Some population models in periodic or random environments

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- multi-type linear birth-and-death processes in a periodic environment

- random environment without demographic stochasticity

- multi-type linear birth-and-death processes in a random environment

Periodic environment

Kendall (1948)

$a(t)$: birth rate, $b(t)$: death rate

$\omega(t_0)$: extinction probability starting at t_0

$$\omega(t_0) = 1 - \frac{1}{1 + \int_{t_0}^{\infty} b(t)\, \exp\left[\int_{t_0}^{t} (b(s) - a(s))\, ds\right] dt}$$

$$a(t+T) = a(t),\ b(t+T) = b(t)$$

$\omega(t_0) = 1$ if and only if $\int_0^T a(t)\, dt \leq \int_0^T b(t)\, dt$

Jagers/Nerman (1985)

branching process in a periodic environment

$n(t)$: expected births per unit of time

$$n(t) = \int_0^\infty K(t,x)\, n(t-x)\, dx$$

$$K(t,x) = a(t,x)\, e^{-\int_0^x b(t-x+s,s)\, ds} = K(t+T,x)$$

$$n(t) \sim e^{rt}\phi(t), \quad \phi(t+T) = \phi(t)$$

$$\phi(t) = \int_0^\infty e^{-rx} K(t,x)\, \phi(t-x)\, dx = (L_r\phi)(t)$$

$$\rho(L_r) = 1, \quad \omega(t_0) = 1 \Leftrightarrow r \leq 0$$

Klein/Macdonald (1980)

multi-type processes

$A_{i,j}(t)$: nonnegative birth matrix

$B_{i,j}(t)$: death and transfer matrix

$$A(t+T) = A(t), \quad B(t+T) = B(t)$$

$g(t, x_1, \ldots, x_m)$: generating function

$$\frac{\partial g}{\partial t} = \sum_{i,j} \left[A_{i,j}(t) x_j - B_{i,j}(t)\right] (x_i - 1) \frac{\partial g}{\partial x_j}$$

population mean: $\frac{dP}{dt} = (A(t) - B(t))P(t)$

Allen/Lahodny (2012) Extinction thresholds in deterministic and stochastic epidemic models. J Biol Dyn

multi-type processes

constant environment

Back to periodic environments

F: dominant Floquet multiplier of

$$\frac{dP}{dt} = (A(t) - B(t))P(t)$$

$$\boxed{\omega(t_0) = 1 \text{ if and only if } F \leq 1}$$

Proof: method of characteristics

$$\frac{dX_j}{dt} = \sum_i \left[A_{i,j}(t)X_j - B_{i,j}(t)\right](1 - X_i)$$

$$\tau > t_0,\ X(\tau) = 0$$

$$g(\tau, 0, \ldots, 0) = \prod_i (X_i(t_0))^{\pi_i(t_0)}$$

$$Y_i(s) = 1 - X_i(\tau - s)$$

$$\frac{dY_i}{ds}(s) \simeq \sum_j \left[A^*_{i,j}(\tau - s) - B^*_{i,j}(\tau - s)\right] Y_j(s)$$

cooperative sublinear system of ODEs

Similar result for discrete-time population models in a periodic environment

$$P(t+1) = (A(t) + B(t))P(t)$$

The basic reproduction number R_0

J Math Biol (2006...), *Bull Math Biol* (2007...)

