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Contribution to the study of stochastic models and algorithms in population dynamics

Bertrand Cloez

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Université de Montpellier

École doctorale Information, Structures et Systèmes (I2S)
Spécialité: Biostatistique

HABILITATION À DIRIGER DES RECHERCHES

Contribution to the study of stochastic models and algorithms in population dynamics

*Contribution à l'étude de modèles stochastiques et
d'algorithmes en dynamique des populations*

Bertrand CLOEZ

soutenue le 5 janvier 2023 devant

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	Marie DOUMIC	- Inria Paris & E. Polytechnique
	Gersende FORT	- CNRS Toulouse

Je déclare avoir respecté, dans la conception et la rédaction de ce mémoire d'HDR, les valeurs et principes d'intégrité scientifique destinés à garantir le caractère honnête et scientifiquement rigoureux de tout travail de recherche, visés à l'article L.211-2 du Code de la recherche et énoncés par la Charte nationale de déontologie des métiers de la recherche et la Charte d'intégrité scientifique de l'Université de Montpellier. Je m'engage à les promouvoir dans le cadre de mes activités futures d'encadrement de recherche

Remerciements

J'ai écrit cette page presque deux ans après ma soutenance d'HDR. A ce moment cela faisait 13 ans de recherche, dont 3 en thèse. Durant cette période, j'ai accumulé un grand nombre de personnes envers qui je suis reconnaissant. Je n'en ferais pas la liste celle-ci étant trop longue et je vais oublier des personnes qui comptent pour moi.

Néanmoins, comme le veut l'usage, je vais remercier les membres du jury. Au vu de leur emploi du temps chargé, je remercie chaleureusement Djalil Chafai, Benoîte de Saporta, Pierre Del Moral, Marie Doumic, Janos Englander, Gersende Fort, Amaury Lambert et Viet Chi Tran d'avoir accepté de faire parti de mon jury et pour les rapporteurs d'avoir écrit un rapport.

Je remercie les chercheuses et chercheurs de Marne-la-Vallée, Toulouse et Montpellier, et plus généralement de la communauté mathématique et INRAE, qui me rendent heureux de faire le travail que je fais tous les jours.

Enfin, j'ai aussi une pensée pour ma famille, et les personnes qui ne pourront plus lire ces lignes.

Contents

1	Parcours et contributions	9
1.1	Curriculum Vitae	9
1.1.1	Parcours universitaire	9
1.1.2	Responsabilités administratives et scientifiques	9
1.1.3	Membre de jurys	10
1.1.4	Projets de recherche	10
1.1.5	Encadrements	10
1.2	Productions scientifiques	12
2	Introduction	17
2.1	Partie I : modèle aléatoire en dynamique des population	17
2.1.1	Chapitre 3 : processus de branchement	18
2.1.2	Chapitre 4 : modèles de population avec interaction	22
2.2	Partie II : algorithme stochastique	24
2.2.1	Chapitre 5 : Approximation des états quasi-stationnaires	24
2.2.2	Chapitre 6 : autres algorithmes stochastiques	27
I	Stochastic models in population dynamics	29
3	Branching processes	31
3.1	Introduction : the finite dimensional case	31
3.2	Two applications	32
3.2.1	Viability of Pyreneans brown bears	33
3.2.2	The paradoxical growth of the babassu palm tree	33
3.3	Branching processes and non-conservative semi-groups	35
3.4	Age-structured models : the renewal equation and the contour process	43
3.5	Growth-fragmentation models and the asymmetrical division of the E-coli bacteria	46
3.6	Evolutionary models	50

3.7	Perspectives	55
4	Population models with interaction	57
4.1	Introduction : a birth and death process	57
4.2	Chemostat : a consumer-resource population model	60
4.3	Functional responses : how predators eats preys	63
4.4	Around birth and death process	68
4.5	Collective behaviors	71
4.6	Perspectives	72
II	Stochastic algorithm	73
5	Quasi-stationary approximation	75
5.1	Fleming-Viot particle system	76
5.1.1	General results	76
5.1.2	A stimulating example	80
5.1.3	Hidden Markov chain	81
5.2	The Aldous-Flannery-Palacios Algorithm	84
5.2.1	A general result	84
5.2.2	A few word on the proof : the ODE method	86
5.3	Perspectives	87
6	Others stochastic algorithms	89
6.1	A general result for inhomogeneous Markov chain	89
6.1.1	A penalized bandit algorithm	90
6.1.2	Decreasing step Euler scheme	91
6.1.3	Freezing Markov chain and the coin-turning walk	93
6.2	Some others algorithms	95
6.3	Perspectives	95
7	Projet de recherche	99

Parcours et introduction

Chapter 1

Parcours et contributions

1.1 Curriculum Vitae

1.1.1 Parcours universitaire

- 2014-... : Chargé de recherche INRAE (ex. INRA) Montpellier - UMR Mistea
- 2014-2015 : Membre de l'équipe projet INRA-INRIA Modemic
- 2013-2014: Post-doctorant à l'Institut Mathématique de Toulouse à l'Université Paul Sabatier, financé par le Labex CIMI, supervisé par A. Joulin.
- 2010-2013 : Doctorat de mathématiques à l'université Paris-Est Marne-la-Vallée, au sein du LAMA avec D. Chafaï.
- 2009-2010: Master 2 de mathématiques à l'université de Lille et Agrégation de mathématiques.

1.1.2 Responsabilités administratives et scientifiques

- 2020 -2024 : Membre élu de la Commission Scientifique Spécialisée (CSS) Mathématique, Informatique, Sciences et Technologies du numérique (MISTI) de l'INRAE.
- 2018- ...: Membre du comité de pilotage de *Key initiative Muse (KIM) Data for life science* de l'i-site Montpellier Université d'excellence (MUSE)
- 2018-... : Co-organisateur du séminaire de probabilités et statistiques de Montpellier.

- 2016-2020 : Membre élu du conseil de département Mathématiques et Informatiques Appliquées (MIA) de l'INRA.

1.1.3 Membre de jurys

En plus de plusieurs soutenance de master, en 2021, j'ai été examinateur pour la thèse de Josué Corujo-Rodriguez sur les processus de Moran, et rapporteur pour la thèse de Benedetta Cavalli sur les processus de croissance-fragmentation.

1.1.4 Projets de recherche

Je suis ou ai été acteurs dans les projets financés ci-dessous.

- 2020-2024: Membre du projet européen H2020 TechCare, sur les nouvelles technologies pour le bien être animal.
- 2021-2025: Porteur du projet ANR JCJC NOLO, sur les processus de branchement non-locaux (156 029 euros).
- 2018-2021: Membre du projet ANR JCJC MESA, sur la méthode de Stein.
- 2015-2020: Membre du projet ANR franco-chinoise ANSWER, sur la prolifération des micro-algues dans les lacs.
- 2013-2017: Membre du projet ANR JCJC PIECE, sur les processus de Markov déterministes par morceaux.
- 2015-...: Membre de la chaire Polytechnique-Veolia MMB, sur les modèles mathématiques pour la biodiversité.

Plusieurs financements complémentaires provenant de l'INRAE, de labex, etc. m'ont permis de financer des événements où, de manière plus importante, des encadrements. Ces derniers sont donc listés dans la section 1.1.5 ci-dessous.

1.1.5 Encadrements

Durant la période que couvre ce rapport, j'ai encadré plusieurs personnes listées ci-après.

Les résultats obtenus lors de ces encadrements ont donné lieu à des publications de l'étudiant seul, des publications communes ou plus communément à l'absence de publication. Dans la section 1.2 sur mes publications, les auteurs en gras correspondent aux personnes sous mon (co-)encadrement.

Tous les résultats de ces stages sont décrits dans ce rapport.

Masters

- 2021: Adrien Cotel, co-encadré par Jean-Baptiste Menassol, financé par l'institut de convergence # DigitAg, sur la modélisation pour des données de déplacements de bovins et ovins.
- 2021: Adil el Abdouni, co-encadré par Pierre Gabriel, financé par l'ANR NOLO, sur des équations de sélection-mutation inhomogène en temps.
- 2020: Cyril Robert, co-encadré par Bénédicte Fontez et Patrice Loisel, financé par le budget récurrent de MISTEA, sur un modèle de mélange pour la croissance d'un palmier.
- 2020: Marine Perrier, co-encadré par Bénédicte Fontez et Patrice Loisel, non-financée, sur de l'apprentissage non-supervisé (*clustering*) pour des données déplacements de bovins.
- 2018: Jun Zhang, co-encadrée par Réza Akbarinia, Bénédicte Fontez et Florent Masseglia, financée par l'institut de convergence # DigitAg, sur la modélisation et la détection de motifs pour des données de déplacements de bovins.
- 2018: Max Zinsou Débaly, co-encadré par Meïli Baragatti et Céline Casenave, financé par le budget récurrent de MISTEA, sur la méthode ABC appliquée à des modèles déterministes de prolifération d'algues
- 2017: Marion Kerioui, co-encadrée par Bénédicte Fontez, financée par le budget récurrent de MISTEA, sur la viabilité des ours pyrénéens.
- 2016 : Maud Joubaud, co-encadrée par Benoîte de Saporta, financée par le budget récurrent de MISTEA, sur des schéma d'Euler pour des processus de Markov déterministes par morceaux (PDMP).

Doctorant·e-s

- 2021-...: Adrien Cotel, co-encadré par Jean-Baptiste Menassol, financé par l'institut de convergence # DigitAg et le département MathNum de l'INRAE, sur la modélisation mathématique et la détection précoce pour des données de déplacements de bovins et ovins.
- 2021-...: Adil El Abdouni, co-encadré par Pierre Gabriel, financé par le Labex de Mathématique Hadamard, sur des équations de sélection-mutation inhomogène en temps à noyaux non-locaux.

- 2016-2019: Maud Joubaud, co-encadrée par Benoîte de Saporta, financé par l'école doctorale I2S de Montpellier, sur des PDMP à valeurs mesures et des problèmes d'arrêt optimal.

Post-doctorants

- 2018-2021: Tristan Roget, co-encadré par Benoîte de Saporta, financé par le projet FEDER Promesse et la chaire MMB, sur l'asymétrie dans la division de la cellule E-Coli.
- 2018-2020: Alvaro Mateos Gonzalez, co-encadré par Matthieu Alfaro et Guillaume Martin, financé par les labex NUMEV-CEMEB-AGRO, sur des modèles de mutation-sélection pour l'adaptation de micro-organismes.

1.2 Productions scientifiques

Ci-dessous se trouve la liste de toutes mes publications. Dans ce mémoire, je ne détaille cependant pas les travaux [A10, P9, A17] issus de ma thèse [T1], ni [A11] qui en est fortement relié, ni des livres [L2, L1] qui, même s'ils sont en adéquation avec mon travail de recherche, ont une vocation de vulgarisation ou d'enseignement et non de recherche.

Contrairement aux références à la fin du document, ces dernières ne sont pas classées par ordre alphabétique mais par ordre chronologique décroissant. Je rappelle que les autrices et auteurs de la section 1.1.5 sont en gras.

Prépublications

- [P1] Bertrand Cloez and Coralie Fritsch. *Quasi-stationary behavior for an hybrid model of chemostat: the Crump-Young model*. 2022.
- [P2] Bertrand Cloez and Pierre Gabriel. *Fast, slow convergence, and concentration in the house of cards replicator-mutator model*. Mar. 2022. arXiv: 2203.07924 [math.AP].
- [P3] Francesco Piccioni, Céline Casenave, Meïli Baragatti, Bertrand Cloez, and Brigitte Vinçon-Leite. *Automated calibration of a complex aquatic ecological model through Approximate Bayesian Computation and random forest*. 2022.
- [P4] Vincent Bansaye and Bertrand Cloez. *From the distributions of times of interactions to preys and predators dynamical systems*. 2021. arXiv: 2103.16303 [math.DS].

- [P5] Bertrand Cloez and Josué Corujo. *Uniform in time propagation of chaos for a Moran model*. 2021. arXiv: 2107.10794 [math.PR].
- [P6] Reza Akbarinia and Bertrand Cloez. *Efficient matrix profile computation using different distance functions*. 2019. arXiv: 1901.05708 [cs.LG].
- [P7] Bertrand Cloez, Tanguy Daufresne, **Marion Kerioui**, and Bénédicte Fontez. *Galton-Watson process and bayesian inference: A turnkey method for the viability study of small populations*. 2019. arXiv: 1901.09562 [stat.AP].
- [P8] Bertrand Cloez and Benoît Henry. *Markovian tricks for non-Markovian trees: contour process, extinction and scaling limits*. 2018. arXiv: 1801.03284 [math.PR].
- [P9] Bertrand Cloez. *Wasserstein decay of one dimensional jump-diffusions*. 2012. arXiv: 1202.1259 [math.PR].

Articles publiés

- [A1] Vincent Bansaye, Bertrand Cloez, Pierre Gabriel, and Aline Marguet. “A non-conservative Harris’ ergodic theorem”. In: *Journal of the London Mathematical Society* (2022). To appear.
- [A2] Bertrand Cloez, Benoîte de Saporta, and **Tristan Roget**. “Long-time behavior and Darwinian optimality for an asymmetric size-structured branching process”. In: *Journal of Mathematical Biology* 83.6 (2021), pp. 1–30.
- [A3] Bertrand Cloez and Pierre Gabriel. “On an irreducibility type condition for the ergodicity of nonconservative semigroups”. In: *C. R. Math. Acad. Sci. Paris* 358.6 (2020), pp. 733–742.
- [A4] Bertrand Cloez, Benoite de Saporta, and **Maud Joubaud**. “Optimal stopping for measure-valued piecewise deterministic Markov processes”. In: *Journal of Applied Probability* 57.2 (2020), pp. 497–512.
- [A5] Bertrand Cloez and Claire Delplancke. “Intertwinings and Stein’s magic factors for birth–death processes”. In: *Annales de l’Institut Henri Poincaré, Probabilités et Statistiques* 55.1 (2019), pp. 341–377.
- [A6] Michel Benaim, Cloez, Bertrand, and Fabien Panloup. “Stochastic approximation of quasi-stationary distributions on compact spaces and applications”. In: *The Annals of Applied Probability* 28.4 (2018), pp. 2370–2416.

- [A7] Florian Bouguet and Cloez, Bertrand. “Fluctuations of the empirical measure of freezing Markov chains”. In: *Electronic Journal of Probability* 23 (2018).
- [A8] Vincent Bansaye, Bertrand Cloez, and Pierre Gabriel. “Ergodic behavior of non-conservative semigroups via generalized Doeblin’s conditions”. In: *Acta Applicandae Mathematicae* (2017), pp. 1–44.
- [A9] Michel Benaïm, Florian Bouguet, and Cloez, Bertrand. “Ergodicity of inhomogeneous Markov chains through asymptotic pseudotrajectories”. In: *The Annals of Applied Probability* 27.5 (2017), pp. 3004–3049.
- [A10] Bertrand Cloez. “Limit theorems for some branching measure-valued processes”. In: *Advances in Applied Probability* 49.2 (2017), pp. 549–580.
- [A11] Bertrand Cloez, Renaud Dessalles, Alexandre Genadot, Florent Malrieu, Aline Marguet, and Romain Yvinec. “Probabilistic and piecewise deterministic models in biology”. In: *ESAIM: Proceedings and Surveys* 60 (2017), pp. 225–245.
- [A12] Bertrand Cloez and Coralie Fritsch. “Gaussian approximations for chemostat models in finite and infinite dimensions”. In: *Journal of mathematical biology* 75.4 (2017), pp. 805–843.
- [A13] Bertrand Cloez and Marie-Noémie Thai. “Fleming-Viot processes: two explicit examples”. In: *ALEA Lat. Am. J. Probab. Math. Stat.* 13 (2016), pp. 337–356.
- [A14] Bertrand Cloez and Marie-Noémie Thai. “Quantitative results for the Fleming-Viot particle system and quasi-stationary distributions in discrete space”. In: *Stochastic Process. Appl.* 126.3 (2016), pp. 680–702.
- [A15] Matthew J Wade, Jérôme Harmand, Boumediene Benyahia, Théodore Bouchez, Stéphane Chaillou, Bertrand Cloez, J-J Godon, B Moussa Boudjemaa, Alain Rapaport, T Sari, et al. “Perspectives in mathematical modelling for microbial ecology”. In: *Ecological Modelling* 321 (2016), pp. 64–74.
- [A16] Michel Benaïm and Cloez, Bertrand. “A stochastic approximation approach to quasi-stationary distributions on finite spaces”. In: *Electron. Commun. Probab.* 20 (2015), no. 37, 14.
- [A17] Bertrand Cloez and Martin Hairer. “Exponential ergodicity for Markov processes with random switching”. In: *Bernoulli* 21.1 (2015), pp. 505–536.

Livres

- [L1] Bertrand Cloez. *Recueil d'anecdotes mathématiques*. Ellipses, 2022.
- [L2] Vincent Bansaye et al. *Maths la Terminale S*. Ellipses, 2016.

Thèse

- [T1] Bertrand Cloez. "Comportement asymptotique de processus avec sauts et applications pour des modèles avec branchement". PhD thesis. Université Paris-Est, 2013.

Chapter 2

Introduction

Ce document résume mes activités de recherche depuis ma soutenance de thèse de doctorat en 2013. Étant maintenant chercheur en mathématique dans un institut de recherche spécialisé dans les sciences du vivant, ces dernières sont centrées sur des applications en biologie et principalement en dynamique des populations. Elles sont axées autour de deux thèmes principaux qui structureront ce rapport :

1. l'étude du comportement en temps long de modèles aléatoires
2. les propriétés de quelques algorithmes stochastiques pour la biologie.

De plus, dans la lignée de mes travaux de thèse, qui s'intéressaient principalement à des modèles déterministes par morceaux, à la fois les modèles et les algorithmes que j'ai étudiés sont majoritairement non-diffusifs.

Donnons dans ce chapitre introductif, une vue d'ensemble des résultats présentés dans ce manuscrit. En particulier, le contexte bibliographique sera décrit plus en détail dans les parties II et I. Nous reprenons le plan de ces dernières, c'est-à-dire deux parties comportant chacune deux chapitres. Chacun de ces chapitres finit par une section de perspective. En guise de conclusion, ces dernières sont résumées dans mon projet de recherche à moyen terme dans le chapitre 7. Le manuscrit finit par un chapitre sur mon projet de recherche.

2.1 Partie I : modèle aléatoire en dynamique des population

La partie I est consacrée aux modèles aléatoires en dynamique des populations que j'ai étudiés. Ils sont principalement issus de modèles de branchement, et

sont développés dans le chapitre 3. Dans le chapitre 4, je décrirai d'autres modèles que j'ai étudiés. Ces derniers ne satisfont pas la propriété de branchement et la structure d'interaction y est centrale.

2.1.1 Chapitre 3 : processus de branchement

Durant ma thèse de doctorat, j'ai établi des résultats de type loi des grands nombres pour des processus de branchement. Ces résultats [A10, T1] sont dans la lignée de [17, 136, 137] et donnent la convergence de répartition des traits. Les hypothèses et la démonstration de ces précédant résultats reposent sur l'existence préalablement connue d'éléments propres principaux d'un certain opérateur associé à ce processus de branchement. J'ai continué à travailler sur ce sujet, mais au contraire de mon travail de thèse, l'existence et la convergence vers ces éléments propres a été la question centrale. Ce chapitre décrira donc les travaux [A1, P2, A2–A4, P7, P8, A8] en collaboration avec Vincent Bansaye, Tanguy Daufresne, Benoîte de Saporta, Bénédicte Fontez, Pierre Gabriel, Benoît Henry, Maud Joubaud, Marion Kérioui et Tristan Roget. Il reprend aussi les résultats issus des encadrements d'Adil el Abdouni, Alvaro Mateos González, Maud Joubaud, Marion Kerioui, Cyril Robert et Tristan Roget.

Dans les modèles issus de ces recherches, nous considérons une population d'individus possédant chacun un trait. Entre les événements de branchement, ces traits évoluent de manière indépendante et markovienne, typiquement en suivant une équation différentielle ordinaire. On pourrait aussi cependant imaginer une dynamique diffusive de type brownienne. Pour chaque individu, les événements de branchement arrivent à des temps aléatoires dépendant des traits selon des lois de type exponentielle mais indépendamment des autres individus. À ces temps, chaque individu possède un nombre entier de descendants dont le nouveau trait dépend de celui du parent. Après la naissance, ces individus évoluent de manière indépendante et ainsi de suite. Voir la figure 2.1 pour une illustration.

Ce type de modèle inclut naturellement les modèles de Galton-Watson multi-types. Dans ce modèle, le trait est constant entre les divisions et l'espace des traits est fini. Ce modèle est simple et bien connu. En temps discret, les transitions du nombre d'individus correspondent à des lois multinomiales. Dans la section 3.2, je détaille rapidement deux exemples concrets d'applications utilisant cette propriété. Le premier utilise la propriété de conjugaison bayésienne entre la loi multinomiale et la loi de Dirichlet pour étudier simplement la viabilité de la population d'ours pyrénéens. La deuxième application concerne la croissance du palmier Babassu. Nous posons un modèle de mélange et un test de ratio de vraisemblance pour comprendre l'effet de goulot d'étranglement

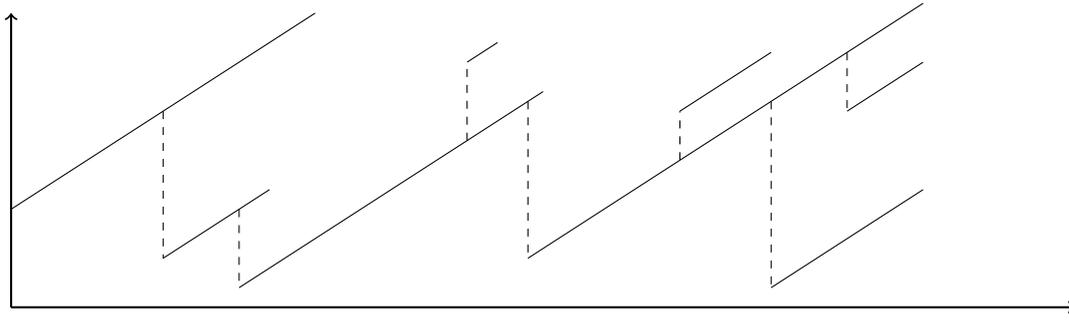


Figure 2.1: Exemple d'une trajectoire d'un processus de branchement. L'abscisse représente le temps, l'ordonnée le trait des individus. Les pointillés désignent les liens de filiations.

dans sa croissance.

Comme pour le modèle discret, en dimension infinie, le comportement des processus de branchement repose principalement sur la valeur des vecteurs propres principaux et la valeur propre principale (au sens de Perron). Dans plusieurs travaux, j'ai donc étudié l'existence de ces éléments propres ainsi que les convergences associées. Ces problèmes dépassent le cadre des probabilités. Ils concernent l'étude des semi-groupes ou semi-flow positifs en analyse fonctionnelle; c'est-à-dire des suites d'opérateurs $(M_{s,t})_{t \geq s \geq 0}$, agissant sur des fonctions (mesurables bornées par exemple) vérifiant

$$M_{s,u} \circ M_{u,t} = M_{s,t}$$

et $M_{s,t}(f) = M_{s,t}f \geq 0$ pour toute fonction positive $f \geq 0$ et réels positifs $t \geq u \geq s \geq 0$. Ils concernent aussi l'étude des équations aux dérivées partielles linéaires du type

$$\partial_t u(t, x) + \nabla_x(u(t, \cdot)F)(x) + au(t, x) = \int_X u(t, y)K(x, dy), \quad (2.1)$$

où $u(t, x)$ représente la densité de population possédant le trait x au temps t , F est un champs de vecteurs et K un noyau de saut. Je me suis intéressé à des asymptotiques du type

$$u(t, x) \sim e^{\lambda t} \gamma(x) \int_X u(0, y)h(y)dy, \quad (2.2)$$

où (h, γ, λ) sont justement les éléments propres associés à ce problème. Ce type de résultats est la première étape pour montrer que si $\lambda > 0$ alors la distribution des traits converge vers une loi de densité γ et que le nombre d'individus

se comporte comme $e^{\lambda t} \int h d\mu$, où μ est une mesure représentant la répartition initiale des traits.

