Coexistence in host-pathogen systems

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Abstract

Lanchier and Neuhauser have initiated the study of host-symbiont systems but have concentrated on the case in which the birth rates for unassociated hosts are equal. Here we allow the birth rates to be different and identify cases in which a host with a specialist pathogen can coexist with a second species. Our calculations suggest that it is possible for two hosts with specialist pathogens to coexist but it is not possible for a host with a specialist mutualist to coexist with a second species.

1 Introduction

Lanchier and Neuhauser (2006ab) introduced spatially explicit host-symbiont systems because these interactions are important in shaping plant community structure. Being a mixture of the contact process and the biased voter model, these processes are also natural from the point of interacting particle systems. In the special case we will consider here, 1 and 3 are two plant species, while state 2 represents a plant of type 1 with its symbiont. That is, species 2 are specialist symbionts which cannot associate with species 3.

Letting f_i, $i = 1, 2, 3$, denote the fraction of neighbors of site $x \in \mathbb{Z}^d$ in state i, we can formulate the evolution of our Markov process $\xi_t : \mathbb{Z}^d \longrightarrow \{1, 2, 3\}$ at site x as follows:

transition	rate
$1 \to 2$	αf_2
$2 \to 1$	$\gamma_2(f_1 + f_2)$
$1 \to 3$	$\gamma_1 f_3$
$2 \to 3$	$\gamma_2 f_3$
$3 \to 1$	$\gamma_3(f_1 + f_2)$.

In words the symbiont spreads like a contact process with rate α on top of species 1, and the rest of the interactions are like a biased voter, in which individuals of type i are replaced at rate γ_i by a birth from a randomly chosen neighbor, with the modification that when a 2 gives birth onto a site a 1 results, since the symbiont is not passed to the individual's offspring.

To get an idea of the properties we can expect, we look at the non-spatial or "mean-field" version of the process that results when all sites are neighbors and the size of the system tends to infinity. Letting u_i denote the fraction of sites of type i, the rates translate into the following system of ordinary differential equations.

$$\begin{aligned}\frac{du_1}{dt} &= (\gamma_2\, u_2 + \gamma_3\, u_3)\,(u_1 + u_2) \;-\; (\alpha\, u_2 + \gamma_1\, u_3)\, u_1 \\ \frac{du_2}{dt} &= (\alpha\, u_1 - \gamma_2)\, u_2 \\ \frac{du_3}{dt} &= (\gamma_1\, u_1 + \gamma_2\, u_2)\, u_3 \;-\; \gamma_3\,(u_1 + u_2)\, u_3.\end{aligned} \tag{1}$$

For most of the paper we will be interested in the situation $\gamma_1 < \gamma_3 < \gamma_2$, so we begin with that case. The reader should refer to the picture of the dynamical system in Figure 1 as we do our computations. In the absence of 2's, the model reduces to a biased voter model and the 1's out compete the 3's. The inequality $\gamma_1 < \gamma_2$ says that the symbiont is a pathogen that reduces the competitive ability of species 1. In the absence of 3's, we get a contact process with 2's the occupied sites and 1's vacant. Thus when $\alpha > \gamma_2$, there is a boundary fixed point given by

$$u_1 = \frac{\gamma_2}{\alpha}, \qquad u_2 = 1 - \frac{\gamma_2}{\alpha} \qquad \text{and} \qquad u_3 = 0.$$

The side of the triangle on which there are no 1's is unstable since 2's will generate 1's when they give birth. Based on results of Durrett (2002), we expect there to be a nontrivial equilibrium if the 3's can invade 1's and 2's in their equilibrium, that is,

$$\gamma_1\,\frac{\gamma_2}{\alpha} \;+\; \gamma_2\left(1 - \frac{\gamma_2}{\alpha}\right) \;-\; \gamma_3 \;>\; 0. \tag{2}$$

To find the interior fixed point note that the second equation in (1) implies that if $u_2 > 0$ then we have $u_1 = \gamma_2/\alpha$ at the equilibrium. The third equation in (1) implies that if $u_3 > 0$ then

$$\gamma_1\, u_1 \;+\; \gamma_2\, u_2 \;=\; \gamma_3\,(1 - u_3). \tag{3}$$

Subtracting $\gamma_1(u_1 + u_2) = \gamma_1(1 - u_3)$ from (3) and $(\gamma_3 - \gamma_1)u_2 = (\gamma_3 - \gamma_1)u_2$ from the result gives

$$(\gamma_2 - \gamma_1)\, u_2 \;=\; (\gamma_3 - \gamma_1)\,(1 - u_3) \quad \text{and} \quad (\gamma_2 - \gamma_3)\, u_2 \;=\; (\gamma_3 - \gamma_1)\, u_1$$

so we have

$$u_1 \;=\; \frac{\gamma_2}{\alpha_1} \qquad u_2 \;=\; \frac{\gamma_3 - \gamma_1}{\gamma_2 - \gamma_3}\,\frac{\gamma_2}{\alpha_1} \qquad u_3 \;=\; 1 - \frac{\gamma_2 - \gamma_1}{\gamma_2 - \gamma_3}\,\frac{\gamma_2}{\alpha_1}. \tag{4}$$

The inequalities $\gamma_1 < \gamma_3 < \gamma_2$ guarantee $u_2 > 0$. In order for $u_3 > 0$ we need

$$\gamma_2 - \gamma_3 \;>\; (\gamma_2 - \gamma_1)\,\frac{\gamma_2}{\alpha}$$

but this is the invadability condition, (2).

We do not know how to prove that the fixed point is attracting, but it is in the examples we have considered, see e.g., Figure 2. We are able to show that the system has a repelling function, i.e., a convex function that tends to infinity and is decreasing along solutions of the ODE (see Section 6). This implies that the three species persist, i.e.,

$$\liminf_{t\to\infty} u_i(t) > 0.$$

The function we construct in Section 6 has the additional technical conditions needed to apply Proposition 3 on page 6 of Durrett (2002), so there is coexistence in the model with fast stirring. That is, there is a translation invariant stationary distribution in which all types have positive density.

Since plants don't move, fast stirring is not a sensible assumption, and we take a different approach.

Theorem 1. *Suppose $\gamma_1 < \gamma_3 < \gamma_2 < \alpha$ and (2). Then if the range of interaction is long enough there is coexistence.*

If we introduce a state 4 that indicates the presence of a pathogen that specializes on species 3 then we can derive conditions for the existence of an interior fixed point by examining when the 4's can invade the equilibrium (4), etc. We will spare the reader the ugly algebra, since in the absence of a repelling function for the ODE (1), we cannot apply the machinery of Durrett (2002). None the less, we

Conjecture 1. *For suitable parameter choices two species and two specialist pathogens can coexist.*

Returning to the three species system, one might naively expect that coexistence is possible if we assume $\gamma_1 > \gamma_3 > \gamma_2$, i.e., the symbiont is a mutualist that helps species 1. Again $u_2 > 0$ in (4), but this time $\gamma_2 - \gamma_3 < 0$ so the condition for $u_3 > 0$ is the opposite of the invadability condition, so there never is a stable interior fixed point. This is easy to understand intuitively. If the 3's can invade the boundary equilibrium then as they take up more of the space the 2's can't spread as well, so their percentage decreases, and 1's become less able to compete with 3's.