$$L_r : \phi(t) \longmapsto \int_0^\infty e^{-rx} K(t,x)\, \phi(t-x)\, dx$$

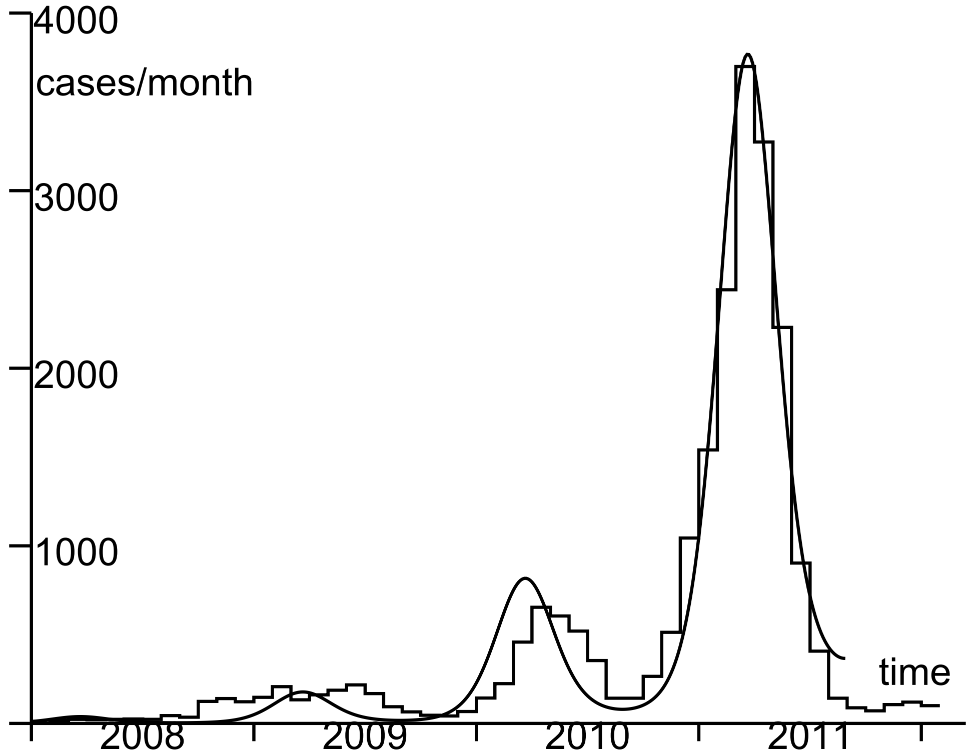
$$\boxed{R_0 = \rho(L_0)} \qquad \boxed{R_0 \gtreqless 1 \Leftrightarrow r \gtreqless 0}$$

$$\frac{dp}{dt} = (a(t) - b(t))p(t) \Rightarrow \boxed{R_0 = \frac{\int_0^T a(t)\, dt}{\int_0^T b(t)\, dt}}$$

$$\frac{dZ}{dt} = \Big(\frac{A(t)}{R_0} - B(t)\Big) Z(t), \qquad f(R_0) = 1, \qquad e^{rT} = F$$

asymptotic per generation growth rate

Example: measles in France



linearized SEIR model

$$\begin{cases} \frac{dE}{dt} &= -c\,E + a(t)(1-v)I \\ \\ \frac{dI}{dt} &= c\,E - b\,I \end{cases}$$

$$a(t) = \bar{a}\Big(1 + \varepsilon \cos(2\pi t/T - \phi)\Big)$$

Effective reproduction number:

$$(1 - v)R_0 \simeq 1.06$$

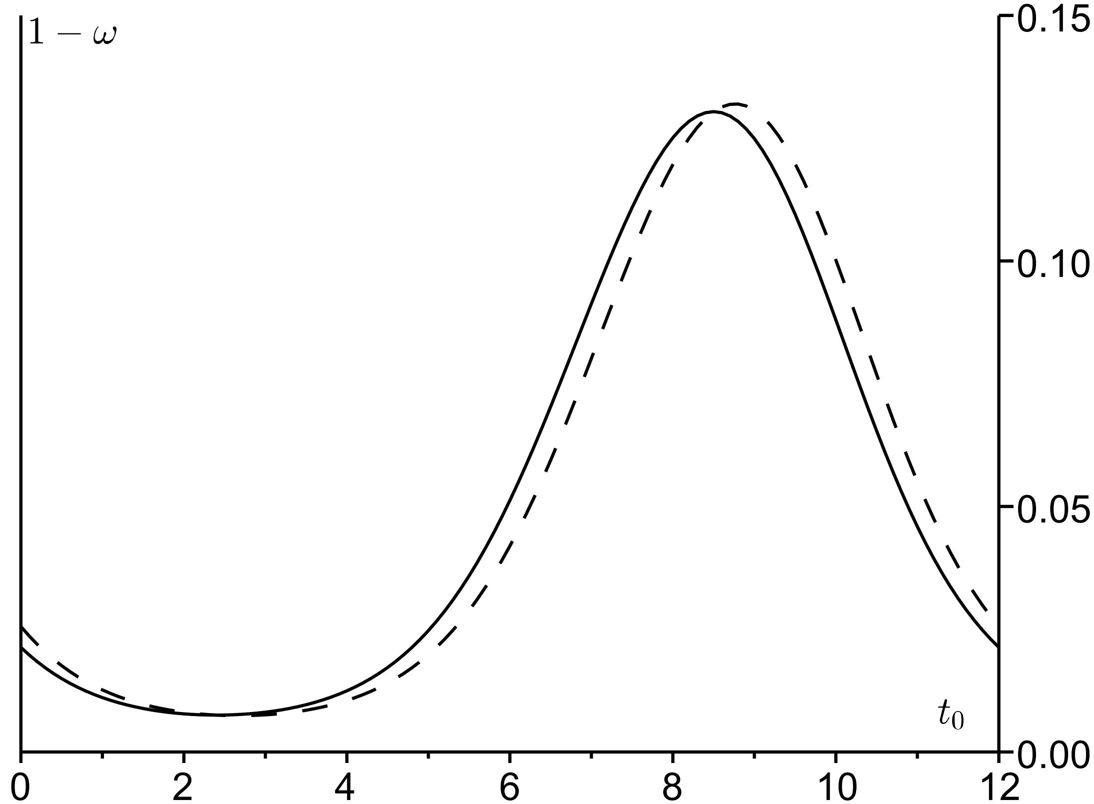
Known vaccine coverage:

$$v \simeq 92\% \Rightarrow R_0 \simeq 13$$

Critical vaccine coverage:

$$v^* = 1 - \frac{1}{R_0} \simeq 92.5\%$$

$t_0 \longmapsto 1 - \omega(t_0)$ (probability of a major epidemic)



R_0 in a random environment

background: periodic discrete-time model

$$P(t+1) = M(t)P(t)$$

$$M(t) = A(t) + B(t)$$

$$A(t+T) = A(t)$$

$$B(t+T) = B(t)$$

stable if $\rho(M(T-1)\cdots M(1)M(0)) < 1$

or equivalently $R_0 = \rho(\mathbf{A}^*\,\mathbf{B}^*) < 1$

$$\mathbf{A}^* = \mathrm{diag}(A(0), \ldots, A(T-1))$$

$$\mathbf{B}^* = \begin{pmatrix} -B(0) & I & 0 & \cdots & 0 \\ 0 & -B(1) & I & \ddots & \vdots \\ \vdots & \ddots & \ddots & \ddots & 0 \\ 0 & & \ddots & \ddots & I \\ I & 0 & \cdots & 0 & -B(T-1) \end{pmatrix}^{-1}$$

$\rightarrow$ *Bull Math Biol* (2009)

Question: what is R_0 if the environment follows a finite Markov chain?

environments $(A^{(k)}, B^{(k)})$

$\Pi_{k,\ell}$: probability that k followed by ℓ

$$\lambda_1 = \lim_{t\to+\infty} \frac{1}{t} \log \|M(t-1)\cdots M(1)M(0)\|$$

$$R_0 \neq R_1 = \rho\left([\Pi_{\ell,k}A^{(\ell)}](I - [\Pi_{\ell,k}B^{(\ell)}])^{-1}\right)$$

