

Stochastic persistence of ecological communities driven by Lévy-noise

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Persistence: preliminaries

The mathematical problem of stochastic coexistence

A simple stochastic LV system of prey-predator type with intraspecific competition driven by Brownian motion (here the flow of biomass is $1 \rightarrow 2$).

$$\begin{aligned}dX_t^{(1)} &= X_t^{(1)}(b_1 - a_{11}X_t^{(1)} - a_{12}X_t^{(2)}) + \sigma_1 X_t^{(1)} dW_t^{(1)} \\dX_t^{(2)} &= X_t^{(2)}(-b_2 + a_{21}X_t^{(1)} - a_{22}X_t^{(2)}) + \sigma_2 X_t^{(2)} dW_t^{(2)}.\end{aligned}\tag{1}$$

Initial conditions for the process $\mathbf{X} = (X^{(1)}, X^{(2)})$ in $\mathbb{R}_+^n =$ positive orthant ($\mathbb{R}_{++}^n =$ strictly positive orthant).

Biological interpretation:

- ① b_i 's: per-capita per-unit time birth-death rates.
- ② a_{ij} 's: if $i \neq j$, interaction strength (increase-decrease of fitting per unit time per prey-predator encounter). If $i = j$: intraspecific competition (due e.g. to competition for space, soil, light, etc.)
- ③ σ_i 's: amount of the random perturbation due to environmental noise.
- ④ $\mathbf{W} = (W^{(1)}, W^{(2)})$: standard 2d Wiener process, carrying the **environmental noise**.

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Modeling issue: it is assumed that the stochastic perturbations of the fitting occur in characteristic times much shorter than the time horizon relevant to our observations

In our work we consider communities of n populations indexed by l engaged in LV dynamics driven by continuous and jump-type noise.

We ask: what are the conditions on the parameters such that the whole community $\mathbf{X} = (X^{(i)} : i = 1, 2, \dots, n)$ **persists**.

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- It can be proved that for initial condition on the strictly positive cone, for every $t > 0$, $X_t^{(1)} > 0, X_t^{(2)} > 0$ a.s. \Rightarrow there is no extinction on finite time. \Rightarrow any notion of stochastic persistence involves a claim on the asymptotic behavior of the laws.

Some different notions of stochastic persistence

Definition

A set of species indexed by $J \subset I$ is said to be **stochastically persistent in probability** if for every $\varepsilon > 0$ there exists a compact set $K_\varepsilon \subset \mathbb{R}_{++}^{|J|}$ such that:

$$\liminf_{t \rightarrow \infty} \mathbb{P}_{\mathbf{x}} \left((X_t^{(i_1)}, X_t^{(i_2)}, \dots, X_t^{(i_l)}) \in K_\varepsilon, (i_1, i_2, \dots, i_l) \in J \right) > 1 - \varepsilon,$$

uniformly on the initial condition $\mathbf{x} \in \mathbb{R}_{++}^I$.

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- Previous work has provided condition for these *weak* form of persistence for Lévy-driven ecological models: [BY11], [Mao11], [BMYY12].

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- We ask: when started from $\mathbf{x} \in \mathbb{R}_{++}^n$,
 - ① when do the laws of \mathbf{X} converges (in an appropriate sense) to a unique invariant probability measure, π ?
 - ② What is the nature of this invariant measure? Namely: does it support the whole community or just a strict subset of the community?

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 - ① when do the laws of \mathbf{X} converges (in an appropriate sense) to a unique invariant probability measure, π ?
 - ② What is the nature of this invariant measure? Namely: does it support the whole community or just a strict subset of the community?
- If π does not change the boundary of the positive cone, then we say that the community is **strongly stochastic persistent**.

Definition

(see [HN18a]) We say that a \mathbb{R}_{++}^n -valued, right-continuous Markov process $(\mathbf{X}_t : t \geq 0)$ is **strongly stochastically persistent (SSP)** if there exists a unique invariant probability measure π supported on \mathbb{R}_{++}^n such that for every $\mathbf{x} \in \mathbb{R}_{++}^n$:

$$d_{TV}(\mathbb{P}_{\mathbf{x}}(\mathbf{X}_t \in \cdot), \pi(\cdot)) \rightarrow 0,$$

as $t \rightarrow \infty$.

