# Coexistence and extinction for stochastic Kolmogorov systems

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# Outline

## Deterministic and Stochastic Models

Real populations do not evolve in isolation and as a result much of ecology is concerned with understanding the characteristics that allow two species to coexist, or one species to take over the habitat of another.

## Deterministic and Stochastic Models

It is of fundamental importance to understand what will happen to an invading species. Will it invade successfully or die out in the attempt? If it does invade, will it coexist with the native population?

The fluctuations of the environment make the dynamics of populations inherently stochastic.

# Deterministic and Stochastic Models

The combined effects of biotic interactions and environmental fluctuations are key when trying to determine species richness.

Sometimes biotic effects can result in species going extinct. However, if one adds the effects of a random environment extinction might be reversed into coexistence.

In other instances deterministic systems that coexist become extinct once one takes into account environmental fluctuations.

## Deterministic and Stochastic Models

A successful way of studying this interplay is modelling the populations as discrete or continuous time Markov processes and looking at the long-term behavior of these processes.

## Deterministic and Stochastic Models

One of the simplest deterministic models of population growth is

$$dX_t = rX_t dt, \quad X_0 = x_0 > 0.$$

1. The growth rate is $r$
2. The solution is given by $X_t = x_0 e^{rt}, t \geq 0$

## Deterministic and Stochastic Models

Note that the long term log growth is given by

$$\lim_{t\to\infty} \frac{\ln X_t}{t} = r.$$

1. The population goes extinct when $r < 0$.

2. The population blows up when $r > 0$.

## Deterministic and Stochastic Models

Now, assume that due to environmental noise the growth rate $r$ is perturbed

$$r \mapsto r + \sigma \dot{W}_t$$

where $\dot{W}_t$ is white noise. We can write the evolution as a stochastic differential equation

$$dX_t = rX_t dt + \sigma X_t dW_t, \quad X_0 = x_0 > 0.$$

## Deterministic and Stochastic Models

In this setting $(W_t)_{t\geq 0}$ is a one dimensional Brownian motion.

Using Ito's formula we get

$$\lim_{t\to\infty}\frac{\ln X_t}{t} = r - \frac{\sigma^2}{2}$$

## Deterministic and Stochastic Models

1. If $r - \frac{\sigma^2}{2} < 0$ the population goes extinct almost surely.
2. If $r - \frac{\sigma^2}{2} > 0$ the population blows up.
3. If $r - \frac{\sigma^2}{2} = 0$ the process is null-recurrent.

## Deterministic and Stochastic Models

The previous model does not take into account competition for resources and therefore it can blow up. This can be ammended by adding a competition term

$$dX_t = X_t(r - kX_t)dt + \sigma X_t dW_t, \quad X_0 = x_0 > 0.$$

## Deterministic and Stochastic Models

One can show in this setting

1. If $r - \frac{\sigma^2}{2} < 0$ the population goes extinct almost surely.
2. If $r - \frac{\sigma^2}{2} > 0$ the population is persistent and converges to its unique invariant probability measure on $(0, \infty)$.
3. If $r - \frac{\sigma^2}{2} = 0$ the process is null-recurrent. This is the **limit case** where the population does not go extinct but also does not have an 'equilibrium' (invariant probability measure).

## Deterministic and Stochastic Models

The factor that determines whether the system persists or goes extinct is the stochastic growth rate

$$r - \frac{\sigma^2}{2}.$$

If the stochastic growth rate is $0$ our methods do not work.

## Deterministic Model

The dynamics of $n$ interacting populations $\mathbf{X}(t) = (X_1(t), \ldots, X_n(t))_{t\geq 0}$ is given by

$$dX_i(t) = X_i(t) f_i(\mathbf{X}(t))dt, \; i = 1, \ldots, n$$

## Stochastic Model

If we add stochastic effects we get

$$dX_i(t) = X_i(t)f_i(\mathbf{X}(t))dt + X_i(t)g_i(\mathbf{X}(t))dE_i(t),\ i = 1, \ldots, n$$

We assume $\mathbf{E}(t) = (E_1(t), \ldots, E_n(t))^T = \Gamma^\top \mathbf{B}(t)$ where $\Gamma$ is a $n \times n$ matrix such that $\Gamma^\top \Gamma = \Sigma = (\sigma_{ij})_{n\times n}$ and $\mathbf{B}(t) = (B_1(t), \ldots, B_n(t))$ is a vector of independent standard Brownian motions.

## General Stochastic Model

If $\pi$ is invariant measure of $\mathbf{X}$ this means that if we start the process with initial distribution $\pi$ then the distribution of $\mathbf{X}(t)$ is $\pi$ for all $t \geq 0$.

