Evolutionary Game Dynamics of Lattice-based Populations: An Introduction to the Standard Stochastic Models

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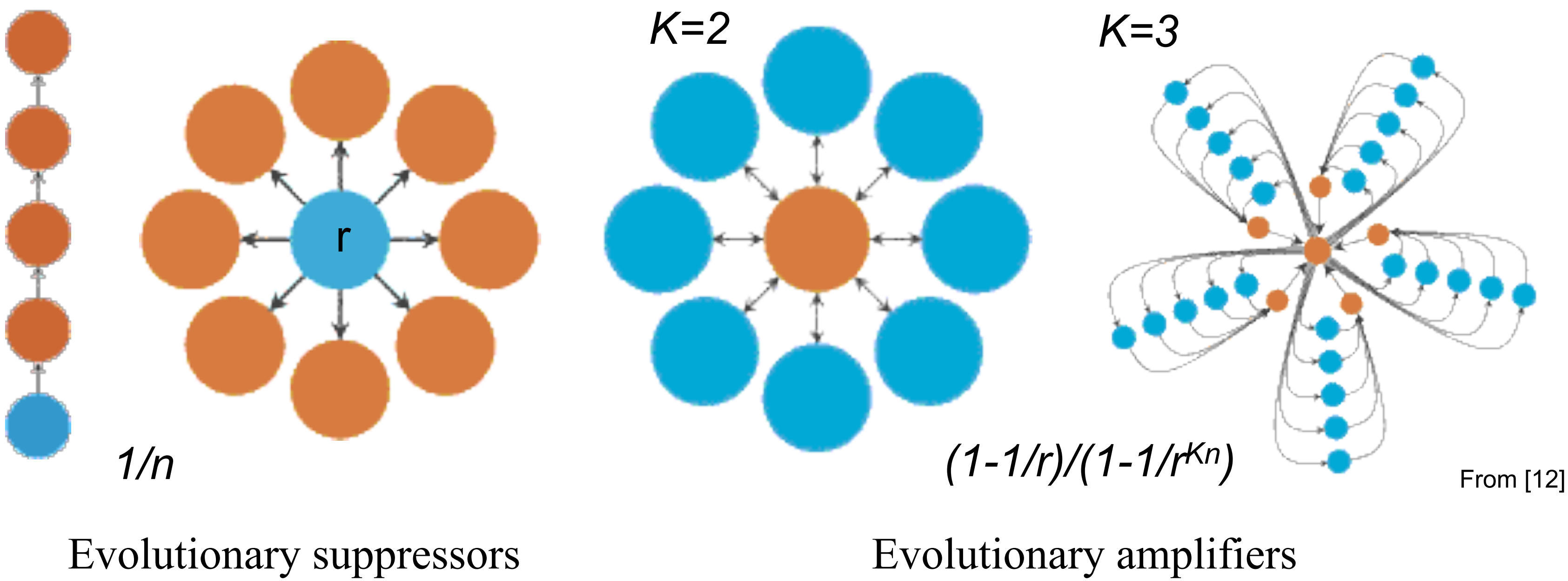
Evolutionary game dynamics

- Population composed of different types of individuals
- Individuals adopting successful strategies tend to survive
- Natural selection process
  - Differential equations
  - Difference equations
  - Reaction-diffusion equations
  - Differential inclusion
- Individuals meet randomly
- How does the population evolves over time?

Why consider spatial structure?

- The spatial location of the individuals may alter the population dynamics
- Spatially explicit models (e.g., lattice-based)
  - Size of the environment
  - Environment divided into various sites
  - Number of individuals per site
  - Individuals lay their offspring in their vicinity

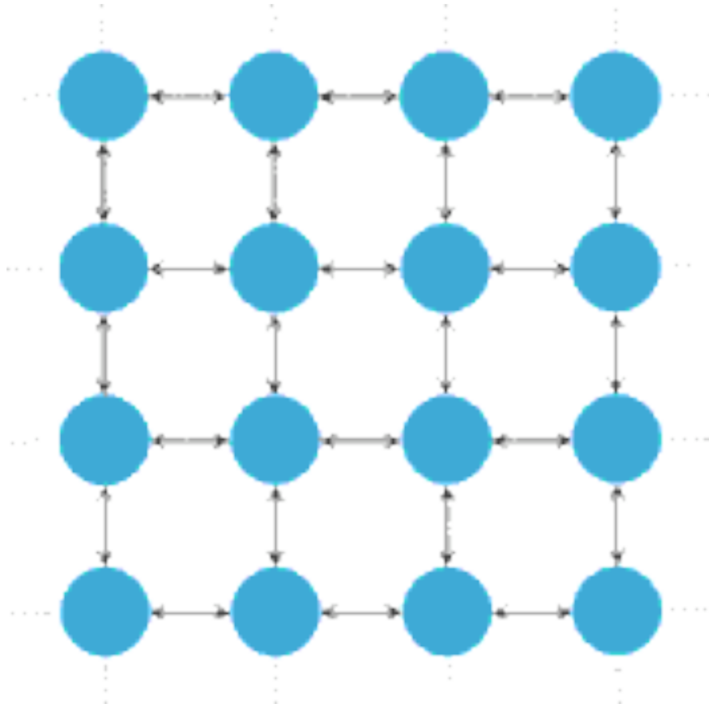
Example: dynamics of natural selection



- Mutants in a non-structured population have fixation probability $(1-1/r)/(1-1/r^n)$
- How do spatial characteristics affect the evolution process?

Why lattice-based?

- Ecological habitats - regular spatial lattices?
- Avoid the complications of simulating models
- Their symmetry allows us to exploit certain relations to non-spatial models
- They neither favor nor suppress natural selection
- Applications: genetics, tumor growth, spread of infections, economics, etc..



