Recombination semigroups on measure spaces

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Abstract

The dynamics of recombination in genetics leads to an interesting nonlinear differential equation, which has a natural generalization to a measure valued version. The latter can be solved explicitly under rather general circumstances. It admits a closed formula for the semigroup of nonlinear positive operators that emerges from the forward flow and is, in general, embedded in a multi-parameter semigroup.

Key Words: recombination, nonlinear ODEs, positive semigroups, measure-valued dynamical systems, Möbius inversion

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1 Introduction

The deterministic limit of the stochastic process of recombination in population genetics leads to an interesting nonlinear ODE system that has been studied for a long time. The first major advances to understand the classical system are due to H. Geiringer [11] in the 1940s (though her formulation was slightly different). A full characterization of solutions (though not in explicit form) was later obtained by Lyubich, compare [12] and references given there, and [8] for general background material.

Motivated by this problem in genetics, a relevant subclass was considered in [4], where an explicit solution to the resulting large system of nonlinear differential equations was constructed. Soon after, this was reformulated as a measure valued differential equation and solved for a more general class of state spaces [6]. In this context, the main focus was not on the functional analytic properties, but on the solution and the interaction with other genetic processes, in particular mutation and selection.

On the other hand, nonlinear semigroups are rarely known explicitly, and if so, this usually rests upon the transformability of the system to a linear one. With this observation in mind, it seems worthwhile to also investigate the semigroup aspect separately. To do so, we will first consider the most elementary semigroup constituents separately. Among them, we will identify mutually commuting ones, which are then used to reconstruct the solution to the full recombination equation of [6] in a simpler than the previous way. Furthermore, generalizations are possible that are less relevant in biological applications, but illustrate that the mathematical analysis may still be pushed considerably.

In view of the origin of the problem, the formulation is oriented towards the application in mathematical biology. Consequently, the formulation is slightly more expository than necessary for a purely mathematical audience. In a separate section, an abstract reformulation of the central observation is added, together with a possible generalization to a wider class of nonlinear operators.

2 Mathematical setting

If $X$ is a locally compact space (by which we always mean to include the Hausdorff property), we denote by $\mathcal{M}(X)$ the Banach space of finite regular Borel measures, equipped with the usual variation norm $\|\cdot\|$, i.e., $\|\omega\| := |\omega|(X)$ where $|\omega|$ denotes the total variation measure of $\omega$. $\mathcal{M}(X)$ is a Banach lattice, and we use $\mathcal{M}_+(X)$ (resp. $\mathcal{P}(X)$) to denote the closed convex cone of positive measures (resp. the closed simplex of probability measures). For positive measures $\omega$, one has $\|\omega\| = \omega(X)$. We will mainly be concerned with the situation that $X$ is itself a product space, e.g., $X = X_1 \times X_2$ with $X_i$ locally compact. Let us first recall a well-known result, compare [7] and [6] Fact 1 for details.
Fact 1. Let $\nu, \nu'$ be two regular Borel measures on the locally compact product space $X = X_1 \times X_2$, and let $\nu, \nu'$ coincide on all “rectangles” $E_1 \times E_2$ where $E_1$ and $E_2$ run through the Borel sets of $X_1$ and $X_2$, respectively. Then, $\nu = \nu'$, i.e., $\nu(E) = \nu'(E)$ for all Borel sets $E$ of $X$. \hfill $\square$

The state space $X$ that we need will have a product structure, described on the basis of sites or nodes. For later convenience, we use $N = \{0, 1, \ldots, n\}$ for the set of nodes, i.e., we start counting with 0 here. To node $i$, we attach the locally compact space $X_i$, and our state space is then

$$X = X_0 \times X_1 \times \ldots \times X_n$$

which is still locally compact. Our dynamics will evolve in the Banach space $\mathcal{M}(X)$ which canonically contains the tensor product $\mathcal{M}(X_0) \otimes \ldots \otimes \mathcal{M}(X_n)$ and also its completion, the corresponding projective tensor product. In fact, product measures $\omega = \omega_0 \otimes \ldots \otimes \omega_n$ with $\omega_i \in \mathcal{M}(X_i)$ will play an important role below.

The main reason for using the above set $N$ of nodes is that we will need ordered partitions of $N$ which are uniquely specified by a set of cuts or crossovers. The possible cut positions are at the links between nodes, which are denoted by half-integers, i.e., by elements of the set $L = \{\frac{1}{2}, \frac{3}{2}, \ldots, \frac{2n-1}{2}\}$. We use Latin indices for nodes and Greek indices for links, and the implicit rule will be that $\alpha = \frac{2i+1}{2}$ is the link between nodes $i$ and $i + 1$.