Dans la section 3.3, nous introduisons clairement la définition du semi-groupe associé à un processus de branchement, et nous décrivons les résultats qui établissent l'existence des éléments propres, ainsi que l'asymptotique (2.2). Les démonstrations sont basées sur la généralisation de méthodes de type Meyn-Tweedie ou Doeblin-Lyapunov aux semi-groupes non-conservatifs. Cela permet de se passer des méthodes de type Krein-Rutman qui nécessitent souvent l'utilisation d'hypothèses plus fortes (propriété de Feller forte, espace d'état compact...). Ces résultats sont établis pour des modèles non homogènes en temps où la convergence vers des éléments propres est remplacée par une contraction traduisant un oubli de la condition initiale.

Par la suite, ces résultats sont appliqués pour quelques modèles particuliers que sont des modèles structurés en âge, en taille ou des modèles de mutation-sélection.

Les modèles structurés en taille (modèle de McKendrick, von Foerster, Bellman, Crump-Mode-Jagers, renouvellement ...) sont très étudiés depuis relativement longtemps. Je me suis principalement intéressé à des modèles inhomogènes en temps et certaines propriétés du processus aléatoire. Nous avons travaillé sur la convergence en temps long du comportement moyen ainsi que d'autres propriétés spécifiques (loi au temps $t \geq 0$, probabilité d'absorption...). Nous obtenons en particulier de nouveaux taux de convergence explicites, même dans le cas homogène. Dans le cas périodique, nous obtenons la croissance exponentielle de la population et la convergence vers un état qui évolue de manière périodique. Nous avons aussi étudié plusieurs autres propriétés du processus aléatoire via la méthode du contour des arbres. Cette méthode consiste à plonger l'ensemble des arbres binaires dans un ensemble de fonctions puis de travailler sur ces fonctions. Ici, le processus de branchement structuré en âge devient un processus de Markov déterministe par morceaux (PDMP) particulier. Tous ces résultats sont décrits dans la section 3.4.

En terme d'opérateurs, le type de générateur \mathcal{A} associé à un processus de branchement structuré en âge a la forme :

$$\mathcal{A}f(x) = f'(x) + B(x) (2f(0) - f(x)),$$

pour $x \in [0, \infty)$ et une fonction f régulière. On peut lire la croissance linéaire de l'âge dans le premier terme, le terme de transport, et le renouvellement dans le terme d'ordre 0. L'espace d'état est non compact mais le fait que les âges des nouveaux nés soient nuls permet d'utiliser des techniques généralement adaptées aux espaces compacts. La situation est différente pour les problèmes

structurés en taille dont le générateur sur le même espace a la forme :

$$\mathcal{A}f(x) = xf'(x) + B(x) (2f(x/2) - f(x)).$$

Encore une fois, le terme de transport $xf'(x)$ retranscrit la croissance exponentielle des cellules et le terme intégral $B(x) (2f(x/2) - f(x))$, le fait qu'à un certain taux, noté $B(x)$ ici, une cellule de masse x se divise en deux cellules de tailles $x/2$.

Ces modèles structurés en taille ont été particulièrement très étudiés ces dix dernières années. A l'aide des résultats présentés dans la section 3.3, nous obtenons de nouveaux résultats du type (2.2), sous différentes hypothèses, décrits dans la section 3.5. Cela nous permet, entre autres, d'apporter des pistes de compréhension sur les raisons de l'asymétrie dans la division de la cellule E-coli. Cette bactérie a une forme tubulaire. Durant sa croissance, elle crée de la masse au centre de ce tube puis se divise en deux. La cellule fille est donc constituée d'un pôle nouveau issu du centre de l'ancienne cellule et un pôle ancien issu du bord de cette cellule mère. En conséquence, lorsque celle-ci se divisera, elle aura une fille issue du pôle nouveau et une du pôle ancien. De récentes études ont montré que la dynamique des cellules nouvelles et des cellules anciennes était différente (alors que ces dernières sont génétiquement identiques). Pour aider à la compréhension de ce phénomène, nous avons montré qu'une dynamique asymétrique est meilleur d'un point de vue évolutif (sous notre modèle et nos hypothèses). La démonstration repose sur l'étude des variations de la valeur propre, non explicite, en fonction des divers paramètres du modèle.

Finalement, le chapitre sur les processus de branchement se termine par les modèles de mutation-sélection. Ces modèles sont encore beaucoup plus étudiés que les modèles de croissance-fragmentation évoqués plus haut. En particulier, il existe une grande variété de modèles. J'en ai étudié trois différents dont le point commun repose sur la sélection. La sélection ajoute en général de l'interaction dans les modèles et est donc, en principe, incompatible avec les méthodes de branchement. Cependant, les modèles de la section 3.6 sont de type *replicator-mutator*, ou modèle de Kimura, qui permettent justement de se ramener à de tels processus. En particulier, dans un des modèles étudiés, les mutations sont réduites au cas le plus simple : le modèle du château de cartes. Ce modèle est très simple, car nous obtenons beaucoup de résultats explicites de taux de convergence, dans des distances variées, exponentielles ou sous-exponentielles. Il peut être aussi relativement complexe, car malgré que sa loi soit à densité pour tout temps, elle converge vers une mesure mélangeant masse de Dirac et densité. Plusieurs questions sont toujours ouvertes sur cette convergence. Il semble que ce type de convergence soit particulière aux semi-groupes

conservatifs et cet exemple représente donc un comportement remarquable et intéressant. Ce phénomène de concentration n'arrive pas lorsque l'on considère un environnement changeant. En effet, nous avons aussi étudié un modèle de mutation-selection dans un environnement in-homogène. Le dernier modèle étudié concerne la prise en compte d'un taux de naissance dépendant du trait pour mieux comprendre la survie évolutionnaire. Finalement, j'ai aussi travaillé sur des modèles de Moran dans [P5]. Une partie des résultats est décrite dans un cas particulier avec une vision plus algorithmique dans la section 5.1.

2.1.2 Chapitre 4 : modèles de population avec interaction

Les processus de branchement sont des processus très complets et très utiles pour la modélisation en biologie (et dans beaucoup d'autres contextes) mais ils ne retranscrivent pas tous les comportements possibles.

J'ai donc étudié divers modèles incluant de la dépendance entre les individus. Ces résultats ont été valorisés dans les articles [P1, P4, A5, A12] en collaboration avec Vincent Bansaye, Coralie Fritsch et Claire Delplancke, ainsi que l'article de type *survey* [A15]. Ils seront exposés dans le chapitre 4 avec les résultats des encadrements d'Adrien Cotil, Marine Perrier et Jun Zhang.

D'un point de vue biologique, on peut modéliser deux types d'interaction: une interaction directe et une interaction indirecte.

Dans une interaction indirecte, les individus n'interagissent qu'à travers une autre quantité. On peut penser naturellement au célèbre modèle proie-prédateur de Lotka-Volterra et donc plus généralement aux modèles de consommateur-ressource. Un des modèles de consommateur-ressource le plus étudié, et en particulier dans mon unité et équipe de recherche, est le modèle du chimostat. Dans ce dernier, une population évolue dans un volume fixe, appelé bioréacteur, dans lequel on ajoute de la nourriture à taux fixe et, pour garder un volume constant, on extrait une partie de ce volume. Ce modèle biologique a majoritairement été étudié à l'aide d'équations déterministes. J'ai étudié une version stochastique de ces modèles, le modèle hybride de Crump-Young, et ses généralisations en dimension infinie. Dans ce modèle, la population est modélisée par un processus de sauts à valeur entière et l'évolution de la ressource par une équation différentielle ordinaire. C'est donc un processus de Markov déterministe par morceaux dont la dynamique est complètement couplée. Voir la figure 2.2 pour une illustration d'une trajectoire de cette dynamique. Nous avons étudié le comportement en temps long et en grande population de tels modèles. Le comportement en temps long est particulièrement délicat du fait de la dynamique hybride. La limite grande population est plus classique mais relativement technique.

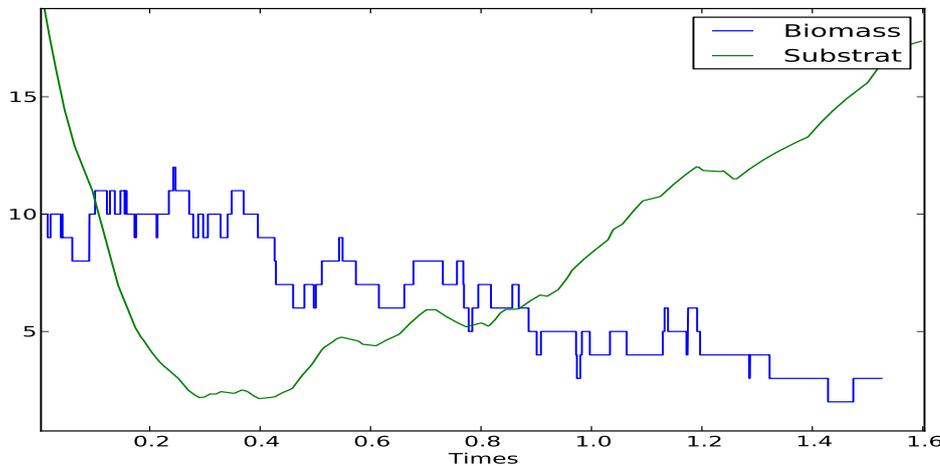


Figure 2.2: Une trajectoire du processus de Crump-Young.

Dans ce type de modèles (chémostat, consommateur-ressource, proie-prédateur), un paramètre important est le taux de consommation de la ressource et sa conversion en nouvel individu. Dans le modèle de Lotka-Volterra, ces derniers sont linéaires. Pour le chémostat, ils sont souvent modélisés par des fonctions concaves, croissantes et convergentes, depuis la thèse de Jacques Monod. En écologie, depuis des travaux de Holling, cette fonction est appelée *réponse fonctionnelle* et sa forme soulève plusieurs controverses (notamment autour de la question de ratio-dépendance, voir [7]). Dans [40], ils démontrent même, en particulier, l'importance de sa calibration pour les conclusions biologiques. Dans la section 4.3, nous justifierons certaines formes de réponses fonctionnelles à partir d'un modèle reposant sur des hypothèses microscopiques. D'un point de vue mathématique, nous faisons une limite d'échelle, où le consommateur et la ressource ne sont pas à la même échelle de temps. On parle de modèle lent-rapide. Cela donne lieu à l'utilisation de nouvelles techniques originales sur les objets que l'on manipule (mesures d'occupations) et les topologies associées.

Les interactions directes peuvent être modélisées simplement à partir de processus de naissance et mort. Ces derniers sont très bien connus et beaucoup de résultats existent sur leur comportement en temps long. Dans la section 4.4, nous utilisons ces processus non pas pour modéliser un phénomène biologique mais pour établir de nouveaux résultats mathématiques dans d'autres contextes. En effet, depuis les travaux de Stein et Chen, les solutions des équations de Poisson (ou de Stein) associées à ces processus permettent d'avoir des

bornes précises de convergence dans des théorèmes d'approximation du type binomiale/Poisson. Nous donnons des bornes sur ces solutions et une application pour des modèles de mélange à partir de nouvelles propriétés sur certains processus de naissance et mort.

Finalement, sur les modèles avec interactions, je me suis intéressé à l'influence des réseaux sociaux dans des déplacements d'animaux afin à terme de détecter en avance des mal-être chez les animaux d'élevage. Ces travaux, surtout issus d'encadrements divers, sont encore en cours d'élaboration et sont décrits dans la section 4.5. Les outils mathématiques sont variés: l'utilisation d'algorithmes de *clustering* pour des graphes de proximités, l'inférence d'une chaîne de Markov à espace d'état fini ou l'étude mathématique d'un modèle déterministe d'alignement.

2.2 Partie II : algorithme stochastique

Motivé par les applications en biologie et par la proximité mathématique de certains algorithmes avec certains modèles biologiques, j'ai étudié divers algorithmes stochastiques. La majorité concerne l'approximation des distributions quasi-stationnaires, d'autres sont des algorithmes proches souvent issus d'algorithmes dit d'*approximation stochastique*.

2.2.1 Chapitre 5 : Approximation des états quasi-stationnaires

Les éléments propres et les résultats limites évoqués par l'équation 2.2 sont aussi importants pour l'étude des processus de branchement en dimension infini que pour des processus $(X_t)_{t \geq 0}$ possédant un état absorbant ∂ . En effet, avant d'être absorbé, ces processus peuvent converger vers un état d'équilibre que l'on appelle état quasi-stationnaire. Si on note $x \mapsto u(t, x)$ la densité de probabilité de la variable aléatoire X_t , au temps $t \geq 0$, et que l'équation (2.2) est vérifiée, alors on a

$$\mathbb{P}_x(X_t \neq \partial) \sim e^{\lambda t} h(x), \quad \mathbb{P}_x(X_t \in dx \mid X_t \neq \partial) \sim \gamma(x) dx,$$

avec $\lambda < 0$. La connaissance de ces quantités est donc très importante pour la compréhension du comportement de $(X_t)_{t \geq 0}$.

Dans la section 5, je décris les résultats sur les différents algorithmes que j'ai étudiés pour l'approximation de ces éléments propres. Il reprend mes collaborations [P5, A6, A13, A14, A16] avec Michel Benaïm, Josué Corujo Rodriguez, Fabien Panloup et Marie-Noémie Thai. Ces articles portent sur les processus de Fleming-Viot et d'Aldous-Flannery-Palacios.

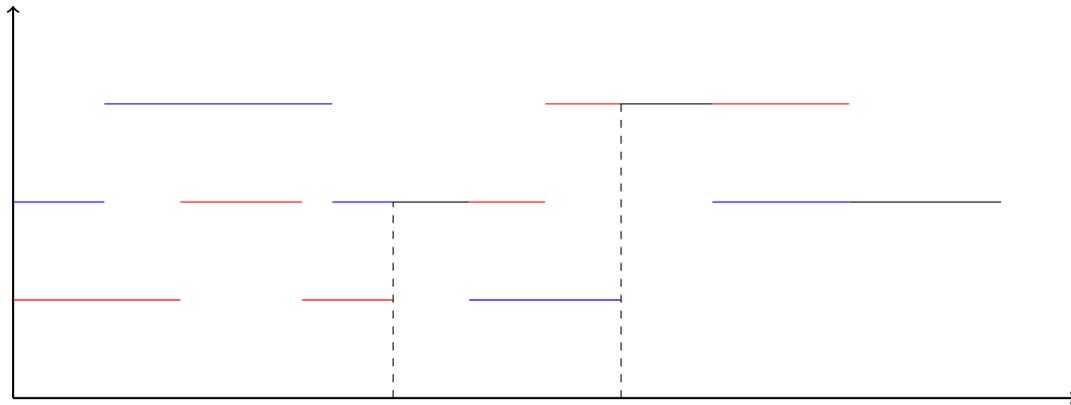


Figure 2.3: Exemple d'une trajectoire d'un processus de Fleming-Viot avec deux particules. Il y a deux particules, représentées en rouge et en bleu. Lorsqu'elles se situent au même endroit, leur valeur superposée est représentée par un trait noir. Les redistributions aux instants d'absorption sont représentées par des lignes pointillées verticales.

L'algorithme de Fleming-Viot a été introduit indépendamment par Burdzy, Holyst, March [53] et Del Moral, Guionnet Miclo [106, 113]. Celui-ci est basé sur un système de particules évoluant indépendamment entre les instants d'absorption comme $(X_t)_{t \geq 0}$. A ces temps, au lieu d'être absorbées, ces dernières sont redistribuées uniformément sur les autres particules. La figure 2.4 représente une trajectoire.

Dans la section 5.1, nous détaillons divers résultats pour ce type de modèle sous des hypothèses très générales. La difficulté de ce type d'algorithme est qu'il repose sur deux paramètres (le temps et le nombre de particules) que nous souhaitons prendre les plus grands possibles. Cependant, rien ne garantit que les deux limites, en temps et en particules, commutent. Pour le garantir, il faut démontrer des bornes fines de convergences. Certaines bornes quantitatives sont décrites dans la section 5.1, dans des cadres généraux, dans le but d'assurer cette commutation de limites et donc la justesse de l'approximation. Nous évoquerons aussi l'exemple particulier du modèle à deux points qui illustre très bien quelques difficultés. Nous évoquerons aussi rapidement le lien avec les chaînes de Markov cachées ainsi qu'un travail en cours autour du filtre de Kalman pour des données comprenant un grand nombre de données aberrantes.

Un algorithme alternatif pour simuler les distributions quasi-stationnaires est de simuler une seule trajectoire, au lieu d'un système de particules, et de redistribuer le processus sur son passé aux instants d'absorption. Ce modèle perd la propriété de Markov. Il a été introduit par Aldous, Flannery et Palacios [2].

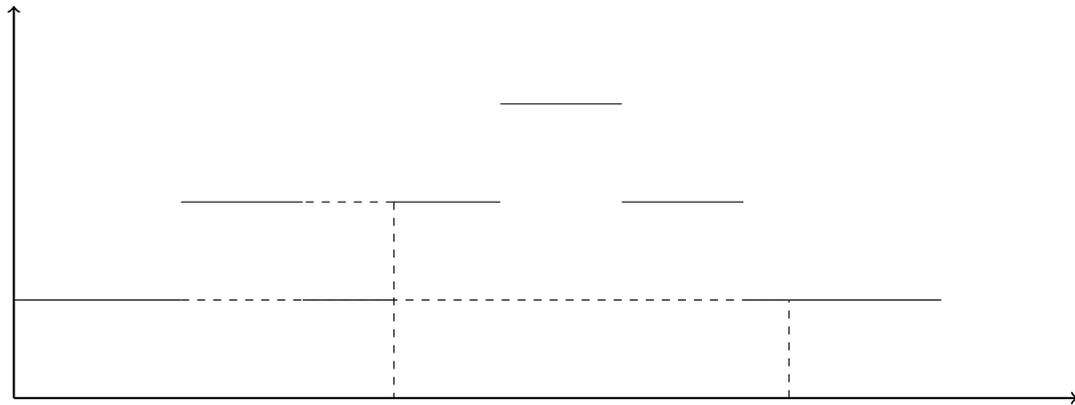


Figure 2.4: Exemple d'une trajectoire d'un processus d'Aldous-Flannery-Palacios (en trait plein). Les redistributions aux instants d'absorption sont représentées par des lignes pointillées. Les lignes pointillées verticales montrent le saut instantané de la particule absorbée et les lignes horizontales représentent les nouveaux points de départ de ce processus et les points du passé associés qui ont été tiré uniformément au hasard.

Voir la figure pour un exemple de trajectoire.

On peut montrer que la mesure empirique d'un tel processus suit ce que l'on appelle un algorithme d'approximation stochastique. En particulier, on peut le considérer comme le schéma d'Euler à pas décroissant d'une certaine équation différentielle ordinaire. On peut donc utiliser la méthode de l'EDO qui consiste à déduire de ce modèle déterministe le comportement du modèle aléatoire. Dans la section 5.2, je décris comment cette méthode donne des résultats pour cet algorithme lorsque l'espace d'état de $(X_t)_{t \geq 0}$ est un compact quelconque. La méthode de l'EDO est donc appliquée en dimension infinie. L'équation différentielle ordinaire sous-jacente est donc une équation à valeurs mesures.

En dimension finie, nous obtenons divers taux de convergence explicites. En particulier, des vitesses de convergence presque-sûr et un théorème central limite.

Nous l'appliquons à deux exemples : l'exemple à deux points et le schéma d'Euler associé à un processus de diffusion absorbé au bord d'un compact. Le premier est intéressant d'un point de vue théorique, et le second pour les applications.

2.2.2 Chapitre 6 : autres algorithmes stochastiques

La dernière section de ce manuscrit reprend les travaux [P3, P6, A7, A9]. Les travaux [A7, A9], en collaboration avec Michel Benaïm et Florian Bouguet, ont une visée plus théorique et portent sur des méthodes d'approximation stochastique en dimension infinie. Les travaux [P3, P6], en collaboration avec Reza Akbarinia, Meili Baragatti, Céline Casenave, Francesco Piccioni et Brigitte Vinçon-Leite, sont des applications d'algorithmes mathématiques.

Comme évoqué précédemment, la section 5.2 décrit le comportement asymptotique d'une chaîne de Markov in-homogène à partir du comportement d'une équation différentielle ordinaire à valeurs mesures.

Dans la section 6.1, nous décrivons un cadre général similaire où cela est possible et l'EDO correspond à la loi d'un processus de Markov.

Prenons un exemple inspiré de [228] pour montrer le cadre dans lequel s'applique les résultats de la section 6.1.

Soit $(U_k)_{k \geq 1}$ une suite de variables aléatoires indépendantes et uniformément distribuées sur $[0, 1]$. La suite associée aux maximums empiriques va trivialement converger vers 1. Pour établir une vitesse de convergence, posons, pour $n \geq 0$, $Y_n = (1 - \max_{1 \leq k \leq n} U_k)n$. Conditionnellement à Y_n , on a facilement

$$\begin{cases} Y_{n+1} = \frac{n+1}{n}Y_n \text{ avec probabilité } 1 - Y_n/n \\ Y_{n+1} \sim \mathcal{U}\left[0, \frac{Y_n}{n}\right] \text{ avec probabilité } Y_n/n \end{cases}$$

La suite $(Y_n)_{n \geq 1}$ est donc une chaîne de Markov non homogène en temps. Via un développement limité et une limite, la formule précédente donne

$$n\mathbb{E}[f(Y_{n+1}) - f(Y_n) \mid Y_n = y] \rightarrow yf'(y) + y \left(\frac{1}{y} \int_0^y f(z)dz - f(y) \right),$$

pour tout $y \geq 0$ et fonction f suffisamment régulière. A droite de l'équation précédente, on observe le générateur d'un processus de Markov dont la dynamique est de croître exponentiellement et d'avoir des sauts uniformes entre sa position et 0 à des temps aléatoires aussi rares que le processus est proche de 0. On peut montrer que ce processus converge vers un état stationnaire π . Avec les arguments de [A9], et quelques résultats techniques supplémentaires, cela montre que la suite (Y_n) tend vers π . On a alors le bon ordre de convergence ainsi que la loi limite (et donc par exemple la possibilité de faire des intervalles de confiance).

Dans la section 6.1, nous détaillons divers exemples sur lesquels cette approche se généralise. Ceci inclut des algorithmes de bandits et des schémas d'Euler à pas décroissant.

Nous étudions aussi en détail le cas particulier de chaînes de Markov inhomogènes en temps discret dont les noyaux de transition $(Q_n)_{n \geq 0}$ vérifient

$$\lim_{n \rightarrow \infty} p_n^{-1} Q_n = Q,$$

pour une certaine suite de réels (p_n) et un noyau fixé Q . Le comportement en temps long de cette chaîne est relativement simple et converge vers une valeur fixe presque sûrement ou en loi vers la mesure invariante de Q selon la sommabilité ou non de (p_n) . Nous avons cependant étudié la convergence de sa moyenne empirique en temps long. Si la suite (p_n) tend lentement vers 0 alors on retrouve les résultats classiques du cas homogène. C'est-à-dire que l'on a une convergence presque-sûr de la moyenne empirique vers la loi invariante associée à Q et, après une bonne renormalisation, la convergence de l'erreur vers la loi normale. Cependant, lorsque $p_n \sim a/n$ alors la moyenne empirique, sans renormalisation, converge vers une variable aléatoire dont on peut caractériser la loi comme la mesure invariante d'un certain processus de Markov déterministe par morceaux.

La section 6.2 évoque les autres algorithmes (non nécessairement stochastiques) sur lesquelles j'ai travaillé.

Part I

Stochastic models in population dynamics

Chapter 3

Branching processes

3.1 Introduction : the finite dimensional case

To motivate our goals, we first present some well-known results on discrete-time branching processes on finite state space, also known as multitype Galton-Watson processes.

Those processes model the dynamics of a population where each individual is of a given type belonging to the finite space $E = \{1, \dots, d\}$. At each generation, all individuals produce independently offspring whose type are distributed according to some fixed random variable $\zeta = (\zeta_{i,j})_{i,j \in E}$. At each time $t \in \mathbb{N}$, we can represent the population through a vector X_t such that $X_t(i)$ represents the number of individuals of type i . The dynamics is as follows: for all $j \in E$

$$X_{t+1}(j) = \sum_{i=1}^d X_t(i) \sum_{k=1} \zeta_{i,j,k,t}, \quad (3.1)$$

where the random variables $\zeta_{i,j,k,t}$ are independent and distributed as $\zeta_{i,j}$, which correspond to the number of offspring of type j of the k th individual of type i at time t . Taking expectations in (3.1) gives the linear relation

$$\mathbb{E}[X_{t+1}] = \mathbb{E}[X_t]M = \mathbb{E}[X_0]M^{t+1},$$

where M is the matrix whose entries are $M_{i,j} = \mathbb{E}[\zeta_{i,j}]$. The long-time behavior of (X_t) is then related to the convergence of M^t . Under an irreducibility assumption, Perron-Frobenius theorem [10, Theorem 1 page 185] entails that

$$M_{i,j}^t = \lambda^t u_i v_j + O(\rho^t), \quad (3.2)$$

where u, v are respectively the right and left eigenvectors of M and λ the associated eigenvalue. The constant ρ is related to the so-called spectral gap $\lambda - \rho$. This entails the convergence of the mean normalized by λ^t .