Conjecture 2. *It is not possible for a species with a specialist mutualist to coexist with another species.*

2 Outline of Proof of Theorem 1

The proof of Theorem 1 relies on a block construction (see Bramson and Durrett, 1988, and Durrett, 1995). The idea is to prove that, for given $\delta > 0$, the particle system, when viewed on suitable length and time scales, dominates the set of wet sites of an oriented percolation process on the graph

$$\mathcal{G} = \{(z,n) \in \mathbb{Z}^2 : z + n \text{ is even and } n \geq 0\}$$

in which sites are open with probability $p = 1 - \delta$. For simplicity, we will write the proof in dimension $d = 1$ only. However, it easily extends to higher dimensions.

Let $N_i(x,t)$ denote the number of sites in state i in the interval $[x, x+1]$ at time t. We do not have to worry about the density of 1's since they are created when 2's give birth onto a site.

Survival of species 2. Let $B_0 = \gamma_2 + \alpha$ be the maximum rate at which sites flip. Pick $\rho_0 < 1$ so that $\alpha\rho_0 - \gamma_2 > 0$, let $\eta_0 = (1-\rho_0)/3$ and introduce the following set of parameters:

$$\begin{aligned} p_1 &= e^{-4B_0}(1-e^{-\gamma_1})/8 & (5)\\ a_1 &= -12\log(p_1) & (6)\\ c_1 &= 5a_1/(\gamma_3-\gamma_1) & (7)\\ c_2 &= (2B_0c_1 + 4a_1/3)/(\alpha\rho_0-\gamma_2) & (8)\\ a_2 &= 2B_0(c_1+c_2)+2a_1 & (9)\end{aligned}$$

$T_1 = c_1T$, $T_2 = c_2T$, $I_T = [-\sqrt{T}, \sqrt{T}]$, $I'_T = [-\sqrt{T}, \sqrt{T}-1]$ and $J_T = [-\sqrt{T}/2, \sqrt{T}/2-1]$.

If there were no 2's then 1's and 3's would be a biased voter model, so even if no births of 1's are allowed outside of I_T we will have

$$N_1(x,t) \geq \rho_0 + \eta_0 \text{ for all } x \in J_T \text{ and } t \in [T_1, T_1+T_2]$$

provided $N_1(0,0) \geq L\exp(-2a_1T)$. Here and throughout this section the indicated claims will hold with high probability if T is large and $L \geq L_T$. It is not hard to show that this conclusion holds with $\rho_0 + \eta_0$ replaced by ρ_0 if $N_2(x,t) \leq 2LT^{-1}$ for all $x \in I'_T$ and $t \in [0, T_1+T_2]$. Since $\alpha\rho_0 - \gamma_2 > 0$, when L is large, the 2's are supercritical between time T_1 and time T_1+T_2. If $N_2(0,0) \geq L\exp(-a_1T)$ then an easy argument shows that

$$N_2(0,T_1) \geq (L/2)\exp(-(a_1+B_0c_1)T)$$

and the choice of c_2 guarantees that

$$N_2(0, T_1+T_2) \geq L\exp(-a_1T/3).$$

These calculations have been done under the assumption that $N_2(x,t) \leq 2LT^{-1}$ for all $x \in I'_T$ and $t \in [0, T_1+T_2]$. On the other hand if $N_2(x,t) \geq 2LT^{-1}$ for some $x \in I'_T$ we can show that there is a time $s \leq 2\sqrt{T}$ so that $N_2(0,t+s) \geq L\exp(-a_1T/3)$. Thus in either case if $N_2(0,0) = L\exp(-a_1T)$ then with high probability we will have a time $t \leq T_1+T_2$ with $N_2(0,t) \geq L\exp(-a_1T/3)$. This allows us to keep the 2's around for a long time. It follows from the proof that we have $N_2(0,s) \geq L\exp(-a_2T)$ at all times.

Survival of species 3. Let $\epsilon_0 > 0$ so that

$$b = \gamma_1\left(\frac{\gamma_2}{\alpha} + \epsilon_0\right) + \gamma_2\left(1 - \frac{\gamma_2}{\alpha} - \epsilon_0\right) > \gamma_3 \tag{10}$$

In words if the density of 2's is larger than $1-\gamma_2/\alpha-\epsilon_0$ then the 3's can invade the 1's and 2's. Let

$$\begin{aligned} c_3 &= 2a_2/(\alpha-\gamma_2) &\quad (11)\\ c_4 &= (2B_0c_3+1)/(b-\gamma_3) &\quad (12) \end{aligned}$$

$T_3 = c_3T$ and $T_4 = c_4T$.

The first step is to show that if there are no 3's and $N_2(0,0) \geq L\exp(-a_2T)$ then

$$|N_2(x,t) - L\bar{u}_2| \leq \epsilon_0/2 \text{ for all } x \in J_T \text{ and } t \in [T_3, T_3+T_4],$$

where $\bar{u}_2 = 1-\gamma_2/\alpha$ is the mean-field equilibrium frequency of 2's in the absence of 3's. It is not hard to show that this conclusion holds with $\epsilon_0/2$ replaced by ϵ_0 if $N_3(x,t) \leq 2LT^{-1}$ for all $x \in I'_T$ and $t \in [0, T_3+T_4]$. Since $b-\gamma_3 > 0$, if L is large the 3's are supercritical between time T_3 and time T_3+T_4. If $N_3(0,0) \geq L\exp(-T)$ then an easy argument shows that

$$N_3(0,T_3) \geq (L/2)\exp(-(1+B_0c_3)T),$$

and the choice of c_4 guarantees that

$$N_3(0,T_1+T_2) \geq L\exp(-T/2).$$

These calculations have been done under the assumption that $N_3(x,t) \leq 2LT^{-1}$ for all $x \in I'_T$ and $t \in [0, T_3+T_4]$. On the other hand if $N_3(x,t) \geq 2LT^{-1}$ for some $x \in I'_T$, we can show that there is a time $s \leq 2\sqrt{T}$ so that $N_3(0,t+s) \geq L\exp(-T/2)$. Thus in either case if $N_3(0,0) \geq L\exp(-T)$ and $N_2(0,0) \geq L\exp(-a_2T)$ then with high probability we will have a time $t \leq T_3+T_4$ with $N_3(0,t) \geq L\exp(-T/2)$.

