Extinction time for the weaker of two competing stochastic SIS logistic epidemics

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SIS epidemics

- In an SIS (susceptible-infective-susceptible) epidemic model, each individual is of one of the following two types: susceptible or infective. When an individual recovers from infection, they become susceptible again.
- SIS epidemics are used as models for diseases where there is no lasting immunity following recovery.
- Examples include respiratory diseases apart from influenza, gastrointestinal infections (e.g. rotavirus and norovirus).
- SIS epidemic models are mathematically equivalent to contact processes, introduced by Harris in 1974.

Stochastic logistic SIS epidemic

- We model an SIS (susceptible-infective-susceptible) epidemic in a population of size N.
- $X_N(t)$ is the number of infective individuals at time t.
- Each infective individual encounters a random other member of the population at rate $\lambda > 0$: if the person they meet is currently susceptible, they become infective.
- So the number $X_N(t)$ increases by 1 at rate $\frac{\lambda X_N(t)(N - X_N(t))}{N}$: each individual attempts to infect another at rate λ, and the probability that the encountered individual is currently susceptible is $(N - X_N(t))/N$.
- Each infective person recovers at rate $\mu > 0$, and then becomes susceptible again.

Corresponding deterministic model

- We have an infinite population.
- The proportion of infective individuals at time t is $x(t)$.
- Each infective individual encounters a random other member of the population at rate λ: if the person they meet is currently susceptible, they become infective.
- Each infective person recovers at rate μ, and then becomes susceptible again.
- The proportion $x(t)$ of infective individuals at time t satisfies:

$$\frac{dx(t)}{dt} = \lambda x(t)(1 - x(t)) - \mu x(t).$$

Behaviour of the deterministic model

- We can write
$$\frac{dx(t)}{dt} = \lambda x(t)\big(1 - \mu/\lambda - x(t)\big).$$
- For $\mu \geq \lambda$, the equation has an attractive fixed point at 0. If $x(0) \in [0, 1]$, then $x(t) \to 0$ as $t \to \infty$.
- For $\mu < \lambda$, the equation has a repulsive fixed point at 0, and an attractive fixed point at $1 - \mu/\lambda$. If $x(0) \in (0, 1]$, then $x(t) \to 1 - \mu/\lambda$ as $t \to \infty$.

Solution of the differential equation

In fact, the differential equation is simple enough that it can be solved explicitly: assuming $x(0) \neq 0$,

$$x(t) = \frac{1 - \mu/\lambda}{1 - \left(\frac{\mu/\lambda - 1}{x(0)} + 1\right) e^{(\mu-\lambda)t}}, \qquad t \geq 0 \quad (\mu \neq \lambda);$$

$$x(t) = \frac{x(0)}{\lambda x(0) t + 1}, \qquad t \geq 0 \quad (\mu = \lambda).$$

The solution for $\mu \neq \lambda$ is called the *logistic curve*.

Again, $x(t) \to 0$ if $\mu \geq \lambda$, and $x(t) \to 1 - \mu/\lambda$ if $\mu < \lambda$. The convergence is exponential except in the critical case $\mu = \lambda$.

Stochastic vs deterministic epidemic

The stochastic logistic epidemic is a continuous-time Markov chain with the following transitions:

$$\begin{aligned} X &\to X+1 \quad \text{at rate} \quad \frac{\lambda X(N-X)}{N}; \\ X &\to X-1 \quad \text{at rate} \quad \mu X. \end{aligned}$$

The drift in $\frac{1}{N}X$ is

$$+\frac{1}{N} \times \frac{\lambda X(N-X)}{N} - \frac{1}{N} \times \mu X = \frac{X}{N}\left(\lambda(1 - X/N) - \mu\right),$$

exactly as in the deterministic model.

A (short-term) law of large numbers

- We consider a sequence of stochastic epidemic models, one for each value of N, and assume that the initial number of infectives satisfies $X_N(0)/N \to x(0)$ as $N \to \infty$, where $x(0) \in (0, 1]$.
- Then, regardless of the values of the parameters λ, μ, the scaled process $x_N = X_N/N$ converges in probability, on bounded time intervals, to the solution of the differential equation
$$\frac{dx}{dt} = \lambda x(1 - x) - \mu x,$$
with initial condition $x(0)$.

Law of large numbers

- During this time interval $[0, t_0]$, the number of jumps in the process X_N is typically of order N.
- What happens over longer time intervals, perhaps until the end of the epidemic?

Basic reproductive ratio

- As for the deterministic system, the key parameter is the ratio $R_0 = \lambda/\mu$, and whether it is greater or less than 1.
- In the context of an epidemic, R_0 is called the *basic reproductive ratio*. It is the number of cases one case generates on average over the course of its infectious period.
- If $R_0 \leq 1$, then the probability of an epidemic becoming established (starting with only a few infectives) is close to 0. If $R_0 > 1$, then this probability is positive.