It is well known (see [10, Theorem 2, page 9] and [10, Theorem 1, page 192] for instance) that using a martingale argument, one can in addition prove the following convergence

$$\lim_{t \rightarrow \infty} \frac{X_t(j)}{\sum_{k=1}^d X_t(k)} = \frac{v_j}{\sum_{k=1}^d v_k}, \quad (3.3)$$

which holds almost-surely on the non-extinction event (which is non-empty if and only if $\lambda > 1$). This Law of Large Number (LLN) type result states that the empirical discrete measure converges towards the same limit of its mean (as in the Glivenko-Cantelli or Varadarajan theorems). More precisely, we can set

$$\mu_t = \sum_{j=1}^d X_t(j) \delta_j, \quad \nu_t = \frac{\mu_t}{\mu_t(E)},$$

for all $t \in \mathbb{N}$, where δ_i is the Dirac mass, and (3.3) became the almost-sure convergence of the sequence of discrete measures (ν_t) to γ defined by

$$\gamma = \sum_{j=1}^d \frac{v_j}{\sum_{k=1}^d v_k} \delta_j,$$

A main part of my research was to generalize this picture to continuous-time and infinite dimensional branching processes. That is in the case where time t belongs to \mathbb{R}_+ and trait i belongs to \mathbb{R}^d .

Before introducing an equivalent of the (3.2) for this more general setting, let us outline two simple concrete applications of multi-type Galton-Watson processes. There are given in Section 3.2. Then, we present general results to study infinite dimensional branching processes in Section 3.3. We then describe particular cases that are age-structured model in Section 3.4, size-structured model in Section 3.5 and mutation-selection model in Section 3.6. We end this chapter by a perspective section.

3.2 Two applications

Let us briefly present here two applications in ecology of the finite cases. Both examples are from research internships that I have supervised, which have given results not yet published. The first concerns the question of the viability of brown bears in the Pyrenees and the second, the question of the homogeneity of a Brazilian palm population.

3.2.1 Viability of Pyreneans brown bears

The Pyrenean brown bear (*Ursus arctos*) population is considered as one of the most seriously threatened with extinction in Western Europe. In the 90's and early 2000s, the reinforcement of the population by the introduction of a few individuals from Slovenia allowed to avoid population extinction. Yet, the population remains fragile, and the introduction of new individuals gives rise to tumultuous debates in France.

During the stage of Marion Kerioui in 2018, supervised by Benedicte Fontez, Tanguy Daufresne and myself, we modelled this population with a Galton-Watson process in a Bayesian framework; see [P7]. We used the data from [58]. It corresponds to the exhaustive supervision of all the population between 2005 and 2016 of the French Pyrenean brown bears. This population is split into two different isolated subpopulations. In the western part of the Pyrenees, before 2018, there were only two males (of which only one is indigenous), therefore we will focus on the subpopulation living in the central part of the Pyrenees. We considered the same structure model as [78]. Namely, we only consider the evolution of the number of females and we consider a population structured by age, with $d = 5$ classes. For classes $i \in \{1, \dots, 4\}$, this corresponds to bears whose age is $i - 1$ years. For $i = 5$ this corresponds to the bears whose age is greater than or equal to 4 years. The life of a bear is modelled as follows: during its first 4 age stages, it can either die or pass to the next age. When it is in the last fully developed stage, it can die, survive and reproduce. See [78] for biological motivations.

For the calibration, we consider a Bayesian framework : we assume that all entries of matrix M (as surviving probabilities for instance) are random and distributed according a prior distribution. We consider both uninformative priors or uni-modal laws centered on previous estimates in other contexts. As Galton-Watson transitions are essentially a multinomial law, we can compute explicitly the posterior distribution (that is the law of parameter conditioned on the observed data) after one generation. For instance, the surviving probability are Beta distributed. Markov property and Bayes Theorem enable to generalize this for all generations. As application, we can thus have access to various information (extinction probability, abundance) without greedy algorithm of the MCMC type.

This is for instance illustrated in Figure 3.1 and Figure 3.2.

3.2.2 The paradoxical growth of the babassu palm tree

During the stage of Cyril Robert, we work on babassu palm tree. This one is an endemic specie of the Amazonian forests, and is one of the economic resources

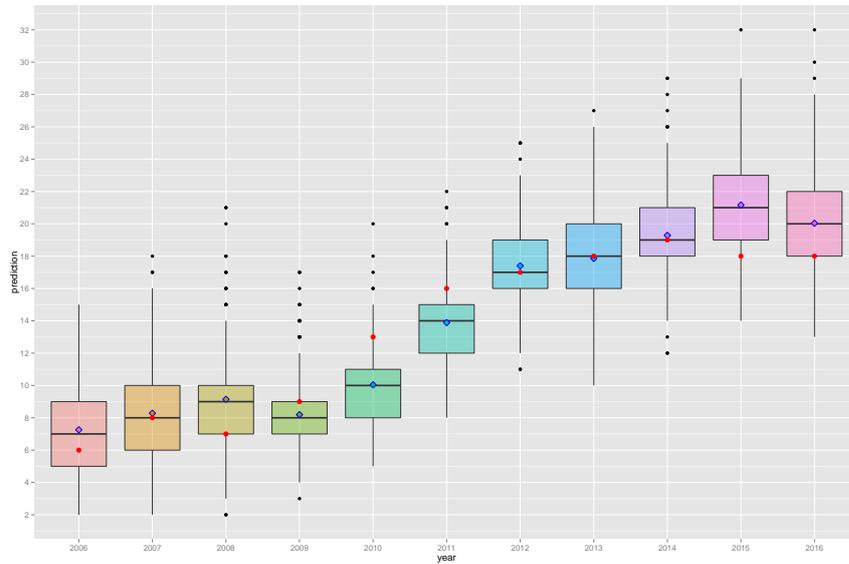


Figure 3.1: Red circles represent the total number of female bears at each year. Boxplots and diamonds both represent prediction of the number of females at each year considering data available on the previous years and a non-informative prior. The boxplot represents the law of the prediction and diamond represents the mean estimator.

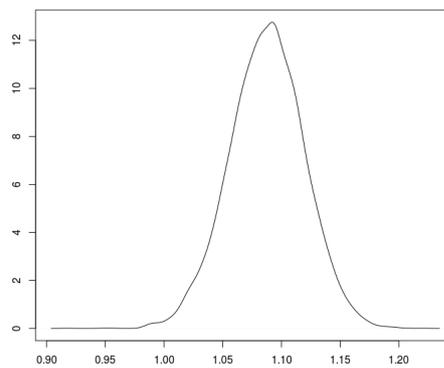


Figure 3.2: Posterior distribution of λ with a non-informative prior. Note that we have $\mathbb{P}(\lambda \leq 1) = 0.0044$

of Brazil. Its related activity involves people among the most disadvantaged and their management is a context of conflict between these people and the owners of pastures. Understanding babassu life cycle is therefore of primary importance.

During its PhD thesis [251, 250], Nikolay Sirakov calibrated an age-structured Galton-Watson processes (even if it is not exactly written on this form). The types did not consist exactly of biological ages but of certain easily identifiable stages of development. He discovered a bottleneck between two particular stages that leads to the following paradox: some plot owners consider the species invasive while the model describes a passage to adulthood in 157 years (See Figure 3.3).

To understand this paradox, Cyril Robert's internship consisted in testing if a mixing model was more likely and thus explain the presence of two distinctly evolving groups. We have worked in a frequentist framework. Without mixing, the maximum likelihood leads to the study of the stage passage ratios. In contrast, adding a mixture assumption leads to non-explicit and non-asymptotic Gaussian estimators. Cyril has therefore set up a computational strategy to perform a likelihood ratio test. He find a negligible p -value, which can be understood as the probability of a result that is at least as "extreme" as the observed result. That means that it is more reasonable to think that there two different populations of palm tree in the data which have different stage passage rates over stage passages 2 – 3 and 3 – 4. Nevertheless, with this data, we do not know if these populations differ genetically, due to their location, due to agricultural practices...

3.3 Branching processes and non-conservative semi-groups

The results that follow are based on publications [A1, A3, A8] in collaboration with Vincent Bansaye, Pierre Gabriel and Aline Marguet.

Let us consider a population whose individuals have a trait belonging to some (now non-necessarily finite) Polish space \mathbb{X} . Individuals can die or give birth to some offsprings with a rate which depends on their trait and independently one from each other. Conditionally on the moments of birth, the subtrees of descendants of individuals are independent; this is the branching property. Moreover, traits may vary in an time in-homogeneous way but without memory (Markov property). See for instance [135, 204].

For a time $t \geq 0$, we write V_t for the set of individuals at time t and $X_i^t \in \mathbb{X}$ for the trait of individual $i \in V_t$. As in Section 3.1, we study the empirical measure

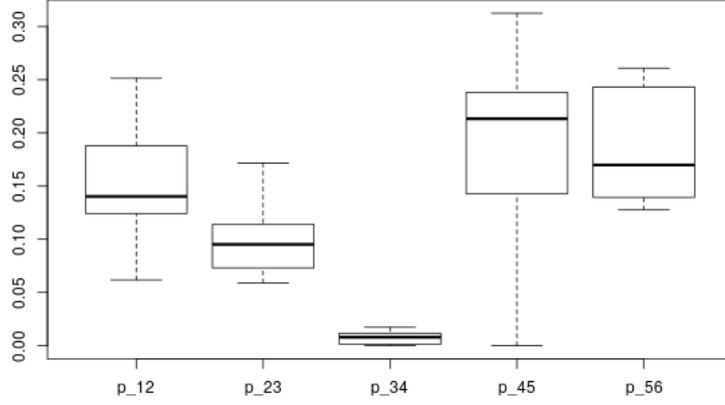


Figure 3.3: Passage frequencies for the six developmental stages in different years of study for the babassu palm tree. The boxes correspond to the variances of the probabilities of the different years (six points per box).

defined by $\mu_t = \sum_{i \in V_t} \delta_{X_t^i}$. For all $t \geq s \geq 0$, we associate to this measure the operator $M_{s,t}$ defined by

$$M_{s,t}f(x) = M_{s,t}(f)(x) = \mathbb{E}[\mu_t(f) \mid \mu_s = \delta_x] = \mathbb{E} \left[\sum_{i \in V_t} f(X_t^i) \mid V_s = \{1\}, X_s^1 = x \right].$$

This operator is called the first moment semi-group in [173] and at least acts on non-negative functions f . However, we will study examples where we are able to prove that $\sup_{s \leq t \leq T} M_{s,t}(V) < +\infty$ for some positive function V and then consider that $(M_{s,t})_{t \geq s \geq 0}$ is a family of linear operators on the space $\mathcal{B}(V)$ of measurable functions such that f/V is bounded.

The branching and Markov properties ensure that the sequence of operators $(M_{s,t})_{t \geq 0}$ is a positive semigroup or a semi-flow. Namely, for $t \geq s \geq u$, we have

$$M_{u,t} = M_{u,s}M_{s,t} = M_{u,s} \circ M_{s,t} \quad (3.4)$$

and if $f \geq 0$ then $M_{s,t}f \geq 0$. Under $\sup_{s \leq t \leq T} M_{s,t}(V) < +\infty$, it is a bounded operator on the Banach space $\mathcal{B}(V)$ embedded with the norm $\|f\|_V = \|f/V\|_\infty$.

Through these properties, we can also define a *left* action of $M_{s,t}$ on the space of positive measures (or on measures integrating V when moreover

$\sup_{s \leq t \leq T} M_{s,t}(V) < +\infty$). Indeed, setting $\mu(f) = \int f d\mu$ for a positive measure μ , we can define $\mu M_{s,t}f$, for any positive function f , by

$$\mu M_{s,t}f = (\mu M_{s,t})f = \mu(M_{s,t}f) = \int M_{s,t}f(x)\mu(dx).$$

When $\mu = \sum_{k=1}^K \delta_{x^k}$ then $\mu M_{s,t}$ describes the behavior of the population at time t when the population at time s consists of K individuals with traits x^1, \dots, x^K .

When the dynamics at a certain time t only depends on the current state at this time and not on this time, we say that the dynamics is (time) homogeneous. Mathematically, that means that $s \mapsto M_{t,t+s}$ does not depend on $t \geq 0$. In this case we set $M_s = M_{t,t+s}$.

From Relation (3.4), and analogously to the discrete case of Section 3.1 (where the mean is described through the iterated power of a matrix M), we can think¹ that $M_{s,t}$ is of the form $e^{\int_s^t \mathcal{A}_u du}$ for some family of linear operators (\mathcal{A}_u) . For this reason, we define

$$\mathcal{A}_t f = \lim_{h \rightarrow 0} \frac{M_{t,t+h}f - f}{h},$$

for every $t \geq 0$ and some function f . The previous limit can be taken point-wisely or in norm. The generator can also be defined through a martingale problem as in [103, 216, 142]. The choice of the definition involves different properties that we will not detail here. At least at the formal point, the last limit implies that

$$\partial_t M_{s,t} = M_{s,t} \mathcal{A}_t = M_{s,t} \circ \mathcal{A}_t, \quad \partial_s M_{s,t} = -\mathcal{A}_s M_{s,t} = -\mathcal{A}_s \circ M_{s,t}.$$

In particular, when $\mathbb{X} \subset \mathbb{R}^d$ and the measure $\mu M_{s,t}$ has a density $u(s, t)$ with respect to the Lebesgue measure, then it is solution to the following P.D.E. :

$$\partial_t u(s, t) = \mathcal{A}_t^* u(s, t),$$

where \mathcal{A}_t^* is the adjoint operator of \mathcal{A}_t with respect to the Lebesgue measure. This equation has, in our application, the form (2.1). It is for this reason that most of the next results can completely go out of the framework of probabilities, both on the scope of results and for the demonstrations.

In general, the semigroup $(M_{s,t})$ is not conservative, since its mass (the mean number of individuals)

$$m_{s,t}(x) = \delta_x M_{s,t} \mathbf{1} = M_{s,t} \mathbf{1}(x) = \mathbb{E} [\#\{i \in V_t\} \mid \mu_s = \delta_x]$$

¹But it does not hold in general, even in discrete space. Operators (\mathcal{A}_t) have to commute.

can decrease due to the deaths of individual or increase by births. Here $\mathbf{1}$ designates the constant function equal to 1.

This particularity is a drawback because there is a rich base of tools to study conservative semigroups. One of them, is for instance, the Doeblin contraction argument in total variation distance. Let us describe it rapidly in the homogeneous and conservative setting. We say that a semigroup (P_t) satisfies the Doeblin minorization condition if there exists $t_0, \epsilon > 0$ and a probability measure such that for all $x \in X$

$$\delta_x P_{t_0} \geq \epsilon \nu. \quad (3.5)$$

This induces,

$$\forall t \geq 0, \quad \|\mu P_t - \eta P_t\|_{TV} \leq \frac{1}{1-\epsilon} e^{-\frac{t}{t_0} \ln(1-\epsilon)} \|\mu - \eta\|_{TV}, \quad (3.6)$$

for any probability distributions μ, η and time $t > 0$. Then, by contraction, there exists a unique stationary measure π and $\lim_{t \rightarrow \infty} \mu P_t = \pi$ exponentially fast.

When the state is not compact Assumption (3.5) generally does not apply on all the whole space. In general this assumption is only supposed to hold on compact set and an additionally assumption is added to prove that the process remains in a compact set for sufficiently long times. This tightness condition is often verified through the existence of a so-called Lyapunov function. This one reads as follow: there exists a positive function V , such that for a certain $t > 0$

$$P_t V \leq CV + D,$$

for some $C, D > 0$. This is often verified by the drift condition:

$$\mathcal{L}V \leq -cV + d, \quad (3.7)$$

where \mathcal{L} is the generator of (P_t) and $c, d > 0$. With this assumption, Doeblin minorization only need to hold on the sublevel set of V to obtain exponential convergence to an invariant measure.

For conservative semigroups, these aspects are well known; see for instance [127, 215, 169, 216].

Recently, several works try to generalize these impressive techniques for non conservative semigroups. Let us cite for instance [223, 190, 191] in a general and continuous-time setting or works on discrete-time Feynman-Kac semigroups [109, 108]. Some works associate Doeblin-Harris techniques with Krein-Rutmann theorem and then often need strong Feller properties [201, 146, 166]. Early but related, Hilbert metric and Birkhoff contraction yield another powerful method for analysis of semigroups, which has been well developed [246, 226, 41]. Unfortunately, these results do not apply or are difficult to apply for

piecewise deterministic dynamics (see our different examples in sections that follow). For growth-fragmentation equations, Articles [34, 36] develop an *ad hoc* Feynman-Kac approach with Krein-Rutman theorem that seems difficult to generalize.

In the homogeneous case, when the existence of a positive eigenvector h is known, we can introduce the so-called h -transform semi-group $(P_t^h)_{t \geq 0}$ defined by

$$P_t^h f = \frac{M_t(fh)}{M_t h}. \quad (3.8)$$

It is a conservative semi-group on which we can apply the classical techniques. Unfortunately, bounds like Equation (3.7) then requires explicit knowledge or sharp bounds on h . See for instance [T1].

In [A1, A3, A8], we developed some theoretical results to generalize Doebelin-Harris methods for some motivated applications in inhomogeneous setting or without knowing the existence of eigenelements. These results are related to [69, 75, 85, 86, 117].

Let us detail our main results in the time homogeneous setting to not dot add technicalities. We will come back later on to the inhomogeneous aspects for the applications.

Theorem 3.3.1 (Theorem 3.5 of [A8]). *Let us assume that*

- *there exist constants $c > 0$, $r > 0$ and a probability measure ν such that for any $x \in X$,*

$$\delta_x M_r \geq c M_r \mathbf{1}(x) \nu. \quad (\text{H1})$$

- *there exists a constant $d > 0$ such that for any $t \geq 0$,*

$$\nu M_t \mathbf{1} \geq d \|M_t \mathbf{1}\|_\infty, \quad (\text{H2})$$

- *The function*

$$t \mapsto \|m_t\|_\infty \quad (\text{H3})$$

is locally bounded on \mathbb{R}_+ .

Then, there exists a unique triplet $(\gamma, h, \lambda) \in \mathcal{P}(X) \times \mathcal{B}(\mathbf{1}) \times \mathbb{R}$ such that $h \geq 0$ and $\int h d\gamma = 1$ and for all $t \geq 0$,

$$\gamma M_t = e^{\lambda t} \gamma \quad \text{and} \quad M_t h = e^{\lambda t} h. \quad (3.9)$$

Additionally $h > 0$ and there exists $C > 0$ such that for all $t \geq 0$ and $\mu \in \mathcal{M}(X)$,

$$\left\| e^{-\lambda t} \mu M_t - \mu(h) \gamma \right\|_{\text{TV}} \leq C \|\mu\|_{\text{TV}} (1 - cd)^{t/r}. \quad (3.10)$$

By differentiating (3.9), the triplet (γ, h, λ) is a triplet of eigenelements for the infinitesimal generator of $(M_t)_{t \geq 0}$, that is $\gamma \mathcal{A} = \lambda \gamma$ and $\mathcal{A}h = \lambda h$ where the (unbounded) operator \mathcal{A} is defined by $\mathcal{A} = \lim_{t \rightarrow 0} \frac{1}{t}(M_t - I)$.

Assumptions of Theorem 3.3.1 holds when (M_t) admits a (upper and lower) bounded density with respect to a fixed measure ν . It is known since the 60's, by Birkhoff [41] for instance, that this type of regularity hypothesis implies the existence of eigen-elements and the convergence. This condition is for instance used in [173, Theorem 10.1] to study infinite dimensional branching processes.

Unfortunately, assuming bounded density does not include simple examples such as the age-structured model of Section 3.4. Briefly (see details in Section 3.4), this model is generated by \mathcal{A} given by

$$\mathcal{A}f(x) = f'(x) + B(2f(x) - f(0)),$$

for smooth function f and $x \geq 0$. Therefore $\delta_x M_t \geq e^{-Bt} \delta_{x+t}$. We then cannot find a reference measure for any starting distribution.

Assumption (H2) overcomes this problem and permits to treat such example. This type of condition seems to appear for the first time in [117]. Indeed, [117, Proposition 3.1] is the analogous of Theorem 3.3.1 and even of its associated time inhomogeneous version [A8, Theorem 2.3]. It only states a contraction inequality, similarly to (3.6), but this is the main step of the proof for such results. In [75], Champagnat and Villemonais highlight this condition and prove that they are in fact equivalent to the exponential convergence (3.10). They deduce the existence of eigenelements in the context of absorbed Markov processes (sub-conservative semigroups). Again results of [75] excludes the age-structured model ; we cannot find a constant $c > 0$ such that $(e^{-ct} M_t)_{t \geq 0}$ is sub-conservative and [117] does not prove the existence of eigenelements.

In [A8], we propose a time-inhomogeneous version of Theorem 3.3.1. In addition to a general theorem, we study two particular cases. In the first, one, we consider the case where the generator \mathcal{A}_t converges to some operator \mathcal{A} when $t \rightarrow \infty$, that we called asymptotically homogeneous. See for instance [16] for an application where this type of model arises naturally. We also study the case where $t \mapsto \mathcal{A}_t$ is periodic. In this case, we can show that, there exists a periodic family of functions (h_t) , a periodic family of measures (γ_t) and a number λ such that

$$\mu M_{s,t} = e^{\lambda(t-s)} \mu(h_{s,t}) \gamma_{s,t} + O\left(e^{(\lambda-\rho)(t-s)}\right),$$

for some $\rho > 0$ et all $t \geq s \geq 0$ and initial measure μ . This result is reminiscent of the Floquet Theory [147]. To our knowledge, even in the conservative setting, there is no general theorem stating this behavior. Nevertheless, it is known for

some P.D.E., see for instance [81, 83]. These last behavior will be detailed in Section 3.4.

As said before, requiring a Doeblin type minorization assumption on the whole space is often too strong when the state space is not compact, we then also extended Harris theorem for non-conservative semi-groups in [A1]. Our result reads:

Theorem 3.3.2 (Theorem 2.1 of [A1]). *(i) If there exist a couple of positive functions (V, ψ) , $\tau > 0$, $\beta > \alpha > 0$, $C > 0$, $(c, d) \in (0, 1]^2$, a subset K and ν a probability supported by K such that $\sup_K V/\psi < \infty$ and*

$$(A1) \quad M_\tau V \leq \alpha V + C \mathbf{1}_K \psi,$$

$$(A2) \quad M_\tau \psi \geq \beta \psi,$$

(A3) *for all positive and measurable function f ,*

$$\inf_{x \in K} \frac{M_\tau(f\psi)(x)}{M_\tau\psi(x)} \geq c \nu(f)$$

(A4) *for all positive integers n*

$$\nu \left(\frac{M_{n\tau}\psi}{\psi} \right) \geq d \sup_{x \in K} \frac{M_{n\tau}\psi(x)}{\psi(x)},$$

then, there exists a unique triplet (γ, h, λ) of eigenelements of M with $\gamma(h) = 1$, i.e. satisfying for all $t \geq 0$

$$\gamma M_t = e^{\lambda t} \gamma \quad \text{and} \quad M_t h = e^{\lambda t} h. \quad (3.11)$$

Moreover, there exist $C, \omega > 0$ such that for all $t \geq 0$ and measure μ ,

$$\sup_{|f/V| \leq 1} \left| e^{-\lambda t} \mu M_t f - \mu(h) \gamma(f) \right| \leq C \mu(V) e^{-\omega t}. \quad (3.12)$$

(ii) Assume that there exist a positive measurable function V , a triplet (γ, h, λ) and constants $C, \omega > 0$ such that (3.11) and (3.12) hold. Then, the couple (V, h) satisfies Assumptions (A1),(A2),(A3), and (A4).