We observe:

- ① \mathbf{X} is not empty (because δ_0 is trivially ergodic).
- ② For every $J \subseteq \{1, 2\}$, the sets:

$$\mathbb{R}_{++}^J := \{\mathbf{x} \in \mathbb{R}_+^n : x_i > 0, i \in J, x_i = 0, i \notin J\},$$

are positively invariant for the dynamics. In general, thus, we can expect to have a lot of invariant probability measures on \mathbb{R}_+^n , many concentrated on $\partial\mathbb{R}_+^n$ (the boundary of the orthant, where at least one of the species is extinct).

Crucial insight

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- Pick an invariant probability measure μ such that at least one of the species is extinct under μ (and thus, μ charges $\partial\mathbb{R}_+^n$). Suppose that the process X , when started from strictly positive abundances, gets close to the part of the extinction boundary that is charged by μ . To guarantee SSP we will need that, in this situation, at least one of the endangered species tend to grow rapidly, avoiding thus the extinction fate.

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- Under some regularity assumption, this will amount to ask that, under any invariant probability measure μ that charges the boundary, at least one of the absent species has positive μ -averaged Lyapunov exponent.

Back to first example

How to ensure SSP for this community?



We have many invariant (indeed, ergodic) p.m. for this system.

- $\delta_{0,0}$.
- An ergodic p.m. μ under which species 1 persists and species 2 is extinct (thus, concentrated on $\{x_1 > 0, x_2 = 0\}$).

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- $\delta_{0,0}$.
- An ergodic p.m. μ under which species 1 persists and species 2 is extinct (thus, concentrated on $\{x_1 > 0, x_2 = 0\}$). This p.m. is unique, and corresponds to the product measure $m \otimes \delta_0$, where m is the law of a Gamma-distributed random variable (the law of the stochastic logistic equation).

Apply (formally!) Ito's formula to $x \mapsto \log(x_1)$ and $x \mapsto \log(x_2)$ to obtain:

$$\frac{\log(X_t^{(1)})}{t} - \frac{\log(X_0^{(1)})}{t} = \frac{1}{t} \int_0^t \left(b_1 - a_{11}X_s^{(1)} - a_{12}X_s^{(2)} - \frac{1}{2}\sigma_1^2 \right) ds + \frac{M_1(t)}{t}$$

$$\frac{\log(X_t^{(2)})}{t} - \frac{\log(X_0^{(2)})}{t} = \frac{1}{t} \int_0^t \left(-b_2 + a_{21}X_s^{(1)} - a_{22}X_s^{(2)} - \frac{1}{2}\sigma_2^2 \right) ds + \frac{M_2(t)}{t}$$

where M_1 and M_2 are local martingales. Put:

$$\Xi_1(x) := b_1 - a_{11}x_1 - a_{12}x_2 - \frac{1}{2}\sigma_1^2$$

$$\Xi_2(x) := -b_2 + a_{21}x_1 - a_{22}x_2 - \frac{1}{2}\sigma_2^2$$

Intuitively...

- ① If X spends a lot of time close to, for example, the support of μ , then for large times the first integrals should be close to $\mu\Xi_1$ and $\mu\Xi_2$.
- ② Since under μ the first species persists, $\mu\Xi_1 = 0$. (resident, stable species do not die or grow exponentially fast.)

So, we require:

- ① $\max_{i=1,2} \delta_{0,0} \bar{\Xi}_i > 0$ (when both are rare, at least one of the species tends to grow exponentially fast).
- ② $\mu \bar{\Xi}_2 > 0$ (when rare, the predator tends to grow exponentially fast).

From the first condition we obtain:

$$b_1 - \frac{1}{2}\sigma_1^2 > 0$$

and from the second one we get:

$$-b_2 + a_{21}\mathbb{E}_{Z\sim m}(Z) - \frac{1}{2}\sigma_2^2 > 0$$

Since $\mu_{\Xi_1} = 0$, we have:

$$\mathbb{E}_{Z\sim m}(Z) = \frac{b_1 - \frac{1}{2}\sigma_1^2}{a_{11}}$$

Thus, still intuitively, a sufficient condition for SSP is:

$$\frac{b_1 - \frac{1}{2}\sigma_1^2}{a_{11}} > \frac{b_2 + \frac{1}{2}\sigma_2^2}{a_{21}}$$

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- In the simple example of the prey-predator community, the above intuition is just right ([Ben18], [HN18b]).
- The aim of this work is to show how these results can be extended to communities such as (2).