Moving the particles. The arguments for the cases in which $N_i(x,t) \geq 2LT^{-1}$, see Lemmas 4.4 and 5.5, imply that if $N_2(0,t) \geq L\exp(-a_1T/3)$ then there is a time $s \leq 2\sqrt{T}$ so that

$$N_2(\sqrt{T}, t+s) \geq L\exp(-a_1T)$$

and that if $N_3(0,t) \geq L\exp(-T/2)$ then there is a time $s \leq 2\sqrt{T}$ so that

$$N_2(\sqrt{T}, t+s) \geq L\exp(-T)$$

Block construction. Let $T^* = 2\sqrt{T} + \max\{T_1+T_2, T_3+T_4\}$. We say that $(0,0)$ is occupied if

$$\begin{aligned} N_2(0,t) &\geq L\exp(-a_1T) \text{ at some time } t \in [0, T^\star - 2\sqrt{T}]\\ N_3(0,t) &\geq L\exp(-T) \text{ at some time } t \in [T^\star, 2T^\star - 2\sqrt{T}] \end{aligned}$$

Our constructions imply

$$\begin{aligned} N_2(0,t) &\geq L\exp(-a_1T/3) \text{ at some time } t \in [T^\star, 2T^\star - 2\sqrt{T}]\\ N_2(0,t) &\geq L\exp(-a_2T) \text{ at all times } t \in [T^\star, 3T^\star]\\ N_3(0,t) &\geq L\exp(-T/2) \text{ at some time } t \in [2T^\star, 3T^\star - 2\sqrt{T}] \end{aligned}$$

Moving the particles we have

$$\begin{aligned} N_2(\sqrt{T},t) &\geq L\exp(-a_1T) \text{ at some time } t\in[T^\star,2T^\star] \\ N_3(\sqrt{T},t) &\geq L\exp(-T) \text{ at some time } t\in[2T^\star,3T^\star] \end{aligned}$$

Using our constructions

$$\begin{aligned} N_2(\sqrt{T},t) &\geq L\exp(-a_1T) \text{ at some time } t\in[2T^\star,3T^\star-2\sqrt{T}] \\ N_2(\sqrt{T},t) &\geq L\exp(-a_2T) \text{ at all times } t\in[2T^\star,4T^\star] \\ N_3(\sqrt{T},t) &\geq L\exp(-T) \text{ at some time } t\in[3T^\star,4T^\star-2\sqrt{T}] \end{aligned}$$

which is the original event shifted in space by $\sqrt{T}$ and in time by $2T^\star$. All of our constructions are defined so that there is a finite range of dependence. The result then follows by a standard application of the block construction, see e.g., Durrett (1995).

The rest of the paper is devoted to filling in the details of the argument sketched above. In Section 3, we will prove some preliminary results that are useful for the two survival arguments. Following the historical order in which the proof was constructed we will tackle the survival of the 3's in Section 4, and then the survival of the 2's in Section 5.

3 Preliminaries

To investigate our process, it is convenient to construct it from a graphical representation, i.e., a collection of independent Poisson processes (see Harris, 1972). Let $\gamma_1<\gamma_3<\gamma_2$ be the voter rates and α be the pathogen infection parameter, and set

$$\lambda_0 \;=\; \alpha, \qquad \lambda_1 \;=\; \gamma_1, \qquad \lambda_2 \;=\; \gamma_3-\gamma_1 \qquad \text{and} \qquad \lambda_3 \;=\; \gamma_2-\gamma_3.$$

For each pair of sites $x,y\in\mathbb{Z}/L$ and $i\in\{0,1,2,3\}$, let $T_n^{i,x,y}$, $n\geq 1$, be independent Poisson processes with rate $q(y-x)\,\lambda_i$, where $q(x)=1/2L$ when $0<|x|\leq 1$, and $q(x)=0$ otherwise. We draw an arrow of type i from site y to site x at time $T_n^{i,x,y}$. Type 1 arrows correspond to a voter interaction for any species so the dual process jumps from site x to site y. At the other arrival times the dual process branches to include site y.

In this section we will prove several preparatory lemmas. The first shows that the number of particles can't decay too fast.

Lemma 3.1. *Let* $B_0=\gamma_2+\alpha$ *and* $i\in\{1,2,3\}$. *Then*

$$P(N_i(0,s)\leq e^{-sB_0}N_i(0,0)/2\leq \exp(-\eta_s N_i(0,0))$$

where $\eta_s=e^{-sB_0}/8$.

Proof. Let $x\in[0,1]\cap\mathbb{Z}/L$. The graphical representation introduced above implies that the state of site x flips at rate at most $B_0=\gamma_2+\alpha$. It follows that if $\xi_0(x)=i$ then

$$P(\xi_t(x)=i \text{ at all times } t\leq s)\geq e^{-sB_0}.$$

Since the no flipping events are independent for different x, the number of $x \in [0,1]$ with $\xi_0(x) = i$ that don't flip by time s is $X = \text{Binomial}(n,p)$ with $n = N_i(0,0)$ and $p = e^{-sB_0}$. A standard large deviations estimate for the Binomial implies

$$P(X \le n(p-z)) \le \exp(-nz^2/2p) \tag{13}$$

Taking $z = p/2$ the desired result follows. $\square$

The dual process of the contact process is the contact process. The dual of the biased voter model is branching coalescing random walk. When the range is large, both of these dual processes are almost branching random walks in which a particle at y dies at rate δ and gives birth at rate β to an offspring that is sent to $y + U$ where U is the uniform law on $[-1,1]$. Let Z_t^x denote the branching random walk starting at $Z_0^x = \{x\}$. Suppose $\beta > \delta$ and let

$$\rho = P(|Z_t^x| > 0 \text{ for all } t)$$

Let $\bar{Z}_t^x$ be the process Z_t^x in which particles that land outside $I_T = [-\sqrt{T}, \sqrt{T}]$ are killed.

Lemma 3.2. *Let* $\bar{Z}_t^x(y) = |\bar{Z}_t^x \cap (y + [0,1])|$. *Suppose* $T \to \infty$, $t/T \to u$, $x/\sqrt{T} \to v$, $y/\sqrt{T} \to w$ *with* $v, w \in [-1/2, 1/2]$.

$$\sqrt{T} e^{-(\beta-\delta)t} \bar{Z}_t^x(y) \to \bar{p}_u(v,w) W$$

in L^2 *and in probability, where* $W = \lim_{s\to\infty} e^{-(\beta-\delta)s} Z_s^x$ *and* $\bar{p}_u(v,w)$ *is the transition probability of a Brownian motion run at rate* $\beta/3$ *killed when it exits* $[-1,1]$.

Proof. If there was no killing this would follow from Asmussen and Kaplan (1976). Their proof extends in a straightforward way to give the desired result. The mean measure for the truncated random walk

$$E(|\bar{Z}_t^x \cap A|) = e^{(\beta-\delta)t} P(\bar{S}_t^x \in A)$$

where $\bar{S}_t^x$ is a random walk that jumps at rate β, takes steps uniformly distributed on $[-1,1]$ and is killed when it steps outside of I_T. If $t/T \to u$, $x/\sqrt{T} \to v$, and $y/\sqrt{T} \to w$ then

$$\sqrt{T} P(\bar{S}_t^x \in y + [0,1]) \to \bar{p}_u(v,w)$$

Let $s = (3/(\beta-\delta)) \log T$ and let $\mathcal{F}_s$ be the σ-field generated by events up to time s. There will be $O(T^3)$ particles in Z_s^x. Since a particle can only move by at most 1 during a jump, simple large deviations estimates for the Poisson imply that there is a constant C so that with high probability no particle in Z_s^x has moved more that Cs from x. Using this with the formula for the mean we see that

$$E(\bar{Z}_t^x(y)|\mathcal{F}_s) \approx Z_s^x e^{(\beta-\delta)(t-s)} \bar{p}_u(v,w)/\sqrt{T}$$