From [12]

Overview

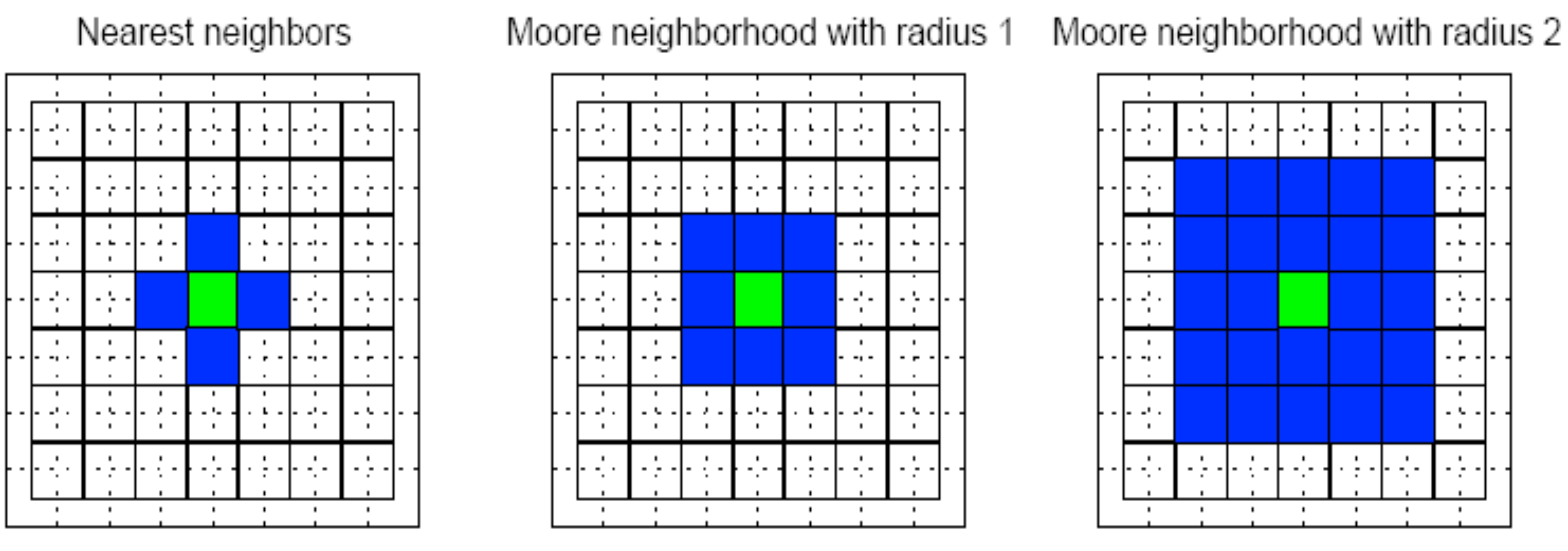
- Environmental and individual constraints
- Stochastic growth models
  - Richardson's model
  - The basic contact process
  - The quadratic contact process
- Stochastic competition models
  - The basic voter model
  - The stepping stone model

Environmental and Individual Constraints

Structured populations

- d-dimensional integer lattice Z^d
- Points in the spatial grid are called sites
  $x_i \in Z^d$
- State of the system - $\xi_t(x_1), \ldots, \xi_t(x_n)$
- Finite set of states - S
- Neighborhood of x_i - N_i

Typical neighborhoods



- Periodic vs. non-periodic boundary conditions
- Open v. close boundary conditions
- Transition between states ξ_t *and* ξ_{t+1} may be determined by the joint behavior of the individuals at site x_i and those at $x_j \in N_i$

Growth Models

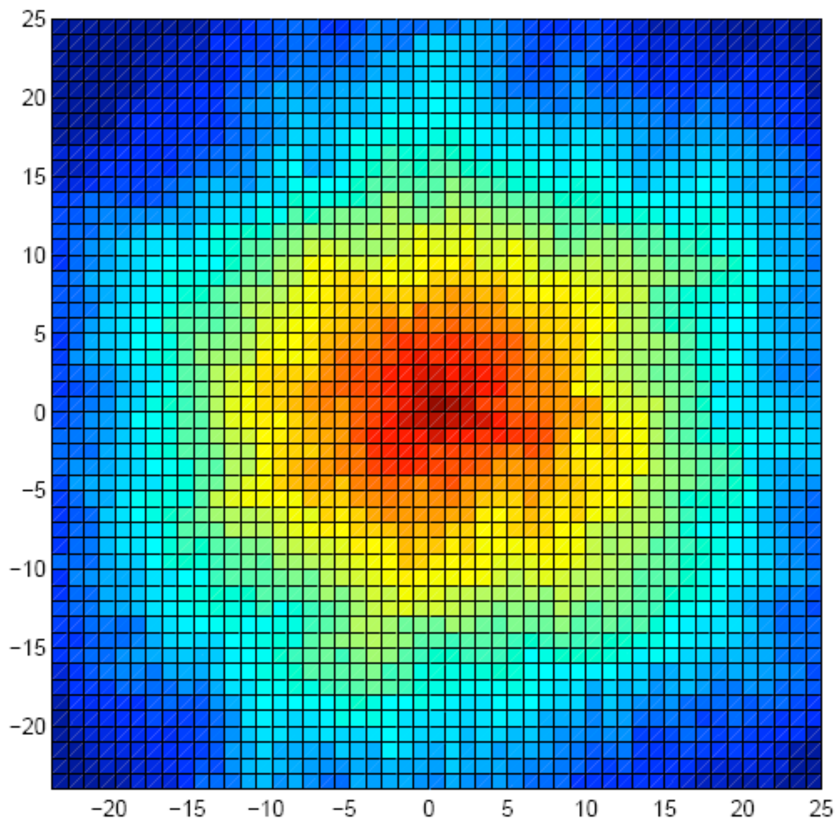
Richardson's Model

- Simplest possible growth model
- An offspring is born near its parents (von Neumann neighborhood)
- If x_i is occupied then $\xi_t(x_i)=1$
- If x_i is vacant $\xi_t(x_i)=0$
- Once a site is occupied remains occupied forever
- A vacant site becomes occupied at a rate equal to the fraction of the four nearest neighbors that are occupied

- Squares with similar color shades represent sites that where occupied at similar time instants.

