Exponential ergodicity of stochastic reaction networks with a single species

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Co-work with Minjoon Kim, Jinsu Kim

Biochemical reaction systems often consider only one species

Schlögl model : Phosphorylation-dephosphorylation cycle,
Cooperative self-activating gene

$$A + 2S \xrightarrow{k_1} 3S \xrightarrow{k_2} A + 2S$$

$$B \xrightarrow{k_3} S \xrightarrow{k_4} B$$

n_A, n_B are very large so that we can assume it is constant

$$2S \xrightarrow{k_1 n_A} 3S \xrightarrow{k_2} 2S$$

$$0 \xrightarrow{k_3 n_B} S \xrightarrow{k_4} 0$$

Vellela, Melissa, and Hong Qian. *Journal of The Royal Society Interface* (2009)

Dynamics of biochemical reactions can be modeled by continuous-time Markov Chain

$$a_1 S \xrightarrow{k_1} b_1 S$$

$$a_2 S \xrightarrow{k_2} b_2 S$$

$$\vdots$$

$$a_n S \xrightarrow{k_n} b_n S$$

The above reaction system can be modeled by continuous-time Markov chain $X_t \in \mathbb{Z}_{\geq 0}$ such that

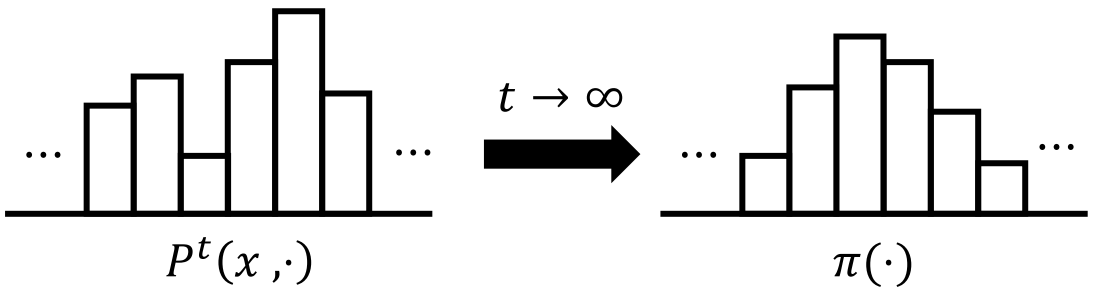
$P(X_{t+\Delta t} = x \mid X_t = x_0) \approx$ (sum of all reaction rates at state x_0 with $b_i - a_i = x - x_0$) x Δt

Assume that all reaction follows mass-action kinetics :

The rate of the reaction $a_i S \xrightarrow{k_i} b_i S$ has reaction rate (intensity) $k_i \frac{x_0!}{(x_0 - a_i)!} \mathbf{1}_{\{x_0 \geq a_i\}}$

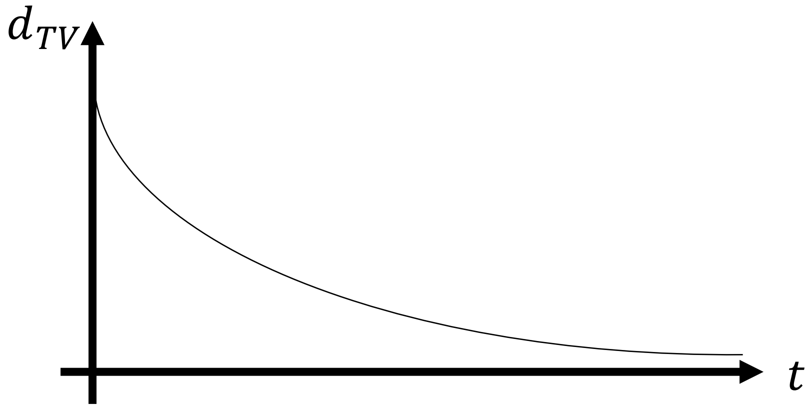
The stability and its convergence rate can be described in terms of positive recurrence (ergodicity) and mixing time