With this notation, the ordered partitions of $N$ are in one-to-one correspondence with the subsets of $L$ as follows. If $A = \{\alpha_1, \ldots, \alpha_p\} \subset L$, with $\alpha_i < \alpha_{i+1}$, let $N_A = \{A_0, A_1, \ldots, A_p\}$ denote the ordered partition

$$A_0 = \{0, \ldots, \lfloor \alpha_1 \rfloor\}, \ A_1 = \{\lfloor \alpha_1 \rfloor, \ldots, \lfloor \alpha_2 \rfloor\}, \ldots, A_p = \{\lfloor \alpha_p \rfloor, \ldots, n\}$$

where $\lfloor \alpha \rfloor$ ($\lceil \alpha \rceil$) is the largest integer below $\alpha$ (the smallest above $\alpha$). So, while $A \subset L$, one has $A_i \subset N$ for $0 \leq i \leq p$. In particular, we have $N_{\emptyset} = N$ and $N_1 = \{\{0\}, \ldots, \{n\}\}$. With this definition, it is clear that $N_B$ is a refinement of $N_A$ if and only if $A \subset B$. Consequently, the lattice of ordered partitions of $N$ now corresponds to the Boolean algebra of all subsets of the finite set $L$, denoted by $\mathcal{B}(L)$, cf. [1] Ch. I.2. We prefer this notation to that with partitions, as it is easier to deal with. If $A \subset B$, we will write $B - A$ for $B \setminus A$, and $\bar{A}$ for the set $L - A$.

Let $X, Y$ be two locally compact spaces with attached measure spaces $\mathcal{M}(X)$ and $\mathcal{M}(Y)$. If $f : X \to Y$ is a continuous function and $\omega \in \mathcal{M}(X)$, $f_\omega := \omega \circ f^{-1}$ is an element of $\mathcal{M}(Y)$, where $f^{-1}(y) := \{x \in X \mid f(x) = y\}$ means the preimage of $y \in Y$ in $X$, with obvious extension to $f^{-1}(B)$, the preimage of a subset $B \subset Y$ in $X$. Due to the continuity of $f$, $f^{-1}(B)$ is a Borel set in $X$ if $B$ is a Borel set in $Y$.

From now on, let $X = X_0 \times \ldots \times X_n$ and let $N$ and $L$ always denote the set of nodes and links as introduced above. Let $\pi_i : X \to X_i$ be the canonical projection, which is continuous. It induces a mapping from $\mathcal{M}(X)$ to $\mathcal{M}(X_i)$ by $\omega \mapsto \pi_i \omega$, where $(\pi_i \omega)(E) = \omega(\pi_i^{-1}(E))$,
for any Borel set $E \subset X_i$. By (slight) abuse of notation, we will use the symbol $\pi_i$ also for this induced mapping. It is clear that $\pi_i$ is linear and preserves the norm of positive measures. In particular, it maps $\mathcal{P}(X)$ to $\mathcal{P}(X_i)$ and may then be understood as marginalization.

Likewise, for any index set $I \subset N$, one defines a projector $\pi_I : \mathcal{M}(X) \to \mathcal{M}(X_I)$ with $X_I := \times_{i \in I} X_i$. With this notation, $X_N = X$. We will frequently also use the abbreviation $\pi_{<\alpha}$ for the projector $\pi_{\{1, \ldots, \lfloor \alpha \rfloor\}}$, and $\pi_{>\alpha}$ for $\pi_{\lceil \alpha \rceil, \ldots, n}$.

This enables us to introduce a class of nonlinear operators, called *recombinators* from now on. For $\alpha \in L$, we first define an elementary recombinator $R_\alpha : \mathcal{M}(X) \to \mathcal{M}(X)$ by

$$R_\alpha(0) = 0 \text{ and, if } \omega \neq 0, \text{ by } R_\alpha(\omega) := \frac{1}{\|\omega\|} \left( (\pi_{<\alpha} \omega) \otimes (\pi_{>\alpha} \omega) \right)$$

which is a (partial) product measure. Here and in what follows, we tacitly identify (if necessary) a product measure with its unique extension to a regular Borel measure on $X$, which is justified by Fact 1. These elementary recombinators satisfy a number of useful properties [6]. In particular, $\|R_\alpha(\omega)\| \leq \|\omega\|$ for all $\omega \in \mathcal{M}(X)$, $R_\alpha$ is globally Lipschitz on $\mathcal{M}(X)$ with Lipschitz constant $\leq 3$, and $R_\alpha(a \omega) = |a| R_\alpha(\omega)$ for all $a \in \mathbb{R}$ and $\omega \in \mathcal{M}(X)$. Moreover, $R_\alpha$ maps $\mathcal{M}_+(X)$ into itself and preserves the norm of positive measures, so that $\mathcal{P}(X)$ is mapped into itself, too. Finally, when restricted to $\mathcal{M}_+(X)$, the elementary recombinators are idempotents and commute, i.e., $R_\alpha^2 = R_\alpha$ and $R_\alpha R_\beta = R_\beta R_\alpha$ for all $\alpha, \beta \in L$.

