

Random Perturbations and Quasi-Stationarity in Stochastic Reaction Networks

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- The quasi-stationary distribution (QSD) is the likely distribution of the state variable, if the system has been running for a "long" time and is not extinct.
- Today, I will focus on the connection with the corresponding deterministic reaction network. In particular, to what extent do we have the following dichotomy, and how are they related?

Deterministic	Stochastic
Attractor	QSD



Motivation - Keizer's paradox

Consider the logistic network

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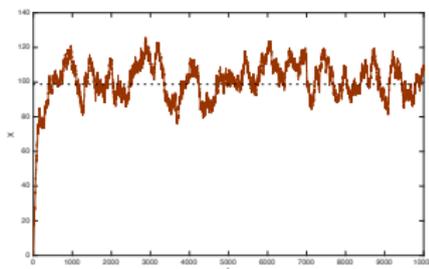


Figure : $X(0) = 1$, $\alpha_1 = 0.05$, $\alpha_2 = 5$, $\alpha_3 = 0.05$.



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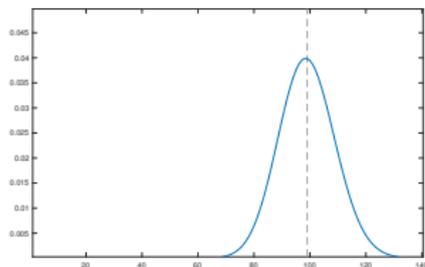
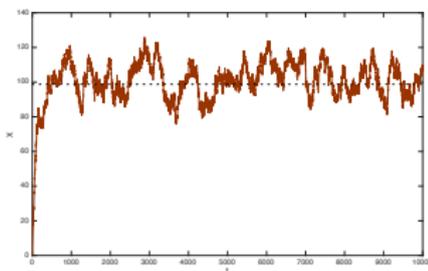


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Main Result - In (CRNT-)Layman Terms

Let a reaction network be given. Under the "**classical scaling**", with ε being the inverse of system size, we may consider the family of Markov processes $\{X_t^\varepsilon\}_{\varepsilon>0}$ associated to the network, as a **random perturbation** of the corresponding deterministic system. Under **appropriate assumptions** the weak* limit of the **quasi-stationary distributions** μ_ε will have support contained in the union of **positive attractors** of the deterministic system.



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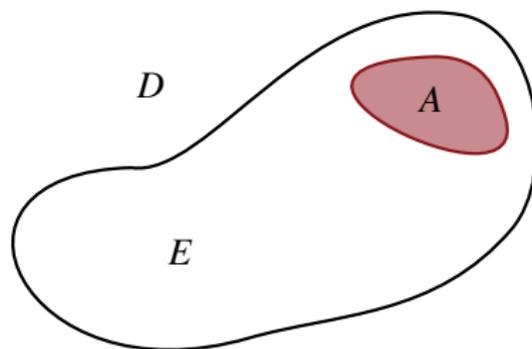
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In particular, for Keizer's paradox, $\mu_\varepsilon \Rightarrow \delta_{x_2^*}$, where x_2^* was the only stable fixed point for the deterministic rate equation.



General Setup of Quasi-Stationarity

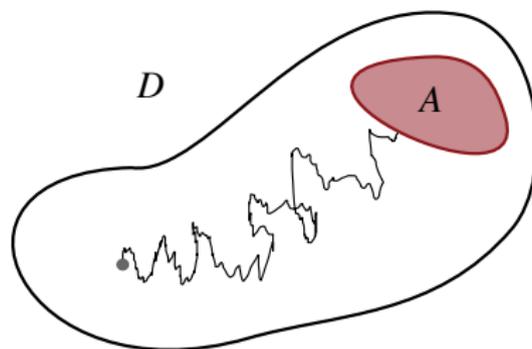
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The process is killed when it hits the trap - assume that this happens almost surely, $\mathbb{P}_x(\tau_A < \infty) = 1$, where $\tau_A = \inf\{t \geq 0 : X_t \in A\}$ is the hitting time of A .

