The competitive exclusion principle in stochastic environments

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Competitive exclusion principle

One of the fundamental principles from ecology, **the competitive exclusion principle** (Gause '32, Volterra '28, Hardin '60), says that when multiple species compete with each other for the same resource, one competitor will win and drive all the others to extinction.

In contrast to this principle, it has been observed in nature that multiple species can coexist despite limited resources.

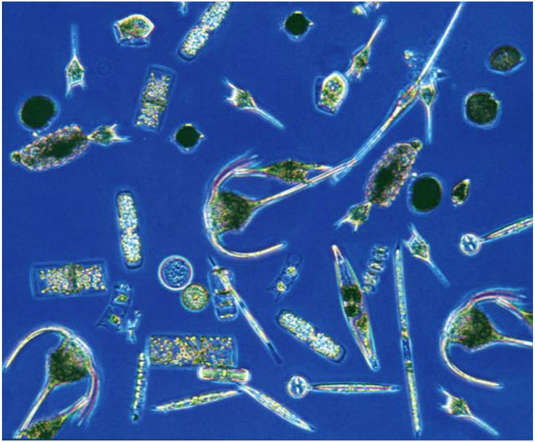


Figure 1: Phytoplankton.

Competitive exclusion principle

Phytoplankton species can coexist even though they all compete for a small number of resources. This apparent violation of the competitive exclusion principle has been called by Hutchinson 'the paradox of the plankton'.

Hutchinson gave a possible explanation by arguing that variations of the environment can keep species away from the deterministic equilibria that are forecasted by the competitive exclusion principle.

A deterministic model for competing species

Two species X_1 and X_2 competing for one resource R.

$$\frac{dX_1(t)}{dt} = X_1(t)(-\alpha_1 + b_1 R(X_1(t), X_2(t))$$
$$\frac{dX_2(t)}{dt} = X_2(t)(-\alpha_2 + b_2 R(X_1(t), X_2(t))$$

where $\alpha_1, \alpha_2 > 0$ are the death rates and b_1, b_2 measure the number of offspring per unit of resource.

A deterministic model for competing species

A natural assumption is that the abiotic resource depends linearly on the density of the species, so that

$$R(x_1, x_2) = \overline{R} - a_1 x_1 - a_2 x_2$$

The dynamics is then given by

$$\frac{dX_1(t)}{dt} = X_1(t)\left(-\alpha_1 + b_1\left[\overline{R} - a_1X_1(t) - a_2X_2(t)\right]\right)$$
$$\frac{dX_2(t)}{dt} = X_2(t)\left(-\alpha_2 + b_2\left[\overline{R} - a_1X_1(t) - a_2X_2(t)\right]\right)$$

It can be shown that the competitive exclusion principle **holds** in this setting, i.e. the two species X_1 and X_2 cannot coexist.

A stochastic model for competing species

Suppose the dynamics switches randomly between two different environments. In environment $u \in \{1, 2\}$ we follow a system of ODE of the form

$$\frac{dX_1(t)}{dt} = X_1(t)\left(-\alpha_1(u) + b_1(u)\left[\overline{R} - a_1(u)X_1(t) - a_2(u)X_2(t)\right]\right)$$
$$\frac{dX_2(t)}{dt} = X_2(t)\left(-\alpha_2(u) + b_2(u)\left[\overline{R} - a_1(u)X_1(t) - a_2(u)X_2(t)\right]\right)$$

Competitive exclusion principle

We spend a random exponential time $T_1 \sim \text{Exp}(\lambda_1)$ in environment 1, after which we switch to environment 2, spend a random exponential time $T_2 \sim \text{Exp}(\lambda_1)$ there and switch to environment 1. Repeat this procedure indefinitely.

What happens with the system as $t \to \infty$?

Competitive exclusion principle

Let us assume that in both environments species X_1 is dominant and drives species X_2 extinct.

Competitive exclusion principle

By suitably choosing the rates of the exponential switching times T_1 and T_2 we can show that one can get coexistence.

By spending time in both environments there can be a **rescue effect** which forces both species to persist.

