Extinction - 2 Case Studies

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Part I: Lifetime of a Branching-Annihilation Process
Part II: Distribution of Epidemic Sizes near Threshold

Extinction Rates - A Real-Space WKB Treatment

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A commentary / extension of Elgart—Kamenev (and Freidlin—Wentzell)
Parallel to Assaf and Meerson

J. Stat. Phys., (2007)

Basic Birth-Death Process

Basic Processes:

$$\begin{aligned} A &\xrightarrow{\alpha} 2A \\ A + A &\xrightarrow{\beta} 0 \end{aligned}$$

Rate Equation:

$$\dot{n} = \alpha n - \beta n(n-1)$$

- Logistic Growth
- Stable state at $n = 1 + \alpha/\beta$
- Unstable state at $n = 0$

Stochastic Process Different:

- State at $n = 1 + \alpha/\beta$ *meta*-stable
- Absorbing state at $n = 0$

What is the extinction rate?

Quasi-stationary State

Consider the master equation:

$$\dot{P}_n = \alpha\left(-nP_n + (n-1)P_{n-1}\right) + \frac{\beta}{2}\left(-n(n-1)P_n + (n+2)(n-1)P_{n+2}\right)$$

Long-time behavior given by $-\Gamma_1$, negative eigenvalue closest to 0

For small β/α, Γ_1 is exponentially small $\Rightarrow$ very slow decay

Associated eigenvector called the quasi-stationary state

$1/\Gamma_1$ is the mean first passage time for the quasi-stationary state

For small β/α, the mean first passage time starting from n is essentially independent of n (unless n is very small), and equal to $1/\Gamma_1$ (implies all other eigenvalues much larger in magnitude)

Small β/α

We want to compute Γ_1 for small β/α

Strategy: Since Γ_1 exponentially small, we can solve *stationary* master equation:

$$0 = \alpha\left(-nP_n + (n-1)P_{n-1}\right) + \frac{\beta}{2}\left(-n(n-1)P_n + (n+2)(n+1)P_{n+2}\right)$$

- Γ_1 determined by leakage to the absorbing state:

$$\Gamma_1 = \frac{\beta P_2}{\sum_n P_n}$$

Use Discrete WKB to solve master equation

Why not Fokker-Planck?

Width of peak near $n = \alpha/\beta$ is $O((\alpha/\beta)^{1/2}) \gg 1$

Approximating Finite-Differences by Derivatives should be good!

Define $y \equiv \sqrt{\beta/\alpha}(n - \alpha/\beta)$

Master equation reads:

$$0 = \left(\frac{3}{2}P'' + (yP)'\right) + \frac{1}{2}\sqrt{\frac{\beta}{\alpha}}\left(P''' + 5yP'' + 8P' + 4yP + 2y^2P\right) + O\left(\frac{\beta}{\alpha}\right)$$

Obtain Fokker-Planck with small corrections!

What is bad???

Why not Fokker-Planck?

$$y \equiv \sqrt{\frac{\beta}{\alpha}}\left(n - \frac{\alpha}{\beta}\right)$$

Leading order solution:

$$P_0(y) \sim e^{-y^2/3}$$

Behavior of correction for large y: $y^3\sqrt{\beta/\alpha}P_0(y)$

Correction no longer small when $y \sim (\alpha/\beta)^{1/6}$ so that $n - \alpha/\beta \sim (\alpha/\beta)^{2/3}$

Can't use Fokker-Planck to get down to n's of order 1.

Can't calculate Γ_1 this way!!

Discrete WKB

WKB Ansatz: $x \equiv \beta n/\alpha$

$$P_n = \exp\left(\frac{\alpha}{\beta}S_0(x) + S_1(x) + \cdots\right)$$

To leading order: $P_{n+k} \approx e^{kS_0'(x)}P_n \equiv \Lambda^k P_n$, where $\Lambda(x) \equiv e^{S_0'(x)}$

Leading Order WKB equation:

$$0 = \alpha(-1 + \frac{1}{\Lambda}) + \frac{\alpha x}{2}(-1 + \Lambda^2)$$

Solution:

$$x = \frac{2}{\Lambda(\Lambda + 1)}$$

Discrete WKB

Solution: $x = 2/(\Lambda(\Lambda+1))$

Connection to Fokker-Planck:

- For $n \approx \alpha/\beta$, $x \approx 1$
- $\Lambda \approx 1 + \frac{2}{3}(1-x)$
- $S_0' = \ln(\Lambda) \approx \frac{2}{3}(1-x) \Rightarrow S_0 \approx -\frac{1}{3}(1-x)^2$
- $P \approx \exp(\frac{\alpha}{\beta}S_0) = e^{-y^2/3}$

As $x \to 0$, $\Lambda \to \infty$

Scale of Γ_1:

$$P_2/P_{\alpha/\beta} \approx \exp\left(\frac{\alpha}{\beta}\int_1^\infty \ln(\Lambda)\frac{dx}{d\Lambda}d\Lambda\right) = \exp\left(-\frac{\alpha}{\beta}\int_1^\infty \frac{x(\Lambda)}{\Lambda}d\Lambda\right)$$

Connection to Elgart-Kamenev

$$\Gamma_1 \sim P_2/P_{\alpha/\beta} \approx \exp\left(-\frac{\alpha}{\beta}\int_1^\infty \frac{x(\Lambda)}{\Lambda} d\Lambda\right)$$

