Spatial Cannings model with catastrophes in random environment

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This talk

- A (population genetics) model for **structured populations**, based on spatially interacting **Cannings processes** in **heterogeneous environment** with the following features:
  - Spatial migration.
  - Cannnings reproduction (in **random environment**).
  - Occasional catastrophes affecting the whole patches of the geographical space (in **random environment**).
- Work in the limit of many individuals: "continuous mass"-limit.
- Study **biodiversity**. Two scenarios:
  - Growth of the mono-type patches: **clustering**.
  - Diverse populations: **coexistence**.

Tools:

- Duality.
- Multi-scale analysis (and renormalization group): how does the dynamics on different scales influence each other?

Geographically structured colonies of individuals

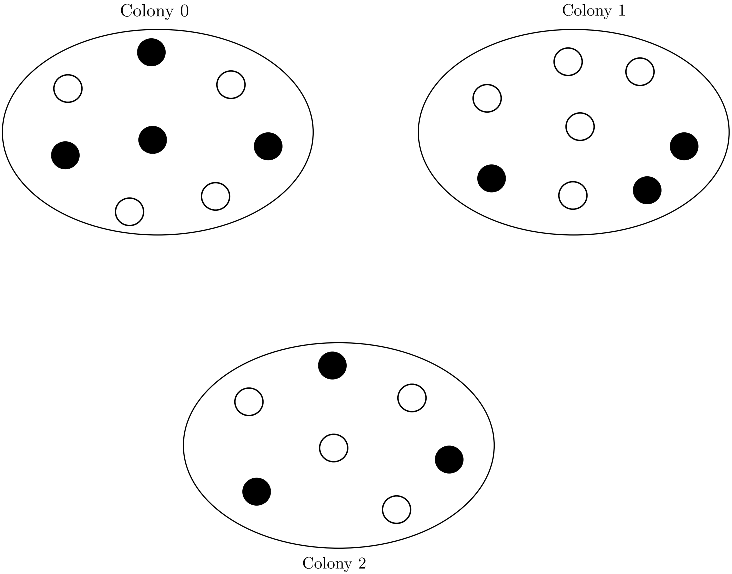


Figure : $N = 3$ colonies with individuals

Migration

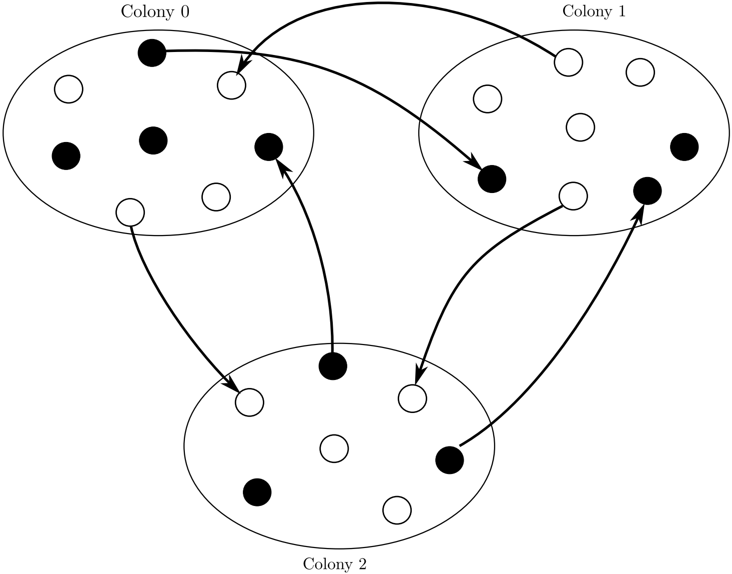
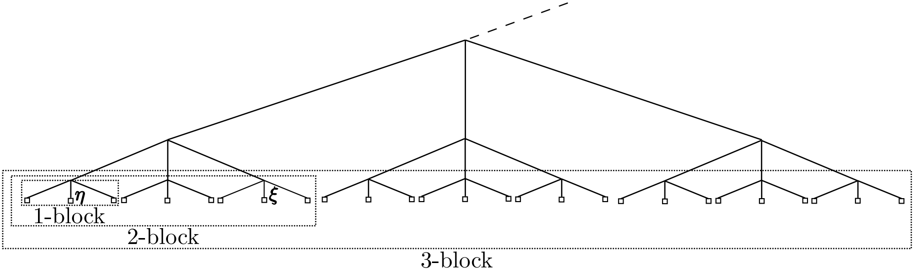