Long-term behaviour of the stochastic model

- The stochastic model we introduced is a continuous-time Markov chain, with a finite state space $\{0, \ldots, N\}$.
- There is an *absorbing state*, namely 0. Once the Markov chain enters this state, it stays there.
- With probability 1, the Markov chain will eventually enter the absorbing state: the epidemic will die out, even when $R_0 > 1$ (i.e. even when $\lambda > \mu$, unlike the deterministic version).

Extinction time: $\lambda > \mu$

- Let $T_N = T_N(X_N(0))$ be the time to extinction for $(X_N(t))$. i.e., the hitting time of the absorbing state 0.
- Whenever $X_N(0) \to \infty$, we have

  $$\mathbb{E}\, T_N(X_N(0)) = \sqrt{2\pi}\frac{\lambda}{(\lambda-\mu)^2}\frac{e^{\gamma N}}{\sqrt{N}}(1-o(1)),$$

  as $N \to \infty$, where
  $\gamma = \log\lambda - \log\mu - \frac{\lambda-\mu}{\lambda} = \log R_0 - 1 + R_0^{-1} > 0.$
- Moreover, the time to extinction is asymptotically an exponential random variable: $\dfrac{T_N}{\mathbb{E}\, T_N} \to Z$ in distribution, where $Z \sim Exp(1)$
- See: Barbour (1976), Andersson and Djehiche (1998), Nåsell (2011).

$\lambda > \mu$

- Conditioning on the event that the chain has not entered state 0 by time t, one obtains a limiting *quasi-stationary distribution*, centred around the attractive fixed point of the differential equation.
- Starting from a fixed state, the chain converges rapidly to the quasi-stationary distribution.
- Moving from near the fixed point to 0 is a *rare event*. The expected time until the rare event occurs can be estimated very precisely, as above.
- One can show that the scaled stochastic process follows the deterministic one for a time period exponential in N.

$\lambda < \mu$: rapid extinction

- In the deterministic model,

$$x(t) = \frac{\mu/\lambda - 1}{(\frac{1}{x(0)}(\mu/\lambda - 1) + 1)e^{(\mu-\lambda)t} - 1},$$

  i.e. the population heads rapidly towards extinction.

- For the stochastic model, in distribution,

$$(\mu-\lambda)T_N - \Big(\log(X_N(0)) + \log(1-\lambda/\mu) - \log\Big(1 + \frac{\lambda X_N(0)}{N(\mu-\lambda)}\Big)\Big) \to W,$$

  where $\Pr(W \leq w) = \exp(-e^{-w})$ (standard Gumbel).

Distribution of extinction time: $\lambda < \mu$

That is,

$$T_N = \frac{1}{\mu(1-R_0)} \left(\log \left\{ \frac{X_N(0)(1-R_0)}{1 + \frac{X_N(0)R_0}{N(1-R_0)}} \right\} + W_N \right),$$

where $W_N \to W$, and μ is the ‘speed’ parameter.

See recent preprint of Brightwell, House and L. (2017).

Extinction time: $\lambda = \mu$ and a critical window

- If $\lambda = \mu$, the time to extinction is somewhere in between (time of order $N^{1/2}$, it turns out).
- Supposing $\lambda = \lambda(N)$ and $\mu = \mu(N)$, there is a "critical window" where $|\mu - \lambda| = O(N^{-1/2})$.
- If $(\mu - \lambda)N^{1/2} \to C$ $(-\infty < C < \infty)$ and $X_0 N^{-1/2} \to b$ $(b > 0)$, then the expected time to extinction is asymptotically $f(C, b)N^{1/2}$, for some function f.
- Also, the time to extinction is of order $\sqrt{N}$, even if the starting state is of order larger than $\sqrt{N}$. (But, for instance, the extinction time starting from state 1 is of order $\log N$.)
- See Doering, Sargsyan and Sander (2005); Dolgoarshinnyk and Lalley (2006).

Scaling window: above threshold

Thinking of a scaling window gives a more sophisticated picture. Suppose again $\lambda = \lambda(N)$ and $\mu = \mu(N)$.

If $\lambda - \mu \to 0$, and $(\lambda - \mu)\sqrt{N} \to \infty$ (sufficiently fast), the epidemic takes a long time to die out
(time of order roughly $\exp(N(\lambda - \mu)^2/2\lambda^2)$).

See work of Nåsell.

Scaling window: below threshold

Whenever $(\mu-\lambda)\sqrt{N} \to \infty$, and $X_N(0)(\mu-\lambda) \to \infty$,

$$(\mu-\lambda)T_N - \big(\log X_N(0) + \log(\mu-\lambda) - \log\big(1 + \frac{\lambda X_N(0)}{(\mu-\lambda)N}\big) - \log\mu\big) \to W,$$

in distribution, where W has the standard Gumbel distribution. (See Brightwell, House and L. 2017.)