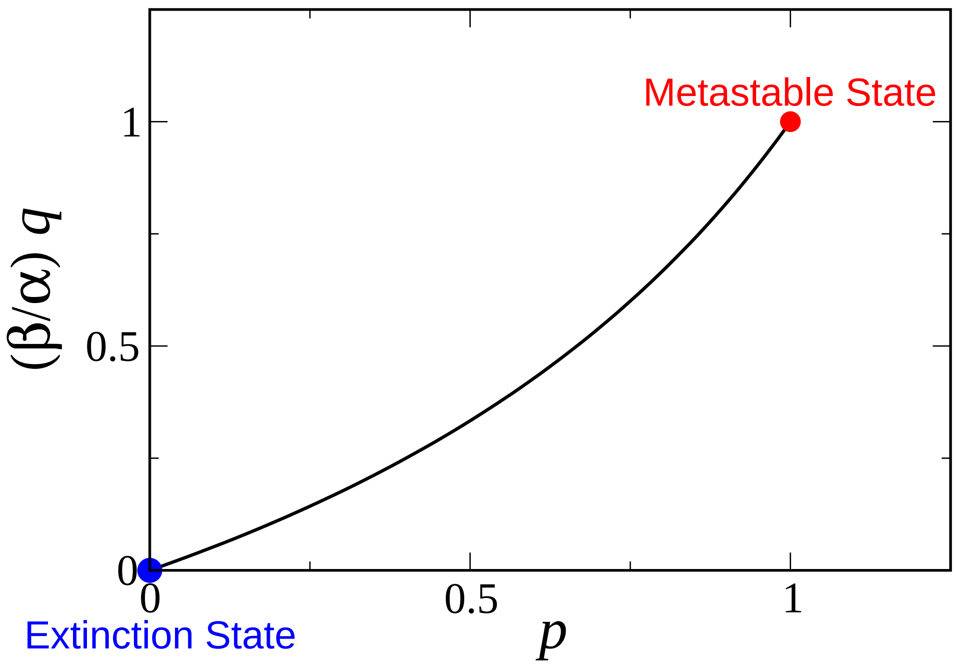
Define coordinate $q = n\Lambda$, momentum $p = 1/\Lambda$

$0 \leq q \leq \alpha/\beta$, $0 \leq p \leq 1$,

$$\Gamma_1 \sim \exp\left(-\int_0^1 q dp\right)$$

where

$$q(p) = \frac{2\alpha}{\beta}\frac{p}{1+p}$$



Physical Optics

To complete the calculation, we need $S_1(x)$ as well.

Answer:

$$Q(x) = Ae^{S_1(x)} = A\frac{\sqrt{\Lambda}(\Lambda+1)^2}{\sqrt{2\Lambda+1}}$$

This works as long as $n \gg 1$. Have to solve small-n problem separately.

For small n, P_n grows rapidly with n.

Leads to approximate master equation:

$$0 = \alpha(-nP_n + (n-1)P_{n-1}) + \frac{\beta}{2}(-n(n-1)P_n + (n+2)(n+1)P_{n+2})$$

Solution:

$$P_n \approx \left(\frac{\alpha}{\beta}\right)^{(n-1)/2} \frac{1}{n\Gamma((n+1)/2)} P_1$$

Physical Optics

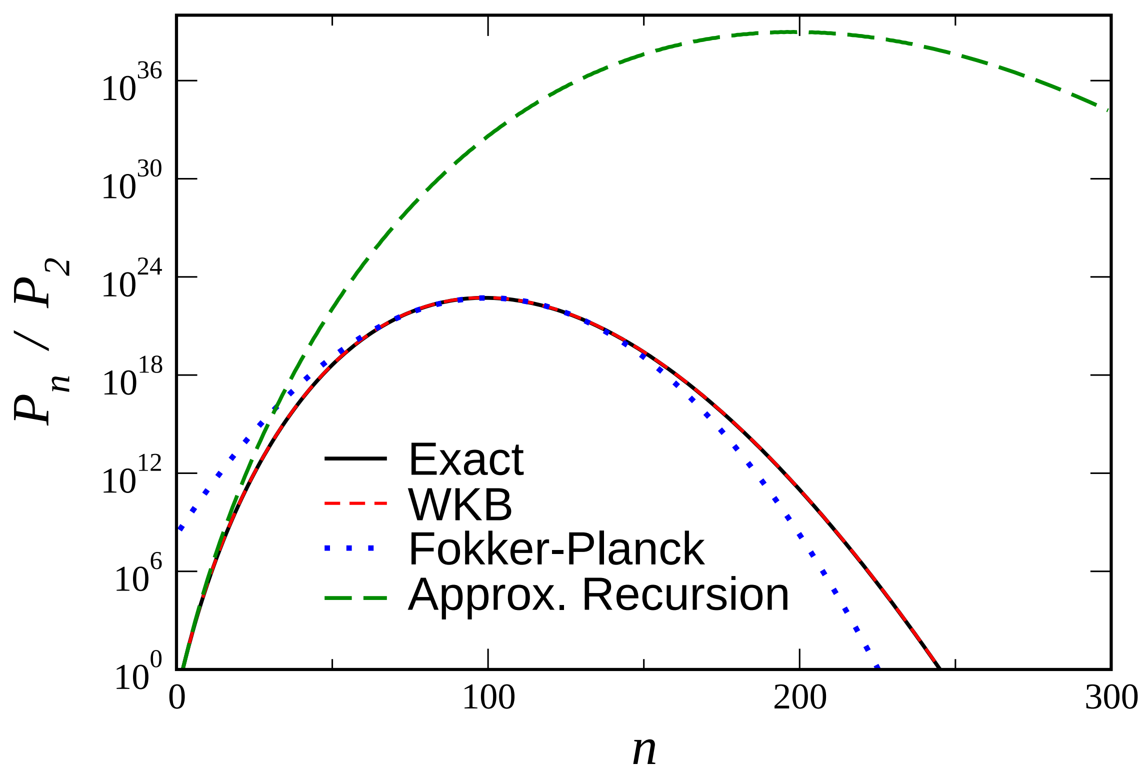
Matching this to WKB solution yields $A = P_1\sqrt{\frac{\beta^3}{4\pi\alpha^3}}$