- Let *B(t)* be the set of sites that are occupied at time *t*

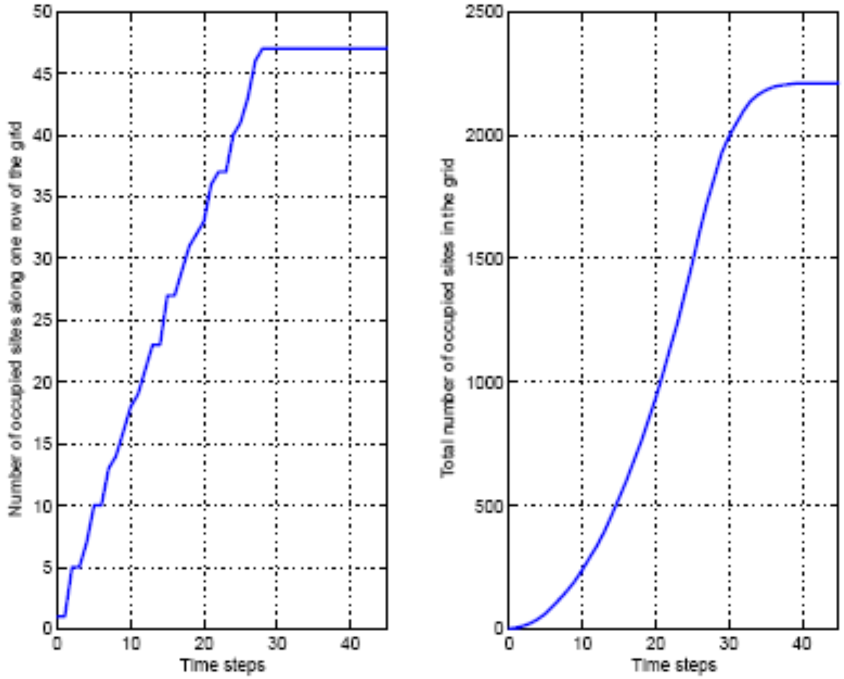
- What is the rate at which the set *B(t)* grows?



Theorem 1: For Richardson's growth model $B(t)/t$ has a limiting shape, which is roughly but not exactly circular.

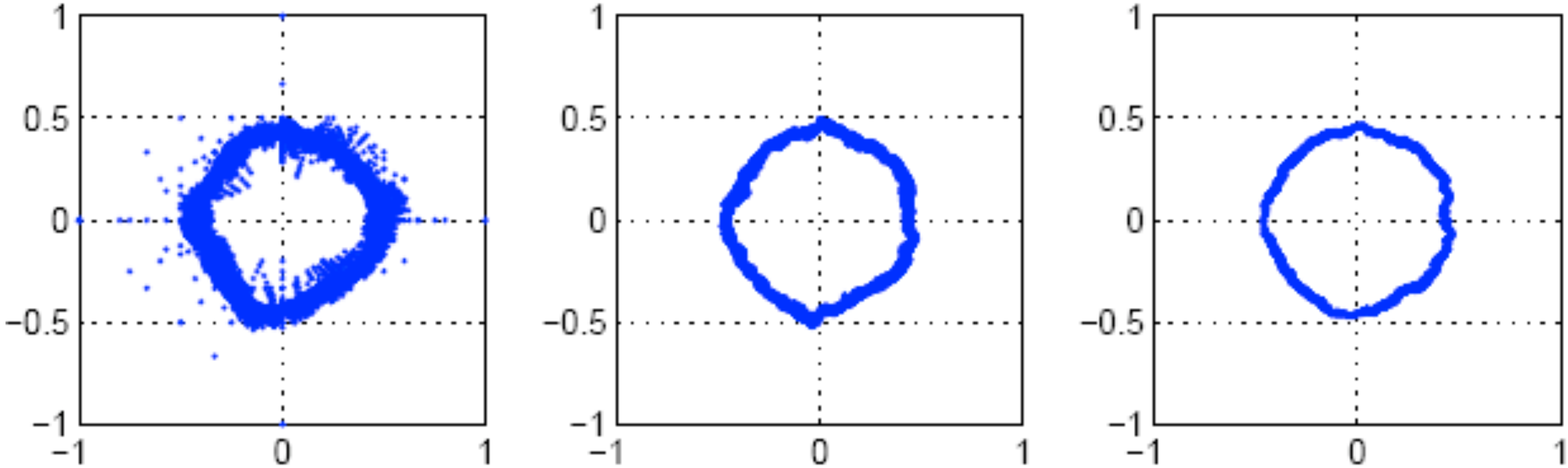
Sketch of the proof: The first step in Richardson's asymptotic shape result is to show that if $t(n,0)$ is the first time the point $(n,0)$ is occupied then $t(n,0)/n$ converges to a constant c (For details see [22]).

- Law of large numbers for $t(n,0)$
- Is there a central limit theorem?
- Standard deviation of $t(n,0)$ is of order $n^{1/3}$ (via simulations)
- Fluctuations are no worse than $n^{1/2}$ [24]



- The number of occupied sites across a single row is roughly a linear function of time
- “Knee” due to finite dimensional lattices

Shape of *B(t)/t*



$0 < t < 70$ $\quad$ $70 < t < 140$ $\quad$ $140 < t < 200$

Remarks

- Application: Model the spread of cancerous cells [24]
- Very simple definition of Richardson's model constrains its applications to real world situations
- It allows us to study the spatial expansion of a population only under very idealistic conditions

- Take into account that individuals may die at a certain rate
- Rate of death *per individual* independent of the number of occupied neighboring sites
- What conditions are required for a population to survive?
- How does the spatial structure of a population affect these conditions?

The Basic Contact Process

- Define $\xi_t(x_i)$ as for Richardson's model
- Individuals occupying sites give birth at a rate β, with a birth from site $x_i \in Z^2$ going to site $x_j \in Z^2$ with probability $p(x_i - x_j)$
- If x_i is occupied, then it becomes vacant at a constant rate δ.

