Population Dynamics in a Random Environment

Mean Field Type Models

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Outline

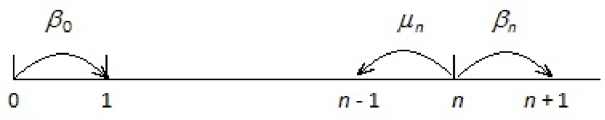
Properties of the random walk in continuous time on $\mathbb{Z}_1^+$

Ergodicity

The process $x(t)$ with generator (*) is ergodic iff

$$S(0) = 1 + \frac{\beta(0)}{\mu(1)} + \frac{\beta(0)\beta(1)}{\mu(1)\mu(2)} + \ldots + \frac{\beta(0)\cdots\beta(n-1)}{\mu(1)\cdots\mu(n)} + \ldots < \infty$$

$$\pi(0) = \frac{1}{S(0)}, \quad \pi(n) = \frac{1}{S(0)} \frac{\beta(0)\cdots\beta(n-1)}{\mu(1)\cdots\mu(n)} \text{ for } n \geq 1$$



(*)

Figure: Generator for Random Walk

The process $x(t)$ is recurrent iff

$$Z = 1 + \frac{\mu(1)}{\beta(1)} + \frac{\mu(1)\mu(2)}{\beta(1)\beta(2)} + \ldots + \frac{\mu(1)\cdots\mu(n)}{\beta(1)\cdots\beta(n)} + \ldots = +\infty$$

Note that the ergodicity of $x(t)$ is equivalent to positive recurrence: for all $m,\ n \geq 0,\ m \neq n$

$$E_m \tau_n < \infty, \quad \tau_n = \min(t : x(t) = n)$$

To calculate $E_x\tau_0 = E_x\tau_{x\to 0} = \varphi(x)$

- Start at 0, RW spends $\theta_1 \sim \exp(\beta_0)$ at 0, jumps to 1 at time $\theta_1 + 0$.
- Returns to 0 after random time T_1, $ET_1 = \varphi(1)$.
- Process repeats.
- n cycles cover time interval $[0, \theta_1 + \ldots + \theta_n + T_1 + \ldots + T_n]$.
- Fraction of time chain spends at site 0 tends to

$$\frac{1}{S(0)} = \pi(0) = \lim_{n\to\infty} \frac{n\frac{1}{\beta_0}}{n\frac{1}{\beta_0} + n\varphi(1)} = \frac{\frac{1}{\beta_0}}{\frac{1}{\beta_0} + \varphi(1)}$$

.

- This gives

$$S(0) = 1 + \beta_0\varphi(1) \Rightarrow$$
$$\varphi(1) = \frac{1}{\mu(1)}\left(1 + \frac{\beta(1)}{\mu(2)} + \frac{\beta(1)\beta(2)}{\mu(2)\mu(3)} + \dots\right) = A(1)$$

- Similarly

$$\varphi(2) = E_2\tau_{2\to 1} + E_1\tau_{1\to 0} = A(1) + A(2)$$

where

$$A(k) = \frac{1}{\mu(k)}\left(1 + \frac{\beta(k)}{\mu(k+1)} + \frac{\beta(k)\beta(k+1)}{\mu(k+1)\mu(k+2)} + \dots\right) \quad (1)$$

- The series $A(1)$, $A(2)$, ... converges if the sum $S(0)$ is finite.

Theorem

Let $A(k)$ be as in Eq. 1. Put $\varphi(x) = A(1) + \ldots + A(x)$ for $x \geq 1$ and $\varphi(0) = 0$. Then, under the condition that $S(0) = 1 + \frac{\beta(0)}{\mu(1)} + \frac{\beta(0)\beta(1)}{\mu(1)\mu(2)} + \ldots + \frac{\beta(0)\cdots\beta(n-1)}{\mu(1)\cdots\mu(n)} + \ldots < \infty$,

$$\mu(x)\varphi(x-1) - (\mu(x) + \beta(x))\varphi(x) + \beta(x)\varphi(x+1) = -1,$$

i.e., $\varphi(x) = E_x\tau_{x\to 0}$. In particular,

$$\varphi(1) = E\tau_{1\to 0} = A(1) = \frac{1}{\mu(1)}\left(1 + \frac{\beta(1)}{\mu(2)} + \frac{\beta(1)\beta(2)}{\mu(2)\mu(3)} + \ldots\right).$$

