable parameter between heterogeneous systems,
- Clear mathematical formalisms: epigenetic mutation rate $\gg$ genetic mutation rate

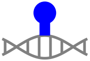
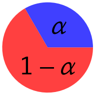
Collaborators:

- E. Rajon & S. Charlat from Laboratoire de Biométrie et Biologie Évolutive, Université de Lyon, Université Lyon 1,
- V. Calvez from Institut Camille Jordan (ICJ), Université Claude Bernard Lyon 1

Approach from E. Rajon & S. Charlat, 2018

Schematic description of individuals



Phenotype: $\phi = (1-\alpha) \times$  $+ \alpha \times$  ⟹ 

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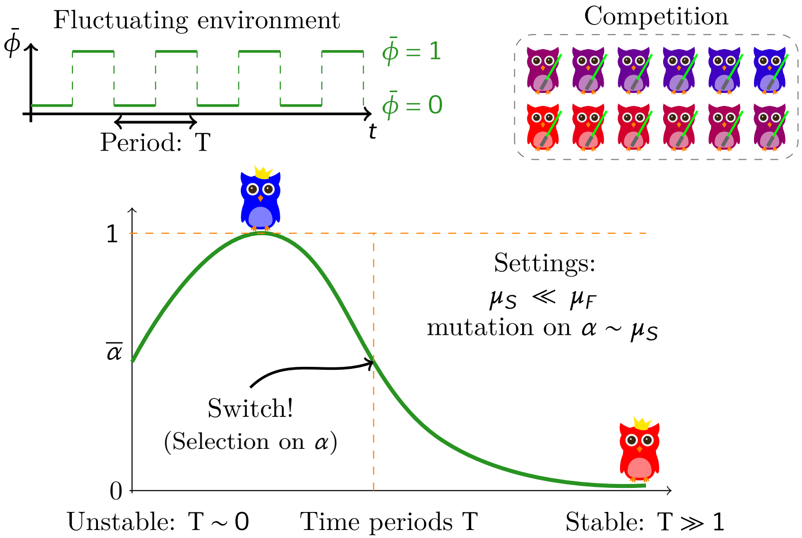
Questions:

- What is the contribution of non-genetic inheritance to evolution?
- Is the contribution of epigenetic (ie. α) under selection?

Approach from E. Rajon & S. Charlat, 2018

Selection in fluctuating environment



Mathematical model

The model is an adaptation of E. Rajon & S. Charlat, 2018.

$$\underbrace{\partial_t \mathrm{G}_i}_{\text{Evolution}} = \underbrace{\mu_\alpha \int_0^1 \mathcal{K}(\alpha,\alpha')\mathrm{G}_i(t,\alpha')\, d\alpha'}_{\text{Modifier locus mutations}} + \underbrace{\eta\left(1-\frac{\rho}{N}\right)\mathrm{G}_i}_{\text{Limited growth}} \underbrace{- s|\phi_i - \bar{\phi}(t)|^\gamma \mathrm{G}_i}_{\text{Fitness selection}} + \underbrace{(M\times\mathcal{G})_i}_{\text{Déterminant's mutation}}$$

Groups	G_1	G_2	G_3	G_4
Determinant set	$\{0,0\}$	$\{0,1\}$	$\{1,0\}$	$\{1,1\}$
Phenotypes: $\boldsymbol{\phi_i}$	0	α	$1-\alpha$	1

- μ_α mutation rate on α (very rare $\implies \mu_\alpha \sim \mu_S$),
- Mutation kernel: $\mathcal{K}(\alpha,\alpha')$ is gaussian law centered in α',
- Maximal growth rate: η,
- Total population size: $\rho(t) = \sum_{i=1}^{4}\int_0^1 G_i(t,\alpha)d\alpha$,

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- Selection rate: s,
- Phenotype of subpopulation: $\phi_i \in \{0,\alpha,1-\alpha,1\}$,
- Phenotype environment promoted: $\bar{\phi}(t) \in \{0,1\}$,
- Mutations:

$$\mathcal{M}\times G = \begin{pmatrix} -\mu_F-\mu_S & \mu_F & \mu_S & 0 \\ \mu_F & -\mu_F-\mu_S & 0 & \mu_S \\ \mu_S & 0 & -\mu_F-\mu_S & \mu_F \\ 0 & \mu_S & \mu_F & -\mu_F-\mu_S \end{pmatrix} \times \begin{pmatrix} G_1 \\ G_2 \\ G_3 \\ G_4 \end{pmatrix}.$$

Mathematical model analysis

Existence of solution

Theorem:

Under mild assumptions, the system has a unique nonnegative solution.

