Effects of discreteness on population persistence in an oasis

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Reaction-diffusion systems and population dynamics

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• **If the density of particles is not very large the discrete nature of the population cannot be neglected** and the continuous description is no longer accurate.

[Durrett and Levin, 1994; Brunet and Derrida, 1997; Doering et al., 2003; Tél et al., 2005; Geyrhofer and Hallatschek, 2013]

Population persistence and demographic stochasticity

• Determining the **conditions for persistence**, or estimating the probability of extinction of species and populations, is essential in population biology.

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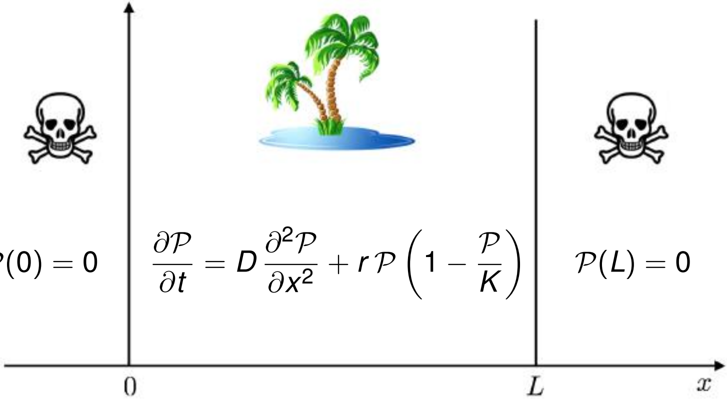
Individual-based reaction-diffusion model

- System of particles diffusing in space and interacting when they get within a given interaction distance.
- Heterogeneous habitat: favorable region surrounded by hostile environment.
- Role of demographic stochasticity and discreteness on extinction dynamics (population persistence).

Continuous KiSS model



$$\mathcal{P}(0) = 0 \qquad \frac{\partial \mathcal{P}}{\partial t} = D\,\frac{\partial^2 \mathcal{P}}{\partial x^2} + r\,\mathcal{P}\left(1 - \frac{\mathcal{P}}{K}\right) \qquad \mathcal{P}(L) = 0$$

$\mathcal{P}(x, t)$ population density field

D diffusion coefficient, r intrinsic growth rate, K carrying capacity

[Skellam, 1951; Kierstead and Slobodkin, 1953]

Continuous KiSS model

- Persistence depends on the patch size L: $\begin{cases} L < L_c & \Rightarrow \text{extinction} \\ L > L_c & \Rightarrow \text{survival} \end{cases}$

Close to extinction: $\mathcal{P} \ll K$, linear growth term $r\,\mathcal{P}$

Eigenvalues of $\mathcal{L} = D\,\partial_x^2 + r$: $\lambda_n = r\left[1 - n^2\left(\frac{L_c}{L}\right)^2\right]$, $n = 1, 2, ...$

Population growth: $\lambda_1 > 0 \Rightarrow \boxed{L > L_c = \pi\sqrt{\frac{D}{r}}}$ critical patch size

used in conservation biology (generalizing the model)

[Diamond and May, 1976; Cantrell and Cosner, 1998, 1999]

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- Nondimensional formulation:

  $t \to r\,t, \;\; x \to x\sqrt{r/D}, \;\; \theta = \mathcal{P}/K$

$$\frac{\partial \theta}{\partial t} = \frac{\partial^2 \theta}{\partial x^2} + \theta\,(1-\theta); \qquad L_c \to L_c = \pi \;\text{ (critical patch size)}$$

[Skellam, 1951; Kierstead and Slobodkin, 1953; Okubo and Levin, 2001; Ryabov and Blasius, 2008]