Positive recurrence (ergodicity) :
Existence of converging
stationary distribution



$$||P^t(x\,,\ \cdot\ ) - \pi(\cdot)||_{TV} \to 0 \text{ as } t \to \infty$$

Exponential ergodicity :
Total variation norm between
stationary distribution and distribution at
each time decays exponentially



$$||P^t(x\,,\cdot\ ) - \pi(\cdot)||_{TV} \leq C(x) \cdot e^{-\eta t}$$

Previous studies characterized the dynamics of stochastic reaction network with a single species

$$2S \xrightarrow{k_1 n_A} 3S$$

$$3S \xrightarrow{k_2} 2S$$

$$0 \xrightarrow{k_3 n_B} S$$

$$S \xrightarrow{k_4} 0$$

For each jump size $\omega \in \Omega$, write the transition rate as

$$\lambda_\omega(x) = a_\omega x^{d_\omega} + b_\omega x^{d_\omega - 1} + O(x^{d_\omega - 2})$$

$$\lambda_1(x) = k_1 n_A x(x-1) + k_3 n_B = k_1 n_A x^2 - k_1 n_A x + k_3 n_B$$

$\Rightarrow$ $d_1 = 2,\ a_1 = k_1 n_A,\ b_1 = -k_1 n_A$

$$\lambda_{-1}(x) = k_2 x(x-1)(x-2) + k_4 x = k_2 x^3 - 3k_2 x^2 + (2k_2 + k_4)x$$

$\Rightarrow$ $d_{-1} = 3,\ a_{-1} = k_2,\ b_{-1} = -3k_2$

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

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$R = \max_{\omega \in \Omega} d_\omega$: maximum order of the reactions (jump)

$\Rightarrow$ $R = \max\{2,3\} = 3$

$$\lambda_1(x) = k_1 n_A x(x-1) + k_3 n_B = k_1 n_A x^2 - k_1 n_A x + k_3 n_B$$

$$\lambda_{-1}(x) = k_2 x(x-1)(x-2) + k_4 x = k_2 x^3 - 3k_2 x^2 + (2k_2 + k_4)x$$

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$$S \xrightarrow{k_4} 0$$

$$\alpha = \sum_{\omega\,:\,d_\omega = R} a_\omega \omega$$: asymptotic largest drift direction

$$\alpha = k_2 \times -1 = -k_2$$

$$\lambda_1(x) = k_1 n_A x(x-1) + k_3 n_B = k_1 n_A x^2 - k_1 n_A x + k_3 n_B$$

$$\lambda_{-1}(x) = k_2 x(x-1)(x-2) + k_4 x = k_2 x^3 - 3k_2 x^2 + (2k_2 + k_4)x$$

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$$S \xrightarrow{k_4} 0$$

$$\gamma = \sum_{\omega\,:\,d_\omega = R} b_\omega \omega + \sum_{\omega\,:\,d_\omega = R-1} a_\omega \omega$$: asymptotic second-largest drift direction

$$\Rightarrow \quad \gamma = -3k_2 \times (-1) + k_1 n_A \times 1 = k_1 n_A + 3k_2$$

$$\lambda_1(x) = k_1 n_A x(x-1) + k_3 n_B = k_1 n_A x^2 - k_1 n_A x + k_3 n_B$$

$$\lambda_{-1}(x) = k_2 x(x-1)(x-2) + k_4 x = k_2 x^3 - 3k_2 x^2 + (2k_2 + k_4)x$$

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

Previous studies characterized the dynamics of stochastic reaction network with a single species