## Lyapunov Exponents

$$\frac{\ln X_i(t)}{t} = \frac{\ln X_i(0)}{t} + \frac{1}{t}\int_0^t \left[ f_i(\mathbf{X}(s)) - \frac{g_i^2(\mathbf{X}(s))\sigma_{ii}}{2} \right] ds + \frac{1}{t}\int_0^t g_i(\mathbf{X}(s)) dE_i(s)$$

## Lyapunov Exponents

If $\mathbf{X}$ is close to the support of an ergodic invariant measure $\mu$ supported on $\partial R_+^n$ for a long time, then

$$\frac{1}{t}\int_0^t \left[f_i(\mathbf{X}(s)) - \frac{g_i^2(\mathbf{X}(s))\sigma_{ii}}{2}\right] ds$$

can be approximated by the average with respect to $\mu$

$$\lambda_i(\mu) = \int_{\partial\mathbb{R}_+^n} \left(f_i(\mathbf{x}) - \frac{g_i^2(\mathbf{x})\sigma_{ii}}{2}\right) \mu(d\mathbf{x}),\ i = 1,\dots,n$$

## Lyapunov Exponents

As $t \to \infty$ the term

$$\frac{\ln X_i(0)}{t} + \frac{1}{t} \int_0^t g_i(\mathbf{X}(s)) dE_i(s)$$

is negligible. This implies that

$$\lambda_i(\mu) = \int_{\partial \mathbb{R}_+^n} \left( f_i(\mathbf{x}) - \frac{g_i^2(\mathbf{x})\sigma_{ii}}{2} \right) \mu(d\mathbf{x}), \ i = 1, \dots, n$$

are the Lyapunov exponents of $\mu$.

## Lyapunov Exponents

It can also be seen that $\lambda_i(\mu)$ gives the long-term growth rate of $X_i(t)$ if $\mathbf{X}$ is close to the support of $\mu$.

Let $\mathcal{M}$ be the set of ergodic invariant probability measures of $\mathbf{X}$ supported on the boundary $\partial\mathbb{R}^n_+ := \mathbb{R}^n_+ \setminus \mathbb{R}^{n,\circ}_+$.

## Lyapunov Exponents

For an ergodic measure $\mu$ the Lyapunov exponents of the components supported by the measure are $0$

$$\lambda_i(\mu) = 0, i \in I_\mu$$

Intuitively this is expected because $\mu$ is in a way an 'equilibrium' so the process should not tend to grow or decay when it evolves in $\mathbb{R}_+^\mu$.

## Lyapunov Exponents

If the process gets close to the boundary $\partial R_+^n$ it is attracted or repelled according to the Lyapunov exponents of the ergodic invariant measures it is close to.

When the process is far from the boundary then our condition on the drift makes the process return to compact sets expnentially fast.

## Persistence

**Condition for persistence**: For any $\mu \in \mathrm{Conv}(\mathcal{M})$ one has

$$\max_{i=1,\ldots,n} \{\lambda_i(\mu)\} > 0$$

This says that any invariant probability measure is a repeller. We can show that $\mathbf{X}$ is persistent and converges exponentially fast to its unique invariant probability measure $\pi^*$ on $\mathbb{R}_+^{n,\circ}$.

## Extinction

**Condition for extinction**: There exists $\mu \in \mathcal{M}$ such that

$$\lambda_i(\mu) < 0, i \in I_\mu^c$$

where $I_\mu^c$ are the directions which are not supported by the ergodic measure $\mu$.

**Theorem**

Suppose that there is at least one transversal attractor, i.e. $\mathcal{M}_1 \neq \emptyset$. Then, there exists $\alpha > 0$ such that for any initial condition $\mathbf{X}(0) = \mathbf{x} \in \mathbb{R}_+^{n,\circ}$ we have with with probability $1$ that

$$\limsup_{t\to\infty} \frac{\ln\left(d\left(\mathbf{X}(t), \partial\mathbb{R}_+^n\right)\right)}{t} \leq -\alpha,$$

where $d(\mathbf{y}, \partial\mathbb{R}_+^n) = \min\{y_1 \ldots, y_n\}$ is the distance to the boundary.

## Extinction

If an ergodic invariant measure $\mu$ with support on the boundary is an "attractor", it will attract solutions starting nearby. Intuitively, the condition

$$\lambda_i(\mu) < 0, i \in I_\mu^c$$

forces $X_i(t), i \in I_\mu^c$ to get close to $0$ (so, to the support $\mathbb{R}_+^\mu$ of $\mu$) if the solution starts close to $\mathbb{R}_+^{\mu,\circ}$.

## Extinction

We need an additional assumption which ensures that apart from those in $\mathrm{Conv}(\mathcal{M}^1)$, invariant probability measures are "repellers". We cannot treat the limit cases when some of the Lyapunov exponents are zero.

# Extinction

**Theorem**

Suppose $\mathcal{M}^1 \neq \emptyset$. Then for any $\mathbf{x} \in \mathbb{R}_+^{n,\circ}$

$$\sum_{\mu \in \mathcal{M}^1} P_{\mathbf{x}}^{\mu} = 1$$

where for $\mathbf{x} \in \mathbb{R}_+^{n,\circ}, \mu \in \mathcal{M}^1$

$$P_{\mathbf{x}}^{\mu} := \mathbb{P}_{\mathbf{x}} \left\{ X \to \mu \text{ and } \lim_{t \to \infty} \frac{\ln X_i(t)}{t} = \lambda_i(\mu) < 0, i \in I_{\mu}^c \right\} > 0.$$

# Thank you for your attention!