Final Answer:

$$\Gamma_1 = \sqrt{\frac{\alpha^3}{4\pi\beta}}e^{-2\alpha(1-\ln(2))/\beta}$$

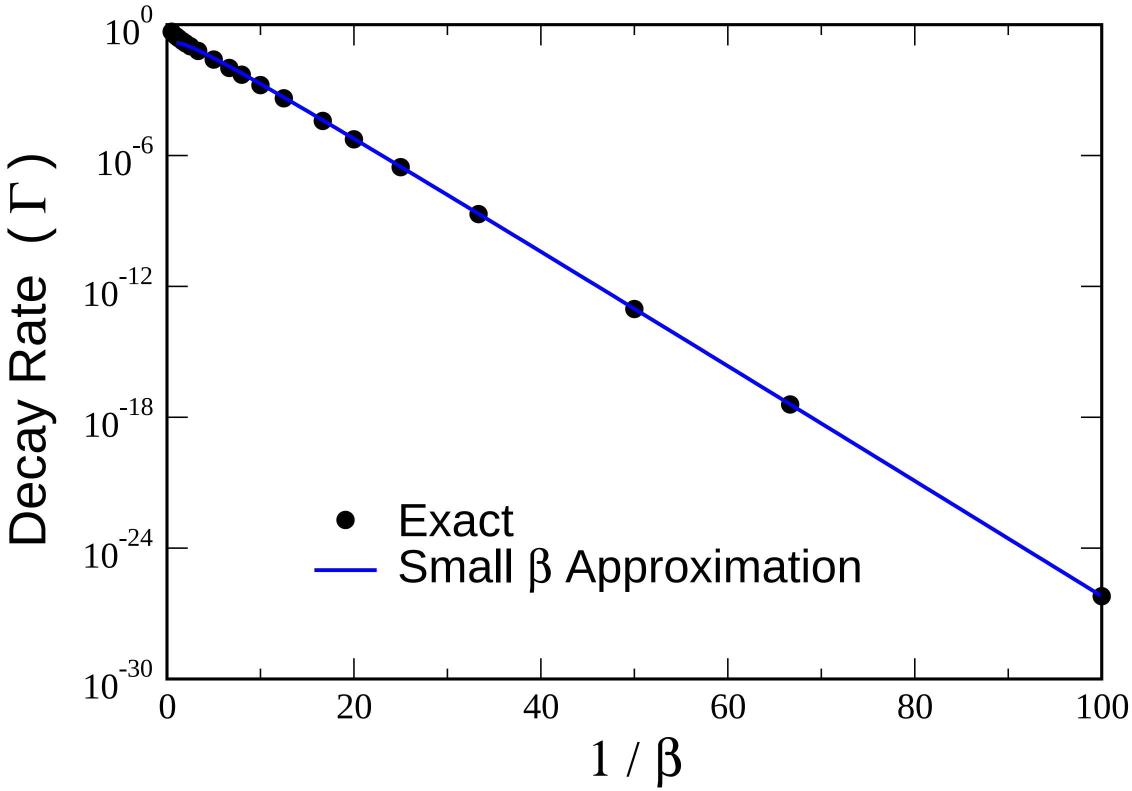
Numerics

Quasistationary Distribution



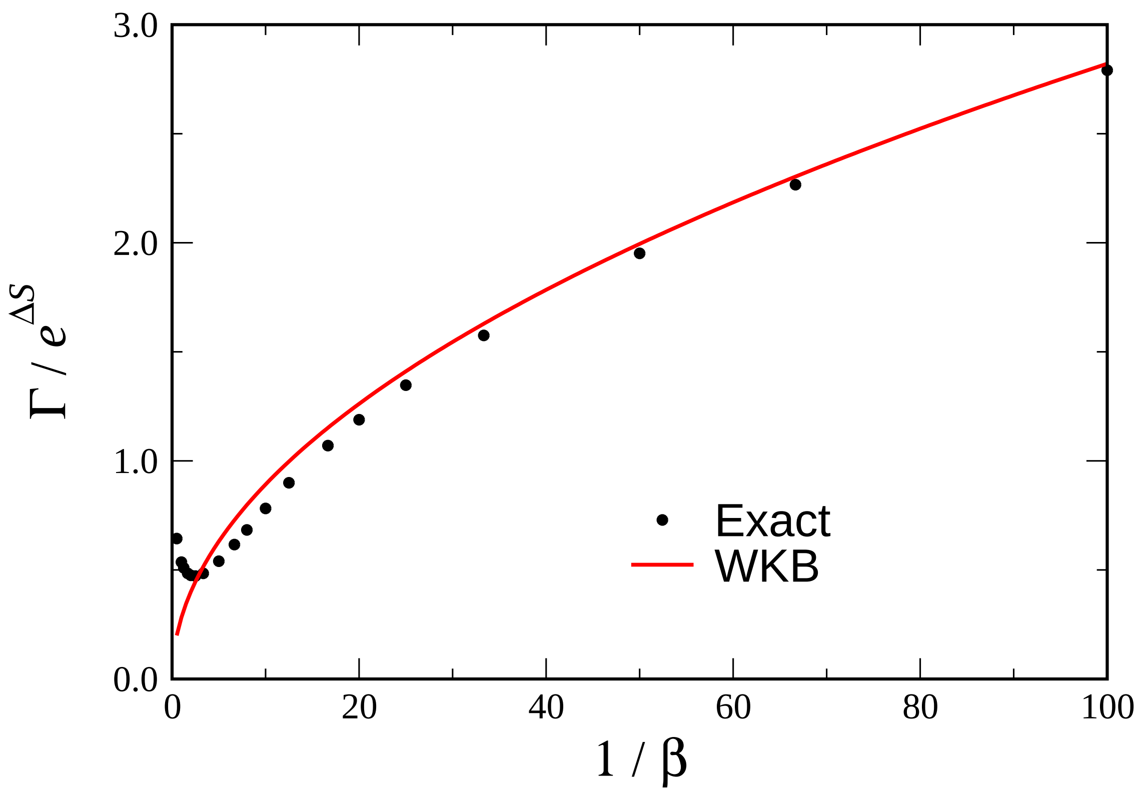
Numerics

Decay Rate



Numerics

Decay Rate



Conclusion

Models with same rate equations yield very different extinction rates, i.e. different ΔS_0.