The main difference between Theorem 3.3.1 and Theorem 3.3.2 (when $\psi = 1$) is the existence of Lyapunov functions. Note that when (M_t) is a conservative semigroup, we recover the classical Harris Theorem by taking $\psi = \mathbf{1}$. This

Lyapunov assumption seems to appear for the first time in [87, Theorem 4.2] and in the proof of [85, Theorem 4.1]. However, combining this assumption with the assumptions (H1) and (H2) to obtain uniqueness of eigenelements and exponential convergence comes from [69]. This significant result has been demonstrated in the framework of sub-conservative semigroups. We generalized their result for non-conservative semi-groups, and non-bounded functions ψ , and prove that these assumptions are in fact necessary. In a follow up paper [76], they proved that results of [69] can cover these two aspects. However, Assumption (A4) of Theorem 3.3.2 seems more simple to verify that the analogous of [76] and our proof leads some estimates on function h .

With this theorem in hand, we are able to handle different examples. Let us comment how to verify the assumptions. From [A1, Section 2.2], Lyapunov conditions hold under the following drift conditions: there exist $\alpha < \beta_- \leq \beta_+$ and $\zeta \geq 0$ such that

$$\mathcal{A}V \leq \alpha V + \zeta \psi, \quad \beta_- \psi \leq \mathcal{A}\psi \leq \beta_+ \psi.$$

We will see in the following sections that, for our examples, these conditions are easily demonstrated by a simple calculation from simple functions. However, they could, of course, be a difficulty. In [A3], we bypass the bound $\mathcal{A}\psi \leq \beta_+ \psi$.

Assumption (A3) is the usual Doeblin condition and is usually not difficult to prove under irreducibly type assumption. We will nevertheless see in Section 3.5 by citing [151, 31], that this assumption also hid an aperiodicity assumption and that aperiodicity can naturally emerge from piecewise deterministic dynamics.

Finally Assumption (A4) is maybe the more original and difficult assumption. In Section 3.6, we will give an example where this assumption is not satisfied and for which the dynamics is somewhat degenerated. The simple non-irreducible example on a two point space also may not satisfy this assumption; see Section 5.1.2 and Subsection 5.2.1 on stochastic algorithms. This assumption leads to a homogeneous growth of the population and thus to the uniqueness of the principal eigenvalue. To our knowledge, there is no an easy way for proving it. For instance, for diffusion processes, it is proved by using Harnack inequality in [69] or by showing that the laws have bounded densities in [70]. In [A3], we show a simple condition which is particularly suitable for one-dimensional type dynamics : starting from one particle of type x , we can have a descendant of type y at a finite random time depending of x, y , for any x, y in some compact space. More rigorously, this reads : there exists $t \geq 0$, and $c > 0$ such that for any $x, y \in K$, there exists a probability measure $\sigma_{x,y}$ on $[0, t]$ such that

$$\int_0^t \delta_x M_s \mathbf{1}_y \sigma_{x,y}(ds) > c. \quad (3.13)$$

In sections that follow, we detail some examples of model for which we apply these conditions and develop some others properties. These models are the age-structured model, the size-structured model and some evolutionary trait-structured models.

3.4 Age-structured models : the renewal equation and the contour process

In the present section, we present some results of [A8] and of the work [P8], with Benoit Henry, both on age-structured models. More precisely, in these models, the traits X_t^i of particles correspond to their ages. We then work on $\mathbb{X} = [0, \infty)$. Between branching events, the ages grow linearly with speed 1 : $X_{t+s}^i = X_t^i + s$. In [A8], we study the case of cell division : at a random time, individuals divided into two new individuals. That means that at branching event, an individual dies and is removed of the population and we add two new individuals in the population. This branching event arises at a rate B which may depends on the current time. Formally, if T^u is the division time of individual u having age a at time t , we have

$$\mathbb{P}(T^u > t + s \mid X_t^u = a) = \exp\left(-\int_0^s B(t+u, a+u)du\right).$$

For this model, the generator reads

$$\mathcal{A}_t f(x) = f'(x) + B(t, x)(2f(0) - f(x)),$$

and the associated P.D.E. is called the renewal equation and reads:

$$\begin{cases} \partial_t u_{s,t}(a) + \partial_a u_{s,t}(a) + B(t, a)u_{s,t}(a) = 0, & t > s, a > 0, \\ u_{s,t}(0) = 2 \int_0^\infty B(t, a)u_{s,t}(a) da, & t > s, \end{cases} \quad (3.14)$$

This model has been introduced by Sharpe and Lotka [249] in a more general context, namely with a birth rate not necessarily equal to twice the death rate. Since then, it has become a very popular model in population dynamics (see for instance [212, 232, 259, 8, 182, 274]).

See also [152] which defines solution measures for this P.D.E., shows the link with the semigroup and use Doeblin minorization argument in the conservative case.

When $B(t, a) = B(a)$, the eigenelements are explicit. The so-called Malthus parameter λ is characterized as the unique real number which satisfies the characteristic equation

$$1 = 2 \int_0^\infty b(a) e^{-\int_0^a (\lambda + B(a')) da'} da,$$

the asymptotic probability measure γ has an explicit density with respect to the Lebesgue measure

$$\gamma(da) = \kappa e^{-\int_0^a (\lambda + b(a')) da'} da$$

where κ is a normalization constant and the harmonic function h is explicitly given by

$$h(a) = 2h(0) \int_a^\infty b(a') e^{-\int_a^{a'} (\lambda + b(a'')) da''} da'.$$

Consequently several sharp results are known such that necessary and sufficient condition to have convergence, see for instance [168, 167, 232, 187, 159, 273, 253, 144]. Nevertheless, no such condition is already known for exponential convergence and with the help of Theorem 3.3.1, we proved a new sufficient condition for exponential convergence. Indeed, even if the state space is not compact, the dynamics is concentrated enough to not need Lyapunov functions.

Theorem 3.4.1 (Theorem 3.8 of [A8]). *Assume that there exist $a_0 > 0$, $p > 0$, $l \in (p/2, p]$, and $\underline{b} > 0$ for which*

$$\forall k \in \mathbb{N}, \forall a \in [a_0 + kp, a_0 + kp + l], \quad B(a) \geq \underline{b}.$$

Then there exists a unique triplet of eigenelements $(\gamma, h, \lambda) \in \mathcal{P}(\mathbb{R}_+) \times \mathcal{B}_b(\mathbb{R}_+) \times \mathbb{R}_+$ verifying $\gamma(h) = 1$ and

$$\forall t \geq 0, \quad \gamma M_t = e^{\lambda t} \gamma, \quad M_t h = e^{\lambda t} h.$$

Moreover there exist $C > 0$ and an explicit $\rho > 0$, such that for all $\mu \in \mathcal{M}(\mathbb{R}_+)$ and all $t \geq 0$,

$$\left\| e^{-\lambda t} \mu M_t - \mu(h) \gamma \right\|_{\text{TV}} \leq C \|\mu\|_{\text{TV}} e^{-\rho t}.$$

The condition $l > p/2$ is only a technical assumption which simplifies the computations and can be removed. The main novelty comes from proving a result of exponential convergence for a rate that can vanish infinitely often.

We also consider the periodic case: there exists $T > 0$ such that $B(t + T, \cdot) = B(t, \cdot)$ for any $t \geq 0$. This model is for instance used for circadian rhythms (see [81, 83] and the references therein).

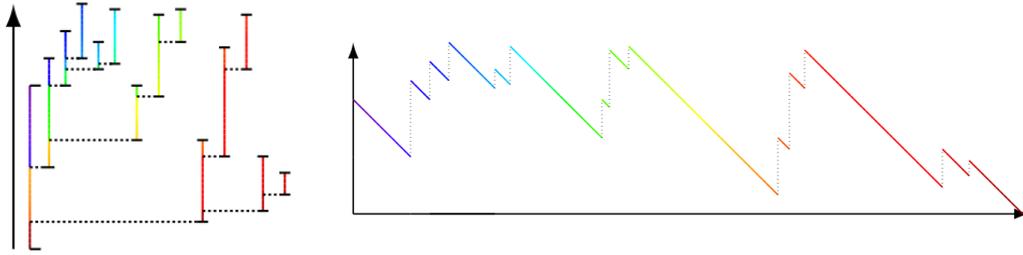


Figure 3.4: In the left, we have the chronological tree and in the right its associated Jump Chronological Contour Process. This one is constructed by going along the tree (following the color gradient) from left to right and by writing a decreasing, linear (with slope 1) function when we are going down (namely we follow the life of an individual) and writing a jump at birth (of size the new lifetime).

Theorem 3.4.2 (Theorem 3.17 of [A8]). *Assume that there exist $A \geq 0$ and $\underline{b} > 0$ such that*

$$\forall t \geq 0, \forall a \geq A, \quad B(t, a) \geq \underline{b}.$$

Then there exists a unique Floquet family $(\lambda_F, \gamma_{s,t}, h_{s,t})_{0 \leq s \leq t}$ for the semigroup $(M_{s,t})_{0 \leq s \leq t}$, some explicit constants $C, \rho > 0$ such that for all $t \geq s \geq 0$ and all $\mu \in \mathcal{M}(\mathbb{R}_+)$,

$$\|e^{-\lambda_F(t-s)} \mu M_{s,t} - \mu(h_{s,s}) \gamma_{s,t}\|_{\text{TV}} \leq C \|\mu\|_{\text{TV}} e^{-\rho(t-s)}.$$

When $B(t, a) = B(t)$ is a continuous T -periodic function, which is not identically zero, we even show that

$$\|e^{-\lambda_F(t-s)} \mu M_{s,t} - \mu(h_{s,s}) \gamma_{s,t}\|_{\text{TV}} \leq C \|\mu\|_{\text{TV}} e^{-2 \int_s^t b(\tau) d\tau},$$

with $\lambda_F = \frac{1}{T} \int_0^T b(\tau) d\tau$. We then recover the spectral gap $2b$ when b is constant.

In [P8], we study the probabilistic properties of the underlying branching process for a slightly different model. In this model birth and death does not arise in the same time. Each individual gives birth at a rate $B(t, a)$ and dies at a rate $D(t, a)$. When B and D are time homogeneous, it correspond to the (binary) Crump-Mode-Jagers model [155]. In [194], it was shown that when B is further constant (in ages) then the contour of the process (see Figure 3.4) is a Levy process. Consequently, several properties were derived such as a backward representation of the tree through a coalescent point process, the age structure,

the probability of extinction... Using contour process for coding random trees seems to date from [1] and is now widely used; see for instance [200] and references therein. However, the definitions of contour differ and Figure 3.4 represents a Jump Chronological Contour Process, which was firstly defined in [194]

In [P8], we follow this approach to understand the time-inhomogeneous dynamics. We also assume that $B(t, a) = B(t)$ does not depend on the age but varies in time and we show that the contour process is no longer a Lévy process but remains a Markov process. This is the piecewise deterministic Markov process generated by

$$Lf(t) = -f'(t) + B(t) \int_0^\infty (f(t+s) - f(t)) D(t, a) e^{-\int_0^a D(t, u) du} da$$

Consequently, we are also able to recover several properties. We give an equation satisfied by the probability of extinction and necessary and sufficient condition or tractable sufficient condition to almost-sure extinction. This is based on the generalization of the notion of scale function (defined for Lévy and diffusion processes) for process generated by L .

Using also the approach of [195], we also obtain some new scaling limit results.

3.5 Growth-fragmentation models and the asymmetrical division of the E-coli bacteria

The results that follow are based on the publications [A1, A2, A4] and a work in progress in collaboration with Benoîte de Saporta, Nathalie Krell and Tristan Roget.

Since my thesis [T1], I have been working on size-structured population models, especially on growth-fragmentation processes. In the latter, I used the results of [233] (giving the existence of the principal eigenelements) to demonstrate a law of large number; that is the convergence in probability in time of the empirical distribution.

In such model, between branching events, the traits X_t^i evolve on $\mathbb{X} = [0, \infty)$ according to an ordinary differential equation of the type :

$$\forall t \geq 0, \quad \partial_t X_t^i = g(X_t^i),$$

for some non-negative growth rate function g . Typically $g : x \mapsto \mathbf{g}x$, for some $\mathbf{g} > 0$, or $g : x \mapsto 1$.

At branching event, an individual divides. It gives birth to a finite number of descendants which share its size. We denote by ρ the fragmentation measure

on $(0, 1)$: an individual of size x produces smaller individuals of size zx , with z distributed by ρ . We assume mass conservation :

$$\int z\rho(dz) = 1.$$

For instance, we have $\rho(dz) = 2\delta_{1/2}(dz)$ in the binary equal mitosis model. Finally, as in Section 3.4, we assume that division events arise at rate B .

For this model, the generator then reads

$$\mathcal{A}f(x) = g(x)f'(x) + B(x) \left(\int_0^1 f(zx)\rho(dz) - f(x) \right), \quad (3.15)$$

for smooth enough function f and $x \geq 0$. The dual, and well-studied, associated partial differential equation is given by

$$\partial_t u_t(x) + \partial_x (g(x)u_t(x)) + B(x)u_t(x) = \int_0^1 B(x/z)u_t(x/z)\rho(dz)/z.$$

This model was first investigated in [160, 121, 174] on compact space. This non-local PDE appears in the modeling of various physical or biological phenomena [15, 244, 212, 232]. From a probabilistic point of view, it was studied in [35, 208, A10, T1, 17] for instance. Probabilistic questions for this type of model is large : existence/non-explosion, long-time behavior of the empirical measure or largest particle, functional estimates, statistical estimation, numerical simulation... For this last question, I co-supervised, with Benoîte de Saporta, the master internship and the PhD of Maud Joubaud. She studied the construction of this process as a branching Piecewise Deterministic Markov Process in line with Davis' construction [103]. In the non-branching case, she studied the construction of an Euler scheme with jumps and studied its long time behavior. She was thus able to deduce sharp bounds of weak and strong errors for this approximation scheme. On this subject one can also consult the works [32, 203, 241]. On the branching process, she has, with B. de Saporta and me, generalized the approach of [164] (see also [245]) for the optimal stopping problem to branching processes. The aim was to calculate

$$\mathbf{V}(\mu) = \sup_{\text{stopping times } S} \mathbb{E} [g(\mu_S) \mid \mu_0 = \mu],$$

where (μ_t) is the empirical measure defined in Section 3.3, μ is a punctual measure and g is a reward function. This problem is solved classically through the associated dynamic programming operators. Thanks to the embedded chain,

the latter are easily calculated (numerically) by iterating some appropriate operators. These results are described in more details in [A4].

From now on, we will focus on the spectral properties of \mathcal{A} . When $g : x \mapsto \mathbf{g}x$, the situation is simple because the right eigenvector is explicit. It is given by $h : x \mapsto x$ and the associated eigenvalue is $\lambda = \mathbf{g}$. We can then use an h -transform, defined in (3.8), and obtain the existence of γ and exponential convergence through classical techniques, as in [216] for instance, applied on the h -transform semi-groups. This type of approach was done in [151, 31, 105, 13, 56]. When B is moreover constant, the associated Markov process is a Lévy process, using known results [33], we can then obtain sharp asymptotic results. See for instance the unpublished Chapter 6 of [T1]. Surprisingly, when $\rho(dz) = 2\delta_{1/2}$ and B is general then there is no convergence; see [151, 31]. This is because in this case the underlying process is aperiodic.

The constant case $\mathbf{g} = 1$ is more challenging because there is no closed formula for the right eigenvector. It captures the difficulties that general growth functions can present while keeping simpler expressions in the calculations because the underlying ODE solutions are explicit. Using the results of Section 3.3, and in particular Theorem 3.3.2 and Condition (3.13), we can show

Theorem 3.5.1. *Assume $\rho(dz) \geq c_0\delta_0$ or*

$$\rho(dz) \geq \frac{c_0}{\varepsilon} \mathbf{1}_{(z_0-\varepsilon, z_0)}(z) dz$$

for some $z_0 \in (0, 1)$, $\varepsilon \in (0, z_0]$ and $c_0 > 0$, and one of the following assumptions

1. *B is C^1 , non-null and increasing;*
2. *$B(x) = 0$ in a neighborhood of the origin and $\lim_{x \rightarrow \infty} xB(x) = +\infty$;*
3. *$\lim_{x \rightarrow 0} xB(x) = 0, \lim_{x \rightarrow \infty} xB(x) = +\infty$ and there exists $k > 0$ such that $\int_0^1 z^{-k} \rho(dz) < +\infty$;*

then the conclusion of Theorem 3.3.2 i) holds true for some V, ψ .

See [A1, Theorem 5.3] and [150, Theorem 3.1] for details. This result is part of a rich list of results on the existence of eigenelements and convergence. In contrast with the previous theorem, existence of eigenelements is traditionally proved through Krein-Rutman theorem (generalization of Perron-Frobenius Theorem for operators on non finite but compact space). The first such result was obtained in [233] where B was supposed to be restricted to small interval of values. This result for existence of eigenelement was extended in [131]. The convergence was proved in [61, 105, 22, 56, 67, 199, 218] on the conservative equation (after normalization or not).

More recently, [34, 38, 36, 37] applies Krein-Rutman Theorem for another operator leading to not use a truncation argument as in [131, 233].

Let us finally cite [267] which now establishes one of the more general result on existence of eigenelements and convergence. As Theorem 3.5.1 below, proofs are based on generalized Harris Theorem [A1, 69], but with a careful construction of the processes and the Lyapunov function. Note that however Theorem 3.5.1 leads to consider non-irreducible dynamics on $(0, +\infty)$, which may be a difficulty as illustrated in Section 3.6 (and especially that prevents from using criteria like (3.13) to show (A4) in Theorem 3.3.2).

For an applied point of view, populations are subject to a time heterogeneous dynamics due, for instance to circadian rhythm [82, 84]. For that purpose, it is interesting to investigate how time variation of the coefficients may modify the population size. See also [186] for an experiment where the temperature is voluntarily regulated at different periodic frequencies to evaluate the impact on the population. On these question, Adil el Abdouni began its PhD with Pierre Gabriel and me. In addition to the modeling application, he will investigate application of this type of convergence result in optimal control in infinite dimension inspired from [88].

Another interesting generalization from an application point of view is the consideration of the asymmetry in the division. Recent biological experiments [235, 272, 255] measured asymmetry in cell division for the species *Escherichia coli*. *E. coli* is a rod shaped bacterium growing exponentially ($g : x \mapsto \mathbf{g}x$) and divides roughly in the middle. Each daughter cell therefore creates a new pole at division and inherits the other pole from its mother. After two divisions, it is possible to distinguish sister cells: one has inherited the old pole of its mother while the other one has inherited the new pole of its mother. The former is called the old pole cell, and the latter the new pole cell. It is possible to track experimentally the status (old pole or new pole) of each cell together with their sizes along time and lineages. These experiments showed that there is a statistically significant difference between the elongation rates of the old pole and new pole cells, even if they are genetically identical; see also [118]. With Benoit de Saporta, I co-supervised the post-doctoral student Tristan Roget on this subject. The aim was to better understand these asymmetry from modeling. For that purpose, in [A2], we propose a size-structured model which takes into account it. In this model, at a certain time $t \geq 0$, each cell i have a trait $Y_t^i = (X_t^i, P_t^i) \in (0, +\infty) \times \{0, 1\}$ composed to its size $X_t^i \in (0, +\infty)$ and its pole $P_t^i \in \{0, 1\}$ (new or old but denoted by 0 or 1). The dynamics is generated by

$$\mathcal{A}f(x, p) = \mathbf{g}_p x \partial_x f(x) + B(x) (f(\theta_0 x, 0) + f(\theta_1 x, 1) - f(x, p)),$$

where $\mathbf{g}_0, \mathbf{g}_1 > 0$ are the growth rate and $1 > \theta_0 = 1 - \theta_1 > 0$ are the proportion of size inherited at birth. See [A2] for details. This is a simple modification of

(3.15). We show that if $\alpha_0 \neq \alpha_1$ and

$$\lim_{x \rightarrow 0} B(x) = 0, \quad \lim_{x \rightarrow +\infty} B(x) = +\infty,$$

then the conclusion of Theorem 3.3.2 i) holds. Note that, we do not consider that division kernel has a density part as in Theorem 3.5.1. Even if this assumption is not necessary for the symmetric growth-fragmentation with constant growth rate, it is necessary when it is linear [151, 31]. However, here the asymmetry prevents aperiodicity and then prevents periodic behavior. We then have a principal eigenvalue λ , which depends in particular in $\epsilon = \mathbf{g}_1 - \mathbf{g}_0$. We then set $\lambda = \lambda_\epsilon$. This parameter represents the rate of the exponential growth of the number of individuals. From an evolutionary point of view, this Malthusian rate λ_ϵ is called the *fitness* and determine if a mutant population can invade a resident one: a mutant with a larger fitness should invade the resident population. We proved that when $B(x) = x$ and $\theta_0 > \theta_1$ then

$$\partial_\epsilon \lambda|_{\epsilon=0} < 0;$$

That is population, whose the largest cells, at birth, grow faster than the smallest ones, have a larger fitness. In particular, the asymmetry is optimal in a Darwinian sense. The proof is based on several semi-explicit expression for the limiting measures γ in the symmetric case extending then some known results [275, 165, 171, 170]. It can surely be extended to $B(x) = x^p$, with $p \leq 1$.

Finally, all models that I introduce were structured by size, in the present section, and by ages, in the previous section. Understand the mechanism of cell division is an active subject of research [213, 272, 12]. From a statistical point of view, let us cite the works [176, 129, 130] which give some estimator of the division rate B . Size-structured models seem to be more accurate than age-structured models [239]. See [128] for a recent survey on the subject. However, biological experiments shows that modeling divisions by size increments rather than by age or size fits the data even better [269]. This is called the adder or incremental model. Some estimators was for instance proposed in [128]. In a work in progress, with B. de Saporta, N. Krell and T. Roget, we work on statistical estimation of an asymmetric model allowing to discriminate if the adder model is more efficient.

3.6 Evolutionary models

This subsection regroups my works [P2, A3] and the unpublished post-doc results of Àlvaro Mateos Gonzàlez.

Simple evolutionary models are often driven by two main forces: the selection and the mutation. The individuals in the population are characterized by some trait x , typically $x \in \mathbb{R}^d$, which can represent its size, growth, reproductive capacity, lifestyle...

The selection part models how a trait translates into competition between individuals for reproduction and death. The latter can, for instance, be simply represented by a function $W(x)$ describing the growth rate as a function of the trait; this is the *fitness* function. By definition, selection imposes interaction terms in the models. They cannot be directly represented by linear PDEs or branching processes. An example of PDE is given by the following model

$$\partial_t v_t(x) = \int (v_t(y) - v_t(x))K(x, y) + v_t(x) \left(W(x) - \int W(y)v_t(y)dy \right), \quad (3.16)$$

where v represents the density of individuals having trait x at time $t \geq 0$, modeling the mutation and W is the fitness function. The integral under the kernel K represents the mutations and we will come back on this aspect a little further. The right term represents the selection term. We can easily see in Equation (3.16) that if $W(x) > \int W(y)v_t(y)dy$ then trait x is more adapted and the associated population will increase and conversely.

This type of model can be derived from individual based models taking into account stochastic interaction [268, 71, 72]. However, this latter model can also be derived from the following linear equation:

$$\partial_t u_t(x) = \int (u_t(y) - u_t(x))K(x, y)dy + W(x)u_t(x), \quad (3.17)$$

by (at least formally) considering

$$v_t = \frac{u_t}{\int u_t(x)dx} \Leftrightarrow u_t(x) = v_t(x) e^{\int_0^t \int v_s(y)dyds}.$$

As seen in Section 3.3, Equations of the type (3.17) are linked to branching processes whose traits evolve as jump processes and where individuals reproduce at rate $\max(W, 0)$ and dies at rate $\max(-W, 0)$. In what follows, we will study selection-mutation with this type of non-linearity which is often called *replicator-mutator* or *Kimura* model [188].

Let us now comment the mutation part. During their life or at the time of the reproductions, a mutation can occur. This results in the creation or replacement of an individual of trait x by an individual of trait y . A classical framework is that this new trait y is a close variation of the previous one x , so it is drawn randomly according to the kernel $K(x, y) = J(x - y)dy$ for some density of measure J ; namely $y = x + \epsilon$ with $\epsilon \sim J$. See [96, 157, 158, 94] for instance. It is

also often assumed that mutation have a small and infinitesimal impact on the trait, this leads to consider a Laplacian, as in (3.16) instead of a kernel K , as in [4, 3, 219] for instance. On the contrary, Kingman proposes in [189] that we can neglect infinitesimal mutations and consider that only large mutations, which change totally the trait, have an impact on the dynamics. He then proposes to consider that the new traits y are choose uniformly at random by a fixed law Q which does not depend on x . This is the so-called *house-of-card* model (a single mutation can destroy the biochemical house of cards built up by evolution).