Proof idea: Banach–Picard fixpoint method (Cf. Transport Equations in Biology - B. Perthame).

Mathematical model analysis

Lyapunov exponent approach in infinite population

Hypothesis: Asymptotically (ie. on a long range of repeated periods) the population is monomorphic with respect to α.

Equilibrium characterisation: Floquet spectral problem, where the Floquet eigenvalue is the average of the fitness over a period :

$$\omega(\alpha) = \exp(\lambda(\alpha)) = \left(\text{eigenvalue}\left(\exp\left(\frac{T}{2}A\right)\exp\left(\frac{T}{2}B\right)\right)\right)^{\frac{1}{T}}$$

where A (resp. B) is the matrix of the evolutionary dynamics in environment $\mathcal{A}$ (resp. $\mathcal{B}$) :

$$A = \begin{pmatrix} 1 & \mu_F & \mu_S & 0 \\ \mu_F & 1-s\alpha^\gamma & 0 & \mu_S \\ \mu_S & 0 & 1-s(1-\alpha)^\gamma & \mu_F \\ 0 & \mu_S & \mu_F & 1-s \end{pmatrix} - \frac{\rho(t)}{N}\mathrm{Id} \qquad (1)$$

Mathematical model analysis

Lyapunov exponent approach in infinite population

Interpretation: In an infinite population setting, where all possible architectures are present in the population, we expect that architectures which are defined via some α will predominate over another architecture β if $\lambda(\alpha) > \lambda(\beta)$.

Assume that the trait fitness function is convex. Then, the Lyapunov exponent $\lambda(\alpha)$ is a convex function of the trait architecture α.

Remark: This result generalises for any number of determinants.

Mathematical model analysis

Interpretation

1. Composite mutation rates are selected against: selection of extremal values of $\alpha \implies \alpha = 0$ or $\alpha = 1$.

   Question: When does it switch from $\alpha = 0$ to $\alpha = 1$?

Mathematical model analysis

Interpretation

1. Composite mutation rates are selected against: selection of extremal values of $\alpha \implies \alpha = 0$ or $\alpha = 1$.

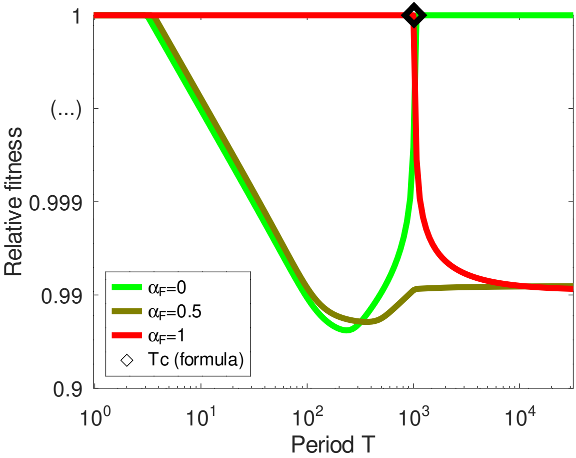
   Question: When does it switch from $\alpha = 0$ to $\alpha = 1$?

2. In the regime $\mu_S \ll \mu_F$ the value of T_c can be computed analytically :

$$\frac{T_c}{2} \approx \frac{1}{\mu_F} \ln\left(\frac{\mu_F}{\mu_S}\right)\left(1 + \frac{\mu_F}{s}\right).$$

Numerical simulation

Relative fitness of the clones & estimation of the switch



Selection on α for polyclonal finite and infinite population Size

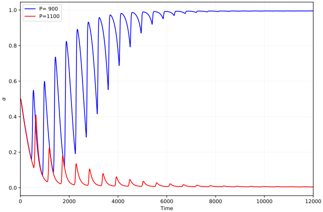
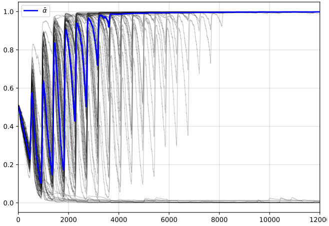
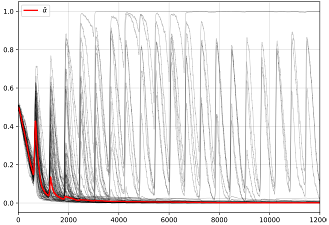


Figure: Simulation of the PDE system $\Longrightarrow$ infinite population

Right side: Monte-Carlo simulations $\Longrightarrow$ finite population.