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$$\beta = \gamma - \frac{1}{2} \sum_{\omega\,:\, d_\omega = R} a_\omega \omega^2$$: asymptotic second-largest drift direction – 1/2 variance

$$\Rightarrow \quad \beta = k_1 n_A + 3k_2 - \frac{1}{2} k_2 (-1)^2 = k_1 n_A + \frac{5}{2} k_2$$

$$\lambda_1(x) = k_1 n_A x(x-1) + k_3 n_B = k_1 n_A x^2 - k_1 n_A x + k_3 n_B$$

$$\lambda_{-1}(x) = k_2 x(x-1)(x-2) + k_4 x = k_2 x^3 - 3k_2 x^2 + (2k_2 + k_4)x$$

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

Previous studies characterized the dynamics of stochastic reaction network with a single species

	$\alpha < 0$	$\alpha = 0$					$\alpha > 0$
		$\gamma < 0$	$\gamma = 0$	$\beta < 0 < \gamma$	$\beta = 0$	$\beta > 0$	
$R = 0$							D
$R = 1$	B		C	C	C	D	D
$R = 2$	E	A	A	A	C	D	F
$R > 2$	E	E	E	E	E	F	F

A ∪ B ∪ E : Positive recurrent

B ∪ E : Exponentially ergodic

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

Previous studies characterized the dynamics of stochastic reaction network with a single species

1D SRN is $\begin{cases} \text{positive recurrent if and only if either (1) } \alpha < 0, \text{ (2) } \alpha = 0,\ \beta < 0,\ R > 1, \text{ (3) } \alpha = \beta = 0,\ R > 2 \\ \text{exponentially ergodic if either (1) } \alpha < 0,\ R \geq 1 \text{ or (2) } \alpha = 0,\ \beta \leq 0,\ R > 2 \end{cases}$

$$2S \xrightarrow{k_1 n_A} 3S$$

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$$R = \max\{2,3\} = 3$$

$$\alpha = k_2 \times -1 = -k_2$$

Positive recurrent
and
Exponentially ergodic

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

Previous studies left the question for the existence of non-exponentially ergodic cases

1D SRN is $\begin{cases} \text{positive recurrent if and only if either (1) } \alpha < 0, \text{ (2) } \alpha = 0, \beta < 0, R > 1, \text{ (3) } \alpha = \beta = 0, R > 2 \\ \text{exponentially ergodic if either (1) } \alpha < 0, R \geq 1 \text{ or (2) } \alpha = 0, \beta \leq 0, R > 2 \end{cases}$

$$2A \xrightarrow{k_1} A$$

$$2A \xrightarrow{k_1} 3A$$

$$A \xrightarrow{k_2} 2A$$

If $0 < k_2 < k_1$: $\alpha = 0$, $\beta = k_2 - k_1 < 0$ and $R = 2$

$\Rightarrow$ Positive recurrent, but we don't know whether this is exponentially ergodic or not

For the case of $\alpha = 0$, $\beta < 0$ and $R = 2$,

it is possible to be non-exponentially ergodic?

Previous studies left the question for the existence of non-exponentially ergodic cases

1D SRN is
- positive recurrent if and only if either (1) $\alpha < 0$, (2) $\alpha = 0$, $\beta < 0$, or (3) $\alpha = 0$, $\beta = 0$, $R > 2$
- exponentially ergodic if either (1) $\alpha < 0$, $R \geq 1$ or (2) $\alpha = 0$, $\beta \leq 0$, $R > 2$

Are there cases that is positive recurrent but non-exponentially ergodic?

In other words, for the case of $\alpha = 0$, $\beta < 0$ and $R \leq 2$,

it is possible to be non-exponentially ergodic?

We show that there are no cases for non-exponential ergodicity.

In other words,
ergodic one-dimensional stochastic reaction networks
are always exponentially ergodic.