Our framework, assumption and results

Our SDE framework

$$d\mathbf{X}_t = \mathbf{X}_t \circ \left((\mathbf{B} + \mathbf{A}\mathbf{X}_t)dt + \Sigma d\mathbf{W}_t + \int_{\mathbb{R}^n \setminus \{0\}} \mathbf{L}(\mathbf{X}, \mathbf{z}) \tilde{N}(dt, dz) \right). \quad (2)$$

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- **Biological interpretation of the jump part:** Other sources of randomness on the biotic or abiotic factors of the ecosystems whose natural time-scale are much longer than those of the perturbation modeled by the Brownian part: sudden migration of resident species or incoming flow of biomass through ecosystem boundaries (see e.g. the excellent compendium on the topic of animal migration [MG11], specially chapter 9) or ENSO effects on habitat compression and deepening of nutricline (see [OMK⁺17]).

Our framework regarding the communities

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- The signs of \mathbf{A} determine a directed graph (with an edge from prey to predators).

Assumptions

- 1 The community is layered.
- 2 (**Assumption 1**): $\int_{\mathbb{R}^n \setminus \{0\}} \|z\|^2 \nu(dz) < \infty$.
- 3 (**Assumption 2**): For every $i = 1, 2, \dots, n$, $\mathbf{x}, \mathbf{z} \in \mathbb{R}^n$:

$$|L_i(\mathbf{x}, \mathbf{z})| \leq |z_i| \mathbf{1}_{z_i > -1}.$$

- 4 (**Assumption 3**): There exists a constant C such that:

$$\|\mathbf{x} \circ \mathbf{L}(\mathbf{x}, \mathbf{z})\| \leq C \|\mathbf{z}\|$$

- 5 (**Assumption 4**): For \mathbf{x}, \mathbf{y} in K compact, $\mathbf{z} \in \mathbb{R}^n$, there exists a constant M_k such that:

$$\|\mathbf{x} \circ \mathbf{L}(\mathbf{x}, \mathbf{z}) - \mathbf{y} \circ \mathbf{L}(\mathbf{y}, \mathbf{z})\| \leq M_k \|\mathbf{x} - \mathbf{y}\| \|\mathbf{z}\|,$$

holds.

Invasibility rates

Just like in our example, define:

$$\Xi_i(\mathbf{x}) := (B_i + (\mathbf{A}\mathbf{x})_i) - \frac{1}{2}\sigma_i^2 - \int_{\mathbb{R}_+^n} L_i(\mathbf{x}, \mathbf{z}) - \ln(1 + L_i(\mathbf{x}, \mathbf{z}))\nu(d\mathbf{z}).$$

More technical assumptions

- ① Observe that any layered community has the following property: there exists $\mathbf{c} \in \mathbb{R}_{++}^n$ such that whenever $i \rightarrow j$:

$$c_i a_{ij} \geq c_j a_{ji}.$$

- ② It is proved that the conditions:

$$\text{For every } \mu \in \mathcal{P}_{erg}(\partial\mathbb{R}_+^n) : \max_i \mu \Xi_i > 0$$

and

There exists $\mathbf{p} := (p_1, \dots, p_n) \in \mathbb{R}_{++}^n$ such that:

$$\inf_{\mu \in \mathcal{P}_{erg}(\partial\mathbb{R}_+^n)} \sum_i p_i \mu \Xi_i := \rho > 0, \quad (3)$$

are equivalent ([SBA11]).

Crucial assumption

(Assumption 5): The condition (3) holds.

log-Lyapunov functions

Define for $\mathbf{x} \in \mathbb{R}_{++}^n$

$$\hat{V}(\mathbf{x}) = \frac{1 + \mathbf{c}^T \mathbf{x}}{\prod_{j=1}^n x_j^{p_j}},$$

and for $\alpha > 0$ define:

$$\tilde{W}(\mathbf{x}) := \hat{V}^\alpha(\mathbf{x}).$$

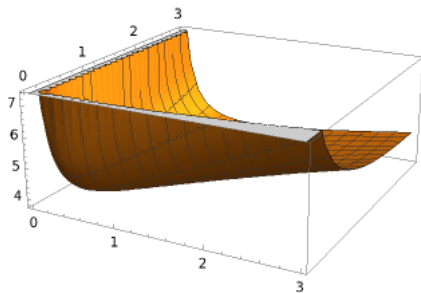
(the c_i 's are those ensured by the layered hypothesis; the p_i 's are *small* and satisfy the condition (3); ; $\alpha > 0$ will be fixed appropriately).