$$P_{n+1}(t+1) = A(t)P_n(t) + B(t)P_{n+1}(t)$$

$$\mathbf{A} : \ell^1(\mathbb{N}, \mathbb{R}^m) \to \ell^1(\mathbb{N}, \mathbb{R}^m) : \begin{cases} (\mathbf{A}x)(0) = 0 \\ (\mathbf{A}x)(t+1) = A(t)x(t) \end{cases}$$

$$\boxed{R_0 = \rho(\mathbf{A}(\mathbf{I} - \mathbf{B})^{-1})} \text{ almost surely}$$

$$\lambda_1 = \lambda_1(A, B) \Rightarrow \boxed{\lambda_1(A/R_0, B) = 0}$$

$*$ single type model:

$$\pi\Pi = \pi \Rightarrow \sum_k \pi_k \log(a_k/R_0 + b_k) = 0$$

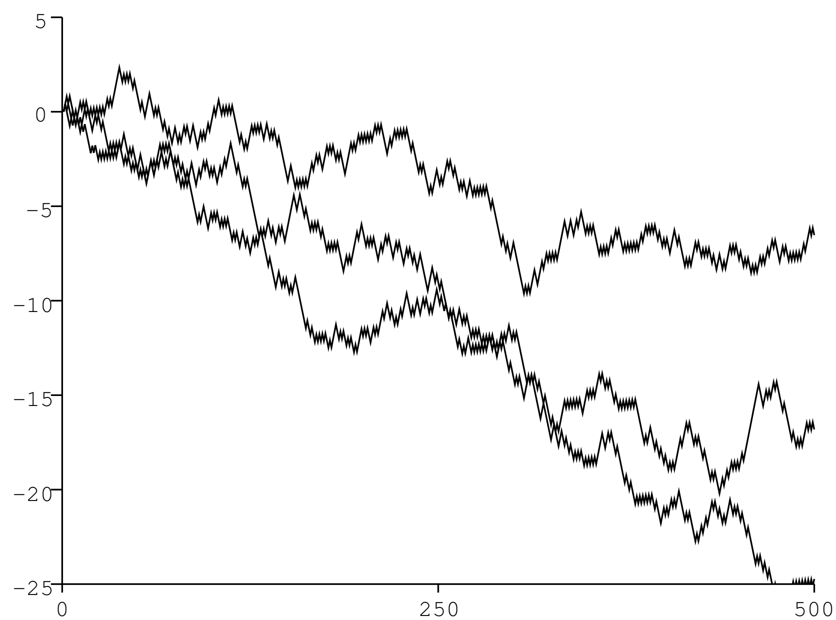
$*$ R_1 decides of the growth the expected population

$*$ continuous-time:

$$\frac{dP}{dt} = (a(t) - b(t))P(t) \Rightarrow R_0 = \frac{\sum a_k \pi_k}{\sum b_k \pi_k}$$

$$(A^{(1)}, B^{(1)}) = (1, 0.5), \quad (A^{(2)}, B^{(2)}) = (0.1, 0.58)$$

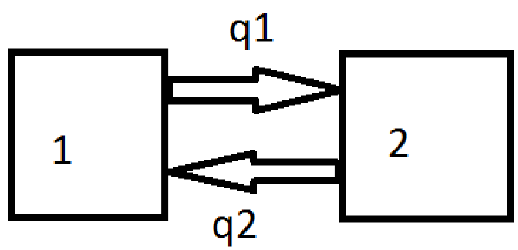
$$M = \begin{pmatrix} 0.3 & 0.7 \\ 0.6 & 0.4 \end{pmatrix}, \quad R_0 < 1, \quad R_1 > 1$$



birth-and-death in a random environment

Continuous-time model.

Finite Markov chain, stationary distribution (π_k).



In environment k, birth-and-death process (a_k, b_k)

Question: how about the extinction probability ω?