- Spatially homogeneous neighborhood around each site
- An offspring born at x_i is sent to $x_j \in N_i$ with probability $p(x_i\text{-}x_j)=\rho(|x_i\text{-}x_j|)$
- The neighborhood of site $\mathrm{x_i}$ is defined by

$$N_i=\{x_j\!: \| x_i\text{-}x_j \|_\infty \leqq R\}$$

- If an offspring is sent to x_j and x_j is vacant it becomes occupied; if it is occupied, then nothing happens
- Let $\beta = 1$ (birth at a rate of at most 1)

Non-structured population case

- All sites are equally likely to receive an offspring from any other site
- The number of occupied sites is a Markov chain $N(t) \in \{0,1,\ldots,n\}$ defined by

$$N(t) \rightarrow N(t)-1 \text{ at a rate of } \delta N(t)$$

$$N(t) \rightarrow N(t)+1 \text{ at a rate of } \beta N(t)\,(1-N(t)/n)$$

- Let $u_n(t)=N(t)/n$ represent the fraction of occupied sites and let $n \rightarrow \infty$

- Reduce the system to an ODE

Mean field equation for the contact process

- The density of occupied sites $u=u_n$ as

  $n\to\infty$ is given by

$$du/dt = -\delta u + \beta u(1-u)$$
$$= \beta u [(\beta-\delta)/\beta - u]$$

- If $\beta = 1$ it is clear that if population structure is ignored then $\delta_c = 1$
- If $\delta_c > 1$ then $du/dt < 0$ for $u \neq 0$
- If $\delta<\delta_c$ the equilibrium density of occupied sites is

  $1-\delta$ (this can be shown by letting $\beta=1$ and solving for $du/dt=0$)

- Non-structured population case:
  - If $\delta > 1$ the contact process will not survive in the sense that it will reach an all-0s state with probability 1

- What happens when the spatial structure of the population is considered?

Terminology

- The *configuration* at time t is described by giving the state of each site x_i, $\xi_t(x)$ for all $i=1, \ldots n$
- To describe the *distribution* of the process at time t, we have to give for each choice of a finite number of sites $x_1, \ldots, x_n$ and of possible states $i_1, \ldots, i_n$, the probability

$$P(\xi_t(x_1) = i_1, \ldots, \xi_t(x_n) = i_n)$$

- The distribution of the process at $t = 0$ is called the *initial distribution*
- An initial distribution for the process which does not change in time is called a *stationary distribution*: For all times t, sites $x_1, \ldots , x_n$, and possible states $i_1, \ldots, i_n$ we have

$$P(\xi_t(x_1) = i_1, \ldots \xi_t(x_n) = i_n) = P(\xi_0(x_1) = i_1, \ldots \xi_0(x_n) = i_n)$$

- *Property 1 (attractiveness):* The contact process is attractive, meaning that increasing the number of individuals adopting strategy 1 increases the total birth rate and decreases the total death rate of the system

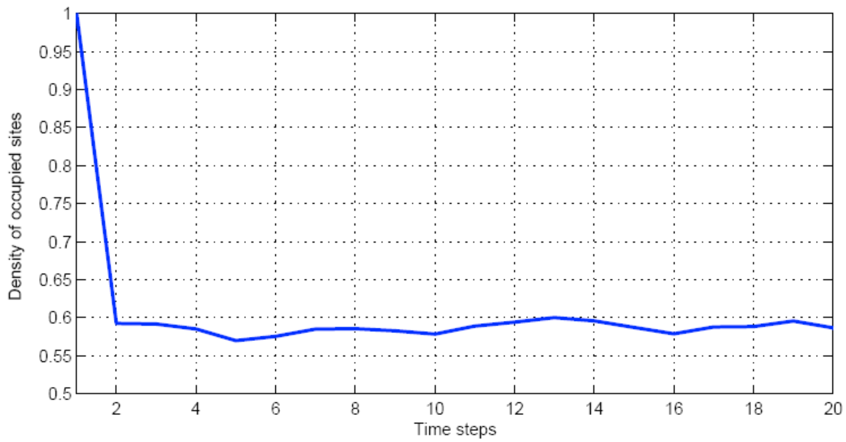
- *Lemma 1:* Let ξ^1_t denote the process starting with all *1*s. If the process ξ_t is attractive, then as $t \to \infty$, ξ^1_t converges in distribution to ξ^1_∞ ($\xi^1_t \Rightarrow \xi^1_\infty$), where ξ^1_∞ represents a stationary distribution

$$P(\xi^1{}_t(x_1)=i_1, \ldots, \xi^1{}_t(x_n)=i_n) = P(\xi^1{}_\infty(x_1)=i_1, \ldots, \xi^1{}_\infty(x_n)=i_n)$$

- However, $\xi^1{}_\infty$ could of course represent the all-0s state (for instance if $\delta > 1$)
- Does there exist a critical value δ_c, so that if $\delta < \delta_c$ the population survives?

Theorem 2: For the basic contact process there is a critical value δ_c, which depends on the dispersal function $\rho(z)$ so that for $\delta<\delta_c$ the process has a non-trivial stationary distribution (for details see [29]).

Density of occupied sites



- Let $\delta = .4$
- Initial configuration $\xi_0(x_1) = \ldots = \xi_0(x_n) = 1$
- Curve seems to level out around 0.6
- Fluctuations around this value due to the fact that we plot the density of a finite lattice
- As $t \rightarrow \infty$ does the process follow a *unique* non-trivial stationary distribution? What is it?

Theorem 3: For the contact process with $\delta<\delta_c$ the following holds:

- If the process survives starting from an finite initial state, then it grows linearly and has an asymptotic shape.
- There exists only one non-trivial stationary distribution which describes the process as

  $t \to \infty$.

  (for details see [30] and [31])