Discrete KiSS model

- Requisite: FKPP dynamics (logistic growth) for large numbers of particles

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- Autocatalytic reaction $A + B \xrightarrow{r} 2B$

$$\frac{\partial \theta_A}{\partial t} = D_A \frac{\partial^2 \theta_A}{\partial x^2} - r\,\theta_A \theta_B$$

$$\frac{\partial \theta_B}{\partial t} = D_B \frac{\partial^2 \theta_B}{\partial x^2} + r\,\theta_A \theta_B$$

with $D_A = D_B = D$ and $\theta_A + \theta_B = 1$

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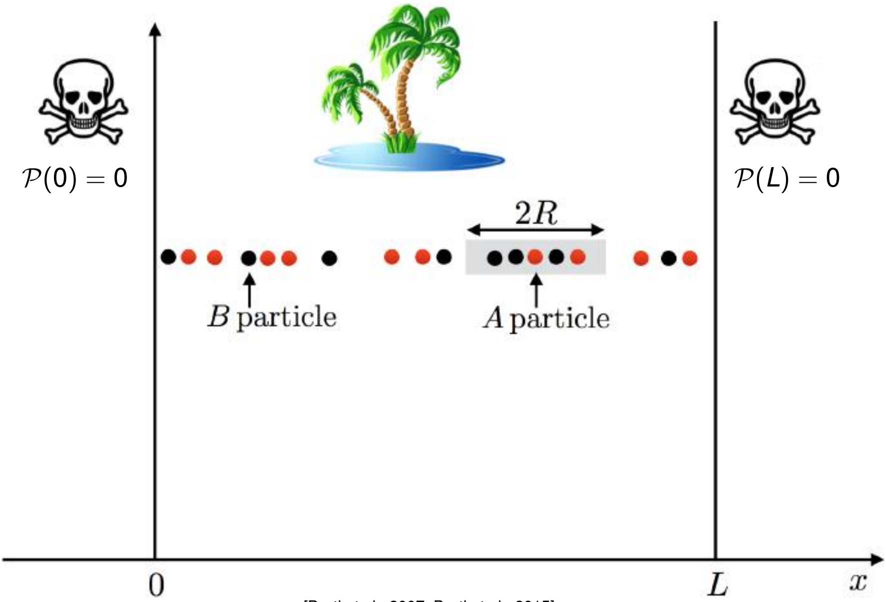
- Discretization:

$$\theta_{A,B} \rightarrow \begin{cases} N_A & \text{particles of type } A \\ N_B & \text{particles of type } B \end{cases}$$

N_A particles of type A	• (red)	auxiliary/nutrient
N_B particles of type B	• (black)	species feeding on A

with $N = N_A + N_B$ fixed

Discrete KiSS model



[Berti et al., 2007; Berti et al., 2015]

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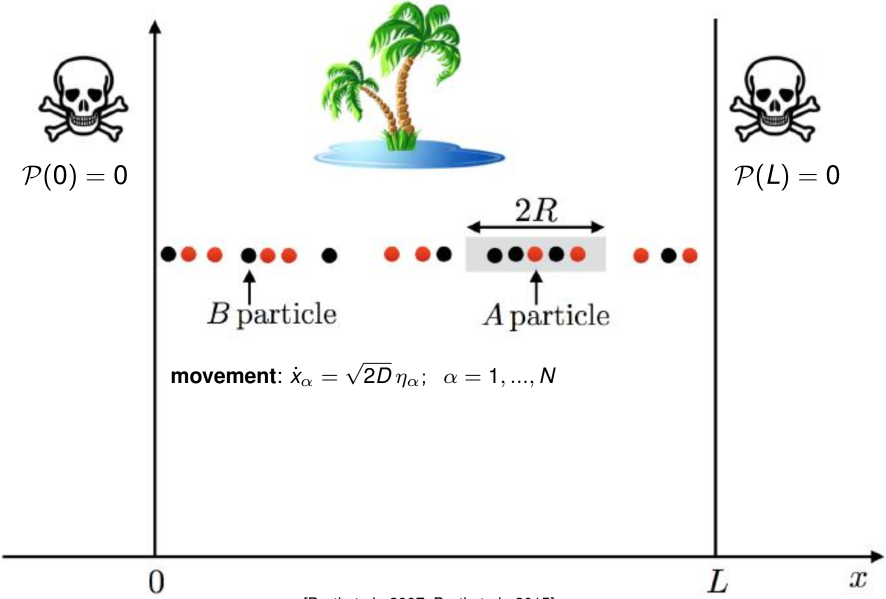

movement: $\dot{x}_\alpha = \sqrt{2D}\,\eta_\alpha; \quad \alpha = 1, ..., N$

[Berti et al., 2007; Berti et al., 2015]