Figure : Migration of individuals between the $N = 3$ colonies (rate c/N random walk)

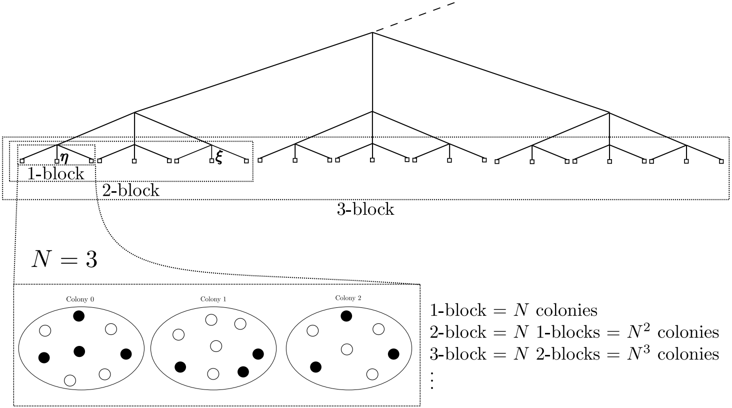
Hierarchical geography



- **Felsenstein, Sawyer (1983)**: migration rates do not depend on the Euclidean distance but rather on the clustering distance (village⇝valley⇝province⇝state⇝country⇝continent).

- (Countable abelian) **Hierarchical group** (and a regular tree): $\Omega_N = \left\{ \eta = (\eta^l)_{l \in \mathbb{N}_0} \in \{0, 1, \ldots, N-1\}^{\mathbb{N}_0} \colon \sum_{l \in \mathbb{N}_0} \eta^l < \infty \right\}$.
- Here $N \in \mathbb{N}$ is a parameter.
- So $\eta \in \Omega_N$ is the **address of a colony**.

Migration on the hierarchical space (Dawson, Gorostiza, Wakolbinger)



Hierarchical random walk:

- **Migration rates:** $\underline{c} := (c_k)_{k\in\mathbb{N}_0} \in (0,N)^{\mathbb{N}_0}$.
- each indiv. at $\eta \in \Omega_N$ jumps unif. in k-block around η at rate c_{k-1}/N^{k-1}.

Reproduction within a colony: Cannings model

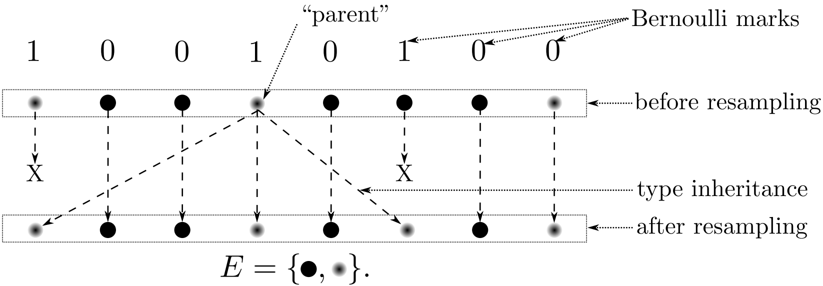
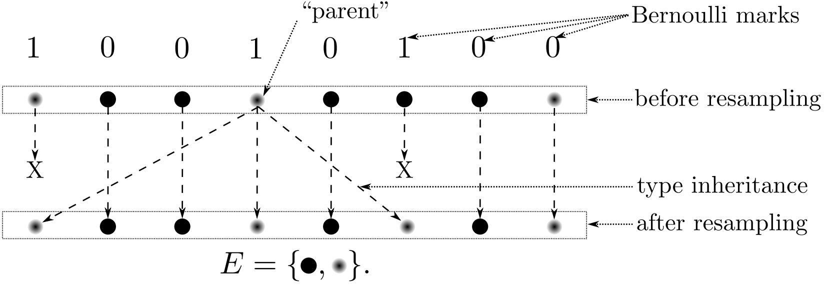


Figure : Resampling

Cannings model (discrete time):

- M fixed (# of individuals).
- **Exchangeable** collection of r.v. $\{v_i^{(M)} \in [0:M] : i \in [1:M]\}$.
- $\sum_{i=1}^{M} v_i^{(M)} = M$.