As the next step, let $A = \{\alpha_1, \ldots, \alpha_p\} \subset L$, with $\alpha_i < \alpha_{i+1}$, and let $N_A$ be the corresponding ordered partition of $N$, as explained above. Then, we define the (composite) recombinators $R_A$ by

$$R_A(\omega) := \frac{1}{\|\omega\|} \left( \bigotimes_{i=0}^{p} (\pi_{A_i} \omega) \right),$$

again with the continuous extension $R_A(0) = 0$. Note that $R_\emptyset = 1$ and $R_{\{\alpha\}} = R_\alpha$ in this notation. As a direct consequence of the definition, or by a simple induction argument based on the properties of the elementary recombinators, one obtains the following result, compare [6] for details.

**Proposition 1** Let $R_A$ be the (composite) recombinator attached to a subset $A$ of $L$. Then, the following assertions hold.

1. $\|R_A(\omega)\| \leq \|\omega\|$ for all $\omega \in \mathcal{M}(X)$, and $R_A$ is globally Lipschitz on $\mathcal{M}(X)$.

2. $R_A$ is positive homogeneous of degree 1, i.e., $R_A(a \omega) = |a| R_A(\omega)$ for all $a \in \mathbb{R}$ and $\omega \in \mathcal{M}(X)$. 


3. $R_A$ maps $\mathcal{M}_+(X)$ into itself and preserves the norm of positive measures. In particular, it maps $\mathcal{P}(X)$ into itself.

4. On $\mathcal{M}_+(X)$, one has $R_A = \prod_{\alpha \in A} R_\alpha$, and the recombinators satisfy the equation

$$R_G R_H = R_{G \cup H},$$

for arbitrary $G, H \subset L$. □

Note that Part 4, when applied to singleton sets, comprises both the idempotency and the commutativity of the elementary recombinators.

### 3 Recombination dynamics

Originally motivated by a problem in biology, compare [4], we are interested in the solutions of the nonlinear ODE

$$\dot{\omega} = \Phi(\omega) := \sum_{G \subset L} \varrho_G \left( R_G - 1 \right)(\omega)$$

(4)

on the Banach space $\mathcal{M}(X)$, with the restriction $\varrho_G \geq 0$. In general, even though the Picard-Lindelöf theorem applies ($\Phi$ is globally Lipschitz) and the time evolution is given by the flow of the ODE, it does not seem possible to write down a closed formula for the corresponding semigroup in forward time.

However, if $\varrho_G > 0$ only for special $G$, namely the singleton sets $\{\alpha\}$ with $\alpha \in L$, it was shown in [6] that the solution in forward time can be given in closed form, if the initial condition is a positive measure. This amounts to constructing an explicit formula for the nonlinear flow of this ODE on the positive cone $\mathcal{M}_+(X)$. In what follows, we will give an independent derivation of this, and an extension to further solvable cases, independent of its biological relevance. Let us start with a general property.

**Proposition 2** The abstract Cauchy problem of the ODE (4) has a unique solution. Furthermore, $\mathcal{M}_+(X)$ is positive invariant under the flow, with the norm of positive measures preserved. In particular, $\mathcal{P}(X)$ is positive invariant.

**Proof:** Existence and uniqueness of the solution follows from the Picard-Lindelöf theorem on Banach spaces, see [2] Thm. 7.6 and Remark 7.10], because $\Phi$ is globally Lipschitz as a consequence of Part 1 of Proposition [1].

Let $\nu \in \mathcal{M}_+(X)$, i.e., $\nu(E) \geq 0$ for all Borel sets $E \subset X$. Let $E$ be any Borel subset of $X$ such that $\nu(E) = 0$. Then

$$\Phi(\nu)(E) = \sum_{G \subset L} \varrho_G R_G(\nu)(E) \geq 0$$

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because each $R_G(\nu)$ is a positive measure and all $\rho_G \geq 0$ by assumption, so $\Phi$ satisfies the positive minimum principle, compare [3]. By a continuity argument, see p. 235, Thm. 16.5 and Remark 16.6 of [2], we obtain the invariance of the cone $M_+(X)$ under the flow in forward time.

Finally, observe that $\Phi(\nu)(X) = 0$ for all $\nu \in M_+(X)$, which is a consequence of Part 3 of Proposition 1. Let $\omega_0 \in M_+(X)$ be the initial condition, and $\omega_t$ the corresponding solution. So, $\omega_t \in M_+(X)$ for all $t \geq 0$ by the previous argument, hence $\|\omega_t\| = \omega_t(X)$. This implies $\frac{d}{dt}\|\omega_t\| = \Phi(\omega_t)(X) = 0$, so $\|\omega_t\| \equiv \|\omega_0\|$ for all $t \geq 0$.