Cogburn, Torrez: J Appl Prob (1981)

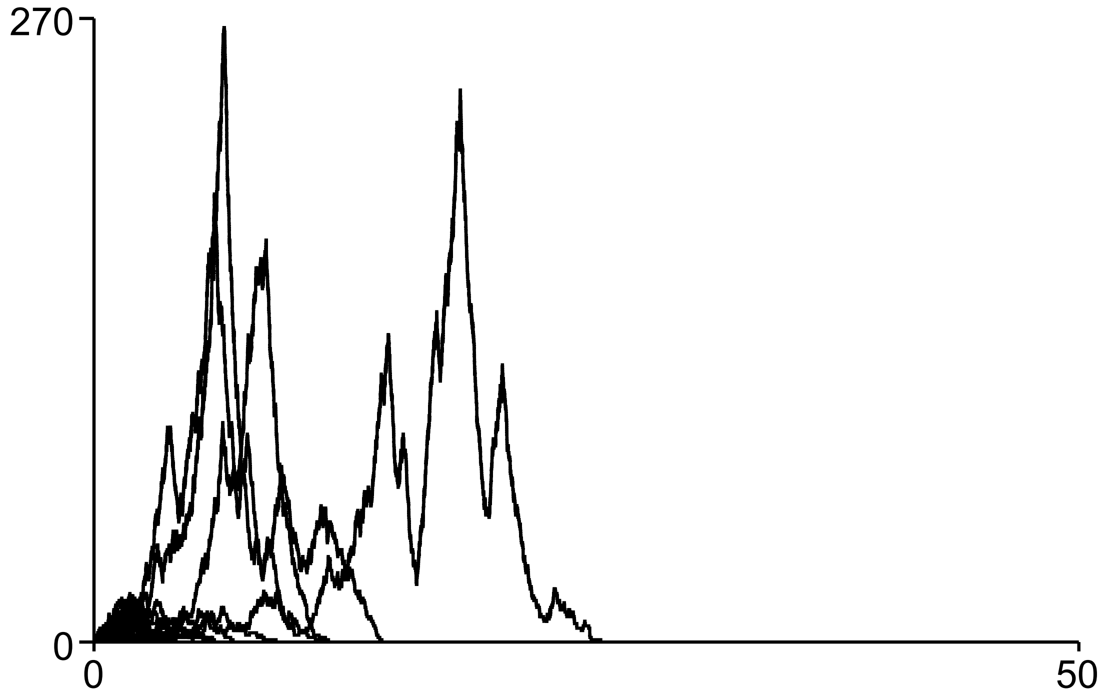
$$R_0 = \frac{\sum a_k \, \pi_k}{\sum b_k \, \pi_k}$$

$$\boxed{\omega = 1 \text{ if and only if } R_0 \leq 1}$$

J Appl Prob (2009): $R_* = m_1 m_2$

$$m_k = \int_0^\infty q_k \, e^{-q_k \tau} e^{(a_k - b_k)\tau} \, d\tau = \frac{q_k}{b_k + q_k - a_k}$$