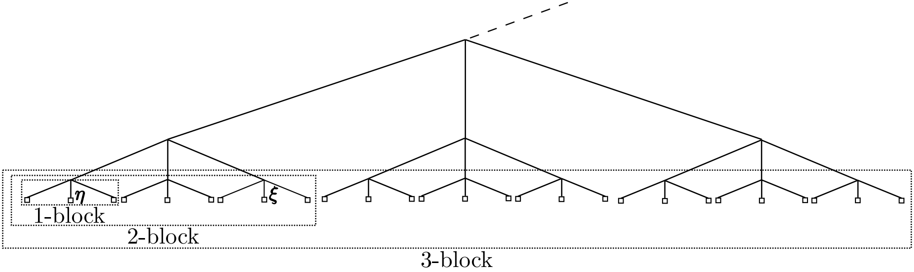
Λ-Cannings model (continous time, continuous mass limit)



A large universality class ($M \to \infty$, Sagitov'1999, Möhle-Sagitov'2001):

- Driven by **PPP** on $\mathbb{R}_+ \times [0,1]$ with $\mathrm{d}t \otimes \Lambda(\mathrm{d}r)/r^2$, where $\Lambda \in \mathscr{M}_{\text{finite}}([0,1])$, $\Lambda(\{0\}) = 0$.
- **Resampling** $(r\delta_1 + (1-r)\delta_0)^{\otimes M}$ (**Bernoulli experiment**).
- For $M \to \infty$, study the **distribution of types**: $X(t) := \frac{1}{M}\sum_{i=1}^{M} \delta_{T(i,t)} \in \mathscr{M}_1(E)$ in a colony.

Catastrophes



Catastrophes affecting the whole blocks:

- E.g, droughts, floods, forest fires, epidemics, meteorite impacts, etc.
- Driven by **PPP** on $\mathbb{R}_+ \times [0,1]$ with $\mathrm{d}t \otimes N^{-2k}\Lambda_k(\mathrm{d}r)/r^2$, where $\Lambda_k \in \mathscr{M}_1([0,1])$, $\Lambda(\{0\}) = 0$.
- Non-local resampling-reshuffling:
  - **Reshuffle** the individuals in the k-block: immediate uniform relocation.
  - **Resample** the individuals in k-block using Λ_k.

Inhomogeneous environment

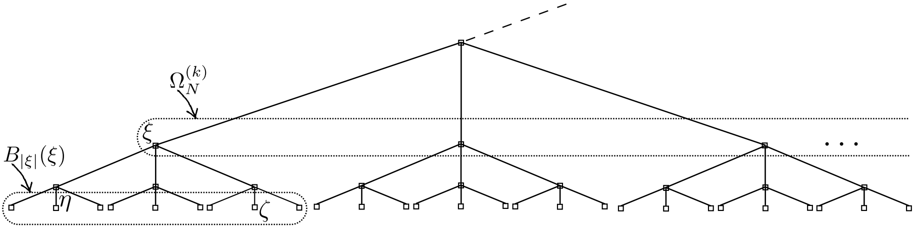


Figure : $\Omega_N^{\mathbb{T}}$ with $N = 3$, $\xi \in \Omega_N^{(k)} \subset \Omega_N^{\mathbb{T}}$, $|\xi| = k = 2$, $\eta, \zeta \in B_{|\xi|}(\xi)$. The elements of $\Omega_N^{\mathbb{T}}$ are the vertices of the tree (indicated by $\square$'s).

Spatially inhomogeneous environment:

- Catastrophes are driven by

$$\underline{\Lambda}(\omega) = \left\{\Lambda^{\xi}(\omega) \in \mathscr{M}_{\mathrm{f}}([0,1]) :\ \xi \in \Omega_N^{\mathbb{T}}\right\}$$

- $\xi \in \Omega_N^{\mathbb{T}}$ is the **address of a $|\xi|$-block**.
- ω is the **random environment**.
- Structural assumption: $\Lambda^{\xi}(\omega) = \lambda_{|\xi|}\chi^{\xi}(\omega)$, where:
  - $\chi^{\xi}(\omega) \in \mathscr{M}_{\mathrm{f}}([0,1])$ is random stationary and λ_k is deterministic.