\section{3.1 Time evolution with one recombinator}

Proposition 2 is important because it allows us to concentrate on the positive cone, and to study the forward flow, which is a nonlinear positive semigroup. Our first step is to analyze the explicit solution, in forward time, of the ODE

$$\dot{\omega} = \rho_A (R_A - 1)(\omega)$$

for an arbitrary, but fixed $A \subset L$, with $\rho_A > 0$.

\textbf{Lemma 1} Let $\nu \in M_+(X)$ and $a \in [0,1]$. Then, we have

$$R_A (a\nu + (1-a)R_A(\nu)) = R_A(\nu).$$

So, $R_A$ acts linearly on this type of convex combination, and we also get

$$(R_A - 1)(a\nu + (1-a)R_A(\nu)) = a(R_A - 1)(\nu).$$

\textbf{Proof:} Since $R_A$ is positive homogeneous of degree 1, it is sufficient to prove the claim for $\nu \in P(X)$, where $\|\nu\| = 1$. If $A = \{\alpha_1, \ldots, \alpha_p\} \subset L$, and $N_A = \{A_0, A_1, \ldots, A_p\}$, with $A_i \subset N$, is the corresponding partition of $N$, we obtain

$$R_A (a\nu + (1-a)R_A(\nu)) = \bigotimes_{i=0}^p \left( a \pi_{A_i} \cdot \nu + (1-a) \pi_{A_i} \cdot R_A(\nu) \right) = \bigotimes_{i=0}^p \left( a \pi_{A_i} \cdot \nu + (1-a) \pi_{A_i} \cdot R_A(\nu) \right).$$

This proves the first claim, while a verification of the second is now straightforward.

\textbf{Proposition 3} Let the initial condition $\omega_0$ for equation (5) be a positive measure. Then, the solution for $t \geq 0$ is $\omega_t = \varphi^A_t(\omega_0)$ where $\{\varphi^A_t \mid t \geq 0\}$ is a semigroup of nonlinear positive operators. They are explicitly given by

$$\varphi^A_t = e^{-\rho_A t} \mathbf{1} + (1-e^{-\rho_A t}) R_A = R_A - e^{-\rho_A t} (R_A - 1)$$
and, on $\mathcal{M}_+(X)$, satisfy the equation
\[
\frac{d}{dt} \varphi^A_t = \varrho_A(R_A - 1) \circ \varphi^A_t.
\]

Finally, $\omega_t \supset \supset R_A(\omega_0)$ as $t \to \infty$, for all $\omega_0 \in \mathcal{M}_+(X)$, with the deviation from the limit decaying exponentially fast in time.

**Proof:** Let $\omega_0$ be a positive measure, and $\omega_t = e^{-\varrho_A t} \omega_0 + (1 - e^{-\varrho_A t}) R_A(\omega_0)$. Then, we have
\[
\dot{\omega}_t = \varrho_A e^{-\varrho_A t} (R_A - 1)(\omega_0).
\]

On the other hand, since $e^{-\varrho_A t} \in [0, 1]$, we can apply Lemma 1 to verify that also
\[
\varrho_A(R_A - 1)(\omega_t) = \varrho_A e^{-\varrho_A t} (R_A - 1)(\omega_0)
\]
which establishes that $\omega_t$ is indeed a solution of the Cauchy problem with initial condition $\omega_0$, while uniqueness follows from Proposition 2.

Let $\{\varphi^A_t \mid t \geq 0\}$ denote the corresponding forward flow, where $\varphi^A_t$ then is the nonlinear operator stated in the proposition. It maps $\mathcal{M}_+(X)$ into itself, preserves the norm of positive measures, and satisfies the equation
\[
\varphi^A_t \circ \varphi^A_s = \varphi^A_{t+s}
\]
by the general properties of the flow. Since the formula for the solution is valid for all initial conditions $\omega_0 \in \mathcal{M}_+(X)$, the formula for the derivative is correct on $\mathcal{M}_+(X)$.

The statement about the norm convergence of $\omega_t$ to the product measure $R_A(\omega_0)$ follows from the form of $\varphi_t$ by standard arguments.

It is somewhat surprising that such a simple formula for the solution emerges. It admits a probabilistic interpretation as follows. If $\varrho_A$ is the rate of the recombination process with $R_A$, the term $e^{-\varrho_A t}$ (resp. $(1 - e^{-\varrho_A t})$) is the probability that recombination has not yet taken place (resp. has happened at least once) until time $t$. This can be substantiated by viewing the ODE (5) as the deterministic limit of an underlying stochastic process, e.g., in the spirit of [10, Sec. 11].

Let us also note that the formula for $\varphi^A_t$ would formally emerge from expanding $\exp(\varrho_A t (R_A - 1))$ as if $R_A$ were a linear idempotent, which it isn’t. Nevertheless, the result is still correct as a consequence of Lemma 1 because linearity on those special convex combinations is all that is needed to derive the formula properly.