Outline

Models in a stationary random environment

Three cases

- In the case of a random environment, all random variables or probabilities are functions of two variables:
  - ω_m: the environment, i.e., sequences of the r.v.s $\{\mu_x\}$, $\{\beta_x\}$, etc.
  - ω: the trajectory of the random walk for fixed ω_m
- Expectations:
  - We use $E_{\omega_m}\tau = f(\omega_m)$ for the expectation with respect to ω_m.
  - We use $\langle E_{\omega_m}\tau \rangle$ for the total expectation of τ.
- We call a random walk ergodic in the "annealed" sense if $\langle E_{\omega_m}\tau_{x\to y} \rangle < \infty$ for all (x, y).
- We call a random walk ergodic in the "quenched" sense if $E_{\omega_m}\tau_{x\to y} < \infty$, $P_{\omega_m} - a.s.$

Models in a stationary random environment

Three cases

- We similarly distinguish annealed and quenched asymptotics with respect to some parameter, say, time t.
- Typically, the quenched and annealed descriptions of processes in a random environment are substantially different.
- The concepts of intermittency and localization are a manifestation of this difference.
- We discuss three cases, all of which are statistically homogeneous.
  - Random walk in a random environment
  - Random walk with immigration in a random environment
  - Mean field Bolker-Pacala model in a random environment

a) *Random walk in a random environment*

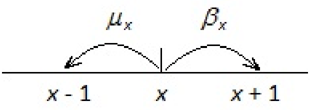


Figure: Random Walk in Random Environment

- Assume that $\beta_x \in [a_1, b_1]$, $0 < a_1 < b_1 < \infty$, $x \geq 0$, are i.i.d. random variables on the underlying probability space $(\Omega_m, \mathcal{F}_m, P_m)$.
- Also assume that $\mu_x \in [a_2, b_2]$, $0 < a_2 < b_2 < \infty$, $x \geq 0$, are i.i.d. random variables, independent of $\{\beta_x, x \geq 0\}$.

b) *Model with immigration*

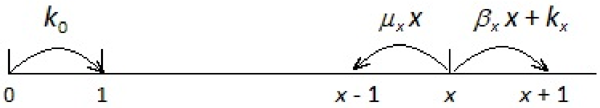


Figure: Random Walk in Random Environment with Immigration

- $\{\mu_x\}$, $\{\beta_x\}$, and $\{k_x\}$ are three independent sequences of i.i.d. random variables, $\beta_x \in [a_1, b_1]$, $\mu_x \in [a_2, b_2]$, and $k_x \in [a_3, b_3]$.
- k_x conveys the probability of immigration occurring at some site, independent of the population.
- This is mean field model of population dynamics.

Models in a stationary random environment

Three cases

c) *Mean field Bolker-Pacala model*

- Initial population of particles lives on a lattice.
- Each particle can split, die, or migrate in space, at respective rates β_x, μ_x, and κ_x.
- Key process: Death may occur due to presence of other particles (competition or suppression), at rate γ_x.
- A mean field treatment is mathematically tractable, and is equivalent to a kind of random walk.

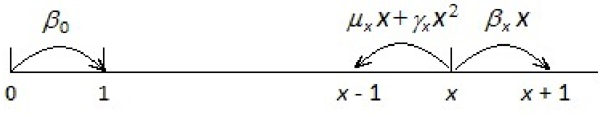


Figure: Mean Field Bolker-Pacala Model in Random Environment

- β_x, μ_x, and γ_x are three independent sequences of i.i.d. random variables, $\beta_x \in [a_1, b_1]$, $\mu_x \in [a_2, b_2]$, and $\gamma_x \in [a_3, b_3]$.
- Migration (rate κ_x) becomes irrelevant in the mean field treatment.
- Quadratic term indicates the negative effect of competition from other members of the population, at rate γ_x.