This house-of-cards model is then represented by the two following P.D.E. :

$$\partial_t u(t, x) + a(x)u(t, x) = \left(\int_X u(t, y) dy \right) Q(x) \quad (3.18)$$

and

$$\partial_t v(t, x) + a(x)v(t, x) = (Q(x) - v(t, x)) + \left(\int a(y)v(t, y) dy \right) v(t, x). \quad (3.19)$$

or equivalently the semigroup $(M_t)_{t \geq 0}$ generated by

$$Af(x) = Q(f) - a(x)f(x).$$

We used the notation $a = -W$ and then a may be understood as a death rate. When a is constant (even equal to 1) then A is the generator of a Markov process. It is even maybe the more trivial Markov process to study. It is direct to see that its law converges at rate 1 in many distances (total variation, Kullback-Leibler, L^2 ...) to Q . Even if we can generalize this result for certain non constant a (and obtaining again the optimal rate of convergence), this simple dynamics encompasses a rich class of different behavior.

Assume that a has only one minimum and, without loss of generality, we assume that $\inf a = a(0) = 0$. In [P2], we show the following exhaustive overview of the possible behaviors:

- If $\int Q/a > 1$ then (u_t) and (v_t) converges, up to scaling, exponentially fast in various senses (total variation distance, L^p , entropy/Kullback-Leibler distance), with an explicit optimal rate, to a unique invariant measure γ . This measure is explicit and admits a density with respect to Q . This case is a textbook case to learn log-Sobolev, Poincaré, Doeblin, the h -transform... See [64, 65, 5].
- If $\int Q/a = 1$ and $1/a \in L^2(Q)$ then (u_t) and (v_t) converges again to a probability measure admitting a density with respect to Q . The convergence is

not at exponential speed. With additional assumptions on the integration of $1/a$ and a , we can prove sub-exponential convergence bounds in various metrics. To that end, we use weakened, seemingly new, versions of Poincaré and log-Sobolev inequalities (see nevertheless [49, 242]) but also the more usual approaches in total variation [126, 261].

- If $\int Q/a = 1$ and $1/a \notin L^2(Q)$ then if u_0 is a measure then u_t tends to $u_0(\{0\})\delta_0$. In particular, if u_0 is/has a Lebesgue density or is equal to δ_x , with $x \neq 0$ then $u_t \rightarrow 0$. In contrast, (v_t) converges weakly to a measure admitting a density in any cases.
- If $\rho = \int Q/a < 1$ then if u_0 is a measure then it tends to $u_0(\{0\})(\delta_0 + (1 - \rho)^{-1}Q/a)$. In particular, if u_0 is/has a Lebesgue density or is equal to δ_x , with $x \neq 0$, then $u_t \rightarrow 0$. In contrast $\frac{1}{t} \int_0^t v_s ds$ converges weakly to $((1 - \rho)\delta_0 + Q/a)$.

In the last case, if u_0, v_0 are Lebesgue density then so are u_t, v_t . The apparition of the Dirac masses, that is the the concentration phenomenon, is abrupt in the sense that the convergence can not hold in total variation distance. These results are proved by *ad hoc* arguments. The fast convergence in total variation could surely have been shown by using Theorem 3.3.2 or Theorem 3.3.1. However, we need to prove criterion A4. The sufficient condition given in (3.13) does not apply here. This example, and counter-example in some cases, illustrates the significance of this assumption. Indeed A4 does not hold in case of concentration and slow convergence. When the initial concentration is too concentrated around 0 then the individuals are fitter and are then more represented in the population. That leads to not have a regular convergence to a regular measure.

Even if the form of γ was known in different contexts [95, 94, 55, 54] and convergence and exponential convergence expected, these convergence results was not complete. Result of [P2] addresses a full portrait of this equation. In particular, the difference of behavior when $\int Q/a = 1$ and $1/a \in L^2$ was unexpected in view of the literature.

To our knowledge, such type of concentration result were only established under explicit formula of the solutions; see [157, 4, 158, 3]. Note that we could have chosen to put the argmin of a at infinity rather than 0, and the concentration becomes a result of acceleration as in [4, 3].

Let us compare this result with the pioneer work of Kingman [189]. Instead of our four different regimes, he finds three that he names democracy, meritocracy and aristocracy. The democracy pattern represents the exponential convergence (without precision in which distance) to a smooth equilibrium, as in case $\int Q/a > 1$. In this case, the effect of the selection is simply to modify the form of the distribution. In the meritocracy pattern, he shows that the convergence

to a distribution having a Dirac mass similarly to our last case. In this case, the Dirac mass emerges from the growth of new class of highly fit individuals. The smooth part consists of the descendant of these mutants. Finally, if $0 \notin \text{Supp}(Q)$ but is in the support of the initial condition then a Dirac masses always remains in the law. Initial individuals are always fitter than mutant, consequently, the final population consist of these individuals plus their descendants. We do not treat this case but it is a relatively simple case to deal with. Finally, we see that the model we consider is richer because there are two other behaviors that emerge.

We study this particular choice of mutation kernel because it enables to use explicit limiting eigen-elements. However, due to the theoretical result [95, 94, 55, 54], supported by the simulation [43], we can think that this convergence portrait is similar when $K(x, y) = J(x - y)$. Let us now continue with this type of kernel. A slight variation of this model, which makes sense for applications [93, 96, 30] is described by a model of mutation-selection in a varying environment. Indeed, when we assume that the environment change at a constant speed, leading to a thinning of the trait. This corresponds to change $W(x)$ into $W(x - ct)$ in (3.16) or (3.17).

Up to a time change, this leads to the study of the PDE

$$\partial_t u(t, x) + c \partial_x u(t, x) + a(x)u(t, x) = \int_{\mathbb{R}} u(t, x + y)J(y)dy$$

Due to the transport term, it is easy to see that our irreducibility criterion (3.13) applies and then concentration is impossible. We can apply Theorem 3.3.2 or Theorem 3.3.1 and show exponential convergence under reasonable assumption. For instance, in [A3], we show that if J is continuous and positive in a neighborhood of 0 and $\lim_{|x| \rightarrow \infty} a(x) = +\infty$ then we have existence of eigen-elements and exponential convergence. This result was used in [175, 57, 229] to study, in reversed time, the associated branching process leading new properties on the ancestral lineage. Without convergence results, [93] established weaker conditions for existence and uniqueness of a family of main eigen-elements.

Finally, with Matthieu Alfaro and Guillaume Martin, we supervised the post-doctorate of Alvaro Mateos-Gonzales. We were motivated by considering $K(x, y) = B(x)J(x - y)$ in (3.16) to understand evolutionary rescue problems: when a bacterial population is affected by a biocide, what are the differences in evolutionary responses if the biocide acts on death rates (more deaths) or births (birth limitation). We considered that $W(x) = x$ and $B(x) = \max(x, 0)$ but we studied the following (mean-field type) approximated equation :

$$\partial_t v(t, x) = \int_{\mathbb{R}} xv(t, x)dx \int_{\mathbb{R}} (v(t, x + y) - v(t, x))J(y)dy + v(t, x) \left(x - \int yv(t, y)dy \right).$$

As in [157, 158], we were able to derive the solution of the associated cumulative generative function leading some estimates on the mean of the fitness $\int yv(t, y)dy$ over time. These results are unpublished.

3.7 Perspectives

There are several possibilities to go further than the results of the present chapter. In Section 3.2.1, we present a model that perfectly fit with the data. However, it is possible that on slightly longer time scales, genetic depression due to low numbers of males takes place. One approach may be to use bisexual models [181, 220, 102] but in a multi-type context with a latent variable to model a deleterious trait. The difficulty is to make the data talk more than the model. For example in the modeling of the Section 3.2.1, we do not model hunting, accidents... They are naturally calibrated from the data.

In Section 3.2.2, we prove that there is different populations of palm tree. A main question should be to identify them but it seems to me that more detailed data is needed.

From a theoretical point of view. Theorem 3.3.2 generalizes the condition CD3 of [216], which gives exponential convergence. It will be very useful to generalize all the drift conditions of [216] for non conservative semi-groups. For instance, having a very simple drift conditions (plus a *small set* one / Doeblin minorization on compact spaces) to have only existence of main eigenelements (when there is no exponential convergence as in Section 3.6) would have several applications. All the behaviors described for the house of cards model in the Section 3.6 should be easy to check on the generator, this is currently not the case. Such conditions may be weaker than usual Krein-Rutman Theorem.

In the same way, Assumption A4 is currently a difficult assumption to deal with and we have to understand how it may be simplified. Criterion (3.13) is not enough to treat the age-size structured model for instance. A key is maybe to adapt the approach of [263, 264].

Closely related, we have to understand how we can prove the concentration phenomenon. That is convergence to the main eigenelements, when there is no convergence in total variation distance. This problem seems to me to be particular to non-conservative semi-groups.

From the application point of view, understand the dependence of the eigenelements with respect to the parameters, as studied in Section 3.5 or in [227, 217], is of prime interest. See for instance [96] for evolutionary problems as in Section 3.6.

Finally, all the associated statistical procedure is an interesting prolongation of my contributions.

Chapter 4

Population models with interaction

4.1 Introduction : the linear and branching birth and death process

To introduce what follow, let's go first back to branching process and especially to the simplest one. Consider a mono-type Galton-Watson process in continuous time. In this model each individual gives birth and dies at exponential times. We also assume that individuals give birth to only one new individual at reproduction time. The process $(X_t)_{t \geq 0}$, representing the number of individuals, has generator given by

$$Lf(n) = bn(f(n+1) - f(n)) + dn(f(n-1) - f(n)).$$

Several general results exist for this process. Let us expose some of these when $d > b$. In such case, we have

$$T_{\text{Ext}} = \inf \{t \geq 0 \mid X_t = 0\} < \infty.$$

What is more, for every $x \in \mathbb{N}^*$,

$$\lim_{t \rightarrow \infty} e^{(d-b)t} \mathbb{P}_x (T_{\text{Ext}} > t) = \left(1 - \frac{b}{d}\right) x,$$

where \mathbb{P}_x designs classically the probability conditional on $\{X_0 = x\}$, and, for every $k \in \mathbb{N}^*$,

$$\lim_{t \rightarrow \infty} \mathbb{P}_x (X_t = k \mid T_{\text{Ext}} > t) = \left(\frac{b}{d}\right)^{k-1} \left(1 - \frac{b}{d}\right).$$

See [211] for details. In short, the process extincts almost-surely after a random time, which has an explicit exponential tail, and before extinction, the number of individuals follow a geometric distribution. This latter is called a *quasi-stationary* distribution because it remains stationary when conditioning on non-extinction. This limiting behavior is related to results exposed in Section 3.3 and in particular Theorem 3.3.2. Indeed, setting

$$M_t f(x) = \mathbb{E}_x [f(X_t) \mathbf{1}_{T_{\text{Ext}} \leq t}],$$

for $x \in \mathbb{N}^*$, bounded function f and time $t \geq 0$, the family of operators (M_t) is a positive non-conservative semigroup. With the notation of this section, we have

$$\lambda = b - d, \quad h : x \mapsto \left(1 - \frac{b}{d}\right) x, \quad \gamma = \sum_{k \geq 1} \left[\left(\frac{b}{d}\right)^{k-1} \left(1 - \frac{b}{d}\right) \delta_k \right].$$

Results of Section 3.3 is then also useful for the study of finite-dimensional process. See for instance [76, 75] for which this type of spectral properties is developed for the study of quasi-stationary behavior. See also [109, 117, 113] where these techniques are also used in a finite-dimensional setting related to Feynman-Kac formulas. This latter approach is discussed in Section 5.1.3.

The linear birth and death process is often too simple for application. In Chapter 3, we made the individual birth and death rates depend on a trait. However, assuming independence at birth is often an unrealistic assumption for applications.

A natural way to introduce interaction in this simple model is to consider indirect interaction : individual does not interact directly but all depend on the same resource. Let us motivate and describe this type of interaction on the deterministic approximation of the linear birth and death process : the solution x of the equation

$$\dot{x} = gx,$$

where x designs the proportion of individuals and $g \approx b - d$ its associated growth rate. We let g depends on a new variable y which designs the resources that need the individuals to live and reproduce. This resource is also consumed (with the same rate, to be simple) so we have a model of the type:

$$\begin{cases} \dot{x} &= g(y)x \\ \dot{y} &= -g(y)x \end{cases}$$

In such model, the population dynamics is trivial: the resources vanish and the population eventually stabilizes. To have a more interesting behavior, it is

necessary to continuously increase the input of resources. A simple way to do this is to use the framework of a bioreactor: we consider that the population is in an environment in which we add at a fixed rate D some resources y_{in} and extract uniformly what is in this environment (without this last condition, the behavior is also trivial, the population tends to infinity). This gives

$$\begin{cases} \dot{x} &= (g(y) - D)x \\ \dot{y} &= D(y_{in} - y) - g(y)x \end{cases}$$

This deterministic model is called the Chemostat model [172, 252] and is based on the modeling of the continuous culture of bacteria developed for instance by Monod [222]. Even if this process is mainly studied by ODE systems [172, 252], a lot of stochastic processes have been proposed or studied in finite [85, 60, 100] and infinite dimension [A12, 59, 73]. See for instance the survey paper [A15] on which I slightly contribute. In what follow, we answer some questions posed in this article. In particular, as resources dynamics and bacteria reproduction may be considered at a different scaling, keeping a birth-death type dynamic have an interest in practice; see [60, 100]. Namely, we have to study the processes (X_t, Y_t) on $\mathbb{N} \times \mathbb{R}_+$ generated by

$$\begin{aligned} Lf(x, y) &= g(y)x(f(x+1, y) - f(x, y)) + Dx(f(x-1, y) - f(x, y)) \\ &+ [D(y_{in} - y) - g(y)x]\partial_y f(x, y). \end{aligned} \quad (4.1)$$

Omitting the biological consideration, this stochastic process is mathematically challenging. Indeed, it is a piecewise deterministic Markov process [A11, 103] and consequently, this makes difficult the understanding of its long-time behavior. This one is developed in Section 4.2 below.

Another interesting point raised by this model is the form of the function g . This function is often called *reponse* function because it encodes how consumers respond as a function of the number of resources. The determination of g is fundamental in ecology and microbiology and is the subject of the Section 4.3.

Another way to consider interaction is to assume that these rates b and d are not constant and depends on the population. We can consider a direct competition and thus these rates depend on the total number of individuals. This leads to a process generated by L , given for a bounded function f and $n \in \mathbb{N}$ by

$$Lf(n) = b_n(f(n+1) - f(n)) + d_n(f(n-1) - f(n)),$$

where (b_n) and (d_n) are two positive sequence on \mathbb{N}^* and $d_0 = 0$. These rates are therefore no longer "individual" rates. These processes are called birth and death processes. When $b_0 = 0$, these processes have a positive probability of extinction (to be absorbed at 0). Extinction and quasi-stationary behavior have

been well studied for quite a while; see for instance [125, 211, 124, 262]. We contribute to these studies in [A1, Section 5.1] : we exhibit an explicit exponential convergence to the quasi-stationary distribution (and gives bounds of the associated eigenelements) in the case where these rates are constant for $n \geq 2$. We will not describe this result more than this in this manuscript. When $b_0 > 0$, these processes can no longer be absorbed at 0. Either they tend to infinity or converges to some stationary distribution. Condition to convergence and explicit formulas for stationary distributions are well known; see for instance [80, Section 9.3]. Due to their simplicity, these processes are well used in many others contexts than biology. Let us cite for instance the study of queuing system in computer science [240]. In Section 4.4, we will introduce some of these basic properties and the original results we developed in [A5]. The sharp bounds we have demonstrated allow, using Stein's method, to obtain fine quantitative bounds for limit theorems on discrete laws of the type of the law of rare events.

The present chapter is now structured as follow : in Section 4.2, we introduce our results on chemostat model, in Section 4.3 on functional responses, on Section 4.4 on birth-death processes and Stein's method. Then we rapidly evoke some results on collective displacement and end by a perspective section.

4.2 Chemostat : a consumer-resource population model

Let us come back to the model generated by (4.1) to expose the works [P1, 59] with Coralie Fritsch. In the chemostat modeling, the resource is often called substrate and then denoted by s and the growth rate is denoted by μ (for Monod). We then study the process (X_t, S_t) generated by

$$Lf(x, s) = \mu(s)x(f(x + 1, y) - f(x, y)) + Dx(f(x - 1, y) - f(x, y)) + [D(y_{in} - y) - \mu(s)x]\partial_y f(x, y). \quad (4.2)$$

This model was introduced by [100]. Even if it can be considered as a switching dynamical system as studied in [29, 27, A17], any general results apply directly due to some particularities including the possible absorption of the discrete chain (X_t) or the different equilibria of (S_t) when X_t remains constant.

Consequently, as many stochastic processes, the first approach can consist to the approximation by scaling limit. To our knowledge, it was first done in [60]. This paper introduces different models at different scales from the two-dimensional jump and discrete process to deterministic by passing by some hybrid process as (4.2) or two coupled diffusion processes. In the continuity of this work, in [59] they introduce an infinite dimensional model, where all

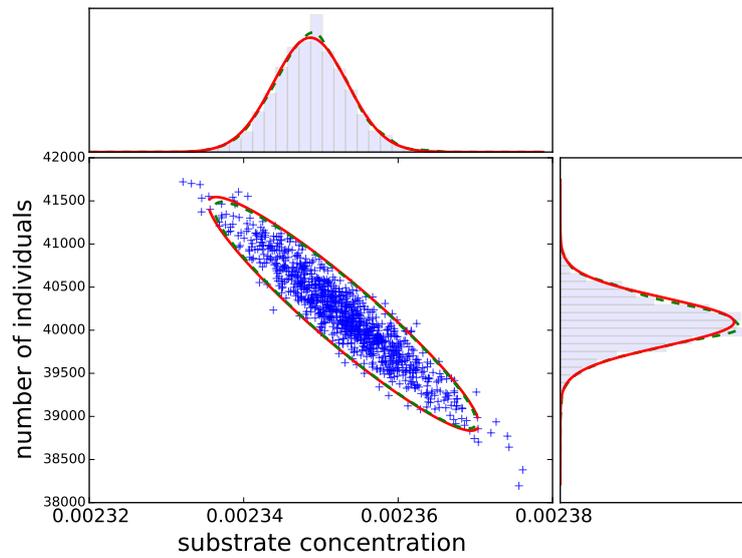


Figure 4.1: Quasi-stationary distribution of the Crump-Young process. In the middle, we have several simulations of the process after a long time (and being not absorbed). The x -axis represents the continuous component and the upper graph is an histogram and a smooth estimation of the associate marginal distribution. The y -axis and the righter graph represent the discrete component.

individuals are structured by their mass, as in Section 3.5, but with indirect interaction as in (4.2). They show the convergence of the empirical distribution to an integro-differential equation which was already introduced for itself in [236, 149].

All these results give a deterministic approximation of the stochastic processes generated by (4.2) or its associated infinite dimensional size-structured model. To better take into account and understand the random dynamics of this process, in [A12], we go one step further in the approximation by proving some central limit theorems. We show that both the finite and infinite dimensional chemostat model converge, after re-normalization, to a Gaussian process in large population. Although the proof for the finite-dimensional process is relatively classic [142], the convergence of the infinite dimensional process is more tricky. Indeed, after re-normalization, we do not study a positive measure but a signed one for which the state space is not metrizable. Consequently, we follow the now well used approach of [210, 260, 209]. We consider the fluctuation process as an element of some appropriate Sobolev space and use Hilbert techniques. The proof was then relatively classical, even technical, but some points were nevertheless tricky and original.

These results then gives a first hint of the long time behavior of this process. Indeed, in large population, the finite dimensional process converges to some degenerate two-dimensional Ornstein-Uhlenbeck process. Consequently, we can expect that its law quickly approaches the normal distribution and remains stationary. However, we can easily prove that the process extincts in finite time (in the sense that the first component is absorbed in 0). These two antagonists behavior are not incompatible. Indeed as for the linear birth and death process of Section 4.1, we can expect that (X_t, S_t) is absorbed after a large time and that before extinction, it converges to a quasi-stationary distribution (close to a normal distribution). Although this result can be expected, no classical result applies. Indeed, the study of birth and death process [124, 262] or diffusion processes [63] generally relies on a reversibility assumption leading to work on an appropriate Hilbert space. The hybrid form of the generator entails that general spectral results do not apply here. Also, the right-eigenvector h is not known as in [193] or in the example of Section 4.1. The only result we know on the quasi-stationary distributions of this or similar processes is [85]. In this work, it was proved, by a compactness argument (based on Lyapunov function similar to those introduced in Section 3.3), that there exist at least one quasi-stationary distribution. Moreover some properties of the form are the QSD are described. In [P1], we show that the process (X_t, S_t) admits a unique quasi-stationary distribution γ , which has exponential moment in its first component and integrate $s \mapsto 1/s$ in the second one. Moreover, for any $(x, s) \in \mathbb{N}^* \times \mathbb{R}_+$,

we have

$$\lim_{t \rightarrow \infty} \mathbb{P}_{(x,s)}((X_t, S_t) \in \cdot \mid X_t \neq 0) = \gamma.$$

We have a uniform exponential bound when the initial distribution is on some compact space. Note that this process is not irreducible, and that even if this does not generally pose a problem for the study of un-absorbed processes, it sometimes generates strange quasi-stationary behaviors; see [77, 24, A6] or Section 5.1.2. The proof is based on Theorem 3.3.2 and a careful study of the path and several Lyapunov functions.

4.3 Functional responses : how predators eats preys

Let us detail here the results of [P4] with Vincent Bansaye.

Functional response is the number of preys/resources successfully attacked/digested per predator/consumer as a function of prey/ressource density. It describes the way a predator responds to the changing density of its prey. This corresponds to the function μ in Section 4.2. Since the work of Holling [120, 178, 177], three main functional responses, called type I, II and III are commonly used. In the type I interaction, the consumption rate is linear $\mu : s \mapsto cs$, for some $c > 0$. This was the functional response assumed independently by Lotka and Volterra in their classic theoretical works on predator-prey interactions. The type II interaction has the form

$$\mu : s \mapsto \frac{as}{b + cs}, \quad (4.3)$$

for some $a, b, c > 0$. This is one of the most used functional response in ecology; see [183, Table 1]. It is also related to the famous Rosenzweig-MacArthur, Monod and Michaelis-Menten equations. The type III interaction has the form $s \mapsto \frac{as^2}{b+cs^2}$.

The form given to functional responses is largely debated for decades, and since the work of Holling, a large number of functional responses has been proposed in the literature depending on the interaction context (see for instance [7]). Form of Equation (4.3) was first derived from empirical study [177, 222] and currently few studies mathematically derive forms of functional responses from microscopic models. Indeed, let us cite [183, 180, 47] which derive such rate by reducing some macroscopic ODE systems, [97] by a game-theoretical approach or also [11] by using properties of random walks. Closer to what we have in mind, [185, 104] starts from a stochastic individual based model. They derive a finite dimensional Markov chain and prove convergence to an ODE

system involving the classical functional responses. They are based on exponential distribution for the interaction times but random times involved in ecological or biological interactions are in general non-exponentially distributed, see [40, 133] and references therein. Consequently, we have to consider an infinite-dimensional process.

In [P4], we propose a microscopic model in the continuation of the "static" model proposed in [40]. In such model, we model preys and predators at a microscopic scale and model each interactions, births and deaths.

Let us describe informally the model. We write $n_1 \in \mathbb{N}$ the number of preys and $n_2 \in \mathbb{N}$ the number of predators. There is two types of predators : predators that are researching a prey and predators manipulating a died prey. The dynamics of predators is as follows:

- Predators search preys during a random time distributed as a random variable $T_S(n_1)$. Typically the more n_1 is large, the smaller $T_S(n_1)$ is.
- After this time, one prey is caught and the number of preys becomes $n_1 - 1$. The predator changes its status and now manipulates during a time distributed as $T_M(n_1 - 1)$.
- At this time, the predator ends to manipulate and returns to the first step.

Several predators follow simultaneously and independently this dynamics, but they live with a common number of preys and impact each other through this common resource. This is the main contrast with [40] which assume that, as the number of individual is large, the population density remains constant over interactions.