An example with $R_0 < 1$ and $R_* > 1$

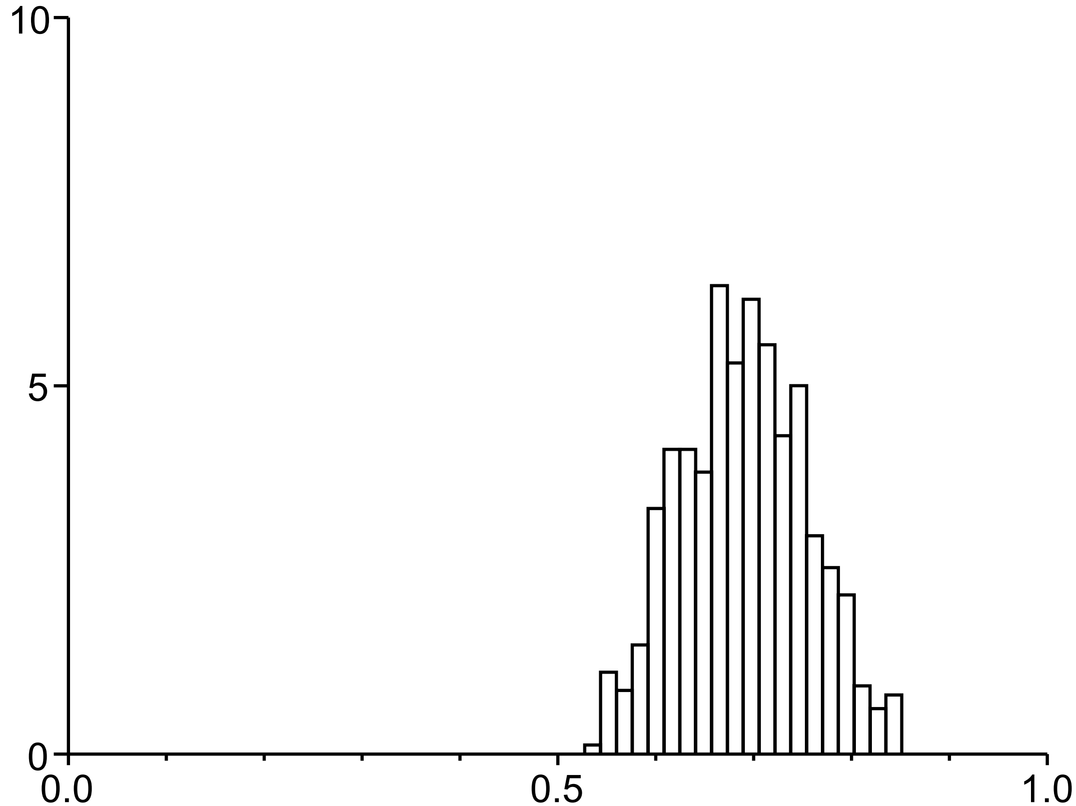


Proof: Kendall (1948) + ergodic theorem

$$\omega = 1 - \frac{1}{1 + \int_0^\infty b(t)\ \exp\left[\int_0^t (b(s) - a(s))\, ds\right] dt}$$

$$\lim_{t \to +\infty} \frac{1}{t} \int_0^t (b(s) - a(s))\, ds = \sum_k (b_k - a_k)\, \pi_k \quad \text{a.s.}$$

Supercritical example



Athreya & Karlin (1971)

environment k during τ followed by k' during τ'

$$\mathbb{P}_{(k,\tau)\to(k',\tau')}\, d\tau' = \frac{Q_{k',k}}{q_k}\, q_{k'}\, e^{-q_{k'}\,\tau'}\, d\tau'$$

stationary distribution : $\varpi_{k,\tau} = \dfrac{q_k \pi_k}{\sum_\ell q_\ell \pi_\ell}\, q_k\, e^{-q_k \tau}$

mean : $\phi'_{k,\tau}(1) = e^{(a_k - b_k)\tau}$

$$\omega = 1 \Leftrightarrow \mathbb{E}(\log \phi'(1)) = \frac{\sum (a_k - b_k)\pi_k}{\sum q_k \pi_k} \leq 0 \Leftrightarrow R_0 \leq 1$$

multi-type populations

λ_1 Lyapunov exponent of $\dfrac{dP}{dt} = (A(t) - B(t))P(t)$

$$M^{(k)}(\tau) = \exp\left[(A^{(k)} - B^{(k)})\tau\right]$$

$$t_n = \tau_0 + \tau_1 + \cdots + \tau_{n-1}$$

$$\lambda_1 = \lim_{n \to +\infty} \frac{1}{t_n} \log \|M^{(k_{n-1})}(\tau_{n-1}) \cdots M^{(k_0)}(\tau_0)\|$$

$$\omega = 1 \Leftrightarrow \lambda_1 \leq 0 \Leftrightarrow R_0 \leq 1$$

$$R^* = \rho \left(\begin{pmatrix} a_1 & 0 \\ 0 & a_2 \end{pmatrix} \begin{pmatrix} b_1 + q_1 & -q_2 \\ -q_1 & b_2 + q_2 \end{pmatrix}^{-1} \right)$$