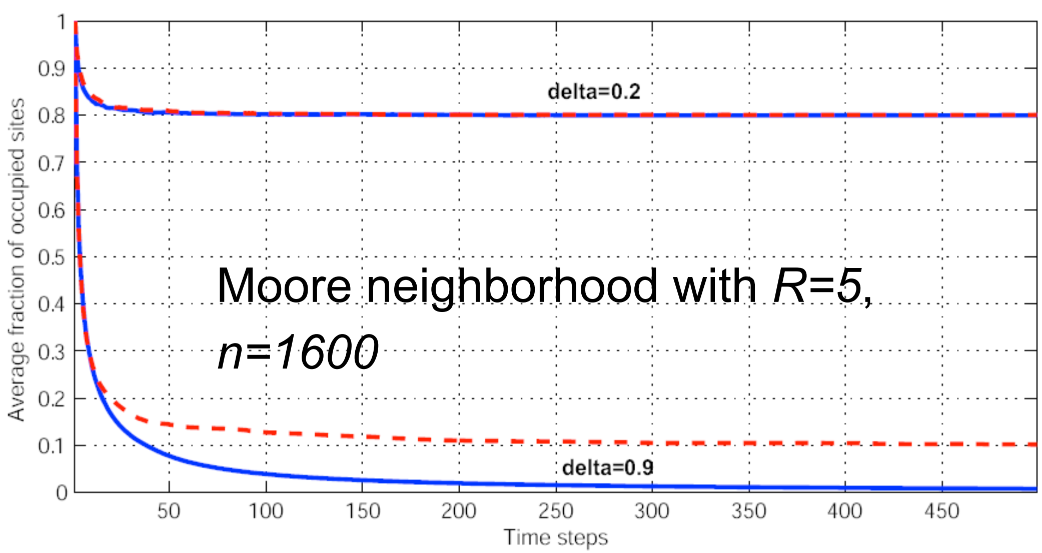
Theorem 4: Let the neighborhood of any site x_i be defined by the set $N_i=\{x_j: \| x_i - x_j \|_\infty \cdot R\}$. As $R \rightarrow \infty$, $\delta_c(r) \rightarrow 1$ and

$$P(\xi_\infty^{1}(x_1)=1, \ldots, \xi_\infty^{1}(x_n)=1) \rightarrow 1 - \delta$$

(for details see [33])

In other words, as r tends to 1, the critical value and equilibrium densities converge to those predicted by the mean field equation

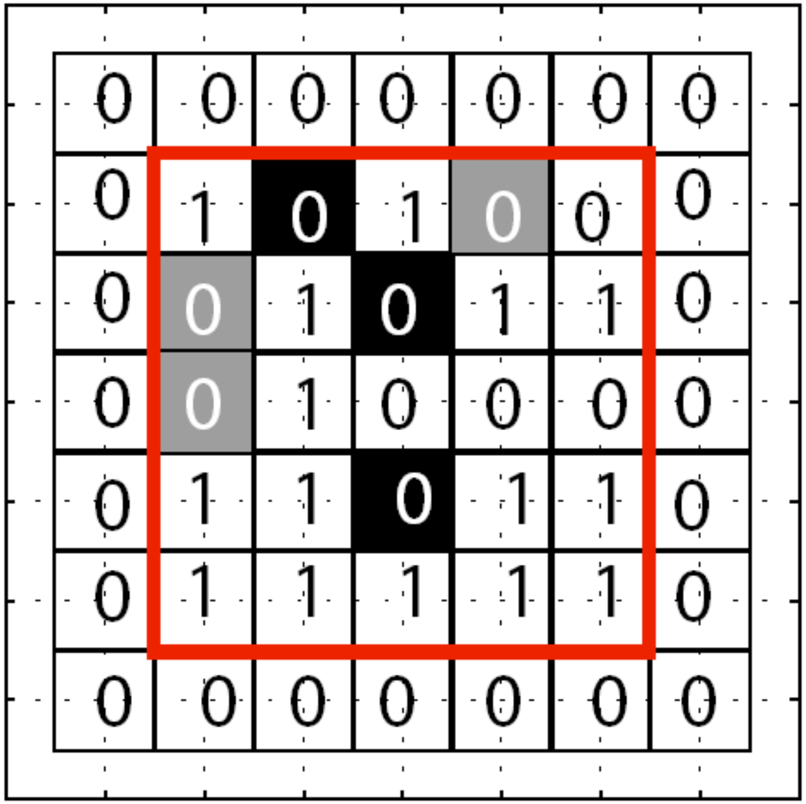
Average fraction of occupied sites for different death rates



- For von Neumann neighborhood $\delta_c \approx 0.607$ (see [34],[35])
- Rate of convergence of *Theorem 4* (see [38])
- Large neighborhoods and fast stirring

The Quadratic Contact Process

- Schloegl's second model
- The sexual reproduction process
- Birth rate is *1*
- An occupied site becomes vacant at rate δ
- A vacant site becomes occupied at a rate *k/4* , where *k* is the number of diagonally adjacent pairs of occupied neighbors



The critical value for survival of the individuals starting from a finite set is $\delta_f = 0$

If the initial configuration has all *1's* then there exists a critical value for the existence of a stationary distribution

Theorem 5: There is a $\delta_0 > 0$ so that if $\delta \leq \delta_0$, then the limit starting from all *1*s is a nontrivial stationary distribution (for details see [41])

- Value of δ_0 in the proof very small
- Via Monte Carlo Simulations $\delta_0 \approx 0.1$

Stirring

A stirring event occurring at time t and involving two neighboring sites x_i and x_j will change the state of the system from $\xi_t(x_1), \ldots, \xi_t(x_n)$ *to* $\xi_{t+1}(x_1), \ldots, \xi_{t+1}(x_n)$, where

$$\xi_{t+1}(x_i) = \xi_t(x_j),$$

$$\xi_{t+1}(x_j) = \xi_t(x_i), \text{ and}$$

$$\xi_{t+1}(x_k) \text{ for } k \neq i,j$$

Scale space by multiplying by $\varepsilon = \nu^{-1/2}$

Scaled model with states ξ^{ε}: $\varepsilon Z^d \in \{0,1\}$

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Theorem 6: For the quadratic contact process, as $\varepsilon \to 0$ the critical value for survival from a an initial state of all *1*s, $\delta_0(\varepsilon) \to 2/9$. If $\delta < 2/9$ then the equilibrium density

$$P(\xi_\infty^1(x_1) = 1, \ldots, \xi_\infty^1(x_n) = 1) \to [1 + (1-4\delta)^{1/2}]/2$$

Simplifies the model of a spatially structured population!!

Competition Models

The Basic Voter Model

- Generalized model of the contact process
  – Multi-type contact process
- One individual per site
- $S \neq \{0,1\}$, the state of the site x_i, $\xi_t(x_i)$ may be 0, or $w \in Z$ with $w>0$
- Example: Rectangular grid of houses, a voter changes its opinion at on average every $1/\delta$

- Type w individuals die at a rate δ_w
- Type w individuals give birth at a rate β_w, with a birth from site x_i going to site x_j with probability $p_w(x_i-x_j)=\rho_w(|x_i-x_j|)$
- If an offspring is sent from x_i to x_j and the number of the invading type at x_i is larger than that of the resident type at x_j, the invader takes over the site
- Otherwise nothing happens

Example: are there bushes in the forest [46]?