Equivalently, whenever $(1-R_0)\sqrt{N} \to \infty$ and $X_N(0)(1-R_0) \to \infty$,

$$T_N = \frac{1}{(1-R_0)\mu}\left(\log\left\{\frac{X_N(0)(1-R_0)}{1+\frac{R_0 X_N(0)}{N(1-R_0)}}\right\} + W_N\right),$$

where $W_N \to W$ in distribution.

Informal description

- From any starting state above about $(1-R_0)N$, $X^N(t)$ moves rapidly to a state of order $(1-R_0)N$.
- The bulk of the time to extinction is spent moving from a state of order $(1-R_0)N$ to a state of order about $1/(1-R_0)$. Here $x_N(t) = N^{-1}X_N(t)$ follows the differential equation closely.
- However, most of the randomness of the extinction time comes from the final phase, from a state around $1/(1-R_0)$ to extinction. Since $(1-R_0)^{-1}N^{-1} \ll 1-R_0$, we can ignore logistic effects and approximate by a linear birth-and-death chain.

Stochastic logistic SIS competition model

- There are two competing SIS epidemics in a population of size N.
- $X_{N,1}(t)$ is the number of infective individuals of type 1 at time t, and $X_{N,2}(t)$ is the number of infective individuals of type 2 at time t.
- Each infective individual of type i encounters a random other member of the population at rate λ_i: if the person they meet is susceptible, they become infective.
- So $X_{N,i}(t)$ increases by 1 at rate $\frac{\lambda_i X_{N,i}(t)(N - X_{N,1}(t) - X_{N,2}(t))}{N}$.
- Each infective person of type i recovers at rate μ_i and becomes susceptible again.
- There is perfect cross-immunity between the two strains.

Two competing epidemics

We assume $\lambda_1, \lambda_2, \mu_1, \mu_2 > 0$.
The stochastic logistic SIS competition model is a Markov chain $(X_N(t))_{t\geq 0} = (X_{N,1}(t), X_{N,2}(t))_{t\geq 0}$.
The transition rates from (X_1, X_2) are as follows:

$$\begin{array}{lclll}
(X_1, X_2) & \to & (X_1+1, X_2) & \text{at rate} & \lambda_1 X_1(1 - X_1/N - X_2/N); \\
(X_1, X_2) & \to & (X_1, X_2+1) & \text{at rate} & \lambda_2 X_2(1 - X_1/N - X_2/N); \\
(X_1, X_2) & \to & (X_1-1, X_2) & \text{at rate} & \mu_1 X_1; \\
(X_1, X_2) & \to & (X_1, X_2-1) & \text{at rate} & \mu_2 X_2.
\end{array}$$

The corresponding deterministic model

- In an infinite population, everyone is either susceptible, infected with subtype 1, or infected with subtype 2.
- $x_i(t)$ represents the proportion of the population infected with subtype i at time t.
- Each person infected with subtype i meets a random other person in the population, and infects them if they are currently susceptible, at rate λ_i.
- Each person infected with subtype i recovers at rate μ_i, and then becomes susceptible.
- Again, if someone is currently infected with one subtype, they are temporarily immune to infection by the other subtype.

Deterministic model: differential equations

- The proportions $x_i(t)$ of infected individuals then satisfy:

$$\frac{dx_1}{dt} = \lambda_1 x_1(1 - x_1 - x_2) - \mu_1 x_1;$$

$$\frac{dx_2}{dt} = \lambda_2 x_2(1 - x_1 - x_2) - \mu_2 x_2.$$

- An explicit solution to these equations is not available.
- Let $R_{0,1} = \frac{\lambda_1}{\mu_1}$, $R_{0,2} = \frac{\lambda_2}{\mu_2}$, the basic reproduction numbers of each of the two strains in the absence of the other.
- We assume that $R_{0,1} > R_{0,2}$; this means that the first strain is "stronger" than the second. We also assume that $R_{0,1} > 1$.

Behaviour of the deterministic model

- The differential equations have fixed points at:

$$(0,0)^T, \quad \left(\frac{\lambda_1 - \mu_1}{\lambda_1}, 0\right)^T, \quad \left(0, \frac{\lambda_2 - \mu_2}{\lambda_2}\right)^T.$$

  The third of these only biologically meaningful if $\lambda_2 > \mu_2$.
- It follows from a general result of Zeeman (1995) that the fixed point at $\left(\frac{\lambda_1-\mu_1}{\lambda_1}, 0\right)^T$ is globally attractive.
- This means that the weaker strain will die out, and the stronger strain will behave as in the deterministic SIS logistic model.

The stochastic model

- As before, we consider a sequence of stochastic models, one for each value of N.
- We assume that the initial values satisfy $X_1(0)/N \to \alpha$, and $X_2(0)/N \to \beta$, where α and β are positive constants with $\alpha + \beta \leq 1$.
- To begin with, we consider the case where $\lambda_1, \mu_1, \lambda_2, \mu_2$ are fixed constants, with $R_{0,1} > R_{0,2}$, and $R_{0,1} > 1$.