$$\begin{aligned} \frac{dp_{k,n}}{dt} = & -(a_k + b_k) n\, p_{k,n} + b_k (n+1) p_{k,n+1} \\ & + a_k (n-1) p_{k,n-1} + \sum_{\ell \neq k} \left(Q_{k,\ell} p_{\ell,n} - Q_{\ell,k} p_{k,n} \right) \end{aligned}$$

$$E_k(t) = \sum_{n \geq 1} n\, p_{k,n}(t)$$

$$\frac{dE_k}{dt} = (a_k - b_k) E_k + \sum_{\ell \neq k} \left(Q_{k,\ell} E_\ell - Q_{\ell,k} E_k \right) .$$

- B., Ait Dads: On the probability of extinction in a periodic environment. *J Math Biol* (2014)

- B., Khaladi: On the basic reproduction number in a random environment. *J Math Biol* (2013)

- B., Ed-Darraz: On linear birth-and-death processes in a random environment. *J Math Biol* (2014)

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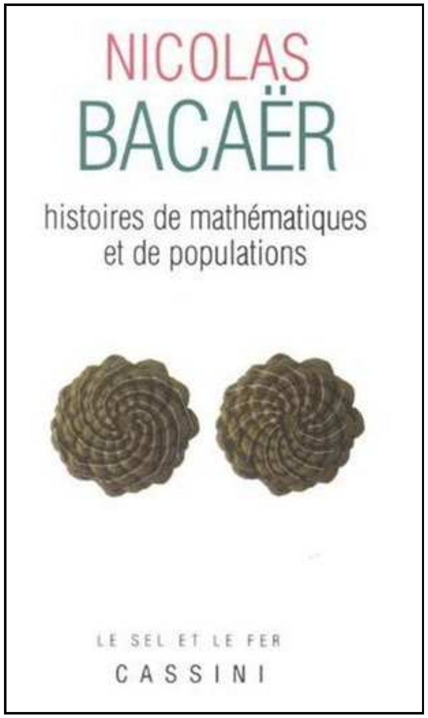

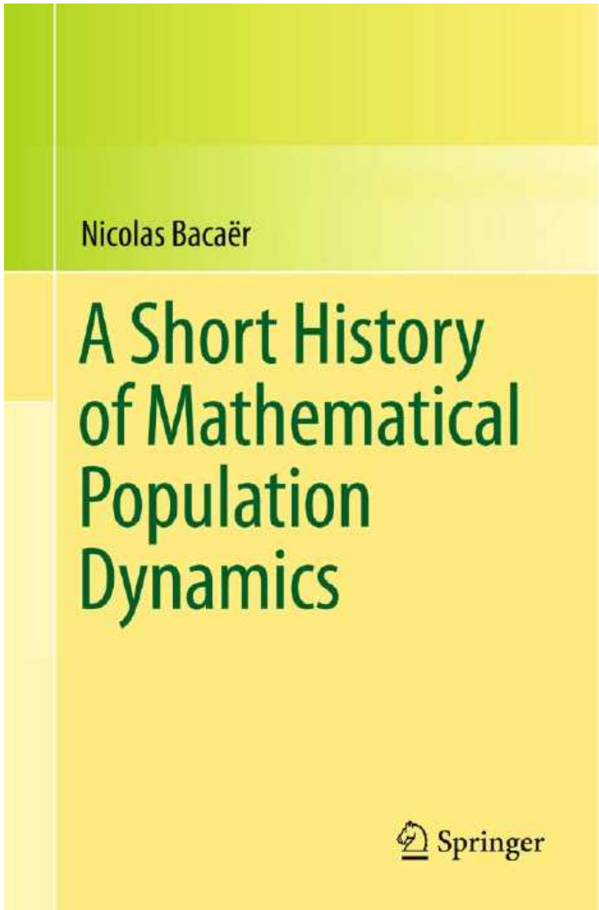

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