Using a trivial bound with a well known result about the second moment of a supercritical branching process

$$\text{var}\,(\bar{Z}_t^x(y)|\mathcal{F}_s) \le Z_s^x E((Z_{t-s}^x)^2) \le C Z_s^x e^{2(\beta-\delta)(t-s)}$$

Using Chebyshev's inequality

$$P\left(\left|\bar{Z}^x_t(y) - E(\bar{Z}^x_t(y)|\mathcal{F}_s)\right| > \epsilon e^{(\beta-\delta)t}/\sqrt{T}\right) \leq \frac{CZ^x_s e^{2(\beta-\delta)(t-s)}}{\epsilon^2 e^{2(\beta-\delta)t}/T}$$
$$\leq Te^{-(\beta-\delta)s} \cdot e^{-(\beta-\delta)s} Z^x_s \leq T^{-1}$$

with probability $\geq 1 - T^{-1}$ since $E(e^{-(\beta-\delta)s}Z^x_s) = 1$. Noting

$$\sqrt{T}e^{-(\beta-\delta)t}E(\bar{Z}^x_t(y)|\mathcal{F}_s) \approx e^{-(\beta-\delta)s}Z^x_s\bar{p}_u(v,w) \approx W\bar{p}_u(v,w)$$

the result now follows. □

From the formula for the expected value in the previous proof we immediately get

Lemma 3.3. *If T is large, then for all $x, y \in [-\sqrt{T}/2, \sqrt{T}/2]$, and $t \in [rT, sT]$*

$$E\bar{Z}^x_t(y) \geq 4e^{(\beta-\delta)t/2}$$

A second consequence that we will need is

Lemma 3.4. *Let $a > 0$, $\eta > 0$, $2a/(\beta-\delta) \leq r < s$, and $\epsilon > 0$ be given. If T is sufficiently large then*

$$|P\left(\bar{Z}^x_t \cap B \neq \emptyset\right) - \rho| \leq \epsilon$$

for all $x \in J_T = [-\sqrt{T}/2, \sqrt{T}/2]$, $t \in [rT, sT]$ and $B \subset [0,1]$ with Lebesgue measure $|B| \geq \exp(-aT)$.

Proof. Lemma 3.2 and the restriction on r imply that if T is large and the branching process does not die out then with high probability there are at least $\exp(3aT/2)$ particles in $[0,1]$ at time $t-1$. Each of these particles has probability $\geq c|B|$ of giving birth before time 1 to a particle that lands in B and that does not die before time 1. Since these events are independent the desired result follows. □

The final general result that we will need is that when the range is large a particle system is almost deterministic. We will apply this twice: (i) when there are no 3's then the 1's and 2's are a contact process in which the 2's are the occupied sites, and (ii) when there are no 2's the 1's and 3's are a biased voter model favoring the 1's. In each case T is fixed and no births are allowed outside $[-\sqrt{T}, \sqrt{T}]$. If we consider the 1's to be the occupied sites then in each case our particle system ξ_t has a dual process $\hat{\xi}_t$. In the next result we will only use this and the fact that B_0 gives an upper bound on the jump rate.

Lemma 3.5. *Let $N(x,t) = |\xi_t \cap [x, x+1]|$, $S < \infty$, and $\epsilon > 0$. As $L \to \infty$ uniformly in the possible nonrandom initial conditions*

$$\lim_{L\to\infty} P(|N(x,t) - EN(x,t)| > 5\epsilon L$$
$$\textit{for some } x \in J_T \textit{ and some } t \in [0,S]) = 0$$

Proof. The first step is to prove that it suffices to control the difference at a finite number of times in a finite number of intervals, where the numbers are independent of L. Let τ be such that $1-\exp(-\tau B_0) \le \epsilon$ where $B_0 = \gamma_2 + \alpha$, and set $m = \min\{n \ge 1 : n\tau \ge S\}$. Repeating the proof of Lemma 3.1 and using a large deviations bound for the upper tail of the Binomial it follows that with probability at least $1 - C\exp(-\eta L)$, the number of sites in $[x, x+1]$ that flip between times $n\tau$ and $(n+1)\tau$ is smaller than $2\epsilon L$.

To make the number of intervals in which the difference has to be estimated independent of L, we let $N_\epsilon(x,t) = |\xi_t \cap [x, x+\epsilon]|$ and observe that if

$$|N_\epsilon(x,t) - EN_\epsilon(x,t)| \le L\epsilon^2 \quad \text{for all} \quad x \in J_{T,\epsilon} \equiv \epsilon\,\mathbb{Z} \cap [-\sqrt{T}/2, \sqrt{T}/2)$$

then $|N(x,t) - EN(x,t)| \le \epsilon^{-1}L\epsilon^2 + 2\epsilon L = 3\epsilon L$ for all $x \in J_T$, since there are at most ϵ^{-1} intervals of length ϵ with endpoints in $J_{T,\epsilon}$ included in $[x, x+1]$, and the second term takes care of the beginning and end segments of $[x, x+1]$ that are not covered.

To estimate $|N_\epsilon(x,t) - EN_\epsilon(x,t)|$ let $\zeta_y = 1$ if $\hat\xi^y_t \cap \xi_0 \ne \emptyset$. A standard construction, see e.g., page 21 in Griffeath (1978), shows that the covariance of ζ_y and ζ_z can be bounded by the probability that the duals do not hit and hence

$$\text{cov}\,(\zeta_y, \zeta_z) \le C/L$$

From this and the trivial bound $\text{var}\,(\zeta_y) \le 1$ it follows that

$$\text{var}\, N_\epsilon(x,t) \le L\epsilon + L^2\epsilon^2 C/L \le C' L\epsilon$$

This together with Chebyschev's inequality implies that

$$P(|N_\epsilon(x,t) - EN_\epsilon(x,t)| > L\epsilon^2) \le C\epsilon^{-3}L^{-1}$$

The number of space and time points at which need this result does not depend on L and the proof is complete. □

4 Survival of species 3

Let $\bar u_2 = 1 - \gamma_2/\alpha$ be the equilibrium density of 2's in the mean field version of the process with no 3's. The first step is to show

Lemma 4.1. *Suppose there are no 3's. If T is large and $L \ge L_T$ then for any initial configuration with $N_2(0,0) \ge L\exp(-a_2 T)$, we will have with high probability*

$$|N_2(x,t) - L\bar u_2| < \epsilon_0/2$$

for all $x \in J_T$ and $t \in [T_3, T_3 + T_4]$, even if no births of 2's are allowed outside I_T.