- For 'parity' model with $A \stackrel{\alpha/2}{\to} 3A$,

$$\Gamma_1 \approx \sqrt{\frac{\alpha^3}{2\pi\beta}} e^{-\alpha/2\beta}$$

In ecology, for example, will never know 'real' model, extinction rate unknowable.

- Leigh (1981) knew the difference between the true extinction rate and the Fokker-Planck value – "equivalent to that accruing from mistaking K" (carrying capacity = metastable population)
- Implication is that since we don't (can't) know K precisely, what does the exact answer matter?

Situation may be better for environmental stochasticity, where distribution is power-law and Fokker-Planck equation is valid.

And now for something completely different!

SIR Infection Model Near Threshold

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http://arxiv.org/pdf/q-bio.PE/0701024
PRE (to appear)
Note added yesterday: Reproduces A. Martin-Löf, J. Appl. Prob. **35**, 671-682 (1998).

Definition of SIR Model

One of the basic models of infection - Kermack and McKendrick (1927)

Well-Mixed Population of N persons - divided into 3 classes

- S $\equiv$ Susceptible - Healthy, Infectible
- I $\equiv$ Infected - Sick, Infectious
- R $\equiv$ Recovered (Removed) - Non-Infectious, Non-Infectible

Fundamental Processes:

$$(S,I,R) \overset{\alpha SI/N}{\rightarrow} (S-1, I+1, \quad R \ ) \qquad \text{Infection}$$

$$(S,I,R) \overset{1}{\rightarrow} (\quad S \ \ , I-1, R+1) \qquad \text{Recovery}$$

2 Parameters, α = infectivity, N

Standard Question: Start with 1 Infected, $(N-1,1,0)$. Process ends when last Infected recovers, $(N-n,0,n)$.

What is epidemic size, n?

First-Pass: Rate Equations

The SIR Equations: (Kermack and McKendrick, 1927)

$$\begin{aligned}\dot{S} &= -\frac{\alpha}{N} SI \\ \dot{I} &= +\frac{\alpha}{N} SI - I \\ \dot{R} &= I\end{aligned}$$

N is conserved $\Rightarrow$ Do not need to track $R(t)$.

S decreases monotonically with time $\Rightarrow$ Sufficient to consider $I(S)$:

$$\frac{dI}{dS} = -1 + \frac{N}{\alpha S}$$

Solution is immediate: $I = N - S + \frac{N}{\alpha} \ln \frac{S}{N-1}$

Rate Equations (Cont'd)

$$\begin{aligned} \frac{dI}{dS} &= -1 + \frac{N}{\alpha S} \\ I &= N - S + \frac{N}{\alpha} \ln \frac{S}{N-1} \end{aligned}$$

Two cases:

- $\alpha < \frac{N}{N-1} \approx 1$: I decreases monotonically to 0, i.e. infection immediately dies out.
- $\alpha > 1$: I first increases, then decreases to 0.

$$n = N - S|_{I=0} = rN$$

where $$e^{-\alpha r} + r = 1$$

$r \sim 2(\alpha - 1)$ as $\alpha \to 1^+$, $\quad r \sim 1 - e^{-\alpha}$ as $\alpha \to \infty$.

Threshold at $\alpha = 1$.

Stochastic Model, Mapping to Random Walk

In principle, we could write down a master equation (or Fokker-Planck equation) for $P(S, I)$. Not stationary. Even to do WKB we would have to solve the semi-classical rate equations - not trivial.

Better idea: Do what we did to rate equations - eliminate time.

Define $T \equiv$ number of transitions. In each transition, I changes by ± 1, Random Walk.

S is given by T and I:

- $I = 1 + T_+ - T_- = 1 + 2T_+ - T \Rightarrow T_+ = \frac{1}{2}(I + T - 1)$
- $S = N - 1 - T_+ = N - \frac{1}{2}(I + T + 1)$

Transition probabilities:

$$p_- = \frac{1}{1 + \alpha S/N} = \frac{1}{1 + \alpha - \alpha(I + T + 1)/(2N)}$$

$$p_+ = 1 - p_-$$

Stochastic Model, Infinite N Limit

$$p_- = \frac{1}{1+\alpha S/N} = \frac{1}{1+\alpha-\alpha(I+T+1)/(2N)}$$
$$p_+ = 1-p_-$$

In initial stages, $I+T+1 \ll N \Rightarrow$ Simple Biased Random Walk, with Trap at Origin

For $\alpha < 1$:

- Walk biased toward origin.
- Avg. number of steps to hit origin from 1:

$$0 = 1 + \bar{T}\left(\frac{\alpha}{1+\alpha} - \frac{1}{1+\alpha}\right) \Rightarrow \bar{T} = \frac{1+\alpha}{1-\alpha}$$

  Finite, so neglect of $(I+T+1)/N$ is always good.
- $\bar{n} = \frac{1}{2}(\bar{T}+1) = \frac{1}{1-\alpha}$, Classic Result (Harris, 1989)
- Diverges as $\alpha \to 1$.

Stochastic Model, Infinite N Limit (Cont'd)

For $\alpha > 1$:

- Cannot use rate equations until I is macroscopic.
- Finite chance that I dies out before this.
- During this time, we can again neglect $(I + T + 1)/N$
- Random Walk biased toward ∞
- Probability of being absorbed at origin = $1/\alpha$.
- If I escapes early extinction, then rate eqn. prediction is reliable. (Watson, 1980)
- Thus,

$$\bar{n} = \left(1 - \frac{1}{\alpha}\right) rN$$

- Always far from naive rate equation answer.
- $\bar{n} \sim 2(\alpha - 1)^2 N$ as $\alpha \to 1^+$.