(Benaim and Lobry AAP '17, H. and Nguyen '18). In the random model we can get the following regimes

- Persistence of X_1 and extinction of X_2.
- Coexistence: Both X_1 and X_2 persist.
- Reversal: Extinction of X_1 and persistence of X_2.
- Bistability: For initial density (x_1^0, x_2^0) persistence of x_1 and extinction of x_2 with probability $p_{(x_1^0, x_2^0)}$ or persistence of x_2 and extinction of x_1 with probability $1 - p_{(x_1^0, x_2^0)}$.

Piecewise deterministic Markov processes

For a PDMP, the process follows a deterministic system of differential equations for a random time, after which the environment changes, and the process switches to a different set of ordinary differential equations (ODE), follows the dynamics given by this ODE for a random time and then the procedure gets repeated.

Piecewise deterministic Markov processes

Suppose $(r(t))$ is a process taking values in the finite state space $\mathcal{N} = \{1, \ldots, N\}$. This process keeps track of the environment, so if $r(t) = i \in \mathcal{N}$ this means that at time t the dynamics takes place in environment i. Once one knows in which environment the system is, the dynamics are given by a system of ODE. We can write

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

Piecewise deterministic Markov processes

Suppose that the switching intensity of $r(t)$ depends on the state of $\mathbf{X}(t)$ as follows

$$\mathbb{P}\{r(t+\Delta) = j \mid r(t) = i, \mathbf{X}(s), r(s), s \leq t\} = q_{ij}(\mathbf{X}(t))\Delta + o(\Delta).$$

Simplest case: $q_{ij}(\mathbf{X}(t)) = q_{ij}$ are constants. Then $r(t)$ is an independent Markov chain and the time $r(t)$ spends in any given state is an independent exponential.

Piecewise deterministic Markov processes

Call μ an **invariant probability measure** for the process $(\mathbf{X}(t), r(t))$ if whenever one starts the process with initial conditions distributed according to $\mu(\cdot,\cdot)$, then for any time $t \geq 0$ the distribution of $(\mathbf{X}(t), r(t))$ is given by $\mu(\cdot,\cdot)$.

Piecewise deterministic Markov processes

$\mathcal{M}$ is the set of ergodic invariant measures of $(\mathbf{X}(t), r(t))$ with support on the boundary $\partial\mathbb{R}_+^n \times \mathcal{N}$.

$\mathrm{Conv}\,\mathcal{M}$ is the set of invariant measures of $(\mathbf{X}(t), r(t))$ with support on the boundary $\partial\mathbb{R}_+^n \times \mathcal{N}$.

Piecewise deterministic Markov processes

If $\mu \in \mathcal{M}$ is an ergodic measure and $\mathbf{X}$ spends a lot of time close to its support, $\operatorname{supp}(\mu)$, then it will get attracted or repelled in the ith direction according to the **Lyapunov exponent**

$$\boxed{\lambda_i(\mu) = \sum_{k \in \mathcal{N}} \int_{\partial \mathbb{R}^n_+} f_i(\mathbf{x}, k) \mu(d\mathbf{x}, k).}$$

We call an invariant probability measure $\mu \in \mathrm{Conv}(\mathcal{M})$ a **repeller** if

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

An ergodic probability measure $\mu \in \mathcal{M}$ is called a **transversal attractor** if

$$\lambda_i(\mu) < 0$$

for all directions i which are not supported by the measure.

Coexistence

Theorem

(Benaim '18, H. and Nguyen '19) If all $\mu \in \mathrm{Conv}(\mathcal{M})$ are repellers, then all species persist.

Theorem

For each transversal attractor $\mu \in \mathcal{M}$ which is accessible we have

$$P^{\mu}_{\mathbf{x},k} := \mathbb{P}_{\mathbf{x},k}\left\{(\mathbf{X}, r) \to \mu,\ \lim_{t\to\infty} \frac{\ln X_i(t)}{t} = \lambda_i(\mu) < 0, i \in I^c_{\mu}\right\} > 0.$$

Furthermore, the process will converge almost surely to one of the transversal attractors.