- Let $S=\{0,1,2\}$
  - If $\xi_t(x_i)=0 \rightarrow$ Grass (or vacant sites)
  - If $\xi_t(x_i)=1 \rightarrow$ Bushes
  - If $\xi_t(x_i)=2 \rightarrow$ Trees
- Trees don't feel the presence of bushes or grass
  - trees will survive if $\delta_2<\delta_c$ (range of the neighborhood
- Bushes are strictly dominated by trees
- What happens to the bushes?
- Do they have enough space in lattice to survive?
- Does spatial structured tend to favor the coexistence of strategies which could not coexist in homogeneous populations?

Terminology

- We will say that the system approaches *complete consensus* if for any set of strategy types *S* and any initial configuration $\xi_0(x_1), \ldots, \xi_0(x_n)$, *as* $t \to \infty$

$$P(\xi_t(x_i) = \xi_t(x_j)) \to 1$$

for all $i,j=1,\ldots,n$

Theorem 6: For a population undergoing the voter model:

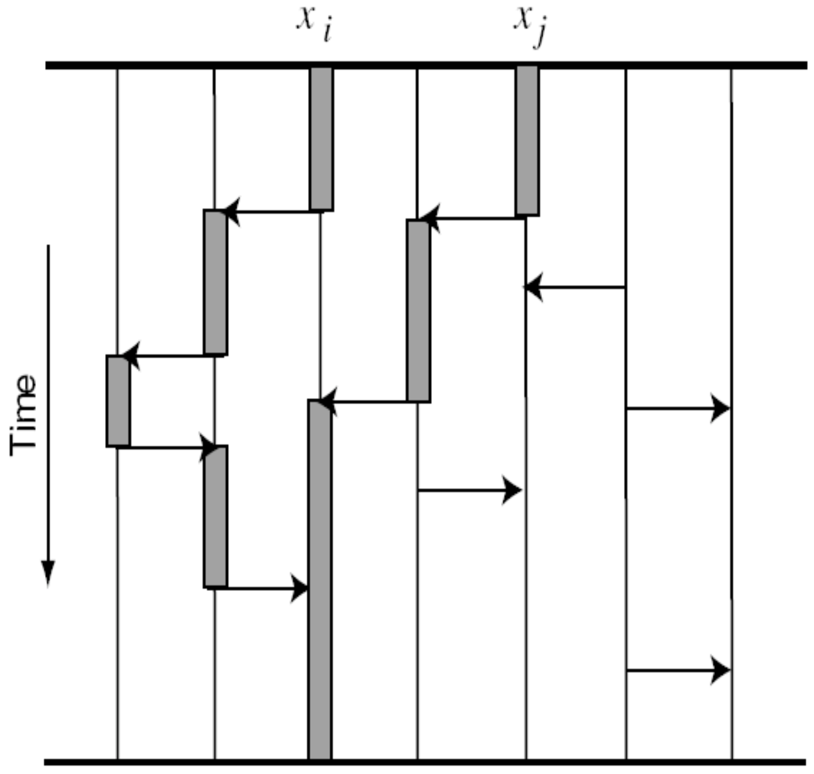
– The system approaches complete consensus (i.e., one type of species survives) for *d· 2*

– Differences in opinion can persist (i.e., different types of species may coexist, however, for $d>2$ (for details see [44])

Proof:

- Construct a "dual process" for the voter model that works backwards in time
- Goal: determine the "source" of the opinion of the individual at site x_i at time t
- Introduce independent Poisson processes for each site x_i, $i=1,\ldots,n$
- Site x_i changes its strategy type at times instants $t^{x_i}_k$, $k \geq 1$, following a Poisson process
- At $t^{x_i}_k$, $k \geq 1$, an individual at site x_i has picked one of its neighboring sites $x^k_j \in N_i$
- At time $t = t^{x_i}_k$ we let $\xi_t(x_i) = \xi_t(x^k_j)$

- Draw arrow from $(x_i, t^{x_i}{}_k)$ to $(x_j{}^k, t^{x_i}{}_k)$
- Dual process for site x_i: $\zeta^{x_i,t}{}_s$
- Let $\zeta^{x_i,t}{}_0 = x_i$
- Stays at x_i until the first time s it finds the tail of an arrow starting from x_i
- If this occurs at at time $t\text{-}s = t_k{}^{x_i}$, then $\zeta^{x_i,t}{}_s = x_j{}^k$
- Work down until we encounter another tail of an arrow



- Opinion of the individual located at x_i at time t is the same as that of $\zeta^{x_i,t}{}_s$ at $t\text{-}s$
- Since $\zeta^{x_i,t}{}_s$ is a continuous time random walk, it stays at a site for an exponential amount of time with mean $1/\delta$, then jumps to another randomly chosen neighbor
- Note that $\zeta^{x_i,t}{}_s$ - $\zeta^{x_j,t}{}_s$ is again a continuous time random walk (but jumps at a rate 2δ)

- For $d=1$ and $d=2$ the difference random walk will hit 0 with probability 1 at some time
- The two ancestral lines will always agree at later times
- However, two random walks $\zeta^{x_i,t}_s$ and $\zeta^{x_j,t}_s$ have positive probability of never hitting each other in dimensions $d > 2$
- What if the number of sites tends to infinity (for $d>2$)?