Long-term behaviour of the competing epidemics model

Theorem (Lopes and L. (2017+))

Under the assumptions given, the extinction time κ_N for subtype 2 is equal to

$$\frac{1}{R_{0,1}-R_{0,2}}\left[\frac{R_{0,1}}{\mu_2}\log\left(N\beta\left(1-\frac{R_{0,2}}{R_{1,0}}\right)\right)+\frac{R_{0,2}}{\mu_1}\log\left(\frac{1-R_{0,1}^{-1}}{\alpha}\right)+W_N\right],$$

where W_N converges to a random variable W with a Gumbel distribution.
Furthermore, the extinction time τ_N of the stronger strain satisfies

$$\mathbb{E}\tau_N=\sqrt{2\pi}\frac{\lambda_1}{(\lambda_1-\mu_1)^2}\frac{e^{\gamma_1 N}}{\sqrt{N}}(1-o(1)),$$

as $N\to\infty$, where
$\gamma_1=\log\lambda_1-\log\mu_1-\frac{\lambda_1-\mu_1}{\lambda_1}=\log R_{0,1}-1+R_{0,1}^{-1}>0.$

Similarly to the single SIS logistic epidemic, there is a phase where the scaled process $x_N(t) = N^{-1}X_N(t)$ follows the differential equation quite closely.

Again, most of the randomness of the extinction time comes from the later phase, where $x_{N,1}(t)$ is quite close to $(\lambda_1 - \mu_1)/\lambda_1$ and $x_{N,2}(t)$ is $o(1)$. Then one can ignore logistic effects and approximate the subsequent evolution of $X_{N,2}(t)$ by a linear birth-and-death chain with birth rate $\lambda_2\mu_1/\lambda_1$ and death rate μ_2.

We have so far only proved a result for $X_{N,1}(0) = N\alpha_N$ and $X_{N,2}(0) = N\beta_N$, where $\alpha_N \to \alpha$ and $\beta_N \to \beta$. There are other interesting starting conditions to consider.

Near-critical epidemics

- In epidemic models, it is important to investigate "near-critical" cases, as these arise naturally in circumstances where a mutation in the strain moves its basic reproduction number across the threshold, or when measures to control the epidemic start to take effect.
- For our model of two competing epidemics, this means we should be interested in cases where either $R_{0,1}$ tends to 1 as $N \to \infty$, or where $R_{0,1} - R_{0,2}$ tends to zero, or both.
- There are a variety of different possibilities: we confine ourselves to considering cases where $\mu_1 = \mu_2 = 1$, $\lambda_1 - \lambda_2$ tends to zero, and is much smaller than $\lambda_1 - 1$. For instance, this is a model of a "supercritical" epidemic where a slightly more infective strain emerges via mutation, and we are interested in the time taken for the new strain to supplant the weaker one in the population.

Result for a near-critical case (Lopes and L.)

Suppose that:

- $(\lambda_1 - \lambda_2)(\lambda_1 - 1)^{-1} \to 0$.
- $N\frac{(\lambda_1-\lambda_2)^4}{(\lambda_1-1)^2} \to \infty$;
- $X_{N,1}(0)/N \to \alpha$ and $X_{N,2}(0)/N \to \beta$ as $N \to \infty$.

Then the extinction time κ_N for the second species is equal to

$$\frac{\log\left(N(\lambda_1 - 1)(\lambda_1 - \lambda_2)\frac{\beta}{\alpha}\right) + W_N}{\lambda_1 - \lambda_2},$$

where W_N converges in distribution to a random variable W with the standard Gumbel distribution.

This extends the result in the case where λ_1 and λ_2 are fixed constants.

Future work

- Different starting conditions
- Different near-critical regimes
- More species

Some ideas of the proof

For simpler computations, we consider the special case where $\mu_1 = \mu_2 = 1$, and $\lambda_1 > 1$, $\lambda_1 > \lambda_2$ are such that $a = 1 - \frac{\lambda_1 - \lambda_2}{\lambda_1(\lambda_1 - 1)} \neq 0$.

Differential equation

We don't know very much about the differential equation, but there is one very useful formula concerning the behaviour of the solutions:

$$\frac{(x_1(t))^{\lambda_2}}{(x_2(t))^{\lambda_1}} = \frac{(x_1(0))^{\lambda_2}}{(x_2(0))^{\lambda_1}} e^{(\mu_2\lambda_1 - \mu_1\lambda_2)t}, \qquad \text{for all } t \geq 0.$$

Hence the time $t_{y \to z}$ spent by $(x(t))_{t \geq 0}$ to travel from a point $x = (y_1, y_2)^T$ to another point $z = (z_1, z_2)^T$ is

$$t_{y \to z} = \frac{\lambda_2}{\mu_2\lambda_1 - \mu_1\lambda_2} \log(z_1/y_1) - \frac{\lambda_1}{\mu_2\lambda_1 - \mu_1\lambda_2} \log(z_2/y_2).$$