Still, the right hand side of (5) is genuinely nonlinear. In general, it is well known, compare [9, p. 91], that $T^A_t(f) := f \circ \varphi^A_t$ defines a semigroup of linear operators on the dual space of $\mathcal{M}(X)$. One can also define the corresponding generator, but this approach does not seem to help in understanding the result of Proposition 3.
However, assume \( \omega_0 \in \mathcal{M}_+(X) \) and define the two signed measures \( \nu_1(t) = R_A(\omega_t) \) and \( \nu_2(t) = (R_A - 1)(\omega_t) \). Then, one has \( \omega_t = \nu_1(t) - \nu_2(t) \), but also \( \nu_1(t) \equiv R_A\omega_0 \) and \( \nu_2(t) = e^{-\varrho_A t}(R_A - 1)(\omega_0) \), by an application of Lemma \( \text{[1]} \). Consequently, these measures satisfy the differential equations

\[
\dot{\nu}_1 \equiv 0 \quad \text{and} \quad \dot{\nu}_2 = -\varrho_A \nu_2
\]

which shows that the ODE \( \text{[5]} \), when restricted to the cone \( \mathcal{M}_+(X) \), is equivalent to a system of two linear ODEs together with special initial conditions. Also, \( \nu_1 \) is the equilibrium, and \( \|\nu_2(t)\| \to 0 \) exponentially fast as \( t \to \infty \).

### 3.2 Abstract reformulation and possible extension

In view of other applications, it might be worth to extract the underlying structure of Proposition \( \text{[3]} \) as follows.

**Theorem 1** Let \( K \) be a closed convex subset of a Banach space \( B \), and let \( \mathcal{R} : K \to K \) be a (nonlinear) Lipschitz map which satisfies

\[
\mathcal{R}(ax + (1-a)\mathcal{R}(x)) = \mathcal{R}(x)
\]

for all \( a \in [0,1] \) and all \( x \in K \). Let \( \varrho \geq 0 \) be arbitrary.

Then, the (nonlinear) Cauchy problem

\[
\dot{x} = \varrho(\mathcal{R} - 1)(x), \quad x(0) = x_0 \in K,
\]

has the unique solution \( x(t) = e^{-\varrho t}x_0 + (1 - e^{-\varrho t})\mathcal{R}(x_0) \) for \( t \geq 0 \), and the entire forward orbit remains in \( K \).

**Proof:** As above, the uniqueness follows from Lipschitz continuity. The formula for the solution is again verified by direct differentiation, using \( \text{[4]} \). Note that this assumed property comprises the linearity on special convex combinations and the idempotency of \( \mathcal{R} \) (by setting \( a = 0 \)). Since \( K \) is a closed convex set which is mapped into itself by \( \mathcal{R} \), its forward invariance under the flow follows by standard arguments, compare \( \text{[2]} \). \( \square \)

Several generalizations seem possible at first sight, but most of them break down rather quickly as soon as genuine nonlinearity of \( \mathcal{R} \) sets in. First, consider the ansatz

\[
\mathcal{R}(ax + (1-a)\mathcal{R}^n(x)) = \mathcal{R}(x),
\]

for some \( n > 1 \), and again for all \( a \in [0,1] \) and all \( x \in K \). This includes the relation \( \mathcal{R}^{n+1}(x) = \mathcal{R}(x) \) for \( x \in K \), a generalization of the idempotency used previously. Here, an explicit solution of the Cauchy problem \( \text{[7]} \) would contain all the terms \( x_0, \mathcal{R}(x_0), \ldots, \mathcal{R}^n(x_0) \), so that \( \text{[8]} \) cannot suffice as a substitute for linearity.
Alternatively, one might consider the ansatz
\[
\mathcal{R}(a_0 x + a_1 \mathcal{R}(x) + \ldots + a_n \mathcal{R}^n(x)) = \mathcal{R}(x)
\]
(on \(K\), where the coefficients \(a_i \geq 0\) with \(a_0 + \ldots + a_n = 1\) define general convex combinations. With \(a_1 = 1\) (hence \(a_i = 0\) for all \(i \neq j\)), this comprises \(\mathcal{R}^{j+1} = \mathcal{R}\) on \(K\), hence also \(\mathcal{R}^2 = \mathcal{R}\), so that this ansatz cannot yield an extension of (6).