Exponential ergodicity of main example

$$2A \xrightarrow{k_1} A$$

$$2A \xrightarrow{k_1} 3A$$

$$A \xrightarrow{k_2} 2A$$

$$0 < k_2 < k_1$$

Theorem) Let X_t be the non-explosive, irreducible **single birth-death** process. The process X_t is exponentially ergodic if and only if

$$\inf_{i\geq 0}(a_i + b_i) > 0 \quad \text{and} \quad \delta \coloneqq \sup_{i>0}\Big(\sum_{j=0}^{i-1}\frac{1}{\mu_j}\Big)\Big(\sum_{j=i}^{\infty}\mu_j\Big) < \infty$$

where a_i and b_i are death and rate at state $i \in \mathbb{Z}_{\geq 0}$, respectively

and $\mu_j = \frac{b_0 b_1 \cdots b_{j-1}}{a_1 a_2 \cdots a_j}$ for $j \geq 1$

Mao, Yong-Hua, and Yu-Hui Zhang. *Journal of Applied Probability* (2004)

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where a_i and b_i are death and rate at state $i \in \mathbb{Z}_{\geq 0}$, respectively

and $\mu_j = \frac{b_0 b_1 \cdots b_{j-1}}{a_1 a_2 \cdots a_j}$ for $j \geq 1$

The left SRN has $a_i = k_1 i(i-1)$, $b_i = k_1 i(i-1) + k_2 i$, and exponentially ergodic

Corollary) One-dimensional irreducible birth-death process with $\alpha = 0$, $\beta < 0$, and $R = 2$ is exponentially ergodic

Mao, Yong-Hua, and Yu-Hui Zhang. *Journal of Applied Probability* (2004)

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{1}{2}} 2A$$

Exponentially ergodic

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{\frac{1}{2}} 4A$$

$$A \xrightarrow{\frac{1}{2}} 2A$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$
$$2A \xrightarrow{1} 3A$$
$$A \xrightarrow{\frac{1}{2}} 2A$$

$$2A \xrightarrow{1} A$$
$$2A \xrightarrow{\frac{1}{2}} 4A$$
$$A \xrightarrow{\frac{1}{2}} 2A$$

Exponentially ergodic

$2A \xrightarrow{1} 3A$ occurs with rate $1n_A(n_A - 1)$ and increases n_A by 1

$2A \xrightarrow{\frac{1}{2}} 4A$ occurs with rate $\frac{1}{2}n_A(n_A - 1)$ and increases n_A by 2

➡ Left and right system has 'almost' same dynamics

Comparison of 1D SRN

$$a_1 S \xrightarrow{k_1} b_1 S$$
$$a_2 S \xrightarrow{k_2} b_2 S$$
$$\vdots$$
$$a_n S \xrightarrow{k_n} b_n S$$

1D SRN is exponentially ergodic if and only if

$$\mathbb{E}_i(e^{\eta \tau_1}) < \infty$$

which is equivalent that for some $\eta > 0$ with $\eta < k_i$ for all reaction i, and for some nonempty finite subset $H \subset Z_{\geq 0}$, the system of inequality

$$\begin{cases} y_i \geq 1, & i \in Z_{\geq 0} \\ \sum_k \lambda_k(n) y_{n+b_i-a_i} \leq \eta y_i, & i \notin H \end{cases}$$

has a finite solution (y_i)

Tweedie, R. L. *Journal of Applied Probability* (1981)

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6}-\kappa} 2A$$

We showed that this SRN exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$ in the first part.

$\Rightarrow$ $^{\exists}(y_i) < \infty$ and $\eta > 0$ satifying

$$\left[\begin{array}{ll} y_i \geq 1, & i \in Z_{\geq 0} \\ \sum_k \lambda_k(n) y_{n+b_i-a_i} \leq \eta y_i, & i \notin H \end{array}\right.$$

We could write as

$$\sum_k \lambda_k(n) y_{n+b_i-a_i} = n(n-1)(y_{n-1} - y_n) + \left\{n(n-1) + \left(\frac{7}{6} - \kappa\right) n\right\} (y_{n+1} - y_n) \leq \eta y_n$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6} - \kappa} 2A$$

Exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1/3} 3A$$

$$A \xrightarrow{7/6} 2A$$

$$2A \xrightarrow{1/3} 4A$$

$\alpha = 0$, $\beta = -1/6$, and $R = 2$

$$\sum_k \lambda_k(n) y_{n+b_i-a_i} = n(n-1)(y_{n-1} - y_n) + \left\{\frac{1}{3}n(n-1) + \frac{7}{6}n\right\}(y_{n+1} - y_n) + \frac{1}{3}n(n-1)(y_{n+2} - y_n)$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6}-\kappa} 2A$$

Exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$

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$$A \xrightarrow{7/6} 2A$$

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$\alpha = 0$, $\beta = -1/6$, and $R = 2$

$$\sum_k \lambda_k(n) y_{n+b_i-a_i} - \sum_k \lambda_k(n) y_{n+b_i-a_i} = \frac{2}{3}n(n-1)(y_{n+1}-y_n) - \frac{1}{3}n(n-1)(y_{n+2}-y_n) - \kappa n(y_{n+1}-y_n)$$

$$= \frac{1}{3}n\{(n-1-3\kappa)(y_{n+1}-y_n) - (n-1)(y_{n+2}-y_n)\}$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6}-\kappa} 2A$$

Exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$

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$$A \xrightarrow{7/6} 2A$$

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$\alpha = 0$, $\beta = -1/6$, and $R = 2$

From the one-step analysis,

$$0 < \eta y_{n+1} = \eta \mathbb{E}_{n+1}(e^{\eta\tau_1}) = \sum_j q_{n+1,j}\left(\mathbb{E}_{n+1}(e^{\eta\tau_1}) - \mathbb{E}_j(e^{\eta\tau_1})\right)$$

$$= \left\{2n(n+1) + \left(\frac{7}{6}-\kappa\right)(n+1)\right\} y_{n+1} - n(n+1)y_n - \left\{n(n+1) + \left(\frac{7}{6}-\kappa\right)(n+1)\right\} y_{n+2}$$

$$= (n+1)\left\{n(y_{n+1}-y_n) - \{(n+\frac{7}{6}-\kappa)\}(y_{n+2}-y_n+1)\right\}$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6}-\kappa} 2A$$

Exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1/3} 3A$$

$$A \xrightarrow{7/6} 2A$$

$$2A \xrightarrow{1/3} 4A$$

$\alpha = 0$, $\beta = -1/6$, and $R = 2$

Therefore,

$$\sum_k \lambda_k(n) y_{n+b_i-a_i} - \sum_k \lambda_k(n) y_{n+b_i-a_i} > 0 \quad \text{for large } n \text{ if } \frac{1}{6} < \kappa < \frac{7}{24}$$

$$\sum_k \lambda_k(n) y_{n+b_i-a_i} < \sum_k \lambda_k(n) y_{n+b_i-a_i} \le \eta y_n$$

Comparison of 1D SRN

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6} - \kappa} 2A$$

Exponentially ergodic if $\frac{1}{6} < \kappa < \frac{7}{6}$

Solution (y_i)