Summary (so far)

Hierarchically interacting $(\underline{c},\underline{\Lambda})$-Cannings process in random environment

$$X^{(\Omega_N)} = \left\{X_\eta^{(\Omega_N)}(\omega;t) \in \mathscr{M}_1(E)\right\}_{t\in\mathbb{R}_+,\eta\in\Omega_N}.$$

Competition between:

- **Migration** $\underline{c} = (c_k)_{k\in\mathbb{Z}_+}$ (spatial movement)
  vs.
  Resampling + Catastrophes in **random environment**
  $\underline{\Lambda} = (\Lambda_k(\omega))_{k\in\mathbb{Z}_+}$ (reproduction under constrained resources).
  plus
- (Hierarchy of) **slow** and **fast time scales** on which the blocks evolve.

N.B. Important features:

- **Non-diffusive behaviour**: PPP driven jumps.
- **Strongly correlated global updates:** non-local reshuffling-resampling.
- **Random environment.**

Long-run behaviour of the spatial process

$$\mathbf{Q}: \mathscr{L}\left[X^{(\Omega_N)}(t)\right] \underset{t\to+\infty}{\Longrightarrow} \ ?$$

Biodiversity in the long run?

Equilibrium

Theorem (Equilibrium)

*Fix $N \in \mathbb{N}\backslash\{1\}$. Suppose that, under the law $\mathbb{P}$, the law of the initial state $X^{(\Omega_N)}(\omega;0)$ is **stationary and ergodic** under translations in $\Omega_N^{\mathbb{T}}$, with mean single-coordinate measure $\theta = \mathbb{E}[X_0^{(\Omega_N)}(\omega;0)] \in \mathscr{M}_1(E)$. Then, there exists an **equilibrium measure** $\nu_\theta^N(\omega) \in \mathscr{M}_1(\mathscr{M}_1(E)^{\Omega_N})$:*

$$\lim_{t\to\infty} \mathscr{L}\left[X^{(\Omega_N)}(\omega;t)\right] = \nu_\theta^N(\omega), \quad \mathbb{P}\text{-a.s. } \omega$$

satisfying

$$\int_{\mathscr{M}_1(E)^{\Omega_N}} x_0 \, \nu_\theta^N(\omega; \mathrm{d}x) = \theta.$$

Moreover, under the law $\mathbb{P}$, $\nu_\theta^N(\omega)$ is stationary and ergodic under translations in $\Omega_N^{\mathbb{T}}$.

Clustering vs. coexistence

Two scenarios for $\nu_\theta^N(\omega)$:

- **Coexistence given ω:**

$$\sup_{\psi \in C_{\mathrm{b}}(E)} \int_{\mathscr{M}_1(E)^{\Omega_N}} \nu_\theta^N(\omega)(\mathrm{d}x) \left[\int_E \psi^2(u) x_0(\mathrm{d}u) - \left(\int_E \psi(u) x_0(\mathrm{d}u) \right)^2 \right] > 0.$$

  In words: The variance of the type distribution is positive.

- **Clustering given ω:**

$$\nu_\theta^N(\omega) = \int_E \delta_{(\delta_u)^{\Omega_N}} \theta(\mathrm{d}u).$$

  In words: The system grows mono-type clusters that cover Ω_N.

Clustering vs. coexistence for $N < \infty$

Theorem (Dichotomy for finite N)

Fix $N \in \mathbb{N}\backslash\{1\}$ and assume that $\rho^{\xi}(\omega) := \chi^{\xi}([0,1],\omega)$ satisfies

$$\mathbb{E}[\rho^{\xi}(\omega)] = 1, \qquad \exists\,\delta > 0\colon\ \delta \le \rho^{\xi}(\omega) \le \delta^{-1}\ \forall\,\xi \in \Omega_N \text{ for } \mathbb{P}\text{-a.e. } \omega.$$

(a) *Let $\mathscr{C}_N := \{\omega\colon$ **coexistence** given ω occurs$\}$. Then $\mathbb{P}(\mathscr{C}_N) \in \{0,1\}$.*

(b) $\mathbb{P}(\mathscr{C}_N) = 1$ *if and only if*

$$\sum_{k\in\mathbb{N}_0} \frac{1}{c_k + N^{-1}\lambda_{k+1}} \sum_{l=0}^{k} \lambda_l < \infty.$$

NB!