We write $x(t) = x(0) + \int_0^t F(x(s))\, ds$, where $F : \mathbb{R}^2 \to \mathbb{R}^2$ is given by

$$F(x) = \begin{pmatrix} F_1(x) \\ F_2(x) \end{pmatrix} = \begin{pmatrix} \lambda_1 x_1 (1 - x_1 - x_2) - x_1 \\ \lambda_2 x_2 (1 - x_1 - x_2) - x_2 \end{pmatrix}.$$

We now decompose: $\quad F(x) = A \begin{pmatrix} x_1 - \frac{\lambda_1 - 1}{\lambda_1} \\ x_2 \end{pmatrix} + G(x),$

$$\text{where} \quad A = \begin{pmatrix} -(\lambda_1 - 1) & -(\lambda_1 - 1) \\ 0 & -\frac{(\lambda_1 - \lambda_2)}{\lambda_1}, \end{pmatrix};$$

$$G(x) = \begin{pmatrix} -\lambda_1 \left(x_1 - \frac{\lambda_1 - 1}{\lambda_1} \right)^2 - \lambda_1 (x_1 - \frac{\lambda_1 - 1}{\lambda_1}) x_2 \\ -\lambda_2 (x_1 - \frac{\lambda_1 - 1}{\lambda_1}) x_2 - \lambda_2 (x_2)^2 \end{pmatrix}.$$

The case where $a \neq 0$ corresponds to matrix A having distinct eigenvalues.

It is then not hard to check that the solution $x(t)$ can also be written as

$$\begin{pmatrix} x_1(t) - \frac{\lambda_1 - 1}{\lambda_1} \\ x_2(t) \end{pmatrix} = e^{tA} \begin{pmatrix} x_1(0) - \frac{\lambda_1 - 1}{\lambda_1} \\ x_2(0) \end{pmatrix} + \int_0^t e^{A(t-s)} G(x(s))\, ds$$

The matrix exponential e^{tA} is given by

$$\begin{aligned} e^{tA} &= \begin{pmatrix} 1 & 1 \\ 0 & -a \end{pmatrix} \begin{pmatrix} e^{-t(\lambda_1 - 1)} & 0 \\ 0 & e^{-t(\lambda_1 - \lambda_2)/\lambda_1} \end{pmatrix} \begin{pmatrix} 1 & \frac{1}{a} \\ 0 & -\frac{1}{a} \end{pmatrix} \\ &= \begin{pmatrix} e^{-t(\lambda_1 - 1)} & \frac{1}{a}\left(e^{-t(\lambda_1 - 1)} - e^{-t(\lambda_1 - \lambda_2)/\lambda_1} \right) \\ 0 & e^{-t(\lambda_1 - \lambda_2)/\lambda_1} \end{pmatrix}. \end{aligned}$$

We can use the above to show that, if

$$\varepsilon = \max\left\{\left|x_1(0) - \frac{\lambda_1 - 1}{\lambda_1}\right|, x_2(0)/a\right\},$$

is small enough, then, for all t, $|x_1(t) - \frac{\lambda_1 - 1}{\lambda_1}| \leq 2\varepsilon e^{-t(\lambda_1 - \lambda_2)/\lambda_1}$, and $x_2(t) \leq 2a\varepsilon e^{-t(\lambda_1 - \lambda_2)/\lambda_1}$.

Hence we show that all solutions $(x_1(t), x_2(t))^T$ decay exponentially towards the fixed point $((\lambda_1 - 1)/\lambda_1, 0)^T$: given an initial condition $x(0)$, there exists $C = C(x(0))$ such that, for all t, $|x_1(t) - \frac{\lambda_1 - 1}{\lambda_1}| \leq Ce^{-t(\lambda_1 - \lambda_2)/\lambda_1}$, and $x_2(t) \leq Ce^{-t(\lambda_1 - \lambda_2)/\lambda_1}$.

The next step is to show that the stochastic process $x_N(t)$ tracks the solution $x(t)$ for a long period of time.

We proceed similarly for the stochastic process. We write $x_N(t) = x_N(0) + \int_0^t F(x_N(s))\,ds + M_N(t)$, where $(M_N(t))$ is a martingale, and decompose

$$\begin{aligned}\begin{pmatrix} x_{N,1}(t) - \frac{\lambda_1 - 1}{\lambda_1} \\ x_{N,2}(t) \end{pmatrix} &= e^{tA} \begin{pmatrix} x_{N,1}(0) - \frac{\lambda_1 - 1}{\lambda_1} \\ x_{N,2}(0) \end{pmatrix} + \int_0^t e^{A(t-s)} G(x_N(s))\,ds \\ &\quad + \int_0^t e^{A(t-s)}\,dM_N(s).\end{aligned}$$

where A and G are as before.