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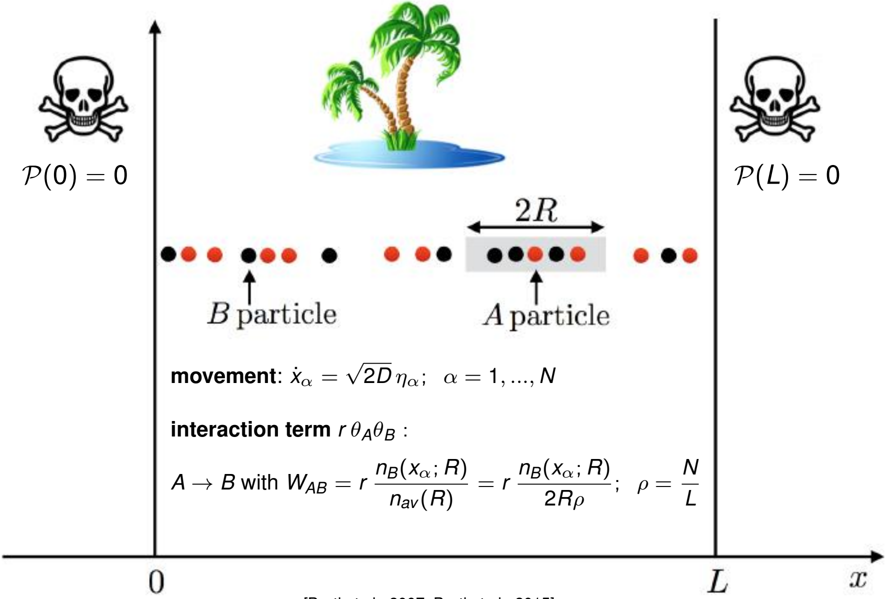

movement: $\dot{x}_\alpha = \sqrt{2D}\,\eta_\alpha; \quad \alpha = 1, ..., N$

interaction term $r\,\theta_A \theta_B$:

$$A \to B \text{ with } W_{AB} = r\,\frac{n_B(x_\alpha; R)}{n_{av}(R)} = r\,\frac{n_B(x_\alpha; R)}{2R\rho}; \quad \rho = \frac{N}{L}$$

[Berti et al., 2007; Berti et al., 2015]

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$\mathcal{P}(0) = 0$

boundary cond.:

reflection of A

absorption of B
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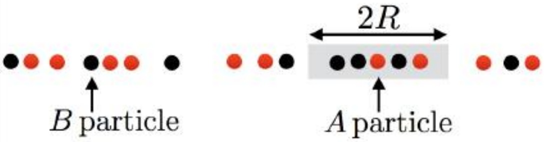

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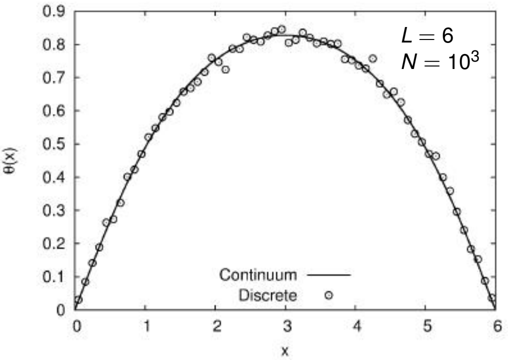
$0 \qquad L \qquad x$

[Berti et al., 2007; Berti et al., 2015]