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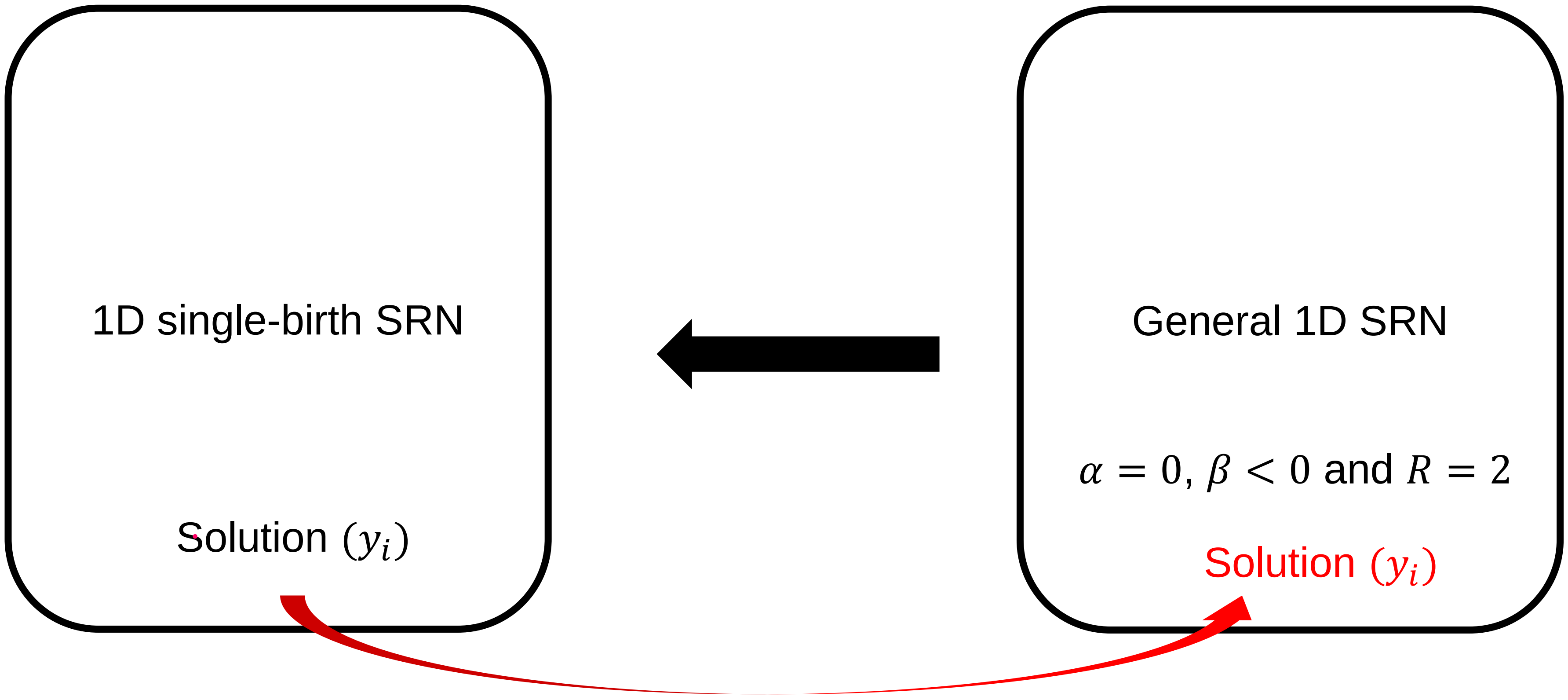
Solution (y_i)

Comparison of 1D SRN



Summary

Theorem) Every ergodic stochastic reaction system with a single species is exponentially ergodic.

1. Exponential ergodicity of single birth-death model

2. Comparison of general 1D SRN with single birth-death model

Summary

Theorem) Every ergodic stochastic reaction system with a single species is exponentially ergodic.