Threshold Region

Clearly, both results $\alpha < 1$ $(n \to \infty)$, $\alpha > 1$ $(n \to 0)$ break down at threshold, $\alpha = 1$.

How wide is threshold region? (Ben-Naim and Krapivsky, 2004)

Define $\alpha - 1 \equiv \delta$.

$\bar{n} \sim O(1/\delta) \qquad \alpha < 1$

$\bar{n} \sim O(\delta^2 N) \qquad \alpha > 1$

$$\Rightarrow \qquad \delta \sim N^{-1/3} \qquad \bar{n} \sim N^{1/3}$$

Solution of Threshold Region

To analyze threshold region, we have to include $(I + T + 1)/N$ term in $p_\pm$.

However, term is nevertheless small in threshold region, so

$$p_\pm \approx \frac{1}{2} \mp \frac{1}{8N}(T + I - 2\delta N)$$

Extra drift is relevant for $T \sim \delta N \sim N^{2/3}$

For random walk, $I \sim T^{1/2}$, so I term in drift is still irrelevant.

We are left with a random walk with a drift that increases linearly in "time".

Solution at Threshold

Look at threshold ($\delta = 0$) case first.

Solution without drift:

$$P(T = 2k+1) = 2^{-2k-1}\left(\binom{2k}{k} - \binom{2k}{k+1}\right) \sim \frac{1}{\sqrt{4\pi k^3}} \quad (k \to \infty)$$

How does drift modify this result at long times?

Pass to Fokker-Planck equation:

$$\frac{\partial P}{\partial T} = \frac{1}{2}\frac{\partial^2 P}{\partial I^2} + \frac{T}{4N}\frac{\partial P}{\partial I}$$

Not separable!

Solution at Threshold (Cont'd)

Trick: Define

$$P \equiv e^{-IT/4N - T^3/(96N^2)}\psi$$

Then,

$$\frac{\partial\psi}{\partial T} = \frac{1}{2}\frac{\partial^2\psi}{\partial I^2} + \frac{I}{4N}\psi.$$

Boundary Conditions: $\psi(0,T) = 0$, $\psi(I,0) = \delta(I-1)$, $\psi(L,T) = 0$ (regularization)

After rescaling I by $a \equiv (2N)^{1/3}$ and T by $2a^2$, we get

$$\frac{\partial\psi}{\partial T} = \frac{\partial^2\psi}{\partial I^2} + I\psi$$

with $\psi(I,0) = \delta(I - 1/a)/a$.

Eigenfunctions satisfy Airy equation!

Properties at Threshold

$$P(n) = \frac{e^{-n^3/(12N^2)}}{\pi^2 a^3} \int_{-\infty}^{\infty} \frac{dE}{\mathrm{Ai}^2(E) + \mathrm{Bi}^2(E)} e^{En/a^2}$$

Asymptotics for small n:

- Dominated by large negative E, where $\mathrm{Ai}^2(E) + \mathrm{Bi}^2(E) \approx (-E)^{-1/2}/\pi$

$$P(n) \approx \frac{1}{\sqrt{4\pi} n^{3/2}}$$

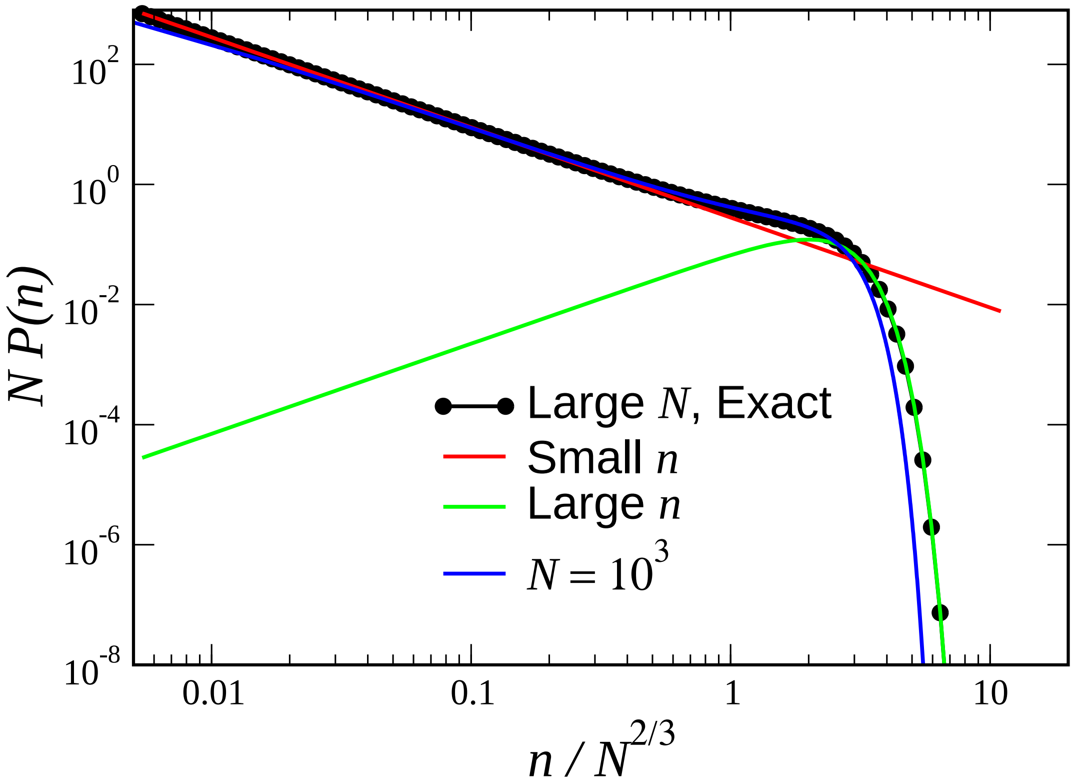
Asymptotics for large n:

- Dominated by $\mathrm{Bi}(E)$ giving maximum at $E \sim n^2$

$$P(n) \approx \frac{1}{8\sqrt{\pi}N^2} n^{3/2} e^{-n^3/(16N^2)}$$

- Strongly suppressed for $n \gg N^{2/3}$
- Suppression found numerically by Ben-Naim & Krapivsky

Properties at Threshold



Solution near Threshold

Return to $\delta \neq 0$.