Any meaningful generalization of (6) seems to require a partial linearity of \(\mathcal{R}\), namely on a subset of the convex combinations used in (9). To construct one possibility, fix \(n \geq 2\), set \(\xi := \exp(2\pi i/n)\), and define
\[
G^{(n)}_k(t) := \frac{1}{n}(e^t + \xi^k e^{\xi t} + \xi^{2k} e^{\xi^2 t} + \ldots + \xi^{(n-1)k} e^{\xi^{n-1} t})
\]
for \(k \in \mathbb{Z}\). Due to \(\xi^n = 1\), this definition is modulo \(n\) in the lower index \(k\). Observing
\[
\frac{1}{n} \sum_{m=0}^{n-1} \xi^{mM} = \begin{cases} 1, & \text{if } n \text{ divides } M \\ 0, & \text{otherwise} \end{cases}
\]
and expanding the exponential factors in (10), one finds (for \(0 \leq k < n\))
\[
G^{(n)}_k(t) = \frac{1}{n} \sum_{\ell \geq 0} \frac{t^\ell}{\ell!} (1 + \xi^{k+\ell} + \xi^{2(k+\ell)} + \ldots + \xi^{(n-1)(k+\ell)})
\]
\[
= \delta_{k,0} + \sum_{m \geq 1} t^{mn-k} \frac{\xi^{mn-k}}{(mn-k)!}
\]
For \(0 \leq k < n\), these functions have the following elementary properties.

1. \(G^{(n)}_k(0) = \delta_{k,0}\)
2. \(\frac{d}{dt} G^{(n)}_k(t) = G^{(n)}_{k+1}(t)\) (with \(G^{(n)}_n \equiv G^{(n)}_0\));
3. \(\sum_{k=0}^{n-1} G^{(n)}_k(t) = e^t\).

Moreover, one has

**Lemma 2** Let \(n \geq 2\) and \(0 \leq k < n\). Then, \(\lim_{t \to \infty} e^{-t} G^{(n)}_k(t) = \frac{1}{n}\).

**Proof:** If \(\gamma \in \mathbb{S}^1\), one has \(\gamma = \cos(\phi) + i \sin(\phi)\) for some \(\phi \in \mathbb{R}\), hence
\[
e^{-t} e^{\gamma t} = e^{(\gamma - 1)t} = e^{(\cos(\phi) - 1)t} e^{i \sin(\phi)t}.
\]
The absolute value is then \(e^{(\cos(\phi) - 1)t}\) which tends to 0 as \(t \to \infty\), unless \(\cos(\phi) = 1\). Using this term by term in (10) proves the claim. \(\square\)
Let us assume, as above, that $R(K) \subset K$ and consider the abstract Cauchy problem (7). Let us also assume, for a fixed $n \geq 2$, that $R^{n+1} = R$ on $K$. Define

$$\phi_t = e^{-t} \left( 1 + (G_0^{(n)}(t) - 1)R^n + \sum_{k=1}^{n-1} G_{n-k}^{(n)}(t)R^k \right)$$

so that $\phi_0 = 1$ and $\phi_t \xrightarrow{t \to \infty} \frac{1}{n}(R + R^2 + \ldots + R^n)$, as a consequence of Lemma 2.

If we now have $[R, \phi] = 0$ for all $t > 0$, one can check, by an explicit calculation, that $\phi_t(x_0)$ solves the Cauchy problem (7). For $n = 2$, it is the solution of Proposition 3.

Let us make this approach more concrete for $n = 3$. Here, one has $R^3 = R$, and the solution $\phi_t(x_0)$ would read

$$x(t) = e^{-t}x_0 + e^{-t}\sinh(t)R(x_0) + e^{-t}(\cosh(t) - 1)R^2(x_0).$$

The coefficients on the right hand side once more admit a probabilistic interpretation. The term $e^{-t}$ is the probability that no “hit” (by $R$) has happened until time $t$, while $e^{-t}\sinh(t) = \frac{1}{2}(1 + e^t)(1 - e^{-t})$ (resp. $e^{-t}(\cosh(t) - 1) = \frac{1}{2}(1 - e^{-t})^2$) is the probability for an odd number of hits (resp. an even number $\geq 2$) until time $t$.

Do such operators $R$ exist that are nonlinear? One possibility to construct an example is the following. For an idempotent $R$ with $R(K) \subset K$, find a map $\sigma: R(K) \to R(K)$ with $\sigma^n = 1$ that commutes with $R$ on $R(K)$ (which is nontrivial). If one defines $R = \sigma R$, one has $R^n = R$ and $R^{n+1} = R$ on $K$.

### 3.3 Dynamics under compatible recombinators

Let us go back to the more concrete setting of simple recombination and look at the situation of compatible semigroups. If $A \subset L$, let

$$I(A) := \{ \beta \mid \min(A) \leq \beta \leq \max(A) \}$$

denote the complete stretch of links associated with $A$.

**Lemma 3** Let $A \subset L$ be fixed and let $\alpha \in L$ be given with $\alpha \notin I(A)$. Let $\{ \varphi^A_t \mid t \geq 0 \}$ denote the corresponding positive semigroup according to Proposition 3. On $\mathcal{M}_+(X)$, one then has

$$\varphi^A_t \circ R_\alpha = R_\alpha \circ \varphi^A_t$$

for all $t \geq 0$.

**Proof**: In view of the formula for the operators $\varphi^A_t$, it is again sufficient to prove the claim on $\mathcal{P}(X)$. The extension to $\mathcal{M}_+(X)$ then follows from the positive homogeneity of the recombinators.