- Sublte inteplay between c and λ.
- If $\lambda_l = 0,\ \forall l \ge 1$ (i.e., no catastrophes), then the criterion reduces to the recurrence condition for the migration.

Idea of proof

Study the **lineages** (backwards in time):

- **Duality**: lineages evolve according to a **spatial coalescent with non-local coalescence in random environment**.

Duality with a spatial coalescent with non-local coalescence in random environment

Relate $X = \{X_t\}_{t\in\mathbb{R}_+}$ with a **simpler process**. Find H and $Y = \{Y_t\}_{t\in\mathbb{R}_+}$:

$$\mathbb{E}_{X_0}[H(X_t, Y_0)] = \mathbb{E}_{Y_0}[H(X_0, Y_t)], \text{ for all } (X_0, Y_0), \quad t \in \mathbb{R}_+.$$

Spatial coalescent with non-local coalescence in random environment

- Backwards in time dynamics of the **coalescing lineages**.
- **Spatial Λ-coalescent** with non-local coalescence: Y_t.
- At start, infinitely many singleton **families**.
- Families move around according to the HRW.
- Driven by **PPP** $\mathrm{d}t \otimes \mathrm{d}\eta \otimes \Big(N^{-2k}\mathrm{d}k \Big[\Lambda_k(\mathrm{d}r)\big(r\delta_1 + (1-r)\delta_0\big)^{\otimes\mathbb{N}}\Big](\mathrm{d}\omega)\Big)$.
- At coalescence event, $k \geq 2$ families in $B_k(\eta)$ coalesce. Afterwards, all families in B_k are reshuffled.

Biodiversity dichotomy: clustering vs. coexistence

Dichotomy seen backwards in time:

- Single family in the long run $\rightsquigarrow$ no **biodiversity** (clustering).
- More then one family $\rightsquigarrow$ **coexistence**.

Exchangeability + Duality $\rightsquigarrow$ enough to consider **two coalescing random walks** $(Z_t^1(\omega), Z_t^2(\omega))_{t\geq 0}$ on Ω_N with migration coefficients $(c_k + \lambda_{k+1} N^{-(k+1)})_{k\in\mathbb{N}_0}$ in random environment and coalescence at rates $(\lambda_k = \Lambda_k([0,1]))_{k\in\mathbb{N}_0}$.

Time-t accumulated hazard for coalescence of this pair

$$H_N(\omega;t) = \sum_{k\in\mathbb{N}_0} N^{-k} \sum_{\substack{\eta,\eta'\in\Omega_N \\ d_{\Omega_N}(\eta,\eta')\leq k}} \lambda^{\mathrm{MC}_k(\eta)}(\omega) \int_0^t 1_{\{Y_s(\omega)=\eta, Y_s'(\omega)=\eta'\}}\,\mathrm{d}s,$$

Lemma

- $\lim_{t\to\infty} H_N(t;\omega) = \infty$ *a.s.* $\rightsquigarrow$ ***no biodiversity*** *(clustering).*
- $\lim_{t\to\infty} H_N(t;\omega) < \infty$ *a.s* $\rightsquigarrow$ ***coexistence****.*

Large space-time scale analysis: $N \to \infty$

Q: $\mathscr{L}\left[k\text{-block average}(t \cdot N^k; \omega)\right] \xrightarrow[N \to +\infty]{} \textbf{?}$

Universal limiting law?