- The integral $\int_0^t e^{A(t-s)}\, dM_N(s)$ is not itself a martingale.
- However, if we fix some time τ, and define

$$M_N^\tau(t) = \begin{cases} \int_0^t e^{A(\tau-s)}\, dM_N(s) & t \leq \tau \\ M_N^\tau(\tau) & t \geq \tau, \end{cases}$$

  then $M_N^\tau(t)$ is a zero-mean martingale.
- We can bound the quadratic variation of the martingale $M_N^\tau(t)$, and hence show that $M_N^\tau(\tau) = \int_0^\tau e^{A(\tau-s)}\, dM_N(s)$ is, with high probability, small at each of a discrete set of times τ.
- As the entries of $\int_0^t e^{A(t-s)}\, dM_N(s)$ do not grow much over a small time interval, this enables us to bound the integral over a long time period, with high probability.

We can then bound the differences $|x_{N,1}(t) - x_1(t)|$ and $|x_{N,2}(t) - x_2(t)|$, with high probability, over a deterministic time interval until the time t_N that $x_2(t_N) = N^{-1/4}$.

At that time, $|x_1(t_N) - (\lambda_1 - 1)/\lambda_1| = o(1)$, as well.

Actually, for simpler calculations, it is easier to work with new variables $\widetilde{x}_{N,1}(t)$ and $\widetilde{x}_{N,2}(t)$, where $\widetilde{x}_{N,1}(t) = x_{N,1}(t) - \frac{\lambda_1 - 1}{\lambda_1} + \frac{1}{a} x_{N,2}(t)$ and $\widetilde{x}_{N,2}(t) = x_{N,2}(t)$.

This amounts to working with eigenvectors of the matrix A.

The left eigenvectors of A are $(1, 1/a)$ and $(0, 1)$, corresponding to the eigenvalues $-(\lambda_1 - 1)$ and $-(\lambda_1 - \lambda_2)/\lambda_1$, respectively.

In terms of the new variables, the differential equation is expressed as:

$$\begin{aligned}\frac{d\widetilde{x}_1(t)}{dt} &= -(\lambda_1-1)\widetilde{x}_1(t) - \lambda_1\widetilde{x}_1(t)^2 - \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)}\Big(\frac{\widetilde{x}_2(t)}{a}\Big)^2 \\ &\quad + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}\widetilde{x}_1(t)\frac{\widetilde{x}_2(t)}{a} \\ \frac{d\widetilde{x}_2(t)}{dt} &= -\frac{\lambda_1-\lambda_2}{\lambda_1}\widetilde{x}_2(t) - \lambda_2\widetilde{x}_2(t)\widetilde{x}_1(t) + \frac{\lambda_2}{\lambda_1 a}\frac{\lambda_1-\lambda_2}{\lambda_1-1}\widetilde{x}_2(t)^2.\end{aligned}$$

We can then write, as before,

$$\widetilde{x}(t) = \widetilde{x}(0) + \int_0^t \widetilde{F}(\widetilde{x}(s))ds,$$

where $\widetilde{F} : \mathbb{R}^2 \to \mathbb{R}^2$ is given by

$$\widetilde{F}(\widetilde{x}) = \begin{pmatrix} \widetilde{F}_1(\widetilde{x}) \\ \widetilde{F}_2(\widetilde{x}) \end{pmatrix} =$$

$$\begin{pmatrix} -(\lambda_1 - 1)\widetilde{x}_1 - \lambda_1 \widetilde{x}_1^2 - \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)}\left(\frac{\widetilde{x}_2}{a}\right)^2 + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}\widetilde{x}_1\frac{\widetilde{x}_2}{a} \\ -\frac{\lambda_1-\lambda_2}{\lambda_1}\widetilde{x}_2 - \lambda_2\widetilde{x}_2\widetilde{x}_1 + \frac{\lambda_2}{\lambda_1 a}\frac{\lambda_1-\lambda_2}{\lambda_1-1}\widetilde{x}_2^2 \end{pmatrix}.$$

We then decompose

$$\widetilde{F}(\widetilde{x}) = \tilde{A}\begin{pmatrix}\widetilde{x}_1\\ \widetilde{x}_2\end{pmatrix} + \widetilde{G}(\widetilde{x}),$$

where

$$\tilde{A} = \begin{pmatrix} -(\lambda_1 - 1) & 0 \\ 0 & -\frac{(\lambda_1-\lambda_2)}{\lambda_1}, \end{pmatrix}$$

and

$$\widetilde{G}(\widetilde{x}) = \begin{pmatrix} -\lambda_1\widetilde{x}_1^2 - \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)}\left(\frac{\widetilde{x}_2}{a}\right)^2 + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}\widetilde{x}_1\frac{\widetilde{x}_2}{a} \\ -\lambda_2\widetilde{x}_2\widetilde{x}_1 + \frac{\lambda_2}{\lambda_1 a}\frac{\lambda_1-\lambda_2}{\lambda_1-1}\widetilde{x}_2^2 \end{pmatrix}.$$