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Let \( \nu \) be an arbitrary probability measure, and assume that \( \alpha < \min(A) \) (the case \( \alpha > \max(A) \) is completely analogous). If \( a \in [0, 1] \), one finds
\[
R_\alpha(a \nu + (1 - a) R_A(\nu)) = (a \pi_{<\alpha} \nu + (1 - a) \pi_{<\alpha} R_A(\nu)) \otimes (a \pi_{>\alpha} \nu + (1 - a) \pi_{>\alpha} R_A(\nu))
\]
\[
= a^2 R_\alpha(\nu) + (1 - a)^2 R_{A \cup \{a\}}(\nu) + a(1 - a)(R_\alpha(\nu) + R_\alpha(R_A(\nu)))
\]
\[
= a R_\alpha(\nu) + (1 - a) R_{A \cup \{a\}}(\nu) = (a 1 + (1 - a) R_A)(R_A(\nu)).
\]

Observe that, due to our assumptions on \( \alpha \), we have \( \pi_{<\alpha} \nu = \pi_{<\alpha} R_A(\nu) \). Using this relation twice in the last line above (once in each direction), one obtains
\[
a^2 R_\alpha(\nu) + (1 - a)^2 R_{A \cup \{a\}}(\nu) + a(1 - a)(R_\alpha(\nu) + R_\alpha(R_A(\nu)))
\]
\[
= a R_\alpha(\nu) + (1 - a) R_{A \cup \{a\}}(\nu) = (a 1 + (1 - a) R_A)(R_A(\nu)).
\]

Since \( \nu \in \mathcal{M}_+(X) \) was arbitrary, this implies the claim. \( \square \)

**Corollary 1** Let \( A, B \subset L \) with \( I(A) \cap I(B) = \emptyset \). Then, on \( \mathcal{M}_+(X) \),
\[
R_B \circ \varphi_t^A = \varphi_t^A \circ R_B.
\]

**Proof:** Let \( \psi = a 1 + (1 - a) R_A \) for an arbitrary, but fixed \( a \in [0, 1] \). Write \( B = \{\beta_1, \ldots, \beta_r\} \) with \( \beta_1 < \cdots < \beta_r \). Then, \( R_B = \prod_{i=1}^r R_{\beta_i} \) by Proposition 4, and a repeated application of Lemma 3 gives
\[
R_B \circ \psi = \left( \prod_{i=1}^r R_{\beta_i} \right) \circ \psi = \ldots = \psi \circ \left( \prod_{i=1}^r R_{\beta_i} \right) = \psi \circ R_B
\]
which is valid on \( \mathcal{M}_+(X) \). This proves the claim because \( \varphi_t^A \) is of the form \( (a 1 + (1 - a) R_A) \), with \( a \in [0, 1] \), for all \( t \geq 0 \). \( \square \)

**Theorem 2** Let \( A, B \subset L \) with \( I(A) \cap I(B) = \emptyset \). Then, the corresponding semigroups commute, i.e.,
\[
\varphi_t^A \circ \varphi_s^B = \varphi_s^B \circ \varphi_t^A
\]
on \( \mathcal{M}_+(X) \), for all \( t, s \geq 0 \).

In particular, \( \{\varphi_t^A \circ \varphi_s^B \mid t, s \geq 0\} \) defines an Abelian two-parameter semigroup of nonlinear positive operators on \( \mathcal{M}_+(X) \).

**Proof:** Let \( \nu \in \mathcal{P}(X) \). With Corollary 1 one finds
\[
((a 1 + (1 - a) R_A) \circ (b 1 + (1 - b) R_B))(\nu)
\]
\[
= ab \nu + a(1 - b) R_B(\nu) + (1 - a)(b 1 + (1 - b) R_B)(R_A(\nu))
\]
\[
= ab \nu + a(1 - b) R_B(\nu) + b(1 - a) R_A(\nu) + (1 - a)(1 - b) R_{A \cup B}(\nu).
\]
Since the last expression is symmetric in \((a,A)\) versus \((b,B)\), the operators in the first line commute.

Since the operators \(\varphi^A_t\) and \(\varphi^B_s\) are of the form used in this argument, for all \(t,s \geq 0\), the claim is true on \(\mathcal{P}(X)\). By positive homogeneity of the recombinators, it extends to all of \(\mathcal{M}_+(X)\). □

This allows to formulate our main result, where we write \(\varphi^L_t\) for the semigroup attached to a set \(L_i \subset L\) of links.