Besides, each predator gives birth and dies with respective individual rates $\gamma_r(u)$ and $\beta_r(u)$, which depends on their status $r \in \{S, M\}$ and the time u from which they are in this status. Typically, the fact that the predator does not find a prey make its death rate $\beta_S(u)$ increase with u . Preys also give birth and die, with fixed rates γ and β .

We assume that the size of the populations of preys is of order of magnitude K_1 and the size of the populations of predators is of order of magnitude K_2 and that $K_1 \gg K_2$. That means that preys are much more numerous than predators. A slow-fast dynamic is considered : the time scale of prey-predator interactions is short compared to the time scale of birth and death of predators and preys. It means that each predator eats many preys during its life and, if a prey is not eaten by a predator then its life length is comparable to that of predators, up to some factor.

After this scaling normalization, we show, that the couple of stochastic processes describing the quantities of preys of predators converges in law in the

Skorokhod space $\mathbb{D}([0, \infty), \mathbb{R}_+^2)$ as K_1, K_2 tend to infinity, to the unique solution (x, y) of an ordinary differential equation:

$$\begin{cases} x'(t) &= (\gamma - \beta)x(t) - y(t)\phi(x(t)) \\ y'(t) &= y(t)\psi(x(t)), \end{cases}$$

where

$$\phi(x) = \frac{1}{\mathbb{E}[T_S(x) + T_M(x)]}, \quad (4.4)$$

and

$$\psi(x) = \frac{\mathbb{E} \left[\int_0^{T_S(x)} (\gamma_S(u) - \beta_S(u)) du + \int_0^{T_M(x)} (\gamma_M(u) - \beta_M(u)) du \right]}{\mathbb{E}[T_S(x) + T_M(x)]}. \quad (4.5)$$

Here x denotes the density of preys and y of predators. Note that at the macroscopic scale, it is no longer necessary to differentiate either the status (searching or manipulating) or the associated residence times. We will not describe here all the details, some of which are technical, but rather describe the main ideas. There is naturally some (uniform) moments assumption to guaranty the convergence. As we associate an age corresponding to the time spent in the current status, we can also be interested by the convergence of the distribution of ages. It converges law to the measure

$$y_r(dt, da) = y(t)\mathbb{P}(T_r(x(t)) > a)\phi(x(t)) dt da.$$

We easily recover the number of predators : $\int_0^\infty y_S(dt, da) + \int_0^\infty y_R(dt, da) = y(t)dt$. The fact that the time of interactions is both density dependent and non-exponentially distributed leads us to extend the state space. This procedure to get the Markov setting is classical and consists here in an additional age structure (as in Section 3.4). The problem arising is then an averaging in infinite dimension. The strategy of proof follows the techniques developed in [185] in finite dimension using the occupation measure. The averaging phenomenon in finite dimension is classical [91, 185, 210, 14]. In infinite dimension, much less work has been done up to our knowledge. See nevertheless [185, 210]. We consider a punctual measure whose atoms give the status and the age of predators. In our slow-fast dynamics, there is an averaging phenomenon and the number of predators in each status are instantaneously at equilibrium. This leads to a reduction of the infinite setting to a finite one describing the number of preys and predators. We do not find such results for slow-fast dynamics.

Classical setting and functional responses : memory less interactions

Let us give some examples and starts by the classical case where memory less property is assumed for each component of the dynamic (interaction, birth, death). Times involved are then exponential. This assumption is probably not realistic for manipulating time in general. For searching time it can be justified with the hypothesis of rapid mixing of the preys in the medium where predators live. In this case, the growth rate ψ of predators simplifies as

$$\psi(x) = \frac{\lambda_S \mathbb{E}[T_S(x)] + \lambda_M \mathbb{E}[T_M(x)]}{\mathbb{E}[T_S(x)] + \mathbb{E}[T_M(x)]}.$$

We recover some classical functional responses with usual supplementary assumptions :

i) *No manipulation and search time inversely proportional to the density:*

$$T_M(x) = 0 \quad \mathbb{E}[T_S(x)] = \frac{1}{cx},$$

for some $c > 0$. This assumption is justified for instance where rapid mixing allows to say that each prey meets independently the predator with a small probability after an exponential time, because the minimum of independent exponential variables is exponentially distributed and its parameter is the sum of each parameter.

It leads to the classical Holling type I functional response and Lotka-Volterra form for the consumption of preys

$$\phi(x) = cx, \quad \psi(x) = (\gamma_S - \beta_S). \quad (4.6)$$

We note that in that case, in contrast to the classical Lotka-Volterra model, the functional response ψ for predators does not increase linearly with respect to the density of preys.

ii) *Fixed mean manipulation time and search time inversely proportional to the density:*

$$\mathbb{E}[T_M(x)] = t_0 > 0, \quad \mathbb{E}[T_S(x)] = \frac{1}{cx},$$

for some $c > 0$. It leads to the classical Holling type II :

$$\phi(x) = \frac{cx}{1 + t_0cx}, \quad \psi(x) = \lambda_S + (\lambda_M - \lambda_S)t_0 \frac{cx}{1 + t_0cx}.$$

Constant $(\lambda_M - \lambda_S)t_0$ is related to the "yield constant" in microbial ecology, as in the chemostat equation for instance.

iii) *Fixed mean manipulation time and generalist predator.* Another usual response make the searching time of the prey increase faster with low density since the predator may dedicate more time to other species. This often leads to the following assumption:

$$\mathbb{E}[T_M(x)] = t_0 > 0, \quad \mathbb{E}[T_S(x)] = \frac{1}{cx^2}.$$

This ensures the Holling type III functional response. To describe this generalist behavior of the predator more precisely, we should consider additional species in our model, see e.g. [40].

Influence of distribution of time interaction

The consumption of prey at a first order macroscopic approximation is only sensitive to mean time of interactions trough the function ϕ . The impact of predatory on the evolution of predators may be more subtle.

Let's give an explicit example. Assume that the individual growth rate is linked to the consumption of preys via the following age dependence

$$\lambda_S : a \mapsto -A + Be^{-Ca}.$$

for some $A, B, C > 0$. It models the fact that the more a predator is waiting for a prey, the less it (successively) reproduces and/or the fastest it dies. For sake of simplicity and, as before, we consider that $T_S(x)$ has exponential distribution with parameter λx . This gives

i) Without manipulation, i.e. $T_M(x) = 0$,

$$\phi(x) = \lambda x, \quad \psi(x) = -A + B \frac{(\lambda x)^2}{C\lambda x + 1}. \quad (4.7)$$

In particular, $\psi(x) \rightarrow -A$ as $x \rightarrow 0$ and $\psi(x) \sim_{x \rightarrow \infty} \frac{B\lambda}{C} x$. That is $\psi(x)$ behaves as $-A + B'x$, with $-A < 0$ and $B' > 0$ as in the Lotka-Volterra model. The associated dynamical system has indeed a similar behavior.

ii) With fixed positive manipulation, i.e. $t_0 = \mathbb{E}[T_M(x)]$ and $\lambda_M(x) = \lambda_M$:

$$\phi(x) = \frac{cx}{1 + t_0\lambda x}, \quad \psi(x) = \frac{cx}{1 + t_0\lambda x} \left(-\frac{A}{\lambda x} + \frac{B\lambda x}{C\lambda x + 1} + \lambda_M t_0 \right)$$

Thus is $\psi(x) \rightarrow -cA/\lambda < 0$ as $x \rightarrow 0$ and $\psi(x) \rightarrow \frac{B}{\lambda t_0} + \lambda_M/\lambda > 0$ as $x \rightarrow \infty$. Then it behaves as classical Holling type II prey-predator model:

$$\psi(x) = -A + \mu \frac{x}{x + K}.$$

We then recover here the two classical dynamical system without directly assuming a conversion of prey into predators as usual.

4.4 Around birth and death process

In this subsection, I detail the result of [A5], with Claire Delplancke, on birth and death processes. A birth and death process is a Markov process (X_t) on \mathbb{N} generated by

$$Lf(n) = b_n(f(n+1) - f(n)) + d_n(f(n-1) - f(n)),$$

for any bounded function f and $n \in \mathbb{N}$, where $(b_n)_n$ and $(d_n)_n$ are two non-negative sequence such that $d_0 = 0$. In this section, we will further assume that $(b_n)_{n \geq 0}$ and $(d_n)_{n \geq 1}$ are positive. This assumption prevents extinction and those process is then different from processes studied in Section 4.2 for instance. This family of processes is well known and has been studied for a long time; see for example [18, 80]. In particular, they are irreducible, positive recurrent and non-explosive when respectively

$$C = \sum_{n=1}^{+\infty} \prod_{k=1}^n \frac{b_{k-1}}{d_k} < +\infty, \quad \sum_{n=1}^{+\infty} \left(\frac{1}{b_n} + \sum_{k=1}^n \frac{1}{b_n} \prod_{i=1}^k \frac{d_{n-i+1}}{b_{n-i}} \right) = +\infty.$$

In this case, the unique stationary distribution π is reversible and is given, for $n \geq 0$, by

$$\pi_n = (1 + C)^{-1} \prod_{k=1}^n \frac{b_{k-1}}{d_k}, \quad \pi_0 = (1 + C)^{-1}. \quad (4.8)$$

This means that the associated semi-group (P_t) of (X_t) is self-adjoint in $L^2(\pi)$. Furthermore, the process is exponentially (or geometrically) ergodic, when $\sigma = \sup_u \sigma_u > 0$ where

$$\sigma_u = \inf_{n \geq 0} \left(d_{n+1} - d_n \frac{u_{n-1}}{u_n} + b_n - b_{n+1} \frac{u_{n+1}}{u_n} \right), \quad (4.9)$$

and the supremum runs over all positive sequence $u = (u_n)$. More precisely, for every $t \geq 0$, we have

$$\|P_t f - \pi(f)\|_{L^2(\pi)} \leq e^{-\sigma t} \|f - \pi(f)\|_{L^2(\pi)}, \quad (4.10)$$

for all function $f \in L^2(\pi)$. Moreover σ is the best constant in these two inequalities; this is the so-called spectral gap.

In [66], they shown the following intertwining (commutation type) relation

$$\partial_u P_t = P_t^u \partial_u, \quad (4.11)$$

where ∂_u is the weighted differential operator defined for a function f by

$$\partial_u f : n \mapsto u_n(f(n+1) - f(n)),$$

for some positive sequence (u_n) . In Equation (4.11), (P_t^u) is a positive (non necessary conservative) and explicit semigroup. For all $t \geq 0$, we have $P_t^u \mathbf{1} \leq e^{-\sigma_u t}$ and consequently if $\partial_u f \leq 1$ then

$$|P_t^u f(m) - P_t^u f(n)| \leq e^{-\sigma_u t} \sum_{k=n}^{m-1} u_k =: e^{-\sigma_u t} d_u(m, n)$$

for all $m \geq n$. This directly induces a quantitative bound in Wasserstein distance :

$$\mathcal{W}_{d_u}(\mu P_t, \pi) \leq e^{-\sigma_u t} \mathcal{W}_{d_u}(\mu P_t, \pi),$$

for every probability measure μ , where we recall that

$$\mathcal{W}_{d_u}(\mu, \pi) = \inf_{X \sim \mu, Y \sim \pi} \mathbb{E} [d_u(X, Y)].$$

In [66], they also prove others consequences including (4.10), entropic inequalities, hitting time estimates, convex domination etc. Since the use of this type of relationship has been successful [44, 179, 254, 9, 45, P9].

In [A5], we take this intertwining relationship one step further by showing various relations of the type

$$\partial_u \partial_v P_t = P_t^{u,v} \partial_v \partial_u.$$

Similarly to the link between Wasserstein distance and gradient type estimates, this new bound induced convergence bound in Zolotarev distance [237, 276]. However our main application was to the estimate of the so-called Stein's magic factors.

Let us rapidly, recall the Stein's method. This is a general method to obtain bounds on the distance between two laws μ, π . Fixing any distribution π , we can find some sequences $(b_n), (d_n)$ such that π is given by (4.8). Then, setting (at least formally) for function f

$$h_f = - \int_0^\infty (P_t f - \pi(f)) dt,$$

it is solution to the Poisson equation : $Lh_f = f - \pi(f)$. Consequently

$$d_{\mathcal{F}}(\mu, \pi) := \sup_{f \in \mathcal{F}} \int f d\mu - \int f d\pi = \sup_{f \in \mathcal{F}} \mu(Lh_f), \quad (4.12)$$

where \mathcal{F} is any set of functions. We may then estimate the total variation, Wasserstein or Kolmogorov distance $d_{\mathcal{F}}$ by considering respectively \mathcal{F} as $\{f \mid 0 \leq f \leq 1\}$, $\{f \mid |\partial_u f| \leq 1\}$ or $\{f = \mathbf{1}_{[0,m]} \mid m \in \mathbb{N}\}$. Equation (4.12) is more often established with the Stein solution g_f verifying (usually up to a shift) $g_f = \partial h_f$. For many problems, we can bound the right-hand side of Equation (4.12) by a quantity of the form

$$\epsilon_0 \|g_f\|_{\infty} + \epsilon_1 \|\partial_u g_f\|_{\infty}$$

for some $\epsilon_0, \epsilon_1 \geq 0$ and positive sequence u, v . See for instance [19] or [20]. In [A5], we established this type of bound for mixture of negative binomial, geometric or Poisson laws.

Also and most importantly, we give precise bounds on $\sup_{f \in \mathcal{F}} \|g_f\|_{\infty}$ and $\sup_{f \in \mathcal{F}} \|\partial_u g_f\|_{\infty}$, in the most general framework. This is based on the intertwining relations plus the identification of the argmax function f for each classes of functions (generalizing the approach of [51]). These bounds depend on the laws at time t of some birth-death processes that can be make precise for some example such as for instance the Galton-Watson processes with immigration (whose laws is explicit).

We compare precisely our results with the literature in [A5]. However, in the well studied Poisson case, we mostly recover the well known bounds [20, 21]. For the negative binomial case, we recover the bound on $\sup_{|\partial f| \leq 1} \|g_f\|_{\infty}$ of [19] but improves the one on $\sup_{|\partial f| \leq 1} \|\partial g_f\|_{\infty}$. We improves results of [50] for $|f| \leq 1$. We gave some bounds for the Stein factor for geometric laws which, to our knowledge, can not be compared to the literature. Note that this example is more difficult since the law at time t of the M/M/1 process is less explicit.

To our knowledge, since then, there are no better results, even if [140] recovers the same type of order for the negative binomial case.

To illustrate our results let us give our bounds on mixtures. If Λ is a positive random variable and $\mathcal{L}(W \mid \Lambda) = \mathcal{P}(\Lambda)$ where, $\mathcal{P}(\lambda)$ is the Poisson law with parameter λ then we derived the new bound

$$\mathcal{W}_{|\cdot|}(\mathcal{L}(W), \mathcal{P}(\lambda)) \leq \left(1 \wedge \frac{8}{3\sqrt{2e\lambda}}\right) \text{Var}(\Lambda)$$

where $\lambda = \mathbb{E}[\Lambda]$. In particular, as the negative binomial law $\text{NB}(r, p)$ is a mixed Poisson law, we have

$$\mathcal{W}_{|\cdot|}(\mathcal{L}(W), \mathcal{P}(r(1-p)/p)) \leq \frac{8}{3\sqrt{2e}} \sqrt{\frac{r(1-p)}{p} \frac{1-p}{p}}.$$

To finish this section, let us point out that a work is currently in progress with Edouart Strickler for the numerical estimation of the spectral gap σ . As

this last one intervenes as the death rate of a coupling, it can be estimated with the methods described in Part II.

4.5 Collective behaviors

Adrien Cotel started his PhD in November 2021 with Jean Baptiste Menassol and me on the subject of animal (sheep and cows) displacements through collective behavior. This subject follows two different internships, those of Jun Zhang and Marine Perrier, that I co-supervised on cattle movements in collaboration with several researchers of the UMR Herbivores, Inria Zenith and my unity UMR Mistea.

Researchers of UMR Herbivores work since several years on the cow behaviors from their locations. These locations are monitored from a real-time location system. They collect the position between 150 and 200 cows every seconds in a building. See for instance [214]. In this work, they explain how they aggregate this large amount of data in a shorter data set centered on the activities of the individuals. Jun Zhang and Marine Perrier study these two data sets (exact positions and activities). Jun Zhang proposed an in-homogeneous time Markov chain in discrete time to model activity changes for individuals. There are 6 different activities and 168 cows representing a state space of around $5 \cdot 10^{130}$ elements. We then impose a certain form of transition highlighting the interaction between individuals. We still need to improve the first results obtained, but they suggest, for the moment, that the interaction between individuals is a secondary factor in the movement choices of individuals. Although uncertain, this result does not surprise the experts because the size of the buildings constrains the individuals. To extend this work, Marine Perrier used various clustering methods on the proximity graphs from the location data.

We decided to work on more mathematically complex models. To this end, Adrien Cotel started his thesis on the mathematical study of alignment models. In particular, in [92], he studies the so-called Cucker-Smale system of equations [101]. In this model, each individual $i \in \llbracket 1, N \rrbracket$ has a position $x_i(t)$ and a speed $v_i(t)$ at each time $t \geq 0$. This model consists of the deterministic model:

$$\begin{cases} \dot{x}_i &= v_i \\ \dot{v}_i &= \frac{\lambda}{N} \sum_{j=1}^N \frac{1}{(1+\|x_i-x_j\|^2)^\beta} (v_j - v_i). \end{cases}$$

We observed that the speed verifies a Kolmogorov type equation. This allowed him to reduce the flocking phenomenon ($\|v_i - v_j\| \rightarrow 0$) to a problem of convergence rate of time-inhomogeneous Markov processes. This property has been generalized for more general interaction scheme of the Cucker-Smale

model. The heart of the mathematical proof of [92] is then to quantify the rate of convergence of Markov chain that are time-inhomogeneous, in discrete space, but for which the topology of the transition graph does not change. See [92] for details.

4.6 Perspectives

It was very successful to have obtained the convergence towards a QSD for a very degenerated process in Section 4.2. We can hope to use the same approach in other similar contexts as in [91]. However, the main challenging question is to study processes in larger dimension. This question is closely related to the problem evoked in Section 3.7. A natural continuity of [P1] is also to give a perfect portrait of the behavior of the Crump-Young model as in [79]. That is to show that the population is large, then the process converges rapidly to its QSD, which is close to a Gaussian, and then became extinct after a large time (See Section 5.1.2 below for a more comprehensive description of [79]).

A challenging and related problem is also to understand the long time behavior of the infinite dimensionnal models [P4, A12] without approximation.

It was also a good step to justify the forms of functional responses used in ecology. However, our first motivation was to go further and give new tools for ecologists. Indeed, let us describe an interesting result of [40]. From data on the vigilance of partridges, they compare two types of regression : the classical one and a least-square estimation with an heteroscedastic noise. In this second method, the variance of the noise take into account the number of individuals. They show that the second method leads to a totally different biological conclusion. It is then of prime interest to establish a central limit theorem for the microscopic model [P4] to build statistical estimators of functional responses. Our approach should enable to consider that the noise in the data depend on both the number of preys (as in [40]) and a temporal correlation.

Finally, due to the digitization of the breeding, several questions and data are beginning to emerge. I would like to continue to study the influence of social network on dynamical system.

Part II

Stochastic algorithm

Chapter 5

Stochastic algorithms for quasi-stationary approximation

Let us consider a continuous-time Markov chain $(X_t)_{t \geq 0}$, on some state \mathbb{X} , which will be absorbed at some random time τ_∂ in some cemetery point $\partial \notin \mathbb{X}$. Some examples were developed in Chapter 4. Under some assumptions, as for instance irreducibly on a finite state space (see also and again Chapter 4), we have the existence of a quasi-stationary measure ν which verifies

$$\lim_{t \rightarrow \infty} \mathbb{P}(X_t \in \cdot \mid \tau_\partial > t) = \nu. \quad (5.1)$$

This distribution is also related to the time of absorption. It can then be of prime importance to simulate it.

The first algorithm we can think of is a Naive Monte Carlo. Let $(X_t^1)_{t \geq 0}, \dots, (X_t^N)_{t \geq 0}$ be N i.i.d. processes, distributed as $(X_t)_{t \geq 0}$ and consider

$$\hat{\nu}_N = \frac{\sum_{i=1}^N \mathbf{1}_{X_t^i \in \cdot}}{\sum_{i=1}^N \mathbf{1}_{X_t^i \neq \partial}} = \frac{\sum_{i=1}^N \delta_{X_t^i}}{\sum_{i=1}^N \mathbf{1}_{X_t^i \neq \partial}}$$

as an estimator of ν for a large time t . The problem is that this mean is based on a very small $N_0 = \sum_{i=1}^N \mathbf{1}_{X_t^i \neq \partial}$ of individuals. Indeed, we have

$$\mathbb{E}[N_0] = N \mathbb{P}(\tau_\partial > t) \xrightarrow[t \rightarrow +\infty]{} 0.$$

It is because we lose all the information of absorbed trajectories. To be efficient, we need to keep a maximum of particles. An alternative is therefore to resurrect the particles lost due to the absorption. The question is then : how to redistribute a particle when it is absorbed ? As we are motivated by making it converge towards ν , a natural choice is to redrawn it with ν . It is not difficult

to prove that a process $(Y_t)_{t \geq 0}$, which evolves as $(X_t)_{t \geq 0}$ between absorption events and is redrawn according to ν at each absorption events, admits ν as invariant measure and converges to it under (5.1). This process is called the ν -return process in [161, 145]. Unfortunately, we are not able to use ν in a numerical strategy. To overcome this problem, we have to use an approximation of it. In this spirit, two main choices are used.

The first one is at the heart of the so-called Fleming-Viot particle system. Be careful, however, as the latter is more of a Moran-type process than the well studied different Fleming-Viot super-process [141]. When considering N independent particles $(X_t^1)_{t \geq 0}, \dots, (X_t^N)_{t \geq 0}$, evolving as $(X_t)_{t \geq 0}$ until one them, say i , is absorbed, then we can redraw it by the (spatial) empirical measure $\frac{1}{N-1} \sum_{j \neq i} \delta_{X_t^j}$. Equivalently we choose $j \neq i$ uniformly at random and we set $X_t^i = X_t^j$. They are no longer independent but become so again when the number of particles increases. This algorithm was introduced in [53, 106, 113] and we worked on various rate of convergence to establish the commutation of the limits between $t \rightarrow +\infty$ and $N \rightarrow \infty$. These ones are developed in Subsection 5.1 below.

Another natural choice is inspired from the ergodic theorem. By (5.1) and this theorem, we can think that $\frac{1}{\tau_\partial} \int_0^{\tau_\partial} \delta_{X_s} ds \approx \nu$. Then, when a particle is absorbed then it is enough to redraw it according to its (time) empirical measure. Equivalently, we choose T uniformly at random in $[0, \tau_\partial)$ and we set $X_{\tau_\partial} = X_T$. It is therefore no longer necessary to simulate several particles and one trajectory is sufficient. However the process is no longer Markovian. This algorithm was first proposed in [2] and brought up to date in [42, A16]. We will come back to this algorithm in Section 5.2.

5.1 Fleming-Viot particle system

In this section, we describe the results of [P5, A13, A14] on quantitative results for the Fleming-Viot particle system in discrete space.

5.1.1 General results

This model consists of finitely many particles, say N , moving independently of the others as $(X_t)_{t \geq 0}$, until one of them hits state ∂ . At that time, it comes back immediately to \mathbb{X} by jumping to the position of one of the other particles chosen uniformly at random. It is convenient to think of particles as being indistinguishable, and to consider the occupation number η with, for $k \in \mathbb{X}$, $\eta(k) = \eta^{(N)}(k)$ representing the number of particles at site k . The configuration

$(\eta_t)_{t \geq 0}$ is a Markov process with state space $E = E^{(N)}$ defined by

$$E = \left\{ \eta : \mathbb{X} \rightarrow \mathbb{N} \mid \sum_{i \in F^*} \eta(i) = N \right\}.$$

Applying its generator to a bounded function f gives

$$\mathcal{L}f(\eta) = \mathcal{L}^{(N)}f(\eta) = \sum_{i \in \mathbb{X}} \eta(i) \left[\sum_{j \in \mathbb{X}} (f(T_{i \rightarrow j}\eta) - f(\eta)) \left(Q_{i,j} + Q_{i,0} \frac{\eta(j)}{N-1} \right) \right], \quad (5.2)$$

for every $\eta \in E$, where, if $\eta(i) \neq 0$, the configuration $T_{i \rightarrow j}\eta$ is defined by

$$T_{i \rightarrow j}\eta(i) = \eta(i) - 1, \quad T_{i \rightarrow j}\eta(j) = \eta(j) + 1, \quad \text{and } T_{i \rightarrow j}\eta(k) = \eta(k) \quad k \notin \{i, j\}.$$

Let μ^N be the associated empirical distribution of the particle system. It is defined, for $\eta \in E$, by

$$\mu_t^N = \frac{1}{N} \sum_{k \in F^*} \eta(k) \delta_{\{k\}}, \quad t \geq 0.$$

In several works [P5, A13, A14], we aim to study the commutation relations in the diagram in Figure 5.1.