$$\sum_{\mu \text{ attractor}} P^{\mu}_{\mathbf{x},k} = 1.$$

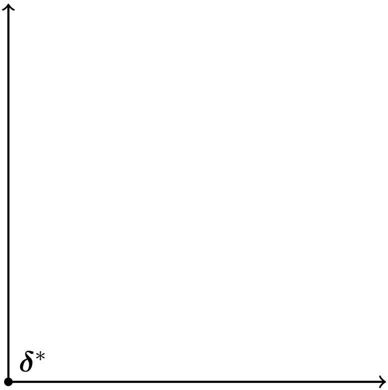
Examples

Two species X_1 and X_2 competing for resources.

$$\frac{dX_1(t)}{dt} = X_1(t)[a(r(t)) - b(r(t))X_2(t) - e(r(t))X_1(t)],$$
$$\frac{dX_2(t)}{dt} = X_2(t)[c(r(t)) - d(r(t))X_1(t) - f(r(t))X_2(t)]$$

where $r(t)$ is an independent irreducible Markov chain which switches between two environments $\{1, 2\}$ and has a stationary distribution (ν_1, ν_2).

Examples



Examples

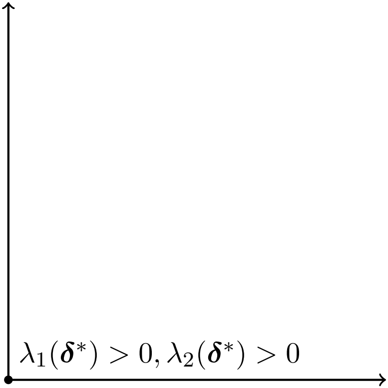
First, we check whether each species can survive on its own, that is we compute the Lyapunov exponents of the measure $\delta^* := \delta \times \nu$ where δ is the Dirac measure at $(0,0)$. Then

$$\lambda_1(\delta^*) = \nu_1 a(1) + \nu_2 a(2)$$

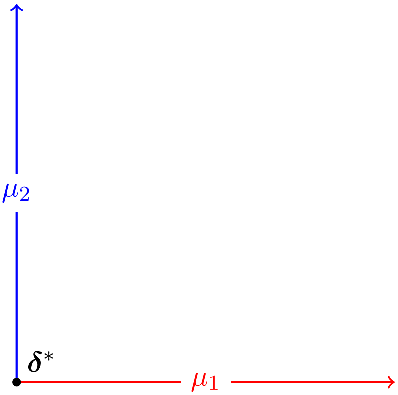
and

$$\lambda_2(\delta^*) = \nu_1 c(1) + \nu_2 c(2).$$

Examples



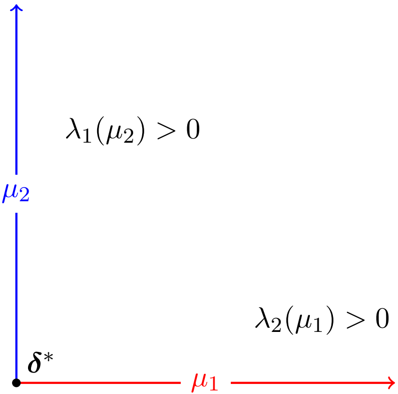
Examples



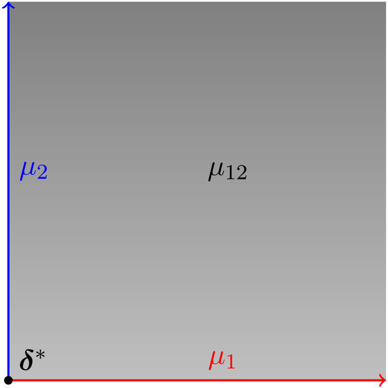
Examples

One can explicitly compute the Lyapunov exponents $\lambda_1(\mu_2)$ and $\lambda_2(\mu_1)$.

Examples



Examples



- If $\lambda_1(\mu_2) > 0$ and $\lambda_2(\mu_1) < 0$ persistence of X_1 and extinction of X_2.
- Coexistence: If $\lambda_1(\mu_2) > 0$ and $\lambda_2(\mu_1) > 0$ then both X_1 and X_2 persist.
- Reversal: If $\lambda_1(\mu_2) < 0$ and $\lambda_2(\mu_1) > 0$ extinction of X_1 and persistence of X_2.
- Bistability: If $\lambda_1(\mu_2) < 0$ and $\lambda_2(\mu_1) < 0$.

Thank you for your attention!