Mean field equations for the Voter model

- The density of species is given by

$$du_1/dt=u_1\,(\,\beta_1(1-u_1-u_2) - \delta_1 - \beta_2 u_2)$$
$$du_2/dt=u_2\,(\,\beta_2(1-u_2) - \delta_2)$$

- The du_2/dt equation derived similarly as the contact process
- The du_1/dt equation:

$\beta_1(1-u_1-u_2)$: births of individuals with strategy type *1* onto vacant sites

δ_1: death rates

$\beta_2 u_2$: births of individuals with strategy type *2* onto sites occupied by individuals with strategy type *1*

- The equilibrium density of individuals with strategy type *2* will be

$$u'_2=(\beta_2-\delta_2)/\beta_2$$

- And $u'_1>0$ if

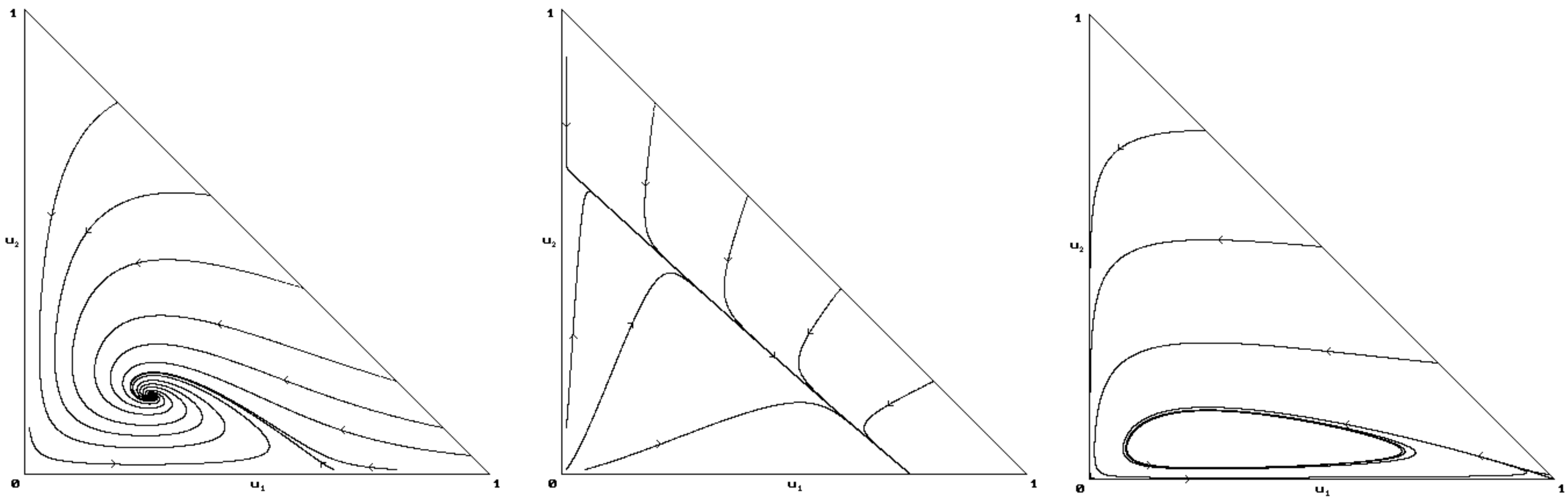
$$\beta_1\delta_2/\beta_2-\delta_1-\beta_2+\delta_2>0 \qquad (*)$$

Theorem 8: When (*) holds, then there exists a stationary distribution that concentrates on configurations with infinitively many sites in each of the possible states (i.e., coexistence of different species occurs). If we have "< " in (1) then whenever the are infinitively many *2*s in the initial distribution,

$$P(\xi_t(x_1)=1,\ \ldots,\ \xi_t(x_n)=1\ ) \to 0$$

as $t \to \infty$. In other words, individuals with strategy type *1* die out.

The bigger picture



Single attracting fixed point

Two locally attracting points

Periodic orbits

From [39]

- The behavior of stochastic spatial models can be determined from the properties of the mean field ODE
- Attempts at defining the moderate length scale precisely (see [48] and [49])

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The Stepping Stone Model

- At each site x_i there is a colony of N individuals labeled $1,\ldots,N$
- Being able to consider colony size $N > 1$ enriches the behavior of the model

Conclusions

- Growth models lay the foundation for competition models
- Spatial structure does not help survival of individual species…but allows co-existence of different ones
- Most theoretical results from the field of Interacting Particle Systems (IPS)

References

[1] J. Hofbauer and K. Sigmund, "Evolutionary game dynamics," *Bulletin of the American Mathematical Society*, vol. 40, pp. 479–519, 2003.

[2] J. Cortés, S. Martinez, and F. Bullo, "Spatially-distributed coverage optimization and control with limited-range interactions," *Control, Optimisation & Calculus of Variations*, vol. 11, pp. 691–719, 2005.

[3] S. Martínez, F. Bullo, J. Corts, and E. Frazzoli, "On synchronous robotic networks -part i: Models, tasks and complexity notions," To appear in the IEEE Transactions on Automatic Control in 2006.

[4] J. Hofbauer and K. Sigmund, "Evolutonary game dynamics," *American Mathematical Society*, vol. 40, pp. 479–519, 2003.

[5] R. Durrett and S. Levin, "The importance of being discrete (and spatial)," *Theoretical Population Biology*, vol. 46, pp. 363–394, 1994.

[6] I. Hansky, "Metapopulation dynamics," *Nature*, vol. 396, pp. 41–49, 1998.

[7] D. Aronson and H. Weinberger, "Multi-dimensional nonlinear diffusion arising in population genetics," *Adv. Math*, vol. 30, pp. 33–76, 1978.

[8] M. Bramson and D. Griffeath, "On the willimas-bjerknes tumor growth model, ii," *Proc. Camb. Phil Soc.*, vol. 88, pp. 339–357, 1980.

[9] M. Bramson and D. Griffeath, "On the willimas-bjerknes tumor growth model, i.," *Ann. Prob.*, vol. 9, pp. 173–185, 1981.

[10] B. Drossel and F. Schwabl, "Self-organized critical forest fire model," *Phys. Rev. Lett.*, vol. 69, pp. 1629–1632, 1992.

[11] I. Eshel, L. Samuelson, and A. Shaked, "Altruists, egoists, and hooligans in a local interaction model," *The American Review*, vol. 88, no. 1, 1998.

[12] E. Libierman, C. Hauert, and M. Nowak, "Evolutionary dynamisc on graphs," *Nature*, vol. 433, 2005.

[13] S. Wolfram, *A New Kind of Science.* Champaign, IL: Wolfram Media, 2002.

[14] C. Hauert, "Fundamental clustes in spatial 2x2 games," *Proc. R. Soc. Lond.*, vol. 26B, 2000.