(a) $P = 900$



(b) $P = 1200$

Selection on α for large polyclonal population

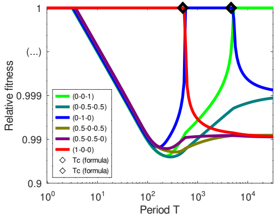
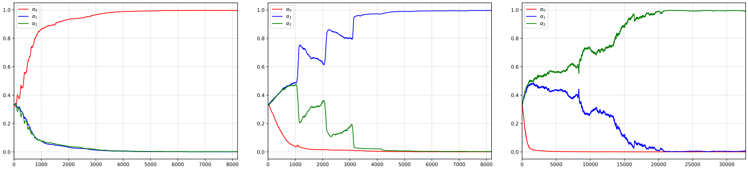


Figure: Relative fitness for 3 media



(a) $P = 900$ (b) $P = 1200$ (c) $P = 10000$

Figure: Monte-Carlo simulations $\implies$ population of finite size

Numerical simulation

what happens if the fitness is non-convex?

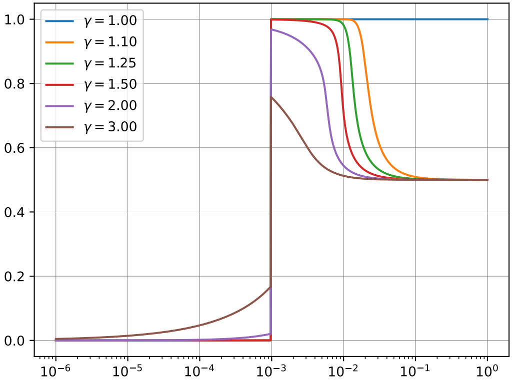
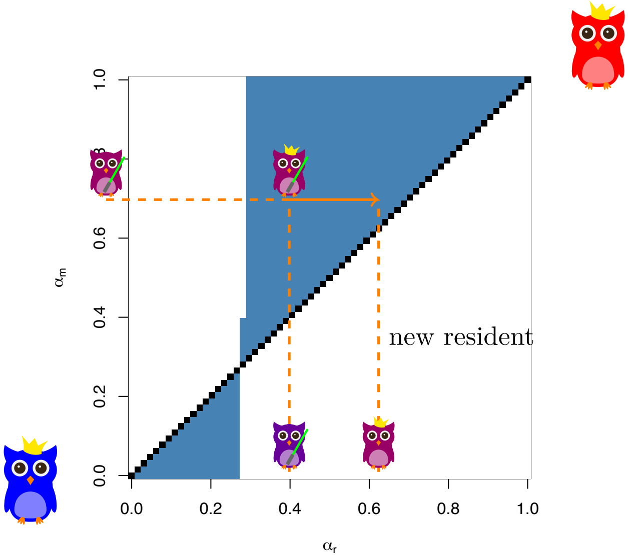


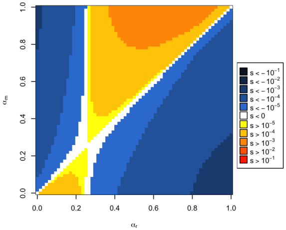
Figure: Selected α with respect to convexity of the selection law: $-s|\phi_i - \bar{\phi}(t)|^\gamma$

Adaptative dynamic & Invasion

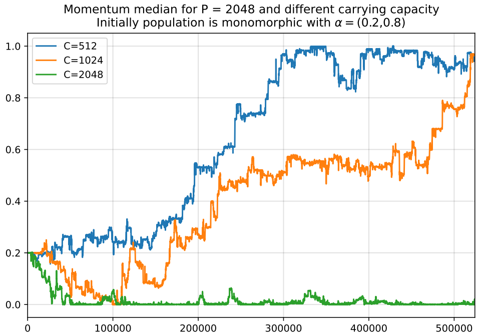
What about the stability of monoclonal populations



Adaptative dynamic & Invasion



(a) $P = 2048$



(b) Median dynamic for monoclonal populations (24 simulations for each period).

Conclusion & Perspectives

Results:

- Structure formation,
- Role of dissolved components in the development of structures,
- Quantification of limiting factors: light, Oxygen, ...
- Optimal strategy quantification for uniform harvest,
- Battlement scrapping harvest induce productivity increase.