Large space-time scale analysis: $N \to \infty$

- **"Separate" slow and fast time scales:** Guaranteed as $N \to \infty$.
- Analyse the system scale by scale.
- **Macroscopic observables:** block averages

$$Y^{(N)}_{\eta,k}(tN^k;\omega) = \frac{1}{N^k} \sum_{\zeta \in B_k(\eta)} X^{(\Omega_N)}_{\zeta}(tN^k;\omega), \qquad \eta \in \Omega_N, k \in \mathbb{Z}_+$$

  (block averages of order $k \in \mathbb{Z}_+$).
- **Single scale** (mean-field) $\rightsquigarrow$ **propagation of chaos** and appearance of **McKean-Vlasov process.**
- **Multiple scales** simultaneously: $\rightsquigarrow$ Markov **interaction chain**.
- All this in the **hierarchical mean-field limit:**

$$\Omega_N \uparrow \Omega_\infty, \quad N \to +\infty.$$

McKean-Vlasov limiting object

Algebra of test functions: $\mathscr{B} \subseteq C_b(\mathscr{M}_1(E), \mathbb{R})$ with $G \in \mathscr{B}$:

$$G(x) = \int_{E^n} x^{\otimes n}(\mathrm{d}u)\,\varphi(u), \qquad x \in \mathscr{M}_1(E), n \in \mathbb{N}, \varphi \in C_{\mathrm{b}}(E^n, \mathbb{R}).$$

Generator:

$$(L_\theta^{c,d,\Lambda} G)(x) = c \int_E (\theta - x)\,(\mathrm{d}a)\,\frac{\partial G(x)}{\partial x}[\delta_a] \leftarrow \textbf{[drift]}$$

$$+\, d \int_E \int_E Q_x(\mathrm{d}u, \mathrm{d}v)\,\frac{\partial^2 G(x)}{\partial x^2}[\delta_u, \delta_v] \leftarrow \textbf{[Fleming-Viot diffision]}$$

$$+ \int_{[0,1]} \Lambda^*(\mathrm{d}r) \int_E x(\mathrm{d}a)\left[G\big((1-r)x + r\delta_a\big) - G(x)\right] \leftarrow \textbf{[jumps]}, \quad G \in \mathscr{B},$$

where

$$Q_x(\mathrm{d}u, \mathrm{d}v) = x(\mathrm{d}u)\,\delta_u(\mathrm{d}v) - x(\mathrm{d}u)\,x(\mathrm{d}v).$$

C^Λ-processes with immigration-emigration:

$$Z_\theta^{c,d,\Lambda} = \left(Z_\theta^{c,d,\Lambda}(t)\right)_{t \geq 0}, \quad Z_\theta^{c,d,\Lambda}(0) = \theta.$$

Asymptotic behaviour of the block averages

Theorem (Behaviour of the macroscopic observables)

Suppose that for each N the random field $X^{(\Omega_N)}(\omega;0)$ is the restriction to Ω_N of a random field $X(\omega)$ indexed by $\Omega_\infty = \bigoplus_{\mathbb{N}} \mathbb{N}$ that is i.i.d. with single-component mean $\theta \in \mathscr{M}_1(E)$. Then, for $\mathbb{P}$-a.e. ω and every $k \in \mathbb{N}$ and $\eta \in \Omega_\infty$,

$$\lim_{N\to\infty} \mathscr{L}\left[\left(Y^{(\Omega_N)}_{\eta,k}(\omega;tN^k)\right)_{t\geq 0}\right] = \mathscr{L}\left[\left(Z^{c_k,d_k,\Lambda^{\mathrm{MC}_k(\eta)}(\omega)}_{\theta}(t)\right)_{t\geq 0}\right].$$

- **Volatility constants:** $\underline{d} = (d_k)_{k\in\mathbb{Z}_+}$,

$$d_0 = 0, \qquad d_{k+1} = \mathbb{E}_{\mathscr{L}_\rho}\left[\frac{c_k(\mu_k\rho + d_k)}{c_k + (\mu_k\rho + d_k)}\right], \quad k \in \mathbb{Z}_+,$$

  where $\mu_k = \lambda_k/2$ and $\mathscr{L}[\rho] = \mathscr{L}[\rho^0]$.
- **N.B.** (inhomogeneous) average of a **random Möbius transformation**.
- **Self-averaging** with respect to the random environment up to and including level k.