There are no non-exponentially ergodic 1D SRN, but there exists in 2D SRN

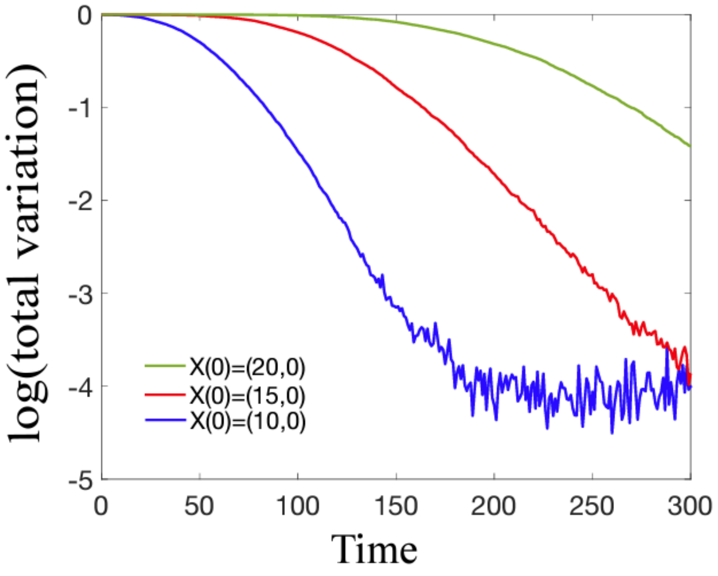
$$0 \xrightarrow{1} A + B$$

$$A + B \xrightarrow{1} 0$$

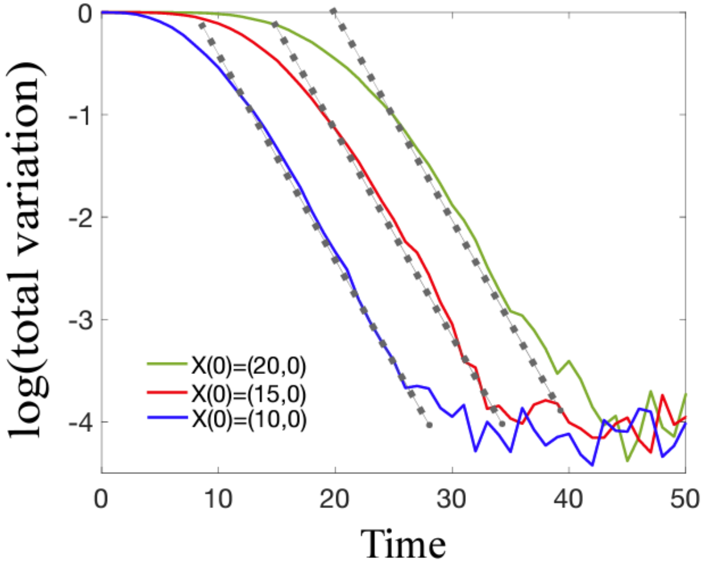
$$B \xrightarrow{1} 2B$$

$$2B \xrightarrow{1} B$$

$$||P^t(x,\cdot) - \pi(\cdot)||_{TV} \nleq C(x) \cdot e^{-\eta t}$$



$\mathrm{Log}(d_{TV})$ of left SRN



$\mathrm{Log}(d_{TV})$ of exponentially ergodic SRN

Kim, Minjoon, and Jinsu Kim. *arXiv preprint* (2024).

Thank you

Appendix

Cases for positive recurrent but not obviously exponentially ergodic

1D SRN is $\begin{cases} \text{positive recurrent if and only if either (1) } \alpha < 0\text{, (2) } \alpha = 0, \beta < 0, R > 1\text{, (3) } \alpha = \beta = 0, R > 2, \\ \text{or (4) } \alpha = 0, \gamma < 0, R = 1 \\ \text{exponentially ergodic if either (1) } \alpha < 0, R \geq 1 \text{ or (2) } \alpha = 0, \beta \leq 0, R > 2 \end{cases}$

- $\alpha < 0$, $R = 0$: From the definition that $R = \max_{\omega \in \Omega} d_\omega$: maximum order of the reactions (jump),
  $R = 0$ means every reaction has the form of $0 \to nA$. i.e. $\omega > 0$ for all $\omega \in \Omega$
  $\alpha = \sum_{\omega \,:\, d_\omega = R} a_\omega \omega$ should be always positive.

- $\alpha = 0$, $\beta < 0$, $R = 2$

- $\alpha = 0$, $\gamma < 0$, $R = 1$: The only possible $\omega < 0$ is the reaction $A \to 0$ and $\lambda_{-1}(x) = a_{-1}x$, therefore $b_{-1} = 0$

$$\gamma = \sum_{\omega \,:\, d_\omega = 1} b_\omega \omega + \sum_{\omega \,:\, d_\omega = 0} a_\omega \omega \text{ is always non-negative.}$$