Observe that for p_i small (namely, $\sum_i p_i < 1$), the function \hat{V} satisfy:

$$\lim_{\|\mathbf{x}\| \rightarrow \infty} \hat{V}(\mathbf{x}) = \liminf_{\mathbf{x}: \min_i x_i \rightarrow 0} \hat{V}(\mathbf{x}) = +\infty$$

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Further assumption

For $\mathbf{x} \in \mathbb{R}_{++}^n$, set:

$$I(\mathbf{x}) := \int_{\mathbb{R}^n} \left\{ \tilde{W}((x_i(1 + L_i(\mathbf{x}, \mathbf{z}))_i) - \tilde{W}(\mathbf{x}) - \alpha \tilde{W}(\mathbf{x}) \sum_{i=1}^n \left(L_i(\mathbf{x}, \mathbf{z}) \left(\frac{c_i x_i}{1 + \mathbf{c}^T \mathbf{x}} - p_i \right) \right) \right\} \nu(d\mathbf{z}).$$

Two further technical assumptions

Assumption 6:

$$I(\mathbf{x}) \leq C\tilde{W}(\mathbf{x})$$

for some positive constant C . Furthermore, for some small positive α_0 , the function $\mathbf{z} \mapsto \exp(\alpha_0\|\mathbf{z}\|)$ is ν -integrable.

Main theorem

Theorem

Suppose Assumptions 1 through 6 hold. Then $(\mathbf{X}_t : t \geq 0)$ is a \mathbb{R}_+^n -valued, right-continuous, C_b -Feller Markov process with the SSP property.

Remark

Define:

$$\text{Safe}(\varepsilon, R) := \{\mathbf{x} \in \mathbb{R}_{++}^n : \min x_i > \varepsilon, \|\mathbf{x}\| \leq R\},$$

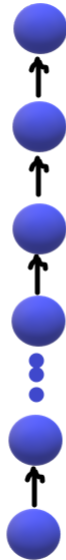
and let $\mathcal{I}(\mathbf{x})$ be a positive Lipschitz function, bounded by 1, that approximates $\mathbf{1}_{\text{Safe}(\varepsilon, R)}(\mathbf{x})$ from below.

Assume that the community is layered and $\nu(d\mathbf{z}) = \lambda\mu(d\mathbf{z})$, with μ the law of a \mathbb{R}^n -valued random variable with compact support contained in $\{z_i > -\gamma, i = 1, \dots, n\}$, where $\gamma \in (0, 1)$. Assume also that

$L_i(\mathbf{x}, \mathbf{z}) = \beta\mathcal{I}(\mathbf{x})z_i$, where $0 < \beta < 1$, $\varepsilon > 0$ and $R > 0$.

On this setting, the hypotheses 1, 2, 3, 4 and 6 required by Theorem 3 are satisfied.

Example: Lévy-driven, Lotka-Volterra food-chains



Parameters

For $i = 1, \dots, n$, let $(N_t^{(i)} : t \geq 0)$ be a family of independent compound Poisson processes on \mathbb{R} with intensity $\tilde{\lambda}_i > 0$ and jump increment distributed according to a law m_i with support contained in $\{z > -1\}$. As before, let \tilde{N}_i be the compensated process. Let $\beta \in (0, 1)$ and $0 < \varepsilon_i < M_i$, $i = 1, \dots, n$ be some constants. Let $\ell_i : \mathbb{R}_+ \rightarrow [0, 1]$ be a Lipschitz function that equals 1 on $[\varepsilon_i, M_i]$ and vanishing outside the interval $[\varepsilon_i/2, 2M_i]$. Set $L_i(\mathbf{x}, \mathbf{z}) = \ell_i(x_i)\beta z_i$.