Outline

Random walk in random environment

- Start from the random walk

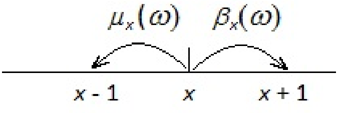


Figure: Random Walk in Random Environment

- Consider the series

$$Z = 1 + \frac{\mu_1}{\beta_1} + \frac{\mu_1 \mu_2}{\beta_1 \beta_2} + \dots$$
$$= 1 + \sum_{n=1}^{\infty} e^{\sum_{i=1}^{n} \ln \frac{\mu_i}{\beta_i}} = 1 + \sum_{n=1}^{\infty} e^{\sum_{i=1}^{n} (\ln \mu_i - \ln \beta_i)}$$

There are three cases

$$\left\langle \ln \frac{\mu}{\beta} \right\rangle < 0, \ \left\langle \ln \frac{\mu}{\beta} \right\rangle = 0, \ \left\langle \ln \frac{\mu}{\beta} \right\rangle > 0.$$

- When $\langle \ln \frac{\mu}{\beta} \rangle = 0$
  - Due to the CLT, the sum $\sum_{i=1}^{n} \ln \frac{\mu_i}{\beta_i} = \sqrt{n} S_n$
  - Where S_n is an asymptotically Gaussian r.v. that oscillates and is greater than 1 infinitely many times.
- Thus, $\left\langle \ln \frac{\mu}{\beta} \right\rangle \geq 0$ implies the recurrence, P_{ω_m}-a.s., of $x(t)$.
- For $\left\langle \ln \frac{\mu}{\beta} \right\rangle < 0$, the random walk is transient, P_{ω_m}-a.s.

- Next, consider the series

$$S_0 = 1 + \frac{\beta_0}{\mu_1} + \frac{\beta_0 \beta_1}{\mu_1 \mu_2} + \dots$$

- A similar calculation shows that the random walk is positively recurrent (i.e., ergodic), P_{ω_m}-a.s., iff $\left\langle \ln \frac{\mu}{\beta} \right\rangle > 0$.
- If $\left\langle \ln \frac{\mu}{\beta} \right\rangle = 0$, then, P_{ω_m}-a.s., the random walk is *zero* recurrent.
- This has been the *quenched* classification. Turn now to the *annealed* classification.

Random walk in random environment

Annealed sense

- Suppose $x(t)$ is ergodic in the annealed sense, that is (for $a = \left\langle \frac{1}{\mu} \right\rangle$, $b = \langle \beta \rangle$)

$$\begin{aligned} \langle \varphi(1) \rangle &= \left\langle \frac{1}{\mu_1} \right\rangle + \langle \beta_1 \rangle \left\langle \frac{1}{\mu_1} \right\rangle \left\langle \frac{1}{\mu_2} \right\rangle + \dots \\ &= a + ba^2 + b^2 a^3 + \dots = a(1 + ab + (ab)^2 + \dots) < \infty \end{aligned}$$

- This holds iff $\langle \beta \rangle \left\langle \frac{1}{\mu} \right\rangle < 1$

- Due to Jensen's inequality

$$\left\langle \ln \frac{\beta}{\mu} \right\rangle < \ln \left\langle \frac{\beta}{\mu} \right\rangle = \ln \left(\langle \beta \rangle \left\langle \frac{1}{\mu} \right\rangle \right).$$

- If $\langle \beta \rangle \left\langle \frac{1}{\mu} \right\rangle < 1$, then, $\left\langle \ln \frac{\beta}{\mu} \right\rangle < 0$ and $x(t)$ is ergodic also in the quenched sense.
- It is possible that the random walk is ergodic in the quenched sense, i.e., P_{ω_m}-a.s., but $\langle \beta \rangle \left\langle \frac{1}{\mu} \right\rangle \geq 1$ and so it is not ergodic in the annealed sense:
  - $\langle \tau_{1 \to 0} \rangle = +\infty$.
  - We have exactly this situation if $\left\langle \frac{1}{\mu} \right\rangle > \frac{1}{\langle \beta \rangle}$ but $\langle \ln \beta \rangle < \langle \ln \mu \rangle$.