Proof. In the absence of 3's, the set of 2's is a contact process with births at rate α and deaths at rate γ_2. $T_3 = c_3 T$ with $c_3 = 2a_2/(\alpha - \gamma_2)$, so Lemma 3.4 implies that if T is large and $L \ge L_T$ then

$$|EN_2(x,t) - L\bar u_2| < \epsilon_0/4$$

for all $x \in J_T$ and $t \in [T_3, T_3 + T_4]$. The desired result now follows from Lemma 3.5. □

Lemma 4.2. *If T is sufficiently large, Lemma 4.1 holds with $\epsilon_0/2$ replaced by ϵ_0 when*

$$N_3(x,t) \le 2LT^{-1} \quad \textit{for all } x \in I'_T \textit{ and all } t \in [0, T_3 + T_4]$$

Proof. Assume first that $N_3(x,t) = 2LT^{-1}$ for all (x,t) belonging to the appropriate space-time region. In this case, the 2's are a contact process with birth rate $\alpha(1-2T^{-1})$ instead of α. The result follows by taking T such that

$$|1 - \gamma_2/\alpha - (1 - \gamma_2/\alpha(1 - 2T^{-1}))| < \epsilon_0/2.$$

Monotonicity of the contact process with respect to its birth rate allows us to conclude that the result holds as well in the general case when $N_3(x,t) \le 2LT^{-1}$. □

Lemma 4.3. *Assume that $N_2(0,0) \ge L\exp(-a_2T)$, $N_3(0,0) \ge L\exp(-T)$ and*

$$N_3(x,t) \le 2LT^{-1} \quad \textit{for all } x \in I'_T \textit{ and all } t \in [0, T_3 + T_4].$$

Then for large T and $L \ge L_T$, with probability close to 1

$$N_3(0, T_3 + T_4) \ge L\exp(-T/2).$$

even if no births of 3's are allowed outside I_T.

Proof. By Lemma 3.1 and Lemma 4.2, we can assume that

$$N_3(0,T_3) \ge (L/2)\exp(-(c_3B_0 + 1)T)$$
$$|N_2(x,t) - L\,\bar{u}_2| \le \epsilon_0 L \text{ for all } x \in J_T \text{ and } t \in [T_3, T_3 + T_4]$$

The idea is to observe that the density of 2's between time T_3 and time $T_3 + T_4$ is sufficiently large so that if L is large the 3's dominate a supercritical branching random walk in which a particle at site y dies at rate γ_3 and gives birth at rate

$$b = \gamma_1\left(\frac{\gamma_2}{\alpha} + \epsilon_0\right) + \gamma_2\left(1 - \frac{\gamma_2}{\alpha} - \epsilon_0\right) > \gamma_3$$

to an offspring that is sent to $y + U$. $c_4 = (2c_3B_0 + 1)/(b - \gamma_3)$ so if T is large, Lemma 3.3 implies that for $x \in [0,1]$

$$E|\bar{Z}^x_{c_4T} \cap [0,1]| \ge 4\exp((c_3B_0 + 1/2)T)$$

Arguing as in the proof of Lemma 3.5 we can estimate the variance and use Chebyshev's inequality to prove the desired result. □

To conclude the proof of step 1, we now deal with the case when the number of 3's exceeds $2LT^{-1}$ in some interval of length 1 included in I_T by time $T_3 + T_4$.

Lemma 4.4. *Assume that*

$$N_3(x,0) \ge 2LT^{-1} \quad \textit{for some } x \in I'_T.$$

Then for T sufficiently large, there is a time $t \le 2\sqrt{T}$ such that

$$\lim_{L\to\infty} P(N_3(0,t) \le L\exp(-T/2)) = 0.$$

Proof. For any integer $n \in \mathbb{Z}$ and any time $t \geq 0$, let

$$B_{x,n} \; = \; [x + n/2, x + (n+1)/2] \quad \text{and} \quad H_{n,t} \; = \; L^{-1} \, |\{z \in B_{x,n} : \xi_t(z) = 3\}|.$$

Without loss of generality, we can assume that $x \in [-\sqrt{T}, 0]$ and $H_{0,0} \geq T^{-1}$. Let $A = 2e^{B_0}$. If $H_{n+1,t} \geq AT^{-1}$ at some $t \in [n, n+1]$ then Lemma 3.1 shows that with a probability that tends to 1 as $L \to \infty$, $H_{n+1,n+1} \geq T^{-1}$. On the other hand if $H_{n+1,t} \leq AT^{-1}$ for all $t \in [n, n+1]$, the probability that a particle of type 3 in $B_{x,n}$ at time n gives birth by time $n+1$ to a particle of type 3 that is sent to $B_{x,n+1}$ and that both particles (the parent and the offspring) die after time $n+1$ is bounded from below by

$$\frac{1}{4} \, e^{-2\gamma_3}(1 - e^{-\gamma_1})(1 - AT^{-1}).$$

The factor 1/4 is the probability that the offspring is sent to $B_{x,n+1}$ and the factor $1 - AT^{-1}$ the probability that it is not sent to a site already occupied by a 3.

Let $p_0 = e^{-2\gamma_3}(1 - e^{-\gamma_1})/8$. As $L \to \infty$, we have with probability $\to 1$

$$H_{n,n} \geq \min\{p_0 \, H_{n-1,n-1}, T^{-1}\}$$

Since it takes at most $2\sqrt{T}$ steps to bring particles to the interval $[0, 1]$, there is a time $t \leq 2\sqrt{T}$ so that

$$N(0,t) \geq p_0^{2\sqrt{T}} T^{-1} \geq L \exp(-T/2)$$

if T is large enough. □

5 Survival of species 2

To begin, we give a lower bound on the number of 1's produced from 2's in one unit of time.

Lemma 5.1. *Assume that* $N_2(0,0) \geq L \exp(-a_1 T)$. *Then for large* T

$$P(N_1(0,1) \leq L \exp(-2a_1 T)) \leq C \exp(-\eta L)$$

Proof. By Lemma 3.1

$$P(N_2(0,t) \leq (L/2) \exp(-a_1 T - B_0) \text{ for some } t \in [0,1]) \leq C \exp(-\eta L).$$

In particular, since each host dies at rate at least γ_1, using the Binomial large deviations result, (13),

$$\begin{aligned} P(|\{x \in [0,1] &: \xi_t(x) \text{ jumps to 1 by time 1}\}| \\ &\leq (L/4)(1 - e^{-\gamma_1}) \exp(-a_1 T - B_0)) \leq C \exp(-\eta L) \end{aligned}$$

By applying (13) again, we obtain

$$P(N_1(0,1) \leq (L/8)(1 - e^{-\gamma_1}) \exp(-a_1 T - 2B_0)) \leq C \exp(-\eta L)$$

If T is large $\exp(-a_1 T) < (1 - e^{-\gamma_1}) \exp(-2B_0)/8$ and the proof is complete. □

Lemma 5.2. *Suppose there are no 2's, no births of 1's are allowed outside* I_T *and* $N_1(0,0) \geq L\exp(-2a_1T)$. *Then, if* T *is large and* $L \geq L_T$ *then*

$$P(N_1(x,t) \leq L(\rho_0 + \eta_0) \text{ for some } x \in J_T \text{ and } t \in [T_1, T_1 + T_2]) = 0.$$

Proof. In the absence of 2's, 1's are a biased voter model. In the dual coalescing random walk particles jump at rate γ_1 and give birth at rate $\gamma_3 - \gamma_1$. $T_1 = c_1T$ where $c_1 = 5a_1(\gamma_3 - \gamma_1)^{-1}$ so Lemma 3.4 implies that if T is large and $L \geq L_T$ then $EN_1(x,t) \geq L(\rho_0 + 2\eta_0)$ for all $x \in J_T$ and $t \in [T_1, T_1 + T_2]$. The desired result now follows from Lemma 3.5. □