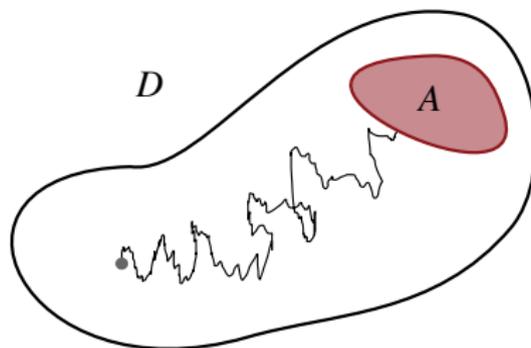


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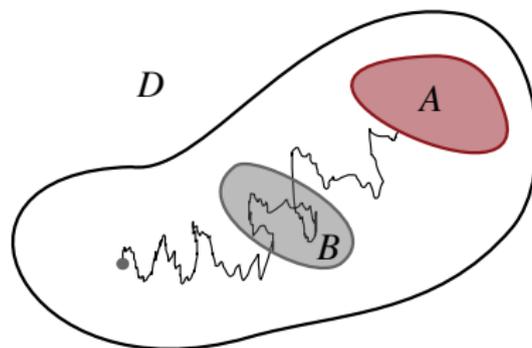
We investigate the behavior of the process before being killed.



Definition

A probability measure ν on $E = D \setminus A$ is called a **quasi-stationary distribution (QSD)** for the process killed at A if for every measurable set $B \subset E$

$$\mathbb{P}_\nu(X_t \in B \mid \tau_A > t) = \nu(B), \quad t \geq 0$$



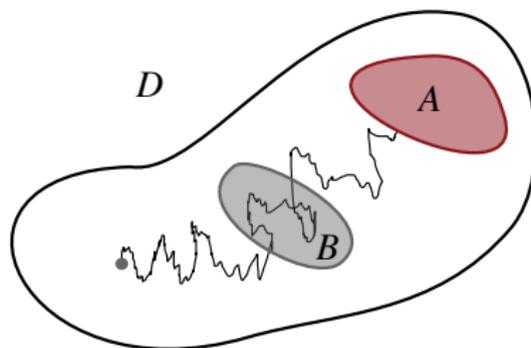
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or equivalently, if there exists a probability measure μ on E such that

$$\lim_{t \rightarrow \infty} \mathbb{P}_\mu(X_t \in B \mid \tau_A > t) = \nu(B)$$



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Let $D \subseteq \mathbb{R}_+^d$ be the state space of a deterministic reaction network.
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Definition

A **random perturbation** of a semi-flow φ_t is a family of homogeneous Markov processes

$$\{(X_t^\varepsilon : t \geq 0)\}_{\varepsilon > 0} \quad \text{on} \quad D \subseteq \mathbb{R}_+^d$$

where $p^\varepsilon(t, x, \Gamma)$ satisfy that for any $\delta > 0, T > 0$ and $K \subset D_1$ compact,

$$\beta_{\delta, K}(\varepsilon) := \sup_{t \in [0, T]} \sup_{x \in K} p^\varepsilon\left(t, x, D \setminus N^\delta(\varphi_t(x))\right) \rightarrow 0 \quad \text{for } \varepsilon \rightarrow 0.$$



Random Perturbations of Reaction Networks

In reaction networks for $\varepsilon > 0$ we may embed the stochastic process $(X_t^\varepsilon : t \geq 0)$ on $\varepsilon\mathbb{N}_0^d$ satisfying the stochastic equation

$$X_t^\varepsilon = X_0^\varepsilon + \sum_{k \in \mathcal{R}} Y_k \left(\int_0^t \lambda_k^\varepsilon(X_s^\varepsilon) ds \right) \varepsilon \xi_k$$

into $D \subseteq [0, \infty)^d$ by allowing X_0^ε to be any point in D and update with the jump rates

$$\lambda_k^\varepsilon(x) = \alpha_k \varepsilon^{\|y_k\|_1 - 1} \prod_{i=1}^d \binom{\lfloor x_i / \varepsilon \rfloor}{y_{ki}} y_{ki}!,$$



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In other words, we consider the **classical scaling** (fluid limit, thermodynamic limit. . .). Kurtz allows us to view these processes as random perturbations of the corresponding deterministic system.



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Lemma

The state space can be written $D = D_0 \sqcup D_1 \subseteq [0, \infty)^d$ where

- (i) $D_0 = \lim_{\varepsilon \rightarrow 0} A^\varepsilon$ is a closed subset of D ;
- (ii) $D_1 = \lim_{\varepsilon \rightarrow 0} E^\varepsilon$ is an open subset of D ;
- (iii) D_0 and D_1 are positively φ -invariant;
- (iv) D_0 is absorbing for the random perturbations,

$$p^\varepsilon(t, x, D_1) = 0 \quad \forall \varepsilon > 0, t > 0, x \in D_0.$$



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$$p^\varepsilon(t, x, D_1) = 0 \quad \forall \varepsilon > 0, t > 0, x \in D_0.$$

We assume that for each $\varepsilon > 0$ there exists at least one QSD μ_ε and, for simplicity, that E^ε is irreducible.



Assuming a Positive Attractor

From a modeling point of view, the applicability of the QSD depends on the expected time to extinction. This scales exponentially in system size ε .