Random walk in random environment

Annealed sense

- Consider, finally

$$EZ = 1 + \sum_{j=1}^{\infty} \langle \mu \rangle^j \left\langle \frac{1}{\beta} \right\rangle^j .$$

- Clearly, $EZ = \infty$ iff $\langle \mu \rangle \left\langle \frac{1}{\beta} \right\rangle \geq 1$.
- Thus, if $\left\langle \ln \frac{\beta}{\mu} \right\rangle < 0$ we have

$$0 < \left\langle \ln \frac{\mu}{\beta} \right\rangle < \ln \left\langle \frac{\mu}{\beta} \right\rangle = \ln \left(\langle \mu \rangle \left\langle \frac{1}{\beta} \right\rangle \right)$$

  so that $\langle \mu \rangle \left\langle \frac{1}{\beta} \right\rangle > 1$.
- Thus, if $x(t)$ is ergodic in the quenched sense, it is at least recurrent in the annealed sense, although possibly only zero recurrent.

Outline

Random walk with immigration in random environment
Quenched sense

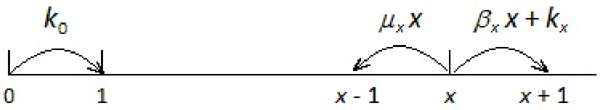


Figure: Random Walk in Random Environment with Immigration

- Rate of increase, $\mu_x(\omega)x + k_x(\omega)$, and rate of decrease, $\mu_x(\omega)$, are random functions of volume of population $x(t) \geq 0$.
- Duplication and mortality rates are multiplied by the population size; immigration rate is not.

Consider the series

$$S_0 = 1 + \frac{k_0}{\mu_1} + \frac{k_0(\beta_1 + k_1)}{2\mu_1\mu_2} + \frac{k_0(\beta_1 + k_1)(2\beta_2 + k_2)}{3!\mu_1\mu_2\mu_3} + \ldots + \frac{k_0 \prod_{i=1}^{n-1}(i\beta_i + k_i)}{n! \prod_{i=1}^{n} \mu_i} + \ldots$$

- Note that

$$\frac{(n-1)\beta_{n-1}(\omega) + k_{n-1}(\omega)}{n\mu_n(\omega)} = \frac{\beta_{n-1}(\omega) + \frac{k_{n-1}(\omega) - \beta_{n-1}(\omega)}{n}}{\mu_n(\omega)} = e^{\ln \beta_{n-1} - \ln \mu_n + o(\frac{1}{n})}.$$

- Thus, using previous analysis for RW, $S_0 < \infty$ and so $x(t)$ is ergodic (P_{ω_m}-a.s.) iff $\langle \ln \frac{\beta_x(\omega)}{\mu_x(\omega)} \rangle = \langle \ln \beta_x \rangle - \langle \ln \mu_x \rangle < 0$.

- Next, consider the series

$$Z = \frac{\mu_1}{\beta_1 + k_1} + \frac{2\mu_1\mu_2}{(\beta_1 + k_1)(2\beta_2 + k_2)} + \ldots + \frac{n!\prod_{i=1}^{n}\mu_i}{\prod_{i=1}^{n}(i\beta_i + k_i)} + \ldots < \infty.$$

- $k.(\omega) \geq a_3 > 0$ implies that $\langle \ln \frac{\mu_x(\omega)}{\beta_x(\omega)} \rangle = 0 \Rightarrow \left\langle \ln \frac{\mu_x(\omega)}{\beta_x(\omega) + \frac{k_x(\omega)}{x}} \right\rangle < 0.$
- Thus, for $\langle \ln \frac{\mu_x(\omega)}{\beta_x(\omega)} \rangle = 0$, $Z < \infty$
- I.e., for $\langle \ln \frac{\beta_x(\omega)}{\mu_x(\omega)} \rangle \geq 0$, the process $x(t)$ is transient (P_{ω_m}-a.s.).