Lemma 5.3. *If* T *is large, Lemma 5.2 holds with* $\rho_0 + \eta_0$ *replaced by* ρ_0 *when*

$$N_2(x,t) \leq 2LT^{-1} \text{ for all } x \in I'_T \text{ and all } t \in [0, T_1 + T_2].$$

Proof. Assume first that $N_2(x,t) = 2LT^{-1}$ for all $(x,t) \in J_T \times [0, T_1 + T_2]$. In this case, the dual process for the 1's is a branching coalescing walk with birth rate $(\gamma_3 - \gamma_1)(1 - 2T^{-1})$ instead of $\gamma_3 - \gamma_1$. The result follows by taking T such that

$$c_1(\gamma_3 - \gamma_1)(1 - 2T^{-1}) > 4a_1$$

Monotonicity of the contact process with respect to its birth rate allows us to conclude that the result holds as well in the general case when $N_2(x,t) \leq 2LT^{-1}$. □

Lemma 5.4. *Assume that* $N_2(0,0) \geq L\exp(-a_1T)$ *and that*

$$N_2(x,t) \leq 2LT^{-1} \text{ for all } x \in I'_T \text{ and all } t \in [0, T_1 + T_2].$$

Then, $N_2(0, T_1 + T_2) \geq L\exp(-a_1T/3)$ *with probability close to 1, even if no births of 2's are allowed outside* I_T.

Proof. First of all, in view of Lemma 3.1 and Lemma 5.3, we can assume that

$$\begin{aligned} &N_2(0,T_1) \geq (L/2)\exp(-(a_1 + B_0c_1)T) \\ &N_1(x,t) \geq L\rho_0 \text{ for all } x \in J_T \text{ and } t \in [T_1, T_1 + T_2]\ . \end{aligned}$$

The idea is to observe that the density of 1's between time T_1 and time $T_1 + T_2$ is sufficiently large so that if L is large, 2's dominate a supercritical branching random walk in which particles die at rate γ_2 and gives birth at rate $\alpha\rho_0$. $c_2 = (2B_0c_1 + 4a_1/3)/(\alpha\rho_0 - \gamma_2)$ so if T is large Lemma 3.3 implies that for all $x \in [0,1]$

$$E|\bar{Z}^x_{c_2T} \cap [0,1]| \geq 4\exp((c_1B_0 + 2a_1/3)T)$$

Arguing as in the proof of Lemma 3.5, we can estimate the variance and use Chebyshev's inequality to prove the desired result. □

The analogue of Lemma 5.4 when the density of 2's exceeds $2LT^{-1}$ in some interval of length 1 included in I_T by time $T_1 + T_2$ is given by

Lemma 5.5. *Assume that*

$$N_2(x,0) \geq 2LT^{-1} \text{ for some } x \in I'_T.$$

Then, for T sufficiently large, there is a time $t \leq 2\sqrt{T}$ such that,

$$\lim_{L\to\infty} P(N_2(0,t) \leq L\exp(-a_1T/3)) = 0.$$

Proof. The proof uses on the same ingredients as the proof of Lemma 4.4 but is harder because 3's can send their offspring to any site, whereas 2's can only give birth onto sites occupied by a 1. To fix this problem, the strategy is to use 2's as a source to produce 1's and then use sites occupied by 1's as a target to produce 2's. To make the argument precise, we introduce, for any integer $n \in \mathbb{Z}$ and any time $t \geq 0$,

$$\begin{aligned} B_{x,n} &= [x + n/2, x + (n+1)/2] \\ H_{n,t} &= L^{-1}|\{z \in B_{x,n} : \xi_t(z) = 1\}| \\ K_{n,t} &= L^{-1}|\{z \in B_{x,n} : \xi_t(z) = 2\}| \end{aligned}$$

Without loss of generality, we can assume that $x \in [-\sqrt{T}, 0]$ and $K_{0,0} \geq T^{-1}$. Let $A = 2e^{B_0}$. If $H_{n+1,t} \geq AT^{-1}$ at some $t \in [n, n+1]$ then Lemma 3.1 shows that with a probability that tends to 1 as $L \to \infty$, $H_{n+1,n+1} \geq T^{-1}$. On the other hand if $H_{n+1,t} \leq AT^{-1}$ for all $t \in [n, n+1]$, the probability that a particle of type 1 in $B_{x,n}$ at time n gives birth by time $n+1$ to a particle of type 1 that is sent to $B_{x,n+1}$ and that both particles (the parent and the offspring) die after time $n+2$ is bounded from below by

$$\frac{1}{4}e^{-4B_0}(1 - e^{-\gamma_1})(1 - AT^{-1}).$$

The factor 1/4 is the probability that the offspring is sent to $B_{x,n+1}$ and the factor $1 - AT^{-1}$ the probability that it is not sent to a site already occupied by a 1. Let $p_1 = e^{-4B_0}(1 - e^{-\gamma_1})/8$. Iterating we have

$$\inf_{t\in[n,n+1]} H_{n,t} \geq p_1^n T^{-1}$$

with probability → 1 as $L \to \infty$.

The probability that a 2 in $B_{x,n}$ at time $n+1$ gives birth by time $n+2$ to a 2 that is sent to $B_{x,n+1}$ and that both particles (the parent and the offspring) die after time $n+3$ is bounded from below by

$$\frac{1}{4}e^{-4B_0}(1 - e^{-\alpha})(1 - T^{-1}) \inf_{t\in[n+1,n+2]} H_{n+1,t}.$$

The factor $\inf_{t\in[n+1,n+2]} H_{n+1,t}$ comes from the fact that 2's can only give birth on sites occupied by 1's. Let $p_2 = e^{-4B_0}(1 - e^{-\alpha})/8$. Since $K_{0,0} \geq T^{-1}$, we get $K_{0,1} \geq e^{-\gamma_2}T^{-1}/2$ and

$$K_{n,n+1} \geq p_2 K_{n-1,n} \inf_{t\in[n,n+1]} H_{n,t} \geq p_1^n p_2 T^{-1} K_{n-1,n}$$

Iterating we have

$$K_{n,n+1} \geq p_1^{1+2+\cdots+n} p_2^n T^{-(2n+1)} e^{-\gamma_2}/2$$

Since it takes at most $n = 2\sqrt{T}$ steps to bring the particles to the interval $[0,1]$, there is a time $t \leq 2\sqrt{T}$ so that, for T large enough,

$$N_2(0,t) \geq L p_1^{4T} = L \exp(-a_1 T/3)$$

where the second equality follows from the definition of a_1. $\square$

6 Repelling function

In this section we will construction a repelling function for the ODE. Recall $\gamma_1 < \gamma_3 < \gamma_2 < \alpha$. First we rewrite the equations

$$\begin{aligned}
\frac{du_1}{dt} &= (\gamma_2 - \alpha)u_1 u_2 + \gamma_2 u_2^2 + (\gamma_3 - \gamma_1)u_1 u_3 + \gamma_3 u_2 u_3 \\
\frac{du_2}{dt} &= u_2(-\gamma_2 + \alpha u_1) \\
\frac{du_3}{dt} &= u_3((\gamma_1 - \gamma_3)u_1 + (\gamma_2 - \gamma_3)u_2)
\end{aligned}$$

The desired function is $f = \sum_i \eta_i (f_i \vee M_i)$ where $f_i = \infty$ on $u_i = 0$.