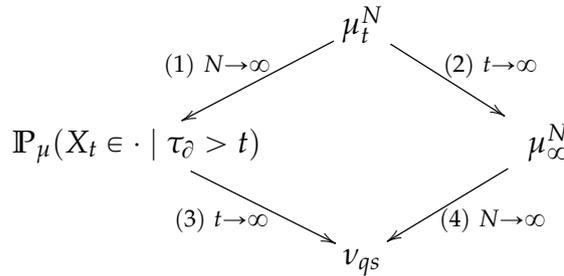


Figure 5.1: Possible limits for the Fleming-Viot particle system

To prove such commutation, one way is to obtain uniform rates for one of limits in (1) or (2) and then pass to the others one (3) or (4). Let us review our results and nowadays known results for each according to each subcases.

Limit (1) : Propagation of chaos

The limit, at fixed time, when the number of particles tends to infinity is the most classical one. When particles became numerous then they evolve as an

independent system of particles : there is a propagation of chaos. This type of asymptotic property is common to models with mean field interaction [68, 256]. The first articles on the Fleming-Viot algorithm established this result; see [53, Theorem 1.3] or [106, Theorem 1.1].

With Josué Corujo, we show a propagation of chaos result with [66, Theorem 1.2]. Let us present it when the starting distribution consists of N i.i.d. particles, the space \mathbb{X} is discrete and the killing rate is bounded. For every $T \geq 0$ and $p \geq 1$, there exists a constant $C_{p,T} > 0$, such that we have

$$\sup_{\|\phi\|_\infty \leq 1} \mathbb{E} \left[\sup_{t \in [0, T]} |\mu_t^N(\phi) - \mu_t(\phi)|^p \right]^{1/p} \leq \frac{C_{p,T}}{\sqrt{N}},$$

where $\mu_t = \mathbb{P}_\mu(X_t \in \cdot \mid \tau_\partial > t)$.

To our knowledge, this is the first result, and the only one, that guarantees a uniform convergence, within the expectation, on compact interval of times, and in L^p , at the good convergence speed. However, it does not capture all Markov processes in contrast with [265] for instance. Finally, see also [114, 99, 98, 110, 111] for related results.

Unfortunately, even if this result guarantees a type of uniformity, it is not enough to commute the limits as in Figure 5.1. To that end, we need a result as the following, which also come from [P5].

Theorem 5.1.1 (Uniform in time propagation of chaos). *Assume there exist a distribution $\mu_\infty \in \mathcal{M}_1(E)$ and $C, \gamma > 0$, such that for every initial distribution $\mu_0 \in \mathcal{M}_1(E)$ and for all $t \geq 0$:*

$$\|\mu_t - \mu_\infty\|_{\text{TV}} \leq C e^{-\gamma t}, \quad (5.3)$$

for every $p \geq 1$, there exists a constant C_p , such that

$$\sup_{\|\phi\|_\infty \leq 1} \sup_{t \geq 0} \mathbb{E} [|\mu_t^N(\phi) - \mu_t(\phi)|^p]^{1/p} \leq \frac{C_p}{\sqrt{N}}.$$

Recall that Theorem 3.3.1 may be used to prove (5.3).

Theorem 5.1.1 generalizes previous results which obtained a bound of order $N^{-\alpha}$, $\alpha < 1/2$ such as [113, Theorem 3.1] (in discrete time), [74, Theorem 2.3] or [A14, Corollary 1.5]. It is strongly based on a generalization of arguments of [243], as the recent work [6]. See [89] for an example where constant in the rate of convergence was precised. Finally see also [109, 108, 115] for related results.

Finally note that results of [P5] are presented in a larger setting than those presented here. Indeed, instead of considering a Moran particle system where

selection only happens at death, we consider, selection at birth. This permits to consider this model not only for approximation purposes but also for an interacting population dynamics model for evolution problems similarly as in Section 3.6.

Limit (2) : Ergodicity of the particle system

For countable space \mathbb{X} , the ergodicity of the Fleming-Viot process is not guaranteed. In finite state space, under assumptions of irreducibility, the Perron-Frobenius theorem gives the exponential convergence of the particle system to an equilibrium state, at a speed which unfortunately should depend on N ; see for instance [A13, Figure 1]. In [A14], we show that under some conditions, the particle system converges exponentially fast to equilibrium for a suitable Wasserstein coupling distance. Let us recall this distance : for $\eta, \eta' \in E$, let d be the distance defined by

$$d(\eta, \eta') = \frac{1}{2} \sum_{j \in \mathbb{X}} |\eta(j) - \eta'(j)|, \quad (5.4)$$

and for any two probability measures μ and μ' on E , let $\mathcal{W}_d(\mu, \mu')$ be the Wasserstein coupling distance between these two laws defined by

$$\mathcal{W}_d(\mu, \mu') = \inf_{\substack{X \sim \mu \\ \bar{X} \sim \mu'}} \mathbb{E} [d(X, \bar{X})], \quad (5.5)$$

where the infimum runs over all the couples of random variables with marginal laws μ and μ' . Distance d is the L^1 distance for the number of particles but is equal to the total variation distance of the associated empirical measures.

Theorem 5.1.2. *Let $\lambda = \inf_{i, i' \in \mathbb{X}} (Q_{i, i'} + Q_{i', i} + \sum_{j \neq i, i'} Q_{i, j} \wedge Q_{i', j})$ and for $i \in \mathbb{X}$, $p_0(i) = Q_{i, 0}$. If $\rho = \lambda - (\sup(p_0) - \inf(p_0))$ then for any processes $(\eta_t)_{t>0}$ and $(\eta'_t)_{t>0}$ generated by (5.2), and for any $t \geq 0$, we have*

$$\mathcal{W}_d(\text{Law}(\eta_t), \text{Law}(\eta'_t)) \leq e^{-\rho t} \mathcal{W}_d(\text{Law}(\eta_0), \text{Law}(\eta'_0)).$$

In particular, if $\rho > 0$ then there exists a unique invariant distribution ν_N satisfying for every $t \geq 0$,

$$\mathcal{W}_d(\text{Law}(\eta_t), \nu_N) \leq e^{-\rho t} \mathcal{W}_d(\text{Law}(\eta_0), \nu_N).$$

To our knowledge, even if there is several result stating a rate of convergence in time for the particle system, as for instance [74, Theorem 2.2] or [266, Theorem 2.1], this is the first result having a bound uniform in N . Since, It seems that the only another one is [90] where this rate of convergence is proved by the calculus of all the spectrum of the particle system.

Proof of Theorem 5.1.2 is original and based on a sharp coupling between two particles system with two different initial conditions. We obtain such rate because we hoped to couple them after only one jump, which is a restrictive assumption. See [184, 221] for similar approaches.

5.1.2 A stimulating example

In [A13], we develop two particular cases of Fleming-Viot particle system. The first one is the complete graph dynamics. That is the underlying Markov chain has the same jump rate for any another state. This Markov chain is relatively simple reducing the study of the Fleming-Viot processes to the interaction mechanism. It is also a particular case of the inclusion process [163, 162, 156]. For this model, we are able to derive exact and closed formulas for the correlations for the family $(\eta_t(k))_k$ for every N, t , an explicit formula for the invariant (and reversible here) distribution ν_N etc.

However, instead of detailing this example, I will develop the second example of this paper. It concerns the general case where the non absorbing state contains two points. In this case, Process $(\eta_t(1))$ is trivially Markovian. Moreover it is a birth and death process (as detailed in Section 4.4). It is generated by

$$Gf(n) = (N - n) \left(Q_{2,1} + Q_{2,0} \frac{n}{N - 1} \right) (f(n + 1) - f(n)) \\ + n \left(Q_{1,2} + Q_{1,0} \frac{N - n}{N - 1} \right) (f(n - 1) - f(n))$$

Indeed, there are $(N - n)$ particles in 2 which can either jumps to 1 directly or, instead of being absorbed at rate $Q_{2,0}$, has a probability $n/(N - 1)$ to be redistributed in 1. If it is redistributed on a particle on 2, this changes nothing. This explain the form of the birth rate and the death rate is similarly build.

When $Q_{1,0} = Q_{2,0}$, it is easy to see that G transforms a polynomial function into another polynomial function without increasing its degree. Consequently, it admits an orthogonal basis of polynomial eigenvectors : all what we want is explicit!

Unfortunately, the most interesting case is when $Q_{1,0} \neq Q_{2,0}$. In this case, Theorem 5.1.2 gives exponential convergence for $Q_{1,2} + Q_{2,1} - |Q_{1,0} - Q_{2,0}| > 0$. In particular if $|Q_{1,0} - Q_{2,0}| \geq Q_{1,2} + Q_{2,1}$ then it does not give convergence. In this case, up to our knowledge, it does not exist any result with an explicit rate of convergence (in long time for the particle system or for this birth and death process) and in particular a rate which does not depend on N . Even if Theorem 5.1.1 gives although that the invariant measure of Fleming-Viot focuses on the QSD.

Using Hardy's inequalities in [A13], we show a lower bound for the spectral gap and then a bound of the type

$$\mathcal{W}_d(\text{Law}(\eta_t), \text{Law}(\eta'_t)) \leq C_N e^{-\rho t} \mathcal{W}_d(\text{Law}(\eta_0), \text{Law}(\eta'_0)),$$

for a certain ρ which does not depend on N , and a constant $C_N > 0$ which depends on N . There is no assumption apart $Q_{1,2}, Q_{2,1} > 0$.

The case $Q_{1,2}$ or $Q_{2,1}$ is equal to 0 is somewhat degenerate because the underlying Markov chain is not irreducible in the non absorbing state. However, it can be an interesting model to understand the behavior of the algorithm.

Let us consider that $Q_{2,1} = 0, Q_{1,0} = 0$ and $Q_{2,0} > Q_{1,2}$. In this case there is two QSD δ_2 and $c\delta_2 + (1-c)\delta_1$, with $c = Q_{1,2}/Q_{2,0}$. If we start in 1, then the conditional law converges to $c\delta_1 + (1-c)\delta_2$. In this other case, there is no dynamics, the process, conditionally to not be absorbed, is constant equal to 2 (and converges to the other QSD).

The birth and death process of the associated Fleming-Viot process is now absorbed at 0. As the state space is finite then it hits 0 at a finite time T_N whatever its initial condition. In particular there is no commutation of the limits : if we let the time going to infinity and then the number of particles, we find δ_2 as QSD, while, if we let $N \rightarrow \infty$ first, then we find the conditional law which tends to $c\delta_2 + (1-c)\delta_1$.

Using [79], we can go further in understanding the failure of Fleming-Viot algorithm. Our process does not exactly satisfy the assumption because, in part, our process belongs to finite state space in contrast with [79]. However, results of [79] may surely be generalizable and we can expect that, when all particles start in 1, the Fleming-Viot evolves as follow : after a random time of order $N \log(N)$ the process is close to its QSD, this one is close to a Gaussian with variance N centered in $c\delta_1 + (1-c)\delta_2$, remains close to this QSD during a very long time (which is exponential on N) and then all particles are in 1.

This type of behavior is not completely proved. Proving and generalizing such behavior is of great interest since the two point space example is a benchmark for more complex non irreducible dynamics [24, A6, 69].

5.1.3 Hidden Markov chain

Hidden Markov model and Fleming-Viot algorithm

As explained in Section 4.1, absorbed Markov chain possesses a sub-conservative semi-group, Fleming-Viot type algorithm can be used in a more general setting than for approximating QSD but to simulate both non-conservative semi-group and its asymptotic (eigenelements of a branching processes for instance).

It is then useful in Hidden Markov chain context. In this case, the Sequential Monte Carlo algorithm [112, 108] can be seen as a discrete time and time-inhomogeneous version of the Fleming-Viot processes. Let us give more detail.

More precisely, assume that $(X_t)_{t \in \mathbb{N}}$ is a (inhomogeneous time) Markov chain. Instead of observing a sample path of this process, we observe one of a process $(Y_t)_{t \in \mathbb{N}}$. This process is not Markovian by itself but the couple $(X_t, Y_t)_{t \in \mathbb{N}}$ is. For sake of presentation, we will assume that at every time $t \geq 0$, variable Y_t only depend on X_t and is sampled with a law admitting a density $g_t(X_t, \cdot)$ for some reference measure; that is, for any positive function f

$$\mathbb{E} [f(Y_t) \mid \mathcal{F}_t] = \int g(X_t, y) \mu(dy),$$

where $(\mathcal{F}_t)_{t \geq 0}$ is the natural filtration associated to $(X_t)_{t \geq 0}$. We could have assumed an additional dependency in Y_{t-1} . In this setting, an iterating argument gives that for any positive function f and sequence $(y_t)_{t \in \llbracket 1, T \rrbracket}$,

$$\mathbb{E} [f((X_t)_{t \in \llbracket 1, T \rrbracket}) \mid (Y_t)_{t \in \llbracket 1, T \rrbracket} = (y_t)_{t \in \llbracket 1, T \rrbracket}] = \frac{\mathbb{E} \left[f((X_t)_{t \in \llbracket 1, T \rrbracket}) \prod_{t=1}^T g_t(X_t, y_t) \right]}{\mathbb{E} \left[\prod_{t=1}^T g_t(X_t, y_t) \right]}. \quad (5.6)$$

See for instance [62, Proposition 3.1.4] or [109, Section 8.4]. When in (5.6) we consider a test function f that only depends on the last term, that is

$$f((X_t)_{t \in \llbracket 1, T \rrbracket}) = f(X_T),$$

estimating this functional is generally called a *filtering* problem. With this choice of function the numerator of the right-hand side is a non-conservative semi-group and the link with Fleming-Viot algorithm is clear (indeed, we can consider the process which evolves as (X_t) and is not absorbed at each time t with probability proportional to $g_t(X_t, y_t)$).

A simple hidden Markov chain and a variant of the Kalman filter

Let us detail a concrete example where we first try to use this algorithm to estimate unobserved data but we finally find another simpler solution.

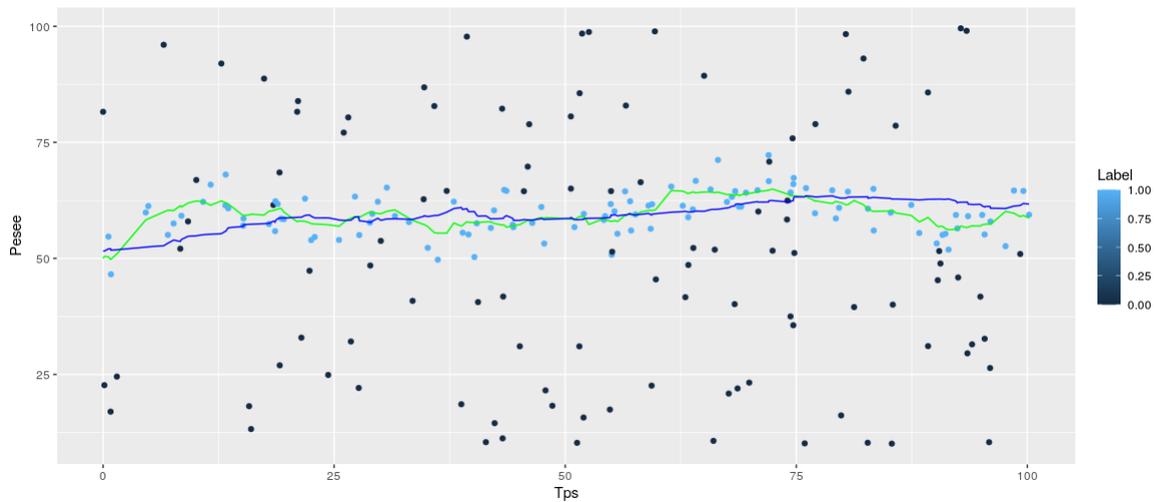


Figure 5.2: The signal (X_t) is the green line and all points are our observations (Y_t) . The blue points are sampled from the signal plus a Gaussian noise while the black ones are sampled uniformly. The blue line is the result of our algorithm. It contains the reconstructed signal (which is smoother because we reconstruct $\mathbb{E}[X_t | (y_k)]$ instead of X_t).

For an agronomic application, we had a time series dataset $(y_k)_{k \in [1, N]}$ whose the structure is general. They came from some captors and are noised version of the signal of interest, in continuous time, $(x_t)_{t \in [0, T]}$. This is the classical setting of Kalman-Filter. A natural modeling choice is to assume that $(x_t)_t$ is a sample path of a Gaussian process $(X_t)_{t \in [0, T]}$ and $(y_k)_{k \in [1, N]}$ are realization of a random variable which correspond to X_t at certain times plus independent Gaussian noises. As the conditional laws of Gaussian are Gaussian, we can give an explicit representation of (5.6) in terms of integrals with respect to normal distribution whose parameters can be calculated easily by an iterative argument. This is the hearth of the Kalman-Bucy filter algorithm.

Unfortunately, our dataset contains some points y_k which can not be seen as noised version of our signal but as totally independent points. Of course, we do not know which points k , it is about. See the points in Figure 5.2 for a numerical simulation of the type of data we have. In a work in preparation, with I. Sanchez and B. Fontez, we propose a branching-type Kalman-Bucy filter for this dynamics, relatively close to switching Kalman-Bucy filter variant [224] to treat this type of data; see for instance the blue line in Figure 5.2.

5.2 The Aldous-Flannery-Palacios Algorithm

5.2.1 A general result

In [A6, A16], with Michel Benaïm and Fabien Panloup, we study another algorithm to approximate quasi-stationary distributions. We consider a discrete time setting : let K be a (Feller) sub-Markov kernel on a compact metric space \mathbb{X} . Let $\delta : \mathbb{X} \mapsto [0, 1]$ be associated killing rate defined by $\delta : x \mapsto 1 - K\mathbf{1}(x) = 1 - K(x, \mathbb{X})$. For a given law μ , we let K_μ denote the Markov kernel on \mathbb{X} defined by

$$K_\mu f(x) = Kf(x) + \delta(x)\mu(f).$$

for all $x \in \mathbb{X}$ and bounded measurable function f . The chain induced by K_μ behaves like the underlying Markov chain, now denoted by (Y_n) , until it is killed and is then redistributed in \mathbb{X} according to μ . An important feature of K_μ is that μ is a QSD for K if and only if it is invariant for K_μ .

A natural discrete time version of the Fleming-Viot process defined in Section 5.1 can be defined using this kernel. Conditionally on the particle system (X_n^1, \dots, X_n^N) at a certain time n , the new position X_{n+1}^i are independently distributed according $K_{\mu_n^N}$ where $\mu_n^N = \frac{1}{N} \sum_{k=1}^N \delta_{X_n^k}$. We should have that μ_n^N tends to the solution of $\mu_{n+1} = K_{\mu_n}$ which should converge to a solution of $\mu = K_\mu$, which is here a quasi-stationary distribution. See [A16, Section 3] for an alternative version of a discrete-time Fleming-Viot particle system, or also [109].

Instead of using this particle system, we consider an \mathbb{X} -valued random process $(X_n)_{n \geq 0}$ verifying

$$\forall n \geq 0, \quad \mathbb{P}(X_{n+1} \in dy \mid X_0, \dots, X_n) = K_{\mu_n}(X_n, dy), \quad \mu_n = \frac{1}{N} \sum_{k=0}^n \delta_{X_k}. \quad (5.7)$$

To be more precise, in [A6, A16], we study a *weighted occupation measure* instead of the uniform measure on the past, as μ_n , leading to large or weak weight on the memory.

This process is a self-interacting Markov process [107, 116, 28].

We then now study a single particle to approach the quasi-stationary distribution in contrast with the Fleming-Viot particle system. We bypass the use of a large number of particles by using a *temporal occupation measure* instead of a *spatial occupation measure*. From a simulation point of view, this is of potential interest, suggesting fewer computations (but more memory) and leading to a recursive method which avoids (at least in name) the trade-off between the number of particles and the time horizon induced by Fleming-Viot algorithm.

We assume that there exists $C, \epsilon > 0$ and a probability measure Ψ on X such that

$$\sum_{n \geq 1} (1 - K(x, X))^n > 0, \quad \sum_{n \geq 1} K^n(x, dy) \geq \epsilon \Psi(dy), \quad \sup_{n \geq 0} \frac{\Psi(K^n \mathbf{1})}{\|K^n \mathbf{1}\|_\infty} \geq C. \quad (5.8)$$

The first assumption guarantees that the process is almost-surely absorbed, the others are not unrelated to Theorem 3.3.1, which is known to be equivalent to exponential convergence to a QSD [75]. In [A6], we can replace the supremum in n in the last term of (5.8) by an inequality holding for any n and a non-constant lower bound $C(n)$ which can tends slowly to 0. Even if we do not write it in this article, the part of the proof enabling this flexibility, may be adapted to have a theorem stating sub-exponential convergence to a quasi-stationary distribution. We are not aware of such result in the literature but weakening this hypothesis seems less useful than weakening Lyapunov conditions on the generator.

Under these assumptions, we prove

Theorem 5.2.1 (Convergence of the algorithm). *Assume (5.8). Then, K has a unique QSD ν and the sequence $(\mu_n)_{n \geq 0}$, defined in (5.7), converges a.s. towards ν . Moreover, $(X_n)_{n \geq 0}$ converges in distribution to ν .*

When the state space is finite, we further give several rate of convergence in [A16]. More precisely, we establish a bound of type

$$\|\mu_n - \nu\|_{\text{TV}} \leq Cn^{-\theta}, \text{ a.s.}$$

for some random variable $C >$ and explicit $\theta \in (0, 1/2]$. Parameter θ depends on the whole spectrum of K (and not only on its spectral gap) and is a trade-off between rate of convergence of the underlying dynamics (given by this spectrum) and the memory loss. We also prove that $\sqrt{n}(\mu_n - \nu)$ tends to some Gaussian distribution. In [A6], we also describe the approximation of the associated eigenvalue, the reducible Markov chain case and an Euler scheme example. In particular, the non-irreducible two point space example of Section 5.1.2 is studied. We can show that if $X_0 = 1$ then (μ_n) has a positive probability to hits $c\delta_2 + (1 - c)\delta_1$. We do not know if it is, or not, equal to 1 when the memory is uniform. However, when the memory is shorter then we are able to show that δ_2 has also a positive probability to be hit.

Let us now place this algorithm in the literature. It was introduced in [2] and the almost-sure convergence was proved by coupling the dynamics with a urn process. Simultaneously and independently, [42, A16] used stochastic algorithm techniques [148, 192, 48, 23] to prove the convergence of (μ_n) . Results of

[A16] enables to use more general memory and exhibits some almost-sure rates of convergence. Both these articles prove a central limit theorem but [42] investigate a Ruppert-Polyak averaging which improve the rate of convergence. Up to our knowledge, the first proof of convergence in a non-finite space as presented here dates from [A6]. Then, due to its application in MCMC techniques [234, 270], several researcher worked on generalization of [A6]. Indeed, as Brownian motions killed at weighted exponential time have explicit quasi-stationary distributions, we can replace the simulation of the stationary distribution of a Langevin process by the simulation of the quasi-stationary distribution of this Brownian motion. The advantage is that we can use perfect simulation in case of killed Brownian motion instead of an Euler scheme. For such application, [271] proves the convergence of the algorithm for diffusion process on compact space with smooth killing (*i.e.* absorption after an exponentially type random time). Article [207] studies the same type of processes but on a non-compact space. The case of hard killing, namely absorption when hitting the boundary of the space, is more tricky. It was shown in [A6, Section 8.3] that the algorithm is generally well defined, in contrast with Fleming-Viot particle system (see [39] where it is shown that the particles can be closer and closer to the boundary, causing a definition problem for the algorithm). The convergence of (μ_n) was proved in [25] for diffusion process with hard killing. There is no general results for the speed of convergence in the non-finite case. Let us nevertheless cite the results of [107, 116] which exhibit a rate of convergence for general self-interacting Markov process which reads, for the Aldous-Flannery-Palacios algorithm, as a perturbative bound as in Theorem 5.1.2. See finally [52] which combine Fleming-Viot and Aldous-Flannery-Palacios algorithm for discrete Markov chain.