**Theorem 3** Let \(A := \bigcup_{1 \leq i \leq r} L_i\) be a subset of \(L\), with \(I(L_i) \cap I(L_j) = \emptyset\) for all \(i \neq j\). Then, the semigroups \(\{\varphi^L_t \mid t \geq 0\}\) mutually commute, and the Cauchy problem

\[
\dot{\omega} = \sum_{i=1}^r \varrho_{L_i} (R_{L_i} - 1)(\omega),
\]

with all \(\varrho_{L_i} > 0\) and initial condition \(\omega_0 \geq 0\), has the unique solution

\[
\omega_t = \left(\prod_{i=1}^r \varphi_i^L_t\right)(\omega_0).
\]

Asymptotically, \(\omega_t \xrightarrow{\|\cdot\|} R_A(\omega_0)\) as \(t \to \infty\), the convergence, once again, being exponentially fast.

**Proof:** Due to commutativity of the participating semigroups by Theorem 2, one can apply Proposition 3 repeatedly to find

\[
\dot{\omega}_t = \left(\sum_{i=1}^r \left(\frac{d}{dt} \varphi^L_i\right) \circ \prod_{j \neq i} \varphi^L_j\right)(\omega_0)
\]

\[
= \left(\sum_{i=1}^r \varrho_{L_i} (R_{L_i} - 1) \circ \prod_{i=1}^r \varphi^L_i\right)(\omega_0)
\]

\[
= \sum_{i=1}^r \varrho_{L_i} (R_{L_i} - 1)(\omega_t).
\]

The convergence result towards the product measure \(R_A(\omega_0)\) is a multiple application of Proposition 3, together with Part 4 of Proposition 1. □

**Corollary 2** Under the assumptions of Theorem 3, the set

\[
\{\prod_{i=1}^r \varphi^L_i \mid t_i \geq 0\}
\]
forms an Abelian \( r \)-parameter semigroup of nonlinear positive operators on \( \mathcal{M}_+(X) \). Each factor is of the form

\[
\varphi_{L_i}^{t_i} = \exp(-\varrho_{L_i} t_i) \mathbf{1} + (1 - \exp(-\varrho_{L_i} t_i)) R_{L_i}
\]

where \( \varrho_{L_i} > 0 \) is the intensity of the underlying process.

Another obvious consequence is that the forward flow of Theorem 3, which is a one-parameter semigroup, is embedded into the \( r \)-parameter semigroup of Corollary 2.

### 3.4 Application to single crossovers and outlook

In [6], the biologically most relevant situation was investigated where \( L \) was written as the disjoint union of all its elements. This resulted in the ODE

\[
\dot{\omega} = \sum_{\alpha \in L} \varrho_{\alpha} (R_{\alpha} - 1)(\omega).
\]

By a different approach, it was shown that the corresponding Cauchy problem with positive initial condition \( \omega_0 \) has the solution

\[
\omega_t = \sum_{G \subseteq L} a_G(t) R_G(\omega_0)
\]

where the coefficient functions are given by

\[
a_G(t) = \prod_{\alpha \in G} \exp(-\varrho_{\alpha} t) \prod_{\beta \not\in G} (1 - \exp(-\varrho_{\beta} t)).
\]

In our new (and more general) formulation, these coefficients can be seen as the result of expanding the product (over \( \alpha \in L \)) of the commuting semigroups \( \{\varphi_{L_i}^{t_i} | t \geq 0\} \). It is an easy exercise to show that the formula of Proposition 3 then gives an independent verification of (14).

In this case, a simple combinatorial transformation is possible, namely

\[
T_G := \sum_{H \supseteq G} (-1)^{|H-G|} R_H,
\]

which admits the inverse \( R_G := \sum_{H \supseteq G} T_H \) by Möbius inversion, compare [11, Thm. 4.18]. It was shown in [6] that the signed measures \( T_G(\omega_t) \) satisfy the linear ODEs

\[
\frac{d}{dt} T_G(\omega_t) = - \left( \sum_{\alpha \in G} \varrho_{\alpha} \right) T_G(\omega_t).
\]
Since $T_G(\omega_t) = b_G(t)T_G(\omega_0)$ with $b_G(t) = \sum_{H \subseteq G} a_H(t)$, $\omega_t$ of (14) also admits the representation

$$\omega_t = \sum_{G \subseteq L} b_G(t)T_G(\omega_0).$$

This shows that (13) can be transformed to a system of $2^{|L|}$ linear ODEs (together with a special set of initial conditions), which, a posteriori, provides an explanation for the appearance of the “almost linear like” behaviour of the nonlinear flow of the original equation (13). At present, I am not aware of any other example of this kind of “Möbius linearization” in the literature.

A similar observation applies to the situation of Theorem 3, which corroborates the intuition that explicit expressions for nonlinear semigroups ought to be related to some linear structure. As the above examples show, there are perhaps more possibilities for such a connection to be discovered.

Our above analysis revolved around ordered partitions, which make the treatment rather simple and transparent. It is clear, however, that there is no principal reason to restrict oneself to this case, and with some extra effort, similar results might also be possible for more general partitions. One difficulty here is to find a good formulation for the cases where the semigroups (and not just the recombinators) commute.

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