Let $\rho = 1 - \gamma_2/\alpha$. $f_3(u) = u_2 - \rho \log u_2 - \epsilon_1 \log u_3$, $\eta_3 = 1$.

$$\begin{aligned}
\frac{d}{dt}(u_2 - \rho \log u_2) &= \left(1 - \frac{\rho}{u_2}\right) u_2(\alpha u_1 - \gamma_2) \\
&= (u_2 - \rho)(\rho - u_2 - u_3)\alpha \\
\frac{d}{dt}(-\epsilon_1 \log u_3) &= -\epsilon_1((\gamma_1 - \gamma_3)u_1 + (\gamma_2 - \gamma_3)u_2)
\end{aligned}$$

Let $\Delta = \{(u_1, u_2, u_3) : u_i \geq 0, \sum_i u_i = 1\}$. Pick $a < \rho/(1-\rho) < b$ so that on $A = \Delta \cap \{u_2/u_1 \in [a,b]\}$ we have $(\gamma_1 - \gamma_3)u_1 + (\gamma_2 - \gamma_3)u_2 > 0$. This is possible because of the invadability condition. If δ_1 is small we have $(u_2 - \rho)(\rho - u_2 - u_3) < 0$ on $B(\delta_1) = \Delta \cap A^c \cap \{u_3 < \delta_1\}$. If ϵ_1 is small $df_3/dt < 0$ on $B(\delta_1)$. By picking $\delta_2 \leq \delta_1$ we will have $df_3/dt < 0$ on $A(\delta_2) = A \cap \{u_3 < \delta_2\}$. This implies

$$df_3/dt < 0 \quad \text{on } \Delta \cap \{u_3 < \delta_2\}$$

Since $f_3 = \infty$ on $u_3 = 0$ and is continuous we can pick M_3 so that $\{f_3 > M_3\} \subset \Delta \cap \{u_3 < \delta_2\}$ and δ_2' so that $\{f_3 > M_3\} \supset R_1 = \Delta \cap \{u_3 < \delta_2'\}$.

$f_2 = -\log u_1 - \epsilon_2 \log u_2$.

$$\begin{aligned}
\frac{d}{dt}(-\log u_1) &= -(\gamma_3 - \gamma_1)u_3 + (\alpha - \gamma_2)u_2 - \frac{1}{u_1}\left[\gamma_2 u_2^2 + +\gamma_3 u_2 u_3\right] \\
\frac{d}{dt}(-\epsilon_2 \log u_2) &= -\epsilon_2(-\gamma_2 + \alpha u_1)
\end{aligned}$$

so we have

$$\frac{df_2}{dt} \le -(\gamma_3 - \gamma_1)u_3 + (\alpha - \gamma_2)u_2 - \epsilon_2(-\gamma_2 + \alpha u_1)$$

From this it is clear that if δ_3 and ϵ_2 are small enough. $df_2/dt < 0$ on $R_2 = \Delta \cap \{u_3 \ge \delta_2', u_2 < \delta_3\}$, and hence if η_2 is small $d[(f_3 \vee M_3) + \eta_2 f_2]/dt < 0$ on $R_1 \cup R_2$. Since $f_2 = \infty$ on $u_2 = 0$ and is continuous we can pick M_2 so that $\{f_2 > M_2\} \subset \Delta \cap \{u_2 < \delta_3\}$ and δ_3' so that $\{f_2 > M_2\} \supset \Delta \cap \{u_2 < \delta_3'\}$.

$f_1 = -\log(1 - u_2) - \epsilon_3 \log u_1$.

$$\begin{aligned} \frac{d}{dt}(-\log(1-u_2)) &= \frac{u_2}{1-u_2}(-\gamma_2 + \alpha u_1) \\ \frac{d}{dt}(-\log(u_1)) &\le -(\gamma_3 - \gamma_1)u_3 + (\alpha - \gamma_2)u_2 \end{aligned}$$

where the second result comes from the computation for f_2. It is easy to see that if δ_4 and ϵ_3 are small enough then $df_1/dt < 0$ on $R_3 = \Delta \cap \{u_2 \ge \delta_3', u_1 \le \delta_4\}$. Since $f_1 = \infty$ on $u_1 = 0$ and is continuous we can pick M_1 so that $\{f_2 > M_1\} \subset \Delta \cap \{u_1 < \delta_4\}$. If η_1 is small enough we have the desired repelling function.

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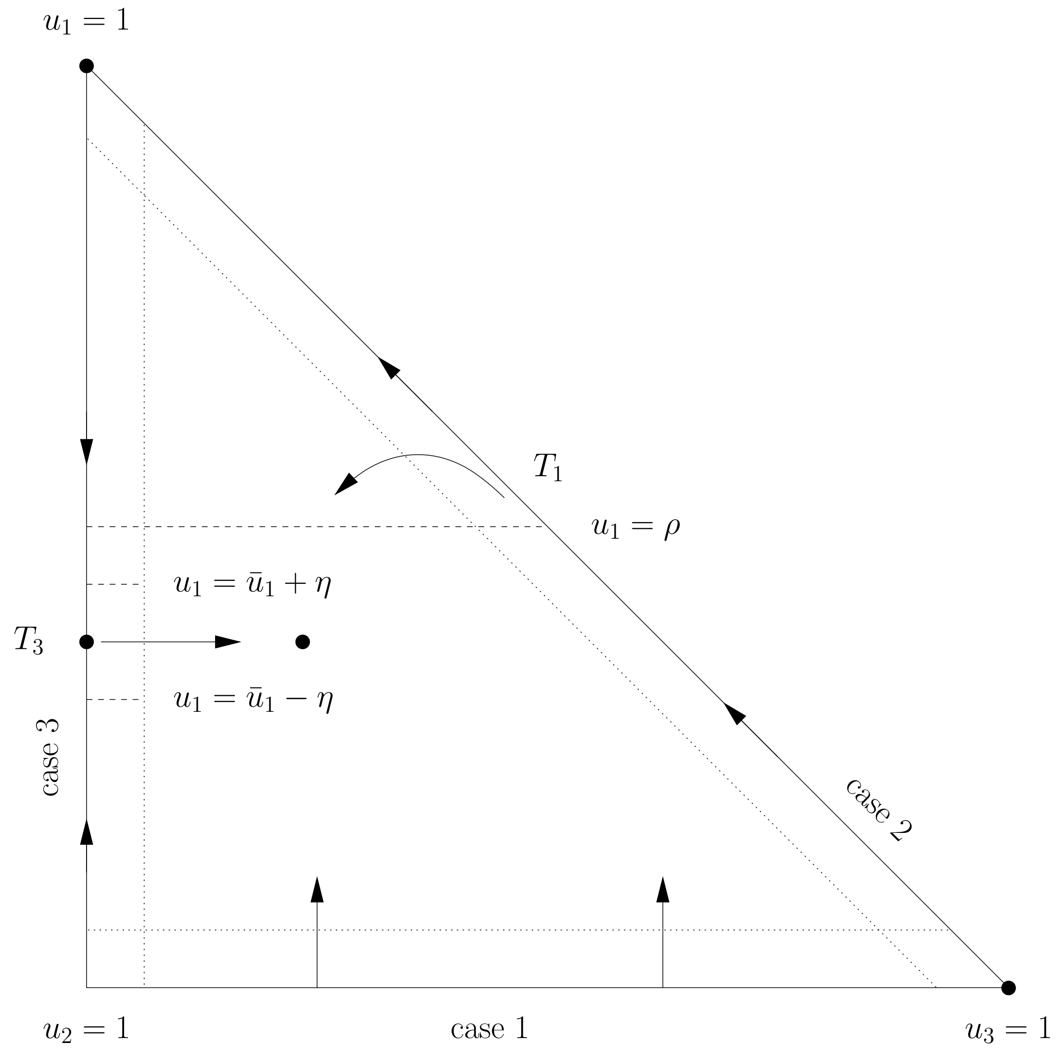