Same Trick works:

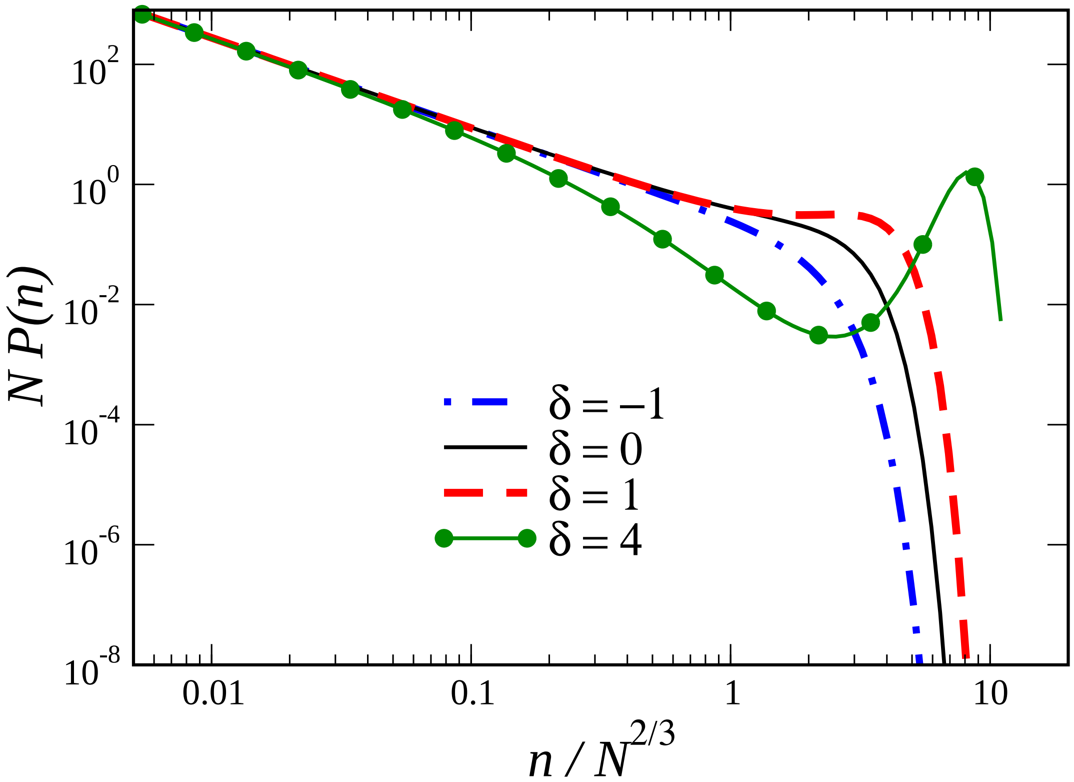
$$P \equiv e^{-\frac{I(T-2\delta N)}{4N} - \frac{(T-2\delta N)^3 - (2\delta N)^3}{96N^2}} \psi$$

so that

$$P_\delta(n) = e^{(n^2\delta N - n\delta^2 N^2)/(3N^2)} P_{\delta=0}(n)$$

For large δ, this generates a second peak at $n \approx 2\delta N$, the "classical" rate equation answer.

Solution near Threshold



Properties near Threshold

Consider $\bar{n}(\delta)$.

Asymptotics for large, negative δ:

- Dominated by small n's:

$$\bar{n} \approx \int_0^\infty dn\, n\, e^{-n\delta^2/4} \frac{1}{2\sqrt{\pi} n^{3/2}} = -1/\delta$$

- Matches on to subcritical result.

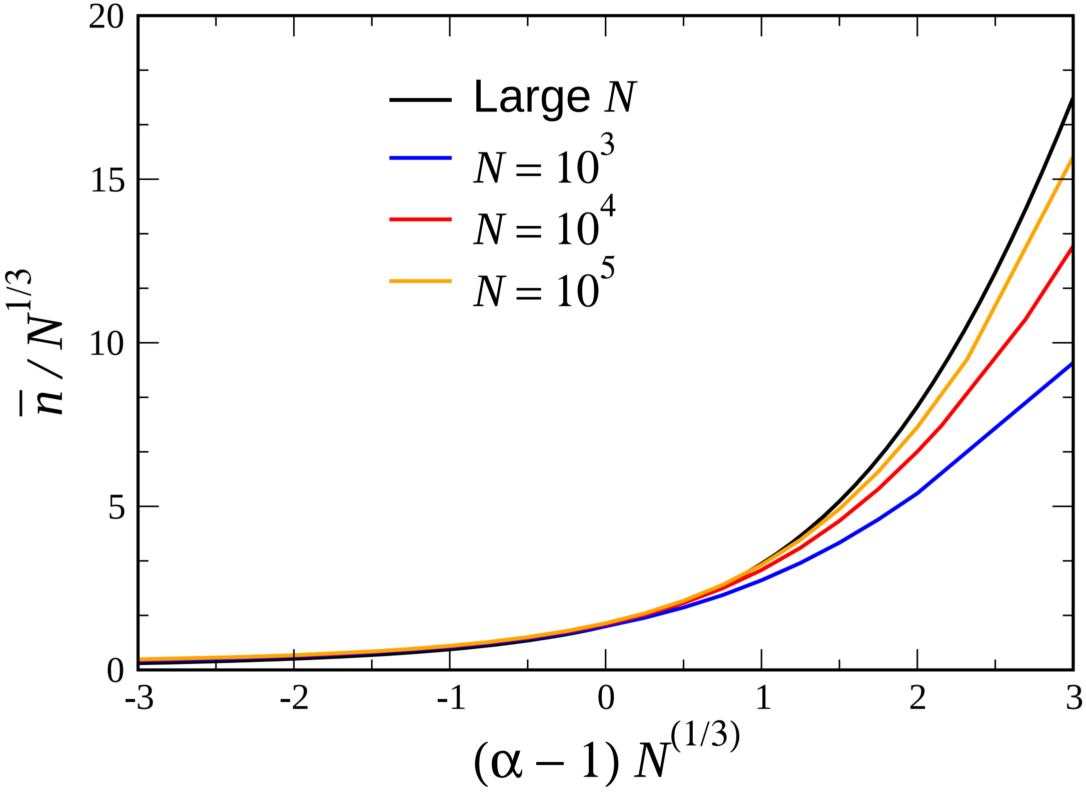
Asymptotics for large, positive δ:

- Dominated by second, classical peak

$$\bar{n} \approx 2\delta^2 N$$

- Matches on to supercritical result.

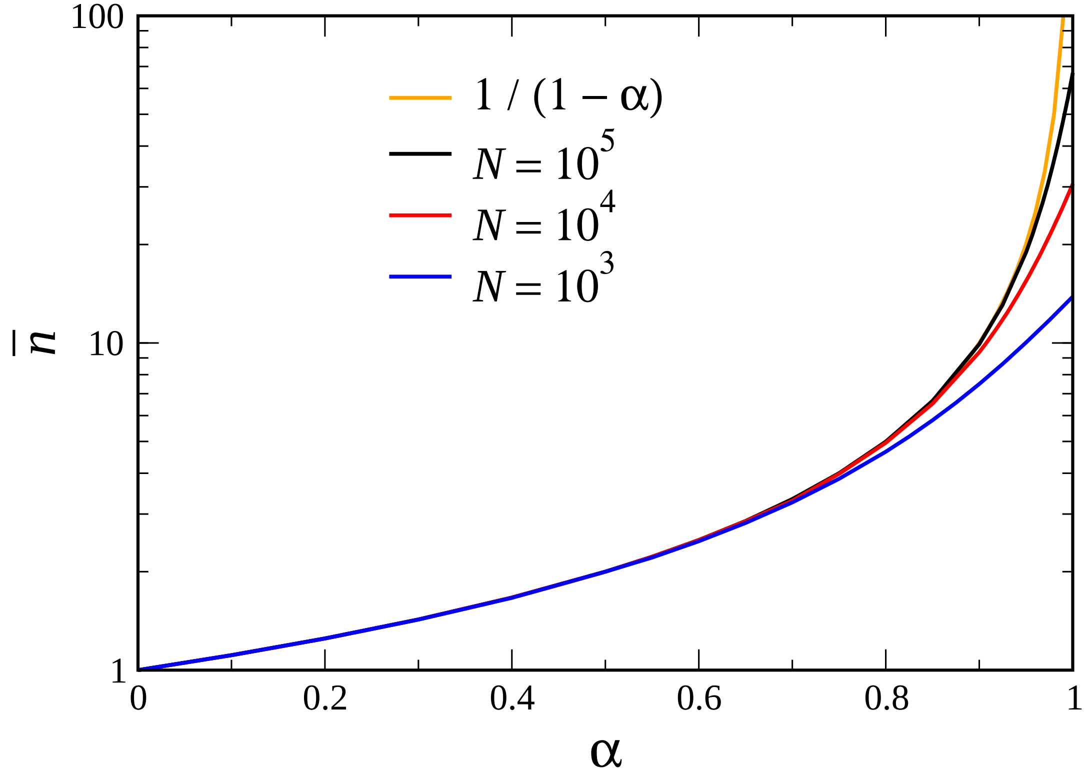
Properties near Threshold



THANK YOU

Does this work?