Numerical simulations: continuous vs discrete model



i.c.: $N/2$ particles of each type
uniformly distributed

$R = 0.1$ $(1/\rho < R < L)$

$N \gtrsim 20$

$\Delta t = 10^{-4}$ $(\sqrt{2D\Delta t} \ll R)$

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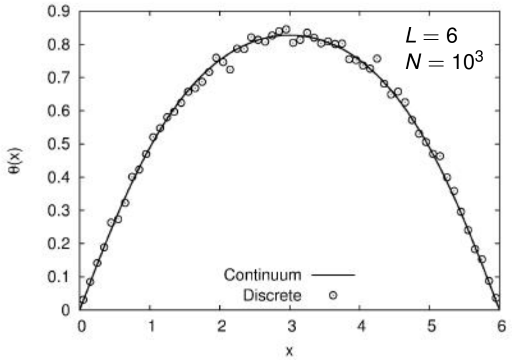

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averages over many realizations n_r

Main difference: $\begin{cases} \text{continuous} & \Rightarrow \quad \theta = 0 \\ \text{discrete} & \Rightarrow \quad N_B = 0 \end{cases}$

continuous ⇒ $\theta = 0$ unstable for $L > L_c$

discrete ⇒ $N_B = 0$ absorbing, always reached

demographic stochasticity

Biomass and the quasi-stationary state

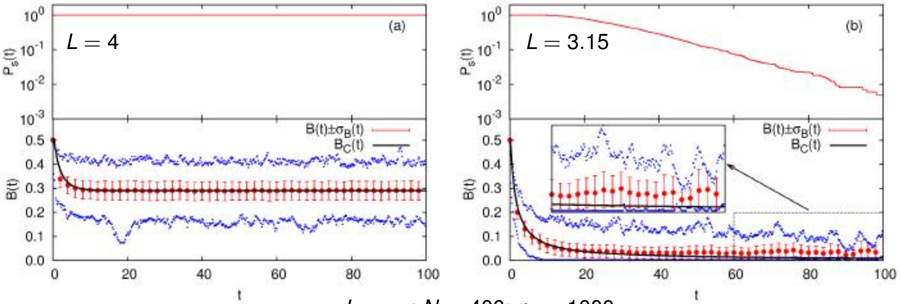
N, L large $\Rightarrow$ **quasi-stationary state**

Continuous biomass:

$$\mathcal{B}_C(t) = \frac{1}{L}\int_0^L \theta(x,t)dx; \quad \mathcal{B}_C^\infty = \lim_{t\to\infty} \mathcal{B}_C(t)$$

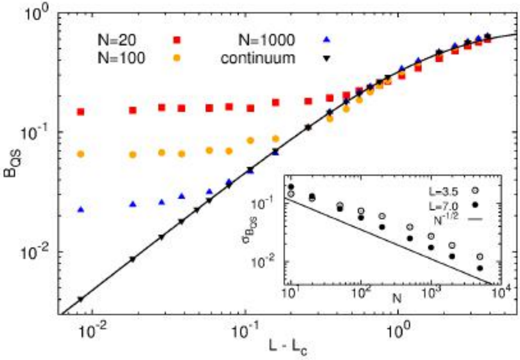
Discrete biomass (conditioning on survival):

$$\mathcal{B}(t) = \left\langle \frac{N_B(t)}{N} \right\rangle; \quad \sigma_{\mathcal{B}}(t) = \left\langle (N_B(t)/N - \mathcal{B})^2 \right\rangle^{1/2}$$



$L_c = \pi$; $N = 400$; $n_r = 1000$

Biomass versus patch size



$\leftarrow \lambda_1$ solid line

$\mathcal{B}_{QS}$ average biomass in the quasi-stationary state

$\mathcal{B}_C^\infty$ long time limiting biomass in the continuum

$L \to L_c$: $\mathcal{B}_{QS} \approx \text{const} > \mathcal{B}_C^\infty \Rightarrow$ **departure** from continuum limit (N-dependence)

$L > L_c$: $\mathcal{B}_{QS} \to \mathcal{B}_C^\infty$ for N large enough (and diverging as $L \to L_c$)

$\mathcal{B}_C^\infty(L) \approx \lambda_1 = 1 - \left(\frac{L_c}{L}\right)^2$ by mean-field argument

Extinction/survival transition

- Continuous KiSS model:

  $L > L_c \Rightarrow$ Population persistence

  $L < L_c \Rightarrow$ Population extinction

- Discrete KiSS model:

  Extinction can happen also for $L > L_c$

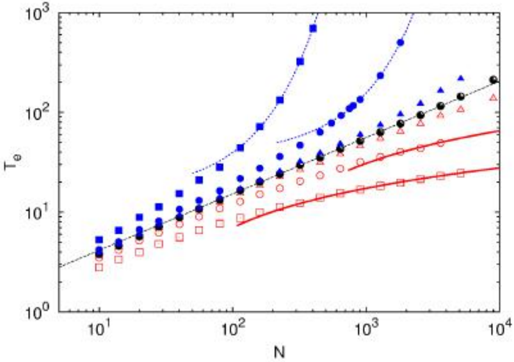
  How does the extinction/survival transition manifest?

  Average time to extinction: $T_e = \int_0^\infty P_s(t)dt$

  where $P_s(t)$ is the survival probability

[Lande, 1993; Redner, 2001; Nåsell, 2001; Doering et al., 2005; Ovaskainen and Meerson, 2010]

Average time to extinction



$L = L_c + \delta L$

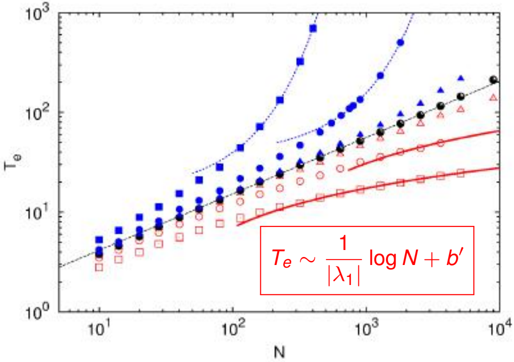
$\delta L = -0.3, -0.1, -0.02, 0, 0.02, 0.1, 0.3$

$n_r = (500 - 5000)$

Extinction region ($L < L_c$):

continuum $\mathcal{B}_C(t) \sim b\, e^{-|\lambda_1|t}$ with $b = \text{const}$, for large t

Average time to extinction



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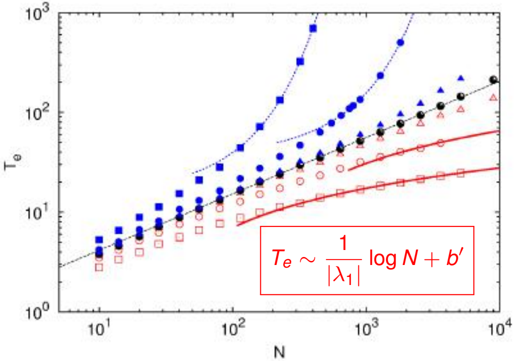

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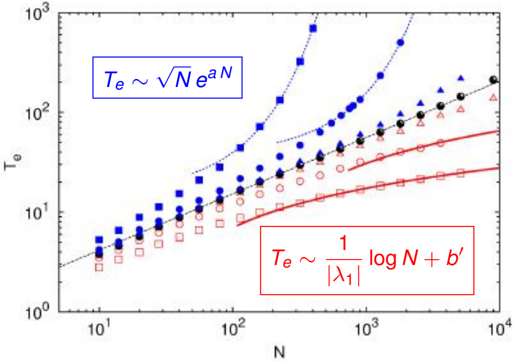
Survival region ($L > L_c$):

$P_{QS}(N_B) \propto 1/\sigma_N \exp\left[-(N_B - \langle N_B \rangle^2)/(2\sigma_N^2)\right]$; extinction: $N_B \approx 1 \to 0$, $T_e \sim 1/P_{QS}(N_B \to 0)$

Average time to extinction



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$\Rightarrow T_e \sim \exp\left(\langle N_B \rangle^2/(2\sigma_N^2)\right) \sim \sqrt{N}\, e^{aN}$ with $a = \text{const}$; using $\langle N_B \rangle = N\,\mathcal{B}_{QS}$, $\sigma_N = N\sigma_{\mathcal{B}_{QS}} \sim \sqrt{N}$