Heuristic derivation of the formula for volatilities

- **Space-time scales separate**, as $N \to \infty$.
- $\Rightarrow$ enough to consider the 1-block averages.
- Duality $\Rightarrow$ study the coalescing lineages.
- Total coalescence rate $=$ volatility.
- At space-time scale Nt, **only pairs of lineages can possibly meet** (cf. Limic, Sturm (2006))
- The lineages coalesce at the rate $\lambda^{(\eta,0)}(\omega) = \Lambda^{(\eta,0)}((0,1])(\omega)$, if they are in the same colony.
- Probability to migrate away before coalescence is $2c_0/(2c_0 + \lambda^{(\eta,0)}(\omega))$.
- $\Rightarrow$ the average **total coalescence rate** equals

$$\mathbb{E}\left[\frac{2c_0\lambda_0\rho(\omega)}{2c_0 + \lambda_0\rho(\omega)}\right].$$

Random environment facilitates biodiversity

The volatility d_k in the random environment can be sandwiched between:

- the volatility d_k^0 in the **zero environment** ($\mathscr{L}_\rho = \delta_0$, i.e., the system without resampling)
- the volatility d_k^1 in the **average environment** ($\mathscr{L}_\rho = \delta_1$, i.e., the system with average resampling).

Theorem (Randomness lowers volatility)

Assume the environment is non-deterministic. If $d_0^0 = d_0 = d_0^1$, then

$$d_k^0 < d_k < d_k^1, \quad k \in \mathbb{N}.$$

Proof.

Jensen's inequality. □

Multi-scale analysis

Theorem (multi-scale behaviour)

Let $(t_N)_{N\in\mathbb{N}}$ be such that $\lim_{N\to\infty} t_N = \infty$ and $\lim_{N\to\infty} t_N/N = 0$. Then, for $\mathbb{P}$-a.e. ω, every $j \in \mathbb{N}$ and every $\eta \in \Omega_\infty$,

$$\lim_{N\to\infty} \mathscr{L}\left[\left(Y^{(\Omega_N)}_{\eta,k}(\omega; t_N N^k)\right)_{k=-(j+1),-j,\dots,0}\right] = \mathscr{L}\left[\left(M^{(j)}_{\eta,k}(\omega)\right)_{k=-(j+1),-j,\dots,0}\right],$$

where $M^{(j)}_\eta(\omega) = (M^{(j)}_{\eta,k}(\omega))_{k=-(j+1),-j,\dots,0}$ is the time-inhomogeneous Markov chain with initial state

$$M^{(j)}_{\eta,-(j+1)}(\omega) := \theta,$$

and transition kernel from time $-(k+1)$ to $-k$ given by

$$K_{\eta,k}(\omega;\theta,\cdot) := \nu_\theta^{c_k,d_k,\Lambda^{\mathrm{MC}_k(\eta)}(\omega)}(\cdot).$$

Summary

The hierarchically interacting Cannings processes in random environment:

- **Dichotomy**: the **clustering vs. local coexistence dichotomy** in the long-time behaviour in terms of $\underline{c}, \underline{\lambda}$ for **finite** N.
- Identified its **space-time scaling behaviour** in the hierarchical mean-field limit $N \to \infty$.
- Volatilities decrease in the inhomogeneous environment. Clusters grow slower.
- Fluctuations in the environment reduce clustering $\rightsquigarrow$ **increased biodiversity**.

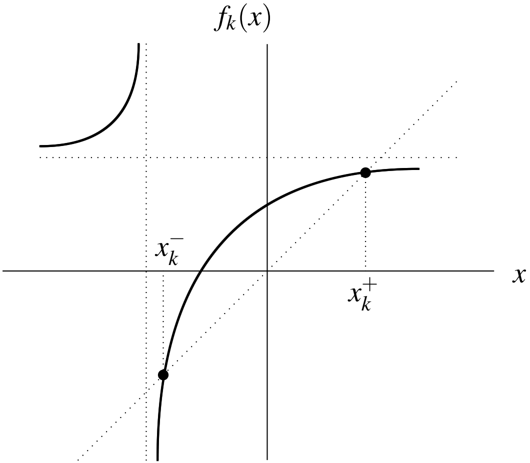


Figure : The Möbius-transformation $x \mapsto f_k(x)$.