Perspectives:

- Include the water flow,
- Take into account the viscosity,
- Multi-species biofilm,
- Calibration and comparison with experimental data.

Conclusions & Perspectives

Conclusions:

- Asymptotic behaviour characterisation,
- Composite mutation rates are selected against (ie. $\alpha = 0$ or 1),
- Analytic expression for T_c.

Perspectives:

- Extend the results for random fluctuation periods,

Open questions:

- What is the dynamic for small populations?

Thank you for your attention!

Questions?

References:

- Understanding photosynthetic biofilm productivity and structure through 2D simulation, B. Polizzi, A. Fanesi, F. Lopes, M. Ribot, O. Bernard, Plos Computational Biology (accepted).
- A time-space model for the growth of microalgae biofilms for biofuel production, B. Polizzi, O. Bernard, M. Ribot, Journal of Theoretical Biology, Volume 432, 7 November 2017, Pages 55-79.
- (In)exhaustible suppliers for evolution? Epistatic selection tunes the adaptive potential of nongenetic inheritance,
  Rajon Etienne and Charlat Sylvain,
  The American Naturalist, 2019.
- The evolution of composite mutation rates,
  Bastien Polizzi, Vincent Calvez, Sylvain Charlat and Etienne Rajon,
  In preparation.

Details about the property proof

$$\partial_t \mathrm{G}_i = \mu_\alpha \int_0^1 \mathcal{K}(\alpha,\alpha')\mathrm{G}_i(t,\alpha')\, d\alpha' + \eta(1-\rho)\mathrm{G}_i - s|\phi_i - \bar{\phi}(t)|\mathrm{G}_i + (M \times \mathcal{G})_i$$

- $\mu_\alpha \sim \mu_S \implies \partial_t \mathrm{G}_i = +\eta(1-\rho)\mathrm{G}_i - s|\phi_i - \bar{\phi}(t)|\mathrm{G}_i + (M \times \mathcal{G})_i,$
- The system to solve is equivalent to $Q \exp(AT)\mathcal{G} = \lambda \mathcal{G}$ with $A = M - s\mathrm{diag}(0, \alpha, 1-\alpha, 1),$
- The eigenvalue of interest is $\lambda = \exp\left(\eta \int_t^{t+T} (\rho(x) - 1)\, dx\right)$ and the ratio in each subpopulation is given by the eigenvector,
- Approximate eigen elements using Taylor expansions.

Remark: Numerically it is easy to extract the largest eigenvalue and its eigenvector.

NUMERICAL METHOD OVERVIEW

- **Semi-implicit approach for the mass balance equations:**

$$\frac{(\theta L)^{n+1} - (\theta L)^n}{dt} + \nabla_x \cdot (\boldsymbol{\theta L V_L})^{\boldsymbol{n}} = \nabla_x \cdot \left(D_\theta \boldsymbol{L^n} \nabla_x \frac{(\boldsymbol{\theta L})^{\boldsymbol{n+1}}}{\boldsymbol{L^n}} \right) + f(\boldsymbol{U^n}) - g(\boldsymbol{U^n})(\boldsymbol{\theta L})^{\boldsymbol{n+1}}$$

$f(U)$ production terms & $g(U)\theta L$ consumption terms

- **Chorin-Temam's projection method for the conservation of momentum:**
  1. Projection step for V_ϕ, $\phi = M, E, L$:

$$\frac{\left(\phi V_\phi\right)^{n+\frac{1}{2}} - \left(\phi V_\phi\right)^n}{dt} + \nabla_x \cdot \left(\boldsymbol{\phi V_\phi \otimes V_\phi}\right)^{\boldsymbol{n}}$$

$$= \frac{1}{\rho_\phi} \left(-\nabla_x \left(\gamma_\phi \boldsymbol{\phi^n}\right) + \sum_{\phi' \neq \phi} m_{\phi,\phi'} \left(\boldsymbol{V_\phi - V_{\phi'}}\right)^{\boldsymbol{n+\frac{1}{2}}} + \left(\boldsymbol{\Gamma_\phi V_\phi}\right)^{\boldsymbol{n}} \right)$$

  2. Elliptic equation for P: Variable coefficients & Nonhomogeneous
  3. Correction step: $V_\phi^{n+1} = V_\phi^{n+\frac{1}{2}} - \frac{\Delta t}{\rho_E} (\nabla_X P)^{n+1}$