C. Xu, M. C. Hansen, and C. Wiuf, *Advances in Applied Probability*, 2023.

Additional explanation about the one-step analysis

Let X_t be the continuous-time Markov chain on a countable state space S,and let $H \subset S$ be an arbitrary nonempty finite subset.
For some $\lambda > 0$ with $\lambda < q_i$ for all $i \in S$, $y_i = E_i(e^{\lambda \tau_1})$ satisfies

$$\begin{cases} y_i \geq 1, & i \in S \\ \sum_j q_{ij} y_j = \lambda y_i \ , & i \notin H \\ \sum_{i \in H} \sum_{j \neq i} q_{ij} y_j < \infty & \end{cases}$$

where τ_1 is the first hitting time of the state {1}

Additional explanation about the one-step analysis

$$2A \xrightarrow{1} A$$

$$2A \xrightarrow{1} 3A$$

$$A \xrightarrow{\frac{7}{6}-\kappa} 2A$$

$$\lambda y_{i+1} = \lambda E_{i+1}\left(e^{\lambda\tau_1}\right) = \sum_j q_{i+1,j}\left(E_{i+1}\left(e^{\lambda\tau_1}\right) - E_j\left(e^{\lambda\tau_1}\right)\right)$$

$$= q_{i+1,i}\left(E_{i+1}\left(e^{\lambda\tau_1}\right) - E_i\left(e^{\lambda\tau_1}\right)\right) + q_{i+1,i+2}\left(E_{i+1}\left(e^{\lambda\tau_1}\right) - E_{i+2}\left(e^{\lambda\tau_1}\right)\right)$$

$$= (i+1)i\left(E_{i+1}\left(e^{\lambda\tau_1}\right) - E_i\left(e^{\lambda\tau_1}\right)\right) + \left\{(i+1)i + \left(\frac{7}{6}-\kappa\right)(i+1)\right\}\left(E_{i+1}\left(e^{\lambda\tau_1}\right) - E_{i+2}\left(e^{\lambda\tau_1}\right)\right)$$

$$= (i+1)i(y_{i+1}-y_i) + \left\{(i+1)i + \left(\frac{7}{6}-\kappa\right)(i+1)\right\}(y_{i+1}-y_{i+2})$$

$$= (i+1)\left\{i(y_{i+1}-y_i) - \left\{\left(i+\frac{7}{6}-\kappa\right)\right\}(y_{i+2}-y_{i+1})\right\}$$

Since $e^{\lambda\tau_1} > 0$, $\lambda y_{i+1} = \lambda E_{i+1}\left(e^{\lambda\tau_1}\right) > 0$

Rewriting, we get $(i-1-3\kappa)(y_{i+1}-y_i) > \frac{i-1-3\kappa}{i}\left(i+\frac{7}{6}-\kappa\right)(y_{i+2}-y_{i+1})$

Additional explanation about the one-step analysis

$$2A \xrightarrow{1} A$$

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Exponentially ergodic
if $\kappa > 1/6$

$$2A \xrightarrow{1} A$$

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$$2A \xrightarrow{1/3} 4A$$

$\alpha = 0$, $\beta = -1/6$, and $R = 2$

$$\sum_j q_{ij}y_j - \sum_j q_{ij}y_j = \frac{1}{3}i\{(i-1-3\kappa)(y_{i+1}-y_i) - (i-1)(y_{i+2}-y_{i+1})\}$$

$$> \frac{1}{3}i\left(\frac{i-1-3\kappa}{i}\left(i+\frac{7}{6}-\kappa\right) - (i-1)\right)(y_{i+2}-y_{i+1})$$

Since $\lim_{i\to\infty}\left(\frac{i-1-3\kappa}{i}\left(i+\frac{7}{6}-\kappa\right)-(i-1)\right) = \frac{7}{6}-4\kappa$, $\sum_j q_{ij}y_j - \sum_j q_{ij}y_j > 0$ for large i if $\kappa < \frac{7}{24}$

Taking $\frac{1}{6} < \kappa < \frac{7}{24}$ makes both SRN exponentially ergodic