$$\widetilde{x}(t) = e^{t\tilde{A}}\widetilde{x}(0) + \int_0^t e^{(t-s)\tilde{A}}\tilde{G}(\widetilde{x}(s))ds,$$

or, equivalently,

$$\begin{pmatrix} \widetilde{x}_1(t) \\ \widetilde{x}_2(t) \end{pmatrix} = \begin{pmatrix} e^{-t(\lambda_1-1)}\widetilde{x}_1(0) \\ e^{-t(\lambda_1-\lambda_2)/\lambda_1}x_2(0) \end{pmatrix} +$$

$$\int_0^t \begin{pmatrix} e^{-(t-s)(\lambda_1-1)}[-\lambda_1\widetilde{x}_1(s)^2 - \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)}\left(\frac{\widetilde{x}_2(s)}{a}\right)^2 + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}\widetilde{x}_1(s)\frac{\widetilde{x}_2(s)}{a}] \\ e^{-(t-s)(\lambda_1-\lambda_2)/\lambda_1}[-\lambda_2\widetilde{x}_2(s)\widetilde{x}_1(s) + \frac{\lambda_2}{\lambda_1 a}\frac{\lambda_1-\lambda_2}{\lambda_1-1}\widetilde{x}_2(s)^2] \end{pmatrix} d$$

We can then prove the following result, showing that, for a suitable starting state, the solution to the differential equation decays exponentially.

Let $L = \min\{\lambda_1 - 1, (\lambda_1 - \lambda_2)/\lambda_1\}$ and
$L_1 = \lambda_1 + \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)} + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}$.
Suppose $\widetilde{x}(0)$ is such that

$$y(0) = \max\{|\widetilde{x}_1(0)|, \widetilde{x}_2(0)/|a|\} \leq L/2L_1.$$

Then, for all $t \geq 0$, $|\widetilde{x}_1(t)| \leq 2y(0)e^{-tL}$, and $\widetilde{x}_2(t) \leq 2|a|y(0)e^{-tL}$.

Moreover, if $y(0) \leq L/8L_1$, then, for all $t \geq 0$,

$$\frac{1}{2}x_2(0)e^{-t(\lambda_1-\lambda_2)/\lambda_1} \leq x_2(t) \leq 2x_2(0)e^{-t(\lambda_1-\lambda_2)/\lambda_1}.$$

We now perform a similar decomposition for the random process.

We write

$$\tilde{x}_N(t) = \tilde{x}_N(0) + \int_0^t \widetilde{F}(\tilde{x}_N(s))ds + M_N(t),$$

where $(M_N(t))$ is a martingale, and $\widetilde{F}(\widetilde{x})$ is the drift of $(\tilde{x}_N(t))$ when in state $\widetilde{x}$.

By analogy with the deterministic process $\widetilde{x}(t)$, we can decompose $\begin{pmatrix}\tilde{x}_{N,1}(t)\\ \tilde{x}_{N,2}(t)\end{pmatrix}$ as

$$e^{\tilde{A}t}\begin{pmatrix}\tilde{x}_{N,1}(0)\\ \tilde{x}_{N,2}(0)\end{pmatrix}+\int_0^t e^{\tilde{A}(t-s)}\tilde{G}(X_N(s))ds+\int_0^t e^{\tilde{A}(t-s)}dM_N(s),$$

where $\tilde{A}$ and $\tilde{G}$ are as before, which is equal to

$$\begin{pmatrix}e^{-t(\lambda_1-1)}\tilde{x}_{N,1}(0)\\ e^{-t\frac{\lambda_1-\lambda_2}{\lambda_1}}\tilde{x}_{N,2}(0)\end{pmatrix}+$$

$$\int_0^t\begin{pmatrix}e^{-(t-s)(\lambda_1-1)}\Big[-\lambda_1\tilde{x}_{N,1}(s)^2-\frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)}\left(\frac{\tilde{x}_{N,2}(s)}{a}\right)^2+\frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}\tilde{x}_{N,1}(s)\frac{\tilde{x}_{N,2}(s)}{a}\Big]\\ e^{-(t-s)\frac{\lambda_1-\lambda_2}{\lambda_1}}\Big[-\lambda_2\tilde{x}_{N,2}(s)\tilde{x}_{N,1}(s)+\frac{\lambda_2}{\lambda_1 a}\frac{\lambda_1-\lambda_2}{\lambda_1-1}\tilde{x}_{N,2}(s)^2\Big]\end{pmatrix}ds$$

$$+\int_0^t\begin{pmatrix}e^{-(t-s)(\lambda_1-1)}dM_{N,1}(s)\\ e^{-(t-s)\frac{\lambda_1-\lambda_2}{\lambda_1}}dM_{N,2}(s)\end{pmatrix}.$$

In order to bound $\int_0^t e^{-(t-s)(\lambda_1-1)} dM_{N,1}(s)$ and $e^{-(t-s)\frac{\lambda_1-\lambda_2}{\lambda_1}} dM_{N,2}(s)$, the key objects to estimate are the quantities $\int_0^t v_{t,i}(\widetilde{x}_N(s),s)ds$, where $v_{t,i}(x,s) = \sum_y q_N(x,x+y)(e^{\tilde{A}(t-s)}y)_i)^2$.