Proposition

Assume that the flow $\{\varphi_t\}$ admits an attractor $K \subset D_1$. Then, starting according to the QSD, μ_ε , the probability of being absorbed by time $t > 0$ is $O(\varepsilon e^{-\gamma/\varepsilon})$ while the mean time to extinction is $O(\varepsilon e^{c/\varepsilon})$, where $\gamma, c > 0$.



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Proposition

Suppose the flow $\{\varphi_t\}$ admits an attractor $K \subset D_1$. Then the set of limit points of $\{\mu_\varepsilon\}$ for the weak topology is a subset of the set of invariant measures for the flow $\{\varphi_t\}$.*



Metastability

We assume μ_ε converges weakly to a Borel probability measure μ for $\varepsilon \rightarrow 0$. By the Poincaré recurrence theorem, one may conclude

$$\text{supp} \mu \subseteq BC(\varphi) := \overline{\{x \in D : x \in \omega(x)\}}.$$

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We also have a complimentary statement excluding metastability

Proposition

Assume that D_0 is a global attractor. Then μ is supported by D_0 .



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To refine these results further, we introduce some terminology.

Assume that the flow allows a global attractor given by

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A **Morse decomposition** of the dynamics of φ_t is a collection of non-empty φ -invariant pairwise disjoint compact sets $\{M_1, \dots, M_m\}$, called Morse sets, such that

- M_i is isolated,
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Morse sets contain all limit sets, and no cycles between Morse sets are allowed. Modulo replacing each M_i with points one may think of φ as being gradient-like, with the flow moving from lower to higher indexed morse sets.



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A Morse decomposition $\{M_1, \dots, M_m\}$ is called finer than a Morse decomposition $\{M'_1, \dots, M'_{m'}\}$ if for all $j \in \{1, \dots, m'\}$ there is $i \in \{1, \dots, m\}$ with $M_i \subset M'_j$.



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Theorem (Main)

Let M_1, \dots, M_m be the finest Morse decomposition for φ_t such that M_j, \dots, M_m are attractors. If

- $M_i \subset D_0$ or $M_i \subset D_1$,*
- $M_i \subset D_1$ for some $i \geq j$.*

then any weak-limit point of $\{\mu^\varepsilon\}_{\varepsilon>0}$ is φ_t -invariant and is supported by the union of attractors in D_1 .*



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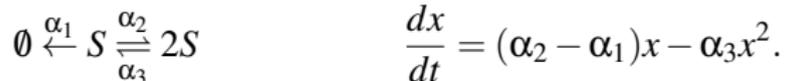
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The proof is based on so called absorption preserving pseudo-orbits, introduced by Schreiber et al. and a large deviations result, generalizing the work of Kifer and Conley.



Resolving Keizer's Paradox

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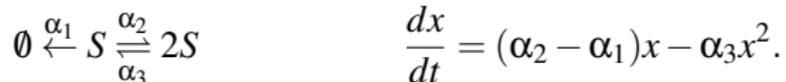


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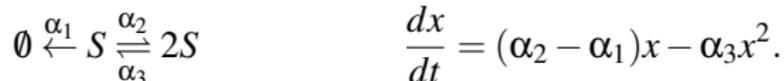
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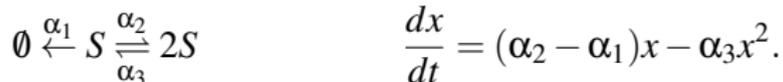
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where M_2 is an attractor. Thus, any weak* limit point of $\{\mu^\varepsilon\}_{\varepsilon>0}$ is supported by M_2 .

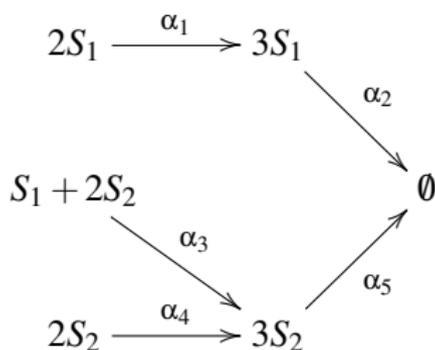


Resolving Keizer's Paradox

Figure : $\varepsilon = 1, 1/2, 1/4, 1/8, 1/16, 1/32, 1/64$.