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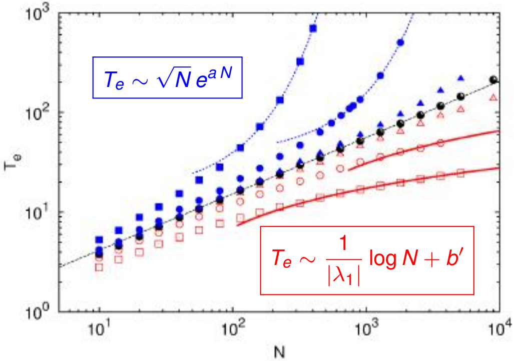

Transition ($L = L_c$):

$T_e \sim N^{\gamma}$, $\gamma = 0.565$

$L = L_c + \delta L$
$\delta L = -0.3, -0.1, -0.02, 0, 0.02, 0.1, 0.3$
$n_r = (500 - 5000)$

Extinction region ($L < L_c$):

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Conclusions

Individual-based reaction-diffusion system of ecological interest that recovers the KiSS model in the continuum limit.

1. Population extinction is always possible, even where the continuum model predicts persistence, due to demographic stochasticity. The time taken by the system to be absorbed can be very long (for large N and L) and a quasi-stationary state can be reached.
2. For $L > L_c$, $\mathcal{B}_{QS} \to \mathcal{B}_C^\infty$ only if N is large enough, otherwise the link between the continuum and discrete biomasses ceases to exist; when $L \to L_c$ the number of individuals required to attain the continuum limit diverges.
3. The extinction/survival transition translates into a transition from logarithmic to exponential behavior of the average time to extinction; at the transition: power-law behavior $T_e \sim N^\gamma$ with $0.5 < \gamma < 0.6$.

S. Berti, M. Cencini, D. Vergni, A. Vulpiani, Phys. Rev. E **92**, 012722 (2015)

Mean-field argument for continuum biomass

$$\frac{\partial \theta}{\partial t} = \frac{\partial^2 \theta}{\partial x^2} + \theta\,(1-\theta) \simeq \frac{\partial^2 \theta}{\partial x^2} + \theta\left(1-\bar{\theta}\right)$$

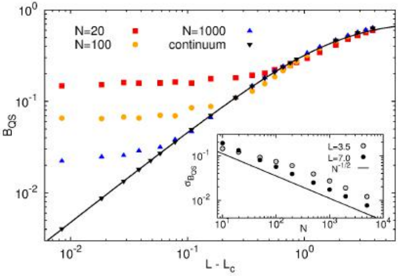
with $\bar{\theta}$ the steady-state spatially averaged value

First eigenvalue: $\lambda_1^* = \lambda_1 - \bar{\theta}$

Stationary solution $\lambda_1^* = 0 \Rightarrow \bar{\theta} = \lambda_1$; at stationarity $\bar{\theta} = \mathcal{B}_C^\infty$

$$\Rightarrow \boxed{\mathcal{B}_C^\infty(L) \approx \lambda_1 = 1 - \left(\frac{L_c}{L}\right)^2}$$

Gaussianity of the distribution of N_B particles

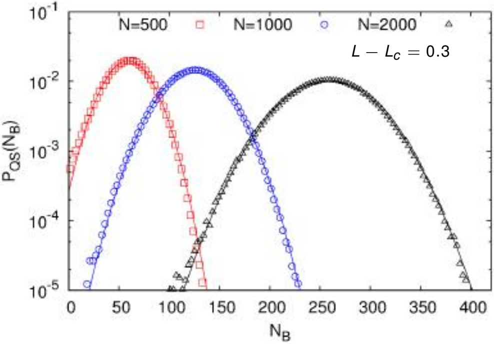


standard deviation of biomass in QS state:

for large L and N, $\sigma_{\mathcal{B}_{QS}} \sim N^{-1/2}$

$\sigma_N = N\sigma_{\mathcal{B}_{QS}} \sim N^{1/2}$ for B particles

suggests a Gaussian distribution of N_B

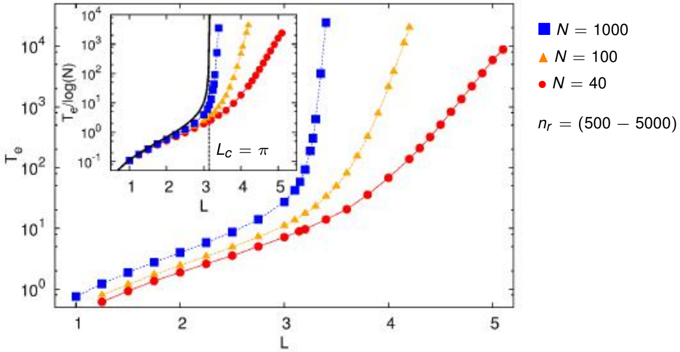


$$P_{QS}(N_B) \propto \frac{1}{\sigma_N} \exp\left[-\frac{(N_B - \langle N_B\rangle^2)}{2\sigma_N^2}\right]$$

$$\langle N_B\rangle = N\,\mathcal{B}_{QS}$$

$$\sigma_N = N\sigma_{\mathcal{B}_{QS}} \sim \sqrt{N}$$

Mean extinction time versus oasis size

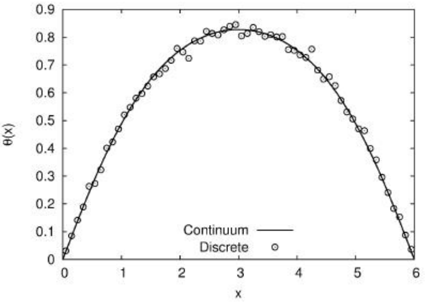


From the continuous model dynamics:

$$\text{when } L < L_c,\ T_e \text{ is mainly controlled by } \lambda_1 = 1 - \left(\frac{L_c}{L}\right)^2$$

$$T_e \sim \frac{1}{|\lambda_1|} \log N + b' \quad \Rightarrow \quad \boxed{T_e \sim \frac{L^2}{L_c^2 - L^2} \log N}$$

Effects of changing the microscopic model's rules



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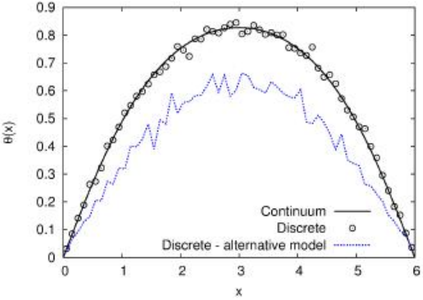

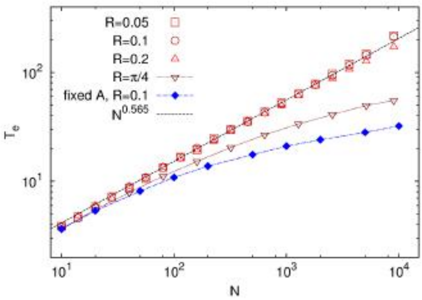

- the model is robust with respect to small changes of R

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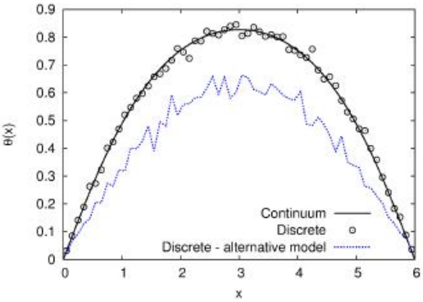

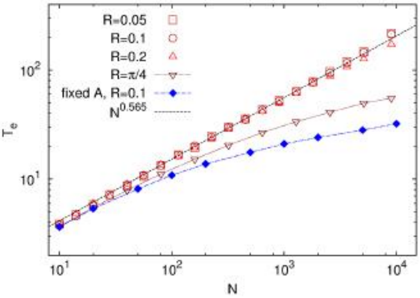

- the model is robust with respect to small changes of R
- model with fixed A particles: deep alteration in the critical behavior ($L = L_c$)

  different continuum limit