5.2.2 A few word on the proof : the ODE method

The occupation measure verifies the following recursion formula

$$\mu_{n+1} = (1 - \gamma_{n+1})\mu_n + \gamma_{n+1}\delta_{X_{n+1}}, \quad (5.9)$$

where $\gamma_n = 1/n$. When K_μ admits a unique invariant probability Π_μ , we can rewrite the evolution of (μ_n) as:

$$\mu_{n+1} = \mu_n + \gamma_{n+1}(-\mu_n + \Pi_{\mu_n}) + \gamma_{n+1}\varepsilon_n \quad (5.10)$$

where $\varepsilon_n = \delta_{X_{n+1}} - \Pi_{\mu_n}$. The process (μ_n) is therefore a *stochastic approximation algorithm*, as for instance the Robbins-Monro algorithm [238] or the SA-EM algorithm [119].

It can be studied through the ODE method, because, from (5.10), it is naturally associated to the following ordinary differential equation (ODE):

$$\dot{\mu} = -\mu + \Pi_{\mu}. \quad (5.11)$$

Indeed, Sequence $(\mu_n)_{n \geq 1}$ can be interpreted as a (noised by $\gamma_n \varepsilon_n$) Euler scheme discretization with decreasing step γ_n . To study it, we then embed it in a continuous-time process $(\bar{\mu}_t)_{t \geq 0}$: for $n \geq 1$, we set $\tau = 0$, $\tau_n = \sum_{k=1}^n \gamma_k$ and for $t \in [\tau_{n-1}, \tau_n)$, $\bar{\mu}_t = \mu_{\tau_{n-1}}$. See for instance Figure 6.1, Figure 6.2 or Figure 6.4 for this type of embedding.

The almost sure convergence of $(\bar{\mu}_t)$ towards μ^* (i.e. the QSD of K) can then be achieved by proving by the two following steps :

- (i) The asymptotic dynamics of $(\bar{\mu}_t)_{t \geq 0}$ matches with that of solutions of the ODE (5.11): more precisely, $(\bar{\mu}_t)_{t \geq 0}$ is an *asymptotic pseudo-trajectory* of the ODE (in the sense of Benaïm and Hirsch [26], see [23] for background).
- (ii) The set $\{\mu \in \mathcal{P}(X), \mu = \Pi_{\mu}\}$ reduces to μ^* and is a global attractor of the ODE.

In finite state space, the sequence of measure $(\mu_n)_n$ belongs to finite-dimensional space. There is then no topological difficulty to combine these two points. In infinite dimension, the distance (or norm) on which we prove these two points are in general not equivalent and is the main difficulty. we nevertheless use the approach of [28].

Step (ii) is close to problems of Section 3.3. Indeed, we can show that Equation (5.11) rewrites

$$\partial_t \mu_t = -\mu_t + \frac{\mu_t \mathcal{A}}{\mu_t \mathbf{A} \mathbf{1}},$$

with $\mathcal{A} = \sum_{n \geq 0} K^n$. In particular, this ODE is of Kimura type as in Section 3.6, and we can study it with linear techniques.

5.3 Perspectives

Commutation of limits for Fleming-Viot processes is not always perfectly understood and may be an interesting continuity of my previous works.

We are finishing the paper introduced in Section 5.1.3 for a variant of Kalman filter algorithm. This algorithm is a variant of switching Kalman Filter, and this last algorithm has been well used since its introduction [224]. Unfortunately, some approximations are done in these two algorithm for which no mathematical justification is known. A work is in progress to obtain quantitative bounds.

With Fabien Panloup, we are working on quantitative rate of convergence for the Aldous-Flannery-Palacios algorithm in non finite space. As results of Section 4.2, this is difficult because the error term is no longer a measure and we need sharp bound from the topological point of view. Nevertheless, in contrast with the Fleming-Viot processes, where we can naturally studied the limit at fixed time for large particles, here we naturally have to combine these two difficulties.

Finally, the behavior of the non-irreducible process is an interesting problem related the trap problem of bandit problem; see Section 6.1.1 below.

Chapter 6

Others stochastic algorithms

6.1 A general result for inhomogeneous Markov chain

Here are exposed results of [A7, A9] with Michel Benaïm and Florian Bouguet. In these work, we use the mathematical methodology used in Section 5.2 to other classical stochastic algorithms based on inhomogenous and freezing Markov chain.

More precisely, let us consider an in-homogeneous Markov chain $(Y_n)_{n \geq 0}$ on \mathbb{R}^d and a sequence $(\gamma_n)_{n \geq 0}$ verifying

$$\lim_{n \rightarrow \infty} \gamma_n = 0, \quad \sum_{n=0}^{+\infty} \gamma_n = +\infty. \quad (6.1)$$

We set, for continuous and bounded function f ,

$$\mathcal{L}_n f(y) = \frac{\mathbb{E} [f(Y_{n+1}) - f(Y_n) \mid Y_n = y]}{\gamma_{n+1}}. \quad (6.2)$$

We shown general quantitative asymptotic results when \mathcal{L}_n converges, in some sense, to the generator \mathcal{L} of an ergodic Markov process $(Y_t)_{t \geq 0}$.

Rather than describe the technical general result of [A9], let us describe in sections that follow, the main example for which these results were applied : A penalized bandit algorithm, decreasing step Euler Scheme and the coin-turning walk.

However, note that the idea to use pseudo-trajectories for in-homogeneous Markov processes has been extended, under more easier and tractable conditions, for continuous-time processes in [206]. These results were used to analyze a Hawkes type process and a Cox-Ingersoll-Ross type jump process. We

can also see that [A9] permits to easily recover and extend some results of [228] which relates maximum of i.i.d. random variables to the invariant distributions of some PDMP.

6.1.1 A penalized bandit algorithm

In [A9, Section 3.2], we slightly generalize the penalized bandit algorithm introduced in [197], and we recover and extend their Theorem 4.

Let us consider two choices A and B , with respective unknown gain probabilities $1 \geq p_A > p_B \geq 0$.

Let us describe a player strategy to optimize the number of gain by doing the better choices between A and B . Let $x_n \in [0, 1]$ be a measure of her trust level in A at time n . She chooses A with probability x_n ¹ independently from the past, and updates x_n as follows:

- If she plays A then $x_{n+1} = x_n + \gamma_{n+1}(1 - x_n)$ in case of gain and $x_{n+1} = x_n - \gamma_{n+1}^2 x_n$ in case of loss.
- If she plays B then $x_{n+1} = x_n - \gamma_{n+1} x_n$ in case of gain and $x_{n+1} = x_n + \gamma_{n+1}^2(1 - x_n)$ in case of loss.

This recursive procedure that we described was designed independently in the fields of mathematical psychology [225], engineering [248], clinical trials or finance [198]. In a financial framework x_n can be related to the managed fund although in a clinical setting x_n can be the proportion tested patient. From a mathematical point of view *bandit algorithm* are important because they are simple examples of stochastic algorithms with a trap [132, 231]. Namely it is possible that x_n does not converge to the attempted value. However, this type of algorithm is not the best type of algorithm to maximize the gain. Indeed, best algorithm are notably based on Upper Confidence Bound (UCB); that is we build two confidence intervals of p_A and p_B and you play the choice which have the larger upper bound; see [154] and reference therein.

If we forgot the square on γ and consider $\gamma_n = 1/n$ then it essentially consists to attribute to A or B their mean gain. This is known to make the algorithm fallible [198]. Replacing the γ_n^2 term is a penalization of the loss to improve the algorithm. To improve further the algorithm, [153] introduces an over-penalized version of this algorithm.

¹ $s(x_n)$ in [A9] with $s : [0, 1] \rightarrow [0, 1]$ be a function, which can be understood as a player's strategy, such that $s(0) = 0, s(1) = 1$. Let us set $s(x) = x$ as in [197] for sake of presentation here.

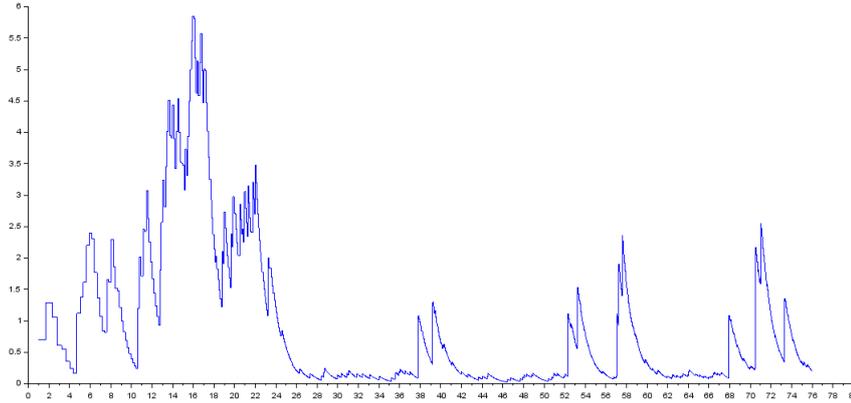


Figure 6.1: Trajectory of an interpolated process of (y_n) in case of penalized bandit.

Theorem 2.8 of [A9] applies for $y_n = \gamma_n^{-1}(1 - x_n)$ and $\gamma_n = n^{-1/2}$. We obtain that the sequence of operators $(\mathcal{L}_n)_{n \geq 1}$ converges to the one of a piece deterministic Markov process with generator

$$\mathcal{L}f(y) = -yp_A f'(y) + yp_B(f(y+1) - f(y)).$$

Consequently, (y_n) converges to the associated invariant measure that have explicit polynomial and exponential moments. This also leads to a functional convergence illustrated in Figure 6.1

We can read in the form of \mathcal{L} that we play a very high number of arm A and that therefore x_n almost decreases in a deterministic way during long time intervals but that at some random time longer and longer (because $\gamma_n \rightarrow 0$), we play the arm B , win and therefore we bias our trust in level A .

6.1.2 Decreasing step Euler scheme

Decreasing step Euler scheme is the classical Markov chain defined by

$$y_{n+1} = y_n + \gamma_{n+1}b(y_n) + \sqrt{\gamma_{n+1}}\sigma(y_n)E_{n+1},$$

where (γ_n) verifies (6.1) and (E_n) is a suitable sequence of reduced and centered random variables, aiming to approximate the stationary measure of the diffusion process solution to

$$X_t^x = x + \int_0^t b(X_s)ds + \int_0^t \sigma(X_s)dW_s,$$

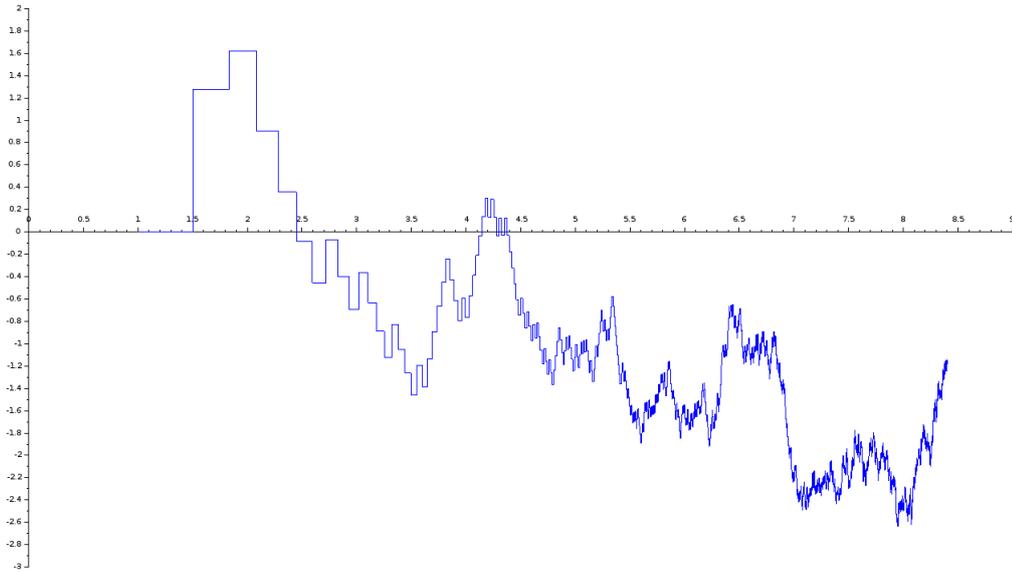


Figure 6.2: Trajectory of an interpolated process of (y_n) in case of decreasing step Euler scheme.

where (W_s) is a Brownian motion. Parameter b, σ will be described hereafter.

This model was studied in [202, 196] and previously for a constant step size in [258, 257].

In [A9, Section 3.3], we assumed that E_n are sub-gaussian, $b, \sigma C^\infty$ whose bounded derivatives of any order and σ is bounded. Moreover, for large y , we assume that

$$-b_2 y^2 \leq b(y)y \leq -b_1 y^2, \sigma_1 \leq \sigma(y),$$

for some $\sigma_1 > 0$ and $b_2 \geq b_1 > 0$. In case of $\gamma_n = 1/n$, we obtain the convergence of (y_n) to the desired invariant distribution π . We moreover have a functional result (illustrated in Figure 6.2) and a rate of convergence of the type, for all $n \geq 0$

$$\left| \mathbb{E}[f(y_n)] - \int f d\pi \right| \leq \frac{C_f}{n^k}$$

for some $k > 0$, explicit $C_f > 0$ and all compactly supported function f^2 . To our knowledge, this was the first result and, from now on, the only result stating a rate of convergence without supposing that σ is constant and b uniformly convex (giving then a uniform contraction properties); see for instance [202, Theorem IV.1], and [134, 196] for such cases.

²To be more precise, bounded functions with bounded derivative of order 1, 2 and 3 may be considered with a uniform constant C_f .

6.1.3 Freezing Markov chain and the coin-turning walk

Let $(i_n)_{n \geq 1}$ be an inhomogeneous-time Markov chain with finite state space $\{1, \dots, D\}$ with the following transitions when $i \neq j$:

$$P(i_{n+1} = j \mid i_n = i) = q_n(i, j) = p_n(q(i, j) + r_n(i, j)),$$

where $(p_n)_{n \geq 1}$ is a decreasing sequence converging toward some $p \in [0, 1]$, the remainders $r_n(i, j)$ tend to 0 (fast enough) and q is the discrete generator of some $\{1, \dots, D\}$ -valued ergodic Markov chain. This model is related to the simulated annealing algorithm, and the sequence $(p_n)_{n \geq 1}$ can be interpreted as the cooling scheme of an underlying Markov chain generated by q . If $p < 1$, since $\lim_{n \rightarrow \infty} q_n(i, j) = pq(i, j)$, the probability of $(i_n)_{n \geq 1}$ to move decreases over time, from which the appellation freezing Markov chain.

The behavior of $(i_n)_{n \geq 1}$ is very simple and relies on the summability of the sequence $(p_n)_{n \geq 1}$. It shall converge in distribution to the unique invariant probability ν associated to q if $\sum_{n \geq 1} p_n = +\infty$. Conversely, if $\sum_{n \geq 1} p_n < +\infty$, the Markov chain shall freeze along the way, as a consequence of the Borel-Cantelli Lemma.

In [A7], we investigate the study of the empirical distribution $x_n = \frac{1}{n} \sum_{k=1}^n \delta_{i_k}$ in case of $\sum_{n \geq 1} p_n = +\infty$. In what follows, for sake of presentation here, we assume $r_n = 0$.

Firstly, when (p_n) decreases slowly to 0, we have the convergence of x_n to ν . This convergence is in probability when $\lim_{n \rightarrow \infty} np_n = +\infty$ and almost-sure when $\sum_{n \geq 0} 1/(n^2 p_n) < +\infty$ (with an explicit rate of convergence). Moreover when

$$\frac{p_{n+1}}{p_n} = 1 + \frac{Y}{n} + o\left(\frac{1}{n}\right),$$

then the sequence whose terms are $y_n = \sqrt{np_n}(x_n - \nu)$ converges to a normal distribution. This includes for instance $p_n = 1/n^Y$. These results may be expected since they generalize the classical setting of convergence of the empirical mean of homogeneous Markov chain.

The situation is more surprising when $p_n \sim a/n$, for some $a > 0$. Indeed, in this case, x_n no longer converge to ν . Indeed, the vector (x_n, i_n) converges in law to some probability measure π on $[0, 1]^D \times \{1, \dots, D\}$. This measure π corresponds to the invariant measure of the exponential zig-zag process that is the Markov process generated by

$$\mathcal{L}f(x, i) = (e_i - x) \cdot \nabla_x f(x, i) + \sum_{j \neq i} aq(i, j)(f(x, j) - f(x, i)),$$

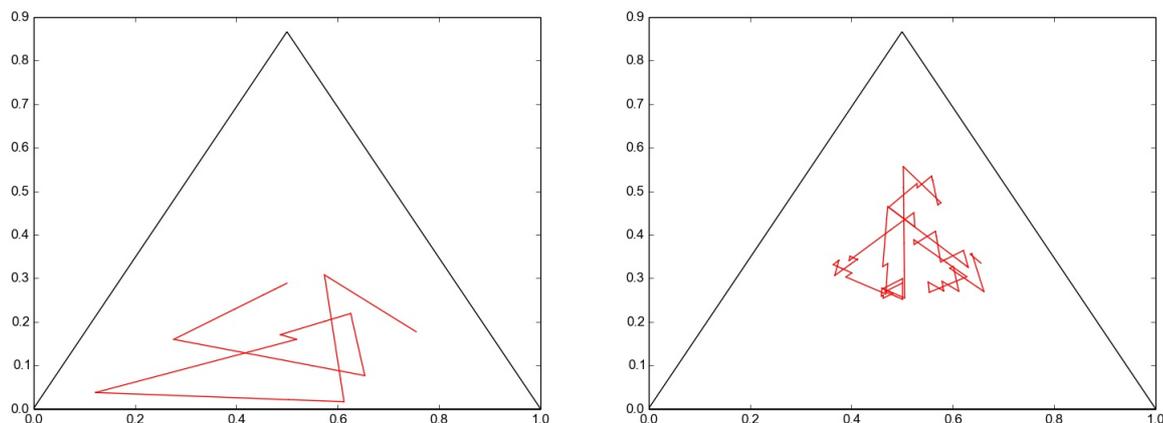


Figure 6.3: Two paths of the exponential zig-zag process. Here \mathbb{R}^3 is represented using a barycentric coordinate system. The vertices of the triangle represent each element of the base of \mathbb{R}^3 and the process starts at the center of the triangle (corresponding to the uniform distribution). We can see in the right that when a is large, the process diffuses and is concentrated.

where $(e_i)_{1 \leq i \leq D}$ is the canonical basis of $[0, 1]^D$. This process runs towards one of the vectors of the base and then at exponential times changes its objective; see Figure 6.3 for a path of this process for $D = 3$. When $q(i, j) = \theta_j$ does not depend on i then the invariant measure is a mixture of Dirichlet distributions. When a tends to infinity the exponential zig-zag process converge to an Ornstein-Uhlenbeck process and there is then a kind of continuity between the two behaviors. Again due to the techniques of the proof, we have several additional results including rate of convergence and functional results as illustrated in Figure 6.4.

The problem of Freezing Markov chain dated from the thesis of Dobrushin [123]. Even if some results can be obtained from the general theory developed in [230, 247], our results can be compared to [139, 138, 122]. Article [122] works on the complete graph dynamics and [138] on the case $D = 2$. They obtained the surprising limits of (x_n) and (y_n) in case of $p_n = 1/n^\theta$ and inspired us to study this model. Their proofs are based on the method of moments which require explicit expression that is not possible for general kernel q and sequence (p_n) . The follow up work [139] is also appealing because it studies another scaling of the deviation sequence (y_n) and obtain the convergence to a non-ergodic linear zig-zag process. It is a Donsker type theorem. The link between exponential and non-exponential zig-zag process is quite similar to the relation between Brownian motion and Ornstein-Uhlenbeck process in the central limit

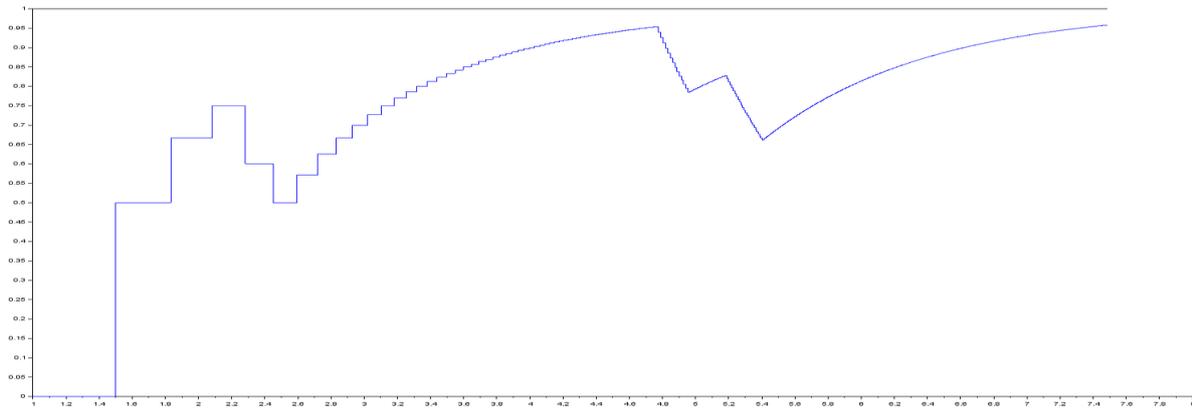


Figure 6.4: Trajectory of an interpolated process of $(x_n(1))_{n \geq 0}$ in case of freezing Markov chain when $D = 2$.

theorem (see for instance [A9, Section 3.1]) . Some techniques we developed in [A7] were used in other context [143] and applied for a stochastic multistate promoter model of dynamic mRNA/protein interactions in [205]. Finally, even if this type of problem seems simple, several questions pointed out in [138] remain open.

6.2 Some others algorithms

I had some weak contribution in [P3, P6] to some works on some numerical algorithm that I list here.

I work with for anomaly Detection in Time Series in [P6] by proposing a new algorithm for calculating the so-called *Matrix profile* of a time series. See [46] for an introduction on the subject. It mainly consists of visiting cleverly a time series to calculate some best functional distances.

I also contribute marginally to [P3] on a variant of ABC algorithm using Random Forest algorithm instead of nearest neighborhood one plus a sensitivity analysis to reduce the number of variables. This is used to propose an automated calibration for a complex aquatic model.

6.3 Perspectives

From a mathematical point of view, results of Section 6.1.2 are interesting but a current issue should be to estimate the dependence on the dimension for such

discretization scheme as in [134] in larger dimension. Also, as already said, several questions of [138] remain unsolved.

Projet de recherche

Chapter 7

Projet de recherche

Dans ce manuscrit, nous avons donné un aperçu de la recherche en dynamique des populations. Bien que les thèmes que j'ai abordés ne couvrent qu'une faible partie des recherches sur le sujet, nous avons pu voir l'étendue des questions mathématiques qui restent ouvertes dans les sections de perspective. Je compte donc travailler sur ces questions avec une articulation particulière entre modèles et algorithmes.

Plus précisément, deux projets de recherche structurent actuellement mon activité : le projet ANR NOLO et le projet H2020 TechCare. Ces derniers reposent sur

- L'étude mathématique de modèles de branchement tels que développés dans le chapitre 3.
- La mise en place d'algorithmes pour le bien-être animal à partir de données de capteurs. Cette partie est liée aux travaux des sections 4.5, 5.1.3 et 6.2.

Bien que ces financements ne couvrent environ que les deux prochaines années, je compte suivre comme direction de recherche ces deux directions dans les années à venir.

Pour les processus de branchement, je vais travailler sur des hypothèses simples et générales pour des lois des grands nombres et théorèmes de la limite centrale pour des processus de branchement, sur les liens entre des théorèmes *à la* Meyn-Tweedie et *à la* Krein-Rutman pour des semi-groupes non-conservatifs positifs, ainsi que la mise en place d'outils pour leur utilisation pour des questions concrètes.

Sur le deuxième axe, j'ai déjà entamé plusieurs travaux. Bien qu'initialement, le but était d'apporter une expertise en statistiques pour les différents problèmes, plusieurs questions mathématiques émergent naturellement

du problèmes. Citons par exemple les travaux d'Adrien Cotil exposés dans la section 4.5 ou la démonstration mathématique de l'efficacité d'algorithmes tels que ceux utilisés dans la section 5.1.3.

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