Letting $\beta_1 = \lambda_1 - 1$ and let $\beta_2 = (\lambda_1 - \lambda_2)/\lambda_1$, we prove that the probability that $\{\sup_{t \leq e^{\omega/8}} | \int_0^t e^{-\beta_i(t-s)} dM_{N,i}(s)ds| > e^{\beta_i}\sqrt{\omega K_i}\}$ for either $i = 1$ or $i = 2$, while at the same time $\int_0^t v_{t,i}(\widetilde{x}_N(s),s)ds \leq K_i$, for $i = 1,2$ and all $t \leq e^{\omega/8}$ is at most $4e^{-\omega/8}$.

We then prove the following.

Let $f_N(t) = \max\{|\widetilde{x}_{N,1}(t) - \widetilde{x}_1(t)|, |\widetilde{x}_{N,2}(t) - \widetilde{x}_2(t)||a|^{-1}\}$.

Suppose that

$$f_N(0) \leq 4e^{\tilde{L}}\left(\frac{\omega a_1}{N}\right)^{1/2}.$$

Suppose also that $y(0) \leq L/8L_1$.

Then

$$\mathbb{P}\left(\sup_{t \leq e^{\omega/8}} f_N(t) > 16e^{\tilde{L}}\left(\frac{\omega a_1}{N}\right)^{1/2}\right) \leq 8e^{-\omega/8}.$$

(Here $a_1 = \frac{b^2(\lambda_1+1)}{\lambda_1-1}$, where $b = \frac{|a|+1}{|a|}$. Also,
$L = \min\{\lambda_1 - 1, (\lambda_1 - \lambda_2)/\lambda_1\}$, $\tilde{L} = \max\{\lambda_1 - 1, (\lambda_1 - \lambda_2)/\lambda_2\}$,
and $L_1 = \lambda_1 + \frac{(\lambda_1-\lambda_2)^2}{\lambda_1(\lambda_1-1)} + \frac{(\lambda_1-\lambda_2)\lambda_1}{\lambda_1-1}$.)

To prove this result, we show that, on some good event (that the martingale terms are not too large and that $f_N(t)$ is not too large),

$$f_N(t) \leq e^{-tL} f_N(0) + 4L_1 y(0) e^{-tL} \int_0^t f_N(s) ds + 4\Big(\frac{\omega a_1}{N}\Big)^{1/2} e^{\tilde{L}}.$$

We can then apply Gronwall's inequality to $f_N(t)e^{tL}$ to deduce the result.

For a suitable choice of ω, $t_N \leq e^{\omega/16}$.

From time t_N onwards, $x_1(t)$, and hence $x_{N,1}(t)$, is very close to $\frac{\lambda_1 - 1}{\lambda_1}$.
Once $X_{N,2}(t)$ has dropped below about $N^{3/4}$, the "logistic effects" become negligible, and the process $(X_{N,2}(t))$ behaves like a sub-critical linear birth-and-death chain, and the distribution of the time to extinction from this point onwards can thus be closely approximated.

The total time taken is approximately the sum of the following two terms:

$$\frac{\lambda_2}{\lambda_1 - \lambda_2} \log(x_1(t_N)/x_1(0)) - \frac{\lambda_1}{\lambda_1 - \lambda_2} \log(x_2(t_N)/x_2(0)),$$

and

$$\frac{\lambda_1}{\lambda_1 - \lambda_2} \left(\log(N x_2(t_N)) + \log\left(1 - \frac{\lambda_2}{\lambda_1}\right) \right) + \frac{\lambda_1}{\lambda_1 - \lambda_2} W_N,$$

where W_N converges in distribution to a standard Gumbel variable G.

The first term corresponds to the phase where the process tracks the differential equation, while the second term comes from the approximation by a linear birth-and-death chain.

In the near-critical case, there is a phase where we do not attempt to prove a differential equation approximation. This is analogous to what happens for a single SIS logistic epidemic.

First we track $X_{N,1}(t) + X_{N,2}(t)$, which behaves very much like a single logistic epidemic with infection rate λ_1 and recovery rate 1, or infection rate λ_2 and recovery rate 1, which are 'almost the same' in this case (the difference is of the order $\lambda_1 - \lambda_2$, which is smaller).

We also consider $X_{N,1}(t)/X_{N,2}(t)$, which is non-increasing, but also stays close to the initial value for a time $o(1/(\lambda_1 - \lambda_2))$.

After time $(\lambda_1 - \lambda_2)^{-1}\psi(N)^{-1}$, we approximate by a differential equation until time $(\lambda_1 - \lambda_2)^{-1}\phi(N)$.

Then we couple with a linear birth-and-death process.