A 2D-example

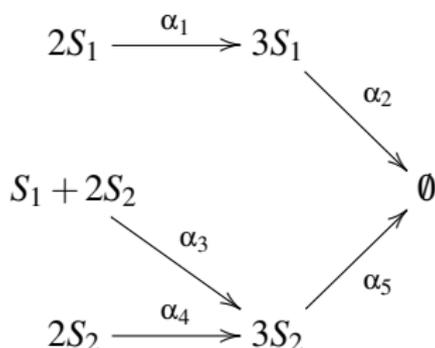


$$\frac{d}{dt} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} \alpha_1 x_1^2 - \alpha_2 x_1^3 - \alpha_3 x_1 x_2^2 \\ \alpha_3 x_1 x_2^2 + \alpha_4 x_2^2 - \alpha_5 x_2^3 \end{pmatrix}$$

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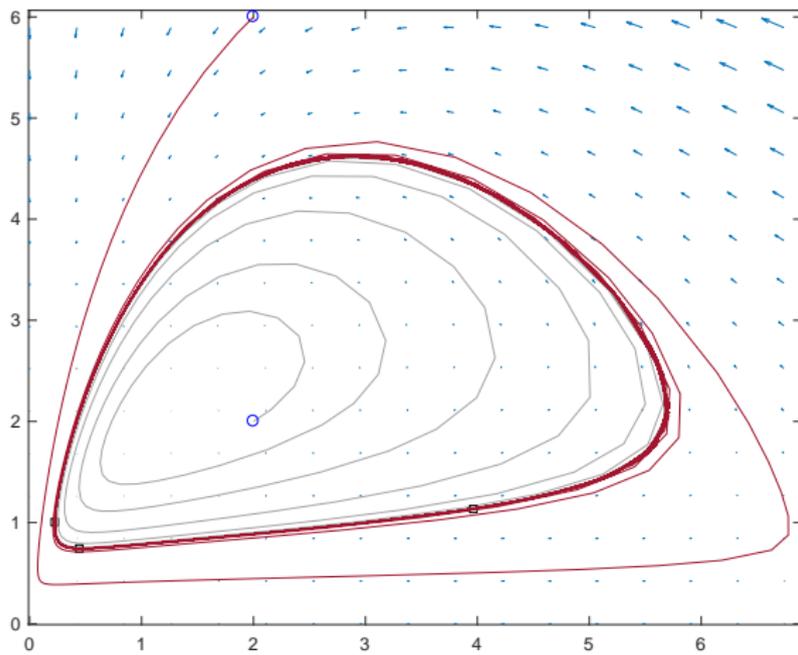
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$$D = \partial \mathbb{R}_+^2 \sqcup (0, \infty)^2$$

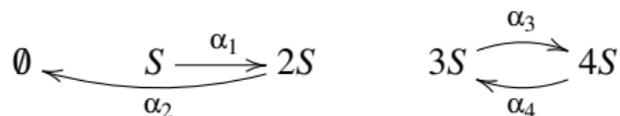


Figure : $\varepsilon = 1/2, 1/4, 1/8, 1/16, 1/32, 1/64$.





Multiple Positive Attractors

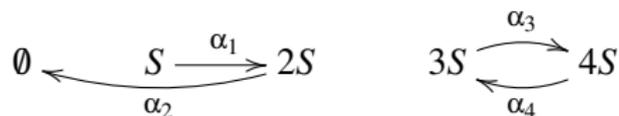


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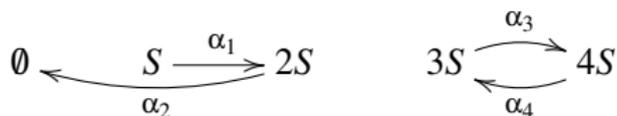
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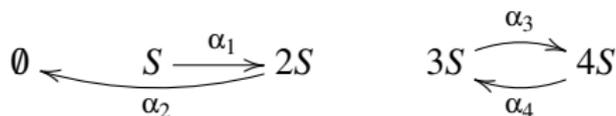
With parameters $\alpha_1 = 900, \alpha_2 = 320, \alpha_3 = 33, \alpha_4 = 1$, the finest Morse decomposition is

$$M_1 = \{0\}, \quad M_2 = \{10\}, \quad M_3 = \{5\}, \quad M_4 = \{18\}$$

with M_3, M_4 being attractors.



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with M_3, M_4 being attractors. Thus

$$\text{supp} \mu \subseteq \{5\} \cup \{18\}. \quad (2)$$





Figure : $\varepsilon = 1/2, 1/4, 1/8, 1/32, 1/64, 1/128, 1/256, 1/512$.

Future (ongoing) work

- When will there exist a QSD for a given reaction network? (Hard)
- When will the limit converge to a single positive attractor? Which one will it be? (Friedlin-Wentzel theory for absorbing processes?)
- If there are no positive attractors, are all the weak* limit points supported by D_0 ?
- Can we determine the rate of convergence to μ (in the total variations norm say)?
- Can we describe the QSDs far away from equilibrium?



Thanks!

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