[15] M. Nowak and R. May, "The spatial dilemmas of evolution," *International Journal of Bifurcation*, vol. 3, 1993.

[16] M. Nowak, S. Bonhoeffer, and R. May, "More spatial games," *International Journal of Bifurcation*, vol. 4, 1994.

[17] T. Liggett, *Stochastic Interacting Systems: Contact Voter and Exclusion Processes.* Heidelberg: Springer, 1999.

[18] C. Hauert, "Effects of 2x2 games," *International Journal of Bifurcation and Chaos*, vol. 12, no. 7, 2002.

[19] M. Porch, A. Pichler, and K. Sigmund, "The efficiency of adapting aspiration levels," *Proc. R. Soc. Lond.*, vol. B 266, 1999.

[20] D. Richardson, "Random growth in a tesselation," *Proc. Camb. Phil. Soc.*, vol. 74, pp. 515–528, 1973.

[21] M. Eden, "A two dimensional growth process," in *Proc. 4th Berkeley Symp.*, vol. IV, pp. 222–239, 1961.

[22] J. Cox and R. Durrett, "Some limit theorems for first passage percolation with necessary and sufficient conditions," *Ann. Prob.*, vol. 9, pp. 583–603, 1981.

[23] C. Newman, "A surface view of first passage percolation," (Zurich, Germany), 1994.

[24] T. Williams and R. Bjerknes, "Stochastic model for abnormal clone spread through epithelial basal layer," *Nature*, vol. 236, pp. 19–21, 1972.

[25] T. Harris, "Contact interactions in a lattice," *Ann. Probab.*, vol. 2, pp. 969–988, 1974.

[26] T. Harris, "On a class of set-valued Marlov processes," *Ann. Probab.*, vol. 4, pp. 175–194, 1976.

[27] D. Griffeath, "Limit theorems for non-ergodic set-valued markov processes," *Ann. Probab.*, vol. 8, pp. 379–387, 1978.

[28] T. Liggett, *Interacting Particle Systems.* New York, NY: Springer-Verlag, 1985.

[29] T. Harris, "A correlation inequality for markov processes in spatially ordered state spaces," *Ann. Probab.*, vol. 6, pp. 355–378, 1977.

[30] R. Durrett, "On the growth of one-dimensional contact processes," *Ann. Probab.*, vol. 8, pp. 890–907, 1980.

[31] R. Durrett and R. Schonmann, "Stochastic growth models," in *Percolation Theory and the Ergodic Theory of Infinite Particle Systems* (H. Kesten, ed.), pp. 85–119, Springer-Verlag, 2002.

[32] C. Bezuidenhout and G. Grimmett, "The critical contact process dies out," *Ann. Probab.*, vol. 18, pp. 1462–1482, 1990.

[33] R. Durrett, "A new method for proving the existance of phase transitions," in *Spatial Stochastic Processes* (K. Alexander and J. Watkins, eds.), pp. 141–170, Birkhäser, 1992.

[34] R. Brower, M. Furman, and M. Moshe, "Critical exponents for the Reggeon quantum spin model," *Phys. Lett. B.*, vol. 76, pp. 213–219, 1978.

[35] P. Grassberger and A. de la Torre, "Reggeon field theory (Schögl's first model) on a lattice: Monte Carlo calculations of critical behavior," *Ann. Phys.*, vol. 122, pp. 373–396, 1979.

[36] T. Liggett, "Improved upper bounds for the contact process critical value," *Ann. Probab.*, vol. 23, pp. 697–723, 1995.

[37] T. Liggett, "Survival of discrete time growth models with applications to oriented percolation," *Ann. Appl. Probab.*, vol. 5, pp. 613–636, 1995.

[38] M. Bramson, R. Durrett, and G. Swindle, "Stochastic mechanics of crabgrass," *Ann. Probab.*, vol. 17, pp. 444–481, 1989.

[39] R. Durrett, "Stochastic spatial models," *SIAM Review*, vol. 41, pp. 677–718, 1999.

[40] F. (Schögl's, "Chemical reaction models for non-equilibrium phase transitions," *Z. Physik*, vol. 253, pp. 147–161, 1972.

[41] M. Bramson and L. Gray, "A useful renormalization argument," in *Random Walks, Brownian Motion, and Intracting Brownian Motion* (R. Durett and H. Kesten, eds.), Birkhauser, Boston, 1991.

[42] D. Griffeath, "Additive and cancellative interacting particle systems," in *Lecture Notes in Math. 724*, New York, NY: Springer-Verlag, 1979.

[43] "Particle systems and reaction diffusion equations," *Ann. Probab.*, vol. 22, pp. 289–333, 1994.

[44] R. Holley and T. Liggett, "Ergodic theorems for weakly interacting systems and the voter model," *Ann. Probab.*, vol. 3, pp. 643–663, 1975.

[45] J. Silvertown, S. Holtier, S. Johnson, and P. Dale, "Cellular automaton models of interspecific competition for space - the effect of pattern on process," *J. Ecol.*, vol. 80, pp. 527–534, 1992.

[46] R. Durrett, , and G. Swindle, "Are there bushes in a forest?," *Stoch. Proc. Appl.*, vol. 37, pp. 19–31, 1991.

[47] R. Durrett and R. Schinazi, "Asymptotic critical value for a competition model," *Ann. Applied. Prob.*, vol. 3, pp. 1047–1066, 1993.

[48] D. Rand and H. Wilson, "Using spatio-temporal chaos and intermediate scale determinism in artificial ecologies to quantify spatially-extended systems," *Proc. Roy. Soc. London*, vol. 259, pp. 111–117, 1995.

[49] M. J. Keeling, I. Mezic, R. J. Hendry, J. Mcglade, and D. A. Rand, "Characteristic length scales of spatial models in ecology via fluctuation analysis."

[50] M. Bramson, J. Cox, and R. Durrett, "A spatial model for the abundance of species," *The Annals of Probability*, vol. 26, no. 2, pp. 658–709, 1998.

[51] J. Cortes, S. Martinez, T. Karatas, and F. Bullo, "Ieee transactions on robotics and automation," vol. 20, pp. 243–255, 2004.