The food-chain equations

$$\begin{aligned}dX_t^{(1)} &= X_t^{(1)} \left((b_1 - a_{11}X_t^{(1)} - a_{12}X_t^{(2)})dt + \sigma_1 dW_t^{(1)} \right. \\ &\quad \left. + \int_{\{z_1 > -1\}} L_1(\mathbf{X}_t, \mathbf{z}) \tilde{N}_1(dz_1, dt) \right), \\ dX_t^{(i)} &= X_t^{(i)} \left((-b_i + a_{i,i-1}X_t^{(i-1)} - a_{i,i}X_t^{(i)} - a_{i,i+1}X_t^{(i+1)})dt + \sigma_i dW_t^{(i)} \right. \\ &\quad \left. + \int_{\{z_i > -1\}} L_i(\mathbf{X}_t, \mathbf{z}) \tilde{N}_i(dz_i, dt) \right), \quad i = 2, \dots, n-1, \\ dX_t^{(n)} &= X_t^{(n)} \left((-b_n + a_{n,n-1}X_t^{(n-1)} - a_{nn}X_t^{(n)})dt + \sigma_n dW_t^{(n)} \right. \\ &\quad \left. + \int_{\{z_n > -1\}} L_n(\mathbf{X}_t, \mathbf{z}) \tilde{N}_n(dz_n, dt) \right).\end{aligned} \tag{4}$$

SSP for Lévy-driven LV food-chains

For $n \geq 2$, set:

$$d_1 = b_1 - \frac{1}{2}\sigma_1^2, \quad d_i = b_i + \frac{1}{2}\sigma_i^2; \quad i = 2, \dots, n$$

$$\Delta_i = \mathbb{E}_{Z \sim m_i}(\beta Z - \ln(1 + \beta Z)) \geq 0; \quad \lambda_i = \tilde{\lambda}_i \Delta_i$$

$$r_1 := d_1 - \lambda_1, \quad r_i := d_i + \lambda_i, \quad i = 2, \dots, n;$$

$$\mathbf{r}_m = (-r_1, r_2, \dots, r_m), \quad 1 \leq m \leq n.$$

SSP for Lévy-driven LV food-chains

Theorem

For $2 \leq m \leq n$, let \mathbf{A}_m be the leading m -dimensional submatrix of \mathbf{A} . Consider the linear systems:

$$\mathbf{A}_m \mathbf{s} = \mathbf{r}_m, \quad 2 \leq m \leq n$$

and let $s^{(*,m)} \in \mathbb{R}^m$ be the unique solution of the m -th system. Assume that:

$$a_{n,n-1} s_{n-1}^{(*,n-1)} > r_n. \quad (5)$$

holds. Then the SDE (4) is SSP.

Remarks:

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- ① The above result extends a Theorem of Hening and Nguyen ([HN18c]), which in turn extends a result of Gard ([GH79]) on deterministic LV food-chains.

Appendix: sketch of the proof

Steps toward the proof

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- To prove that there exists an **embedded chain** with tight laws in \mathbb{R}_{++}^n (uniformly for initial conditions on compact sets). A sufficient condition is:

Proposition

For some continuous log-Lyapunov function \tilde{V} , for some $T^ > 0$, $m \in (0, 1)$ and $C > 0$, the inequality:*

$$\mathbb{E}_{\mathbf{x}}(\tilde{V}(\mathbf{X}_{T^*})) \leq m\tilde{V}(\mathbf{x}) + C,$$

holds for every $\mathbf{x} \in \mathbb{R}_{++}^n$

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- This is the hard part.

Steps toward the proof

We prove:

Lemma

For every $T > 0$ and $\mathbf{X}_0 \in \mathbb{R}_{++}^n$, under $\mathbb{P}_{\mathbf{X}_0}$ the Markov chain $\mathbf{X}^T := (\mathbf{X}_{mT} : m \geq 0)$ is irreducible and aperiodic. Furthermore, every compact set is a petite set for the chain.

By Lemma 5 and Theorem 6.3 of [MT92], there exists a probability measure π such that:

$$\lim_{n \rightarrow \infty} \|\mathbb{P}_{\mathbf{x}}(\mathbf{X}_{nT^*} \in \cdot) - \pi(\cdot)\|_{TV} = 0,$$

and the convergence is geometric.

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and the convergence is geometric. Then, \mathbf{X}^{T^*} is positive Harris recurrent, and thus this chain has hitting times (of open sets) with finite expectation; this in turn also implies that \mathbf{X} is positive Harris recurrent (see theorem 1 of [KM94]), and thus has a unique invariant probability measure in \mathbb{R}_{++}^n . Of course, this probability measure is just π .

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