$\alpha < 1$

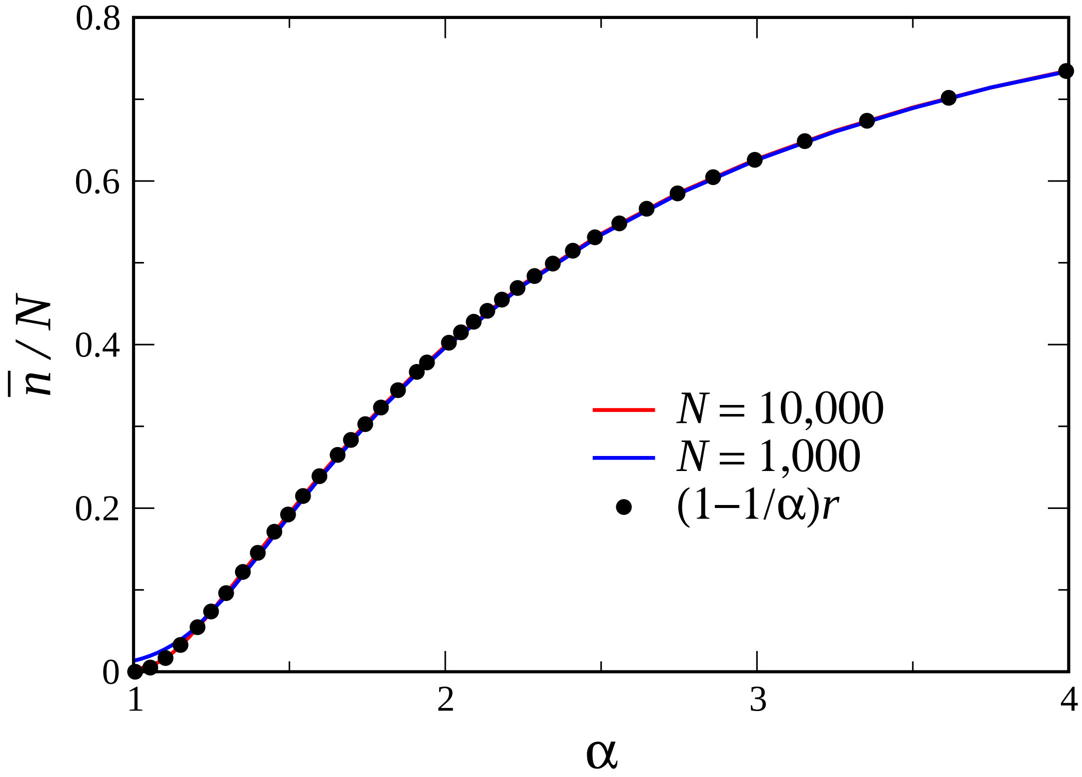


Calculated using exact 1-D master equation

Works as long as α not to close to threshold.

Does this work? (cont'd)

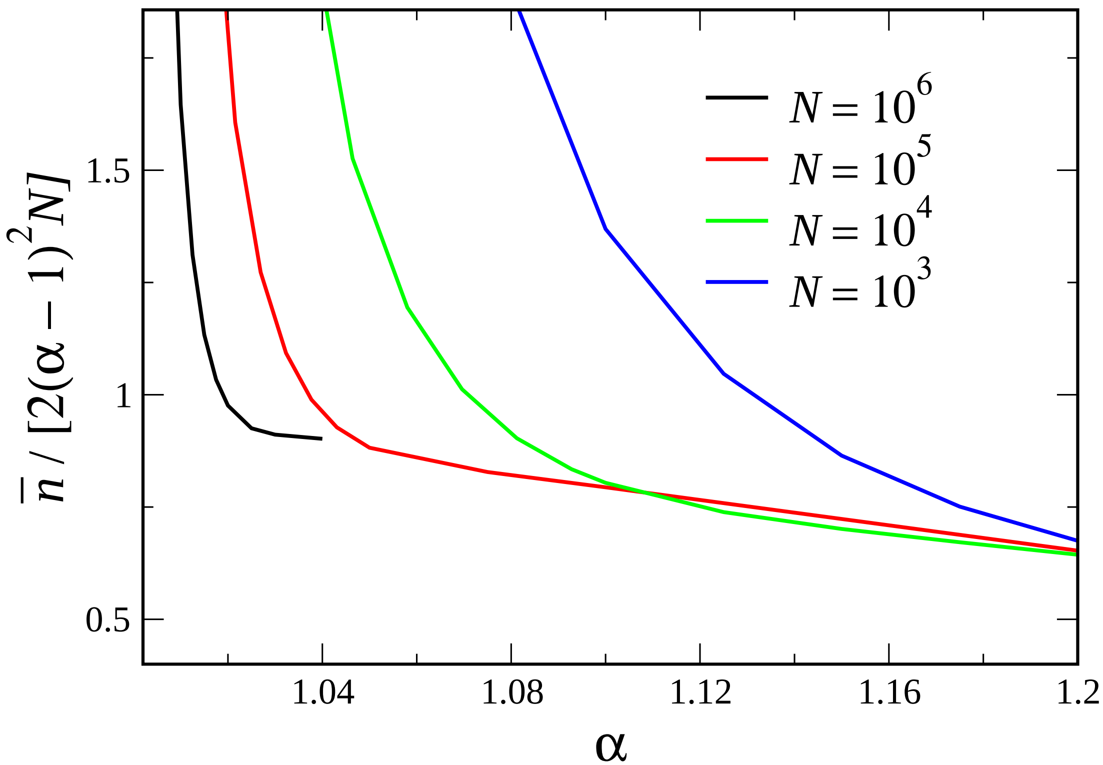
$\alpha > 1$



Hard to see, but again fails as $\alpha \to 1$.

Does this work? (cont'd)

Blow up region near $\alpha = 1$



Again, N-dependent boundary layer near threshold

Solution at Threshold (Cont'd)

Flux of ψ to origin is:

$$\mathcal{F}_\psi = \frac{1}{2}\frac{\partial\psi}{\partial I}\Big|_{I=0} = \frac{1}{2a}\sum_n \phi_n'(0)\phi_n'(\frac{1}{a})e^{E_nT}$$
$$\approx \frac{1}{2a^2}\sum_n (\phi_n'(0))^2 e^{E_nT} \quad (1)$$

Eigenfunctions:

$$\phi_n(I) = A_n\mathsf{Ai}(-x+E_n) + B_n\mathsf{Bi}(-x+E_n)$$

Boundary condition $\phi_n(0)=0$ gives:

$$B_n = -A_n\mathsf{Ai}(E_n)/\mathsf{Bi}(E_n)$$

so,

$$\phi_n'(0) = -\frac{A_n}{\mathsf{Bi}(E_n)}Wr(\mathsf{Ai},\mathsf{Bi}) = -\frac{A_n}{\pi\mathsf{Bi}(E_n)}$$

Solution at Threshold (Cont'd)

A_n given by normalization:

$$\begin{aligned} 1 &= \int_0^L \phi_n^2(I)dI = \left[\phi_n'^2 + (x-E)\phi_n^2\right]_0^L \\ &= \left[(\phi_n'(L))^2 - (\phi_n'(0))^2\right] \approx \frac{(A_n^2 + B_n^2)L^{1/2}}{\pi} \end{aligned} \quad (2)$$

Change sum over n to integral over E. Density of states:

$$\frac{dn}{dE} \approx \frac{L^{1/2}}{\pi}$$

Now, take away the cutoff L and undo the rescalings:

$$P(n) = \frac{e^{-n^3/(12N^2)}}{\pi^2 a^3} \int_{-\infty}^{\infty} \frac{dE}{\mathrm{Ai}^2(E) + \mathrm{Bi}^2(E)} e^{En/a^2}$$