Random walk with immigration in random environment

Annealed sense

- Annealed perspective: $x(t)$ is ergodic iff $\langle \varphi(1) \rangle < \infty$.
- $$\langle \varphi(1) \rangle = \left\langle \frac{1}{\mu} \right\rangle \Big((\langle \beta \rangle + \langle k \rangle) \left\langle \frac{1}{\mu} \right\rangle + \ldots + \\ + (\langle \beta \rangle + \langle k \rangle) \cdots (n\langle \beta \rangle + \langle k \rangle) \frac{1}{n!} \left\langle \frac{1}{\mu} \right\rangle^n + \ldots \Big) \\ = \left\langle \frac{1}{\mu} \right\rangle \sum_{j=1}^{\infty} \left\langle \frac{1}{\mu} \right\rangle^j \prod_{i=1}^{j} \left(\langle \beta \rangle + \frac{\langle k \rangle}{i} \right)$$

  .
- Thus, $\langle \varphi(1) \rangle < \infty$ if and only if $\langle \beta \rangle \left\langle \frac{1}{\mu} \right\rangle < 1$.
- As with random walk, the random walk with immigration can be ergodic in the quenched sense but not in the annealed sense if $\left\langle \frac{1}{\mu} \right\rangle \geq \frac{1}{\langle \beta \rangle}$ but $\langle \ln \beta \rangle < \langle \ln \mu \rangle$.

- Turning to

$$EZ = 1 + \sum_{j=1}^{\infty} \langle\mu\rangle^j \prod_{i=1}^{j} \left\langle \frac{1}{\beta + \frac{k}{i}} \right\rangle$$

.

- Again, $EZ = \infty$ iff $\langle\mu\rangle \left\langle \frac{1}{\beta} \right\rangle \geq 1$.
- As above, if $\left\langle \ln \frac{\beta}{\mu} \right\rangle < 0$, $\langle\mu\rangle \left\langle \frac{1}{\beta} \right\rangle > 1$.
- Thus, as with the random walk without immigration, if $x(t)$ is ergodic in the quenched sense, it is at least recurrent in the annealed sense, although possibly only zero recurrent.

Outline

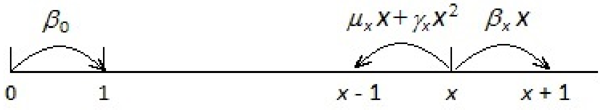


Figure: Mean Field Bolker-Pacala Model in Random Environment

- Once more, calculate

$$S_0 = 1+\frac{\beta_0}{\mu_1+\gamma_1}+\frac{\beta_0\beta_1}{(\mu_1+\gamma_1)(2\mu_2+4\gamma_2)}+\ldots+\frac{(n-1)!\prod_{i=0}^{n-1}\beta_i}{\prod_{i=1}^{n}(i\mu_i+i^2\gamma_i)}+\ldots.$$

- Consider the $n+1$th term of S_0, $n \geq 1$

$$T_{n+1} = \frac{\prod_{i=0}^{n-1} i\beta_i}{\prod_{i=1}^{n}(i\mu_i+i^2\gamma_i)} = \prod_{i=1}^{n}\frac{(\frac{1}{i}-\frac{1}{i^2})\beta_i}{\frac{1}{i}\mu_i+\gamma_i}$$

Mean field Bolker-Pacala model in random environment

Quenched sense

- Recalling that the upper bound for $\beta.$ is b_2 and the lower bound for $\gamma.$ is a_3, let $c = \frac{b_2}{a_3}$.
- Then, using Stirling's Formula

$$T_{n+1} \leq \prod_{i=1}^{n} \frac{c^n}{n!} < \frac{c^n e^n}{\sqrt{2\pi n} n^n} = \left(\frac{c \cdot e}{n}\right)^n \frac{1}{\sqrt{2\pi n}}$$

- Clearly, then, $S_0 = 1 + \sum_{i=1}^{\infty} T_{i+1} < \infty$ and $x(t)$ is ergodic, P_{ω_m}-a.s.
- In other words, as long as the random variable parameters $\beta.$, $\mu.$, and $\gamma.$ are bounded, $x(t)$ is ergodic in the quenched sense.

- Turning to the annealed perspective,

$$\langle\varphi(1)\rangle = \left\langle\frac{1}{\mu}\right\rangle\left(\langle\beta\rangle\left\langle\frac{1}{2\mu+4\gamma}\right\rangle + \ldots + \right.$$
$$\left. + \langle\beta\rangle\cdots\langle(n-1)\beta\rangle\left\langle\frac{1}{(2\mu+4\gamma)\cdots(n\mu+n^2\gamma)}\right\rangle + \ldots\right).$$

- The $(n-1)$th term inside the parentheses can be written

$$\frac{1}{n\cdot n!}\langle\beta\rangle^{n-1}\prod_{j=2}^{n}\left\langle\frac{1}{\gamma_j+\frac{\mu_j}{j}}\right\rangle.$$

- Clearly, again for all $\beta.$, $\mu.$, and $\gamma.$ bounded as given, $\varphi(1)<\infty$.
- The B-P model is ergodic in both annealed and quenched senses.

Summary and discussion

Models and Recurrence Properties

		RW Constant	RW RE	RW I RE	B-P RE
$\langle \ln \frac{\beta}{\mu} \rangle < 0$	Q	Ergodic	Ergodic	Ergodic	Ergodic
	A		E or ZR	E or ZR	Ergodic
$\langle \ln \frac{\beta}{\mu} \rangle = 0$	Q	Z Recurrent	Z Recurrent	Transient	Ergodic
	A		Z Recurrent	Transient	Ergodic
$\langle \ln \frac{\beta}{\mu} \rangle > 0$	Q	Transient	Transient	Transient	Ergodic
	A		Transient	Transient	Ergodic

- The quenched vs. annealed differences for the random walks are worth exploring.
- One phenomenon that may appear with a stationary random environment is *traps*.

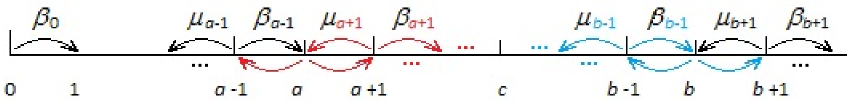


Figure: Random Trap in Random Walk in Random Environment

- Figure:
  - Let c be the center of $[a, b]$.
  - For $x \in [a, b]$, if $x > c$, $\beta_x < \mu_x$ (blue).
  - If $x < c$, $\beta_x > \mu_x$ (red).

Summary and discussion

Traps

- Random trap: random interval $[a_n, b_n]$ where the drift locally is toward the center of the interval.
- Consider situation where $\langle \ln \frac{\beta}{\mu} \rangle < 0$.
  - If $\beta_x < \mu_x$ P-a.s., then, the random walk is ergodic much like the random walk in a constant environment.
  - But if $P\{\beta_x > \mu_x\} \geq \delta > 0$, then, traps will exist, giving ergodicity in the quenched sense.
  - Here, however, in the annealed sense, traps will not exist.
- To leave a trap, $x(t)$ will take time which is the exponential of the size of the trap.

- Traps were explored for a simple random walk in discrete time in the Sinai model (1982).
  - It is well known that a simple symmetric ($\beta = \mu$) random walk in a constant environment in time t is expected to move distance $\sqrt{t}$ from its starting point.
  - Sinai showed that in a stationary random environment, still with $\left\langle \ln \frac{\beta}{\mu} \right\rangle = 0$, that expected time was drastically reduced to $\ln^2 t$.
- For our random walks in random environment with $\left\langle \ln \frac{\beta}{\mu} \right\rangle < 0$ there will be random traps of any width.
- The centers, $c_1, c_2, \ldots$ will be local equilibria.
- $x(t)$ will undergo Gaussian fluctuations around those centers, eventually breaking free, only to end up in another trap.

Summary and discussion

Other conditions

- For homogenization of (1-dimensional) RW in RE, some inner symmetry is necessary.
  - For example, the rates of increase and decrease can be equal on the "edges" of the RW: $\beta^*_x = \mu^*_{x+1}$.
  - This gives a symmetric transition matrix, which is a self-adjoint operator.
  - This RW in random environment becomes like RW in constant environment.
- Another alternative is a *non-stationary* random environment.
  - Above we have considered a *stationary* RE.
  - A non-stationary RE is unlikely to produce traps, because the configuration of rates that produces traps, described above, will evaporate with time.