Figure 1: Picture to explain the proof.

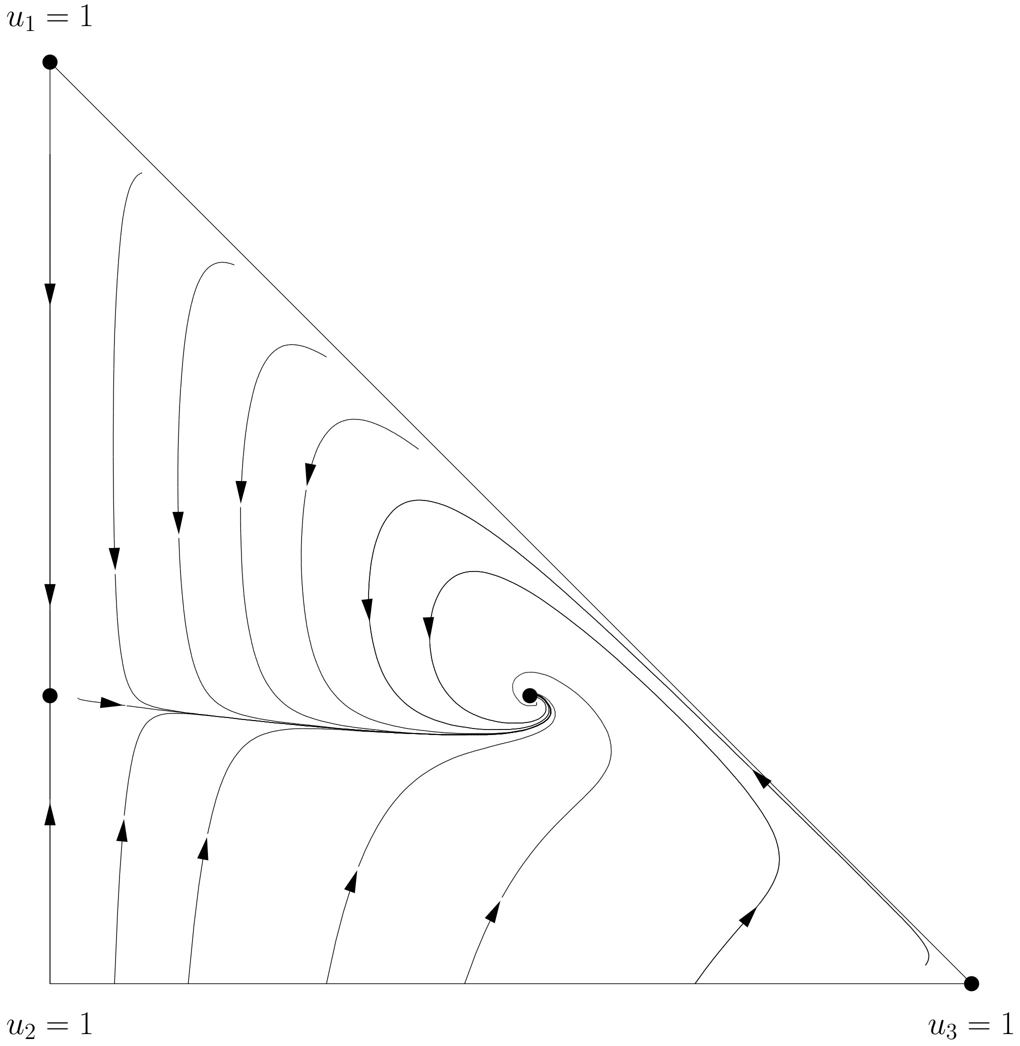

Figure 2: Example of the host-pathogen ODE.

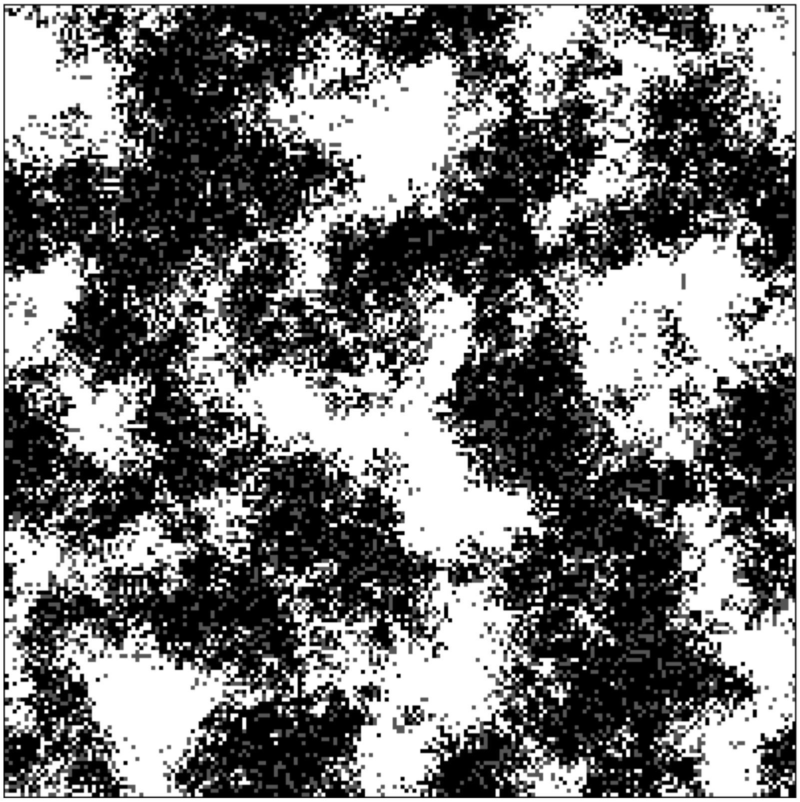

Figure 3: Picture of the range 2 process on the 200×200 square with periodic boundary conditions at time 50 and starting from a Bernoulli product measure. Black sites refer to hosts of type 1 associated with a symbiont, grey sites to unassociated hosts of type 1, and white sites to unassociated hosts of type 2. The parameters are equal to $\gamma_1 = 1$, $\gamma_2 = 0.6$ and $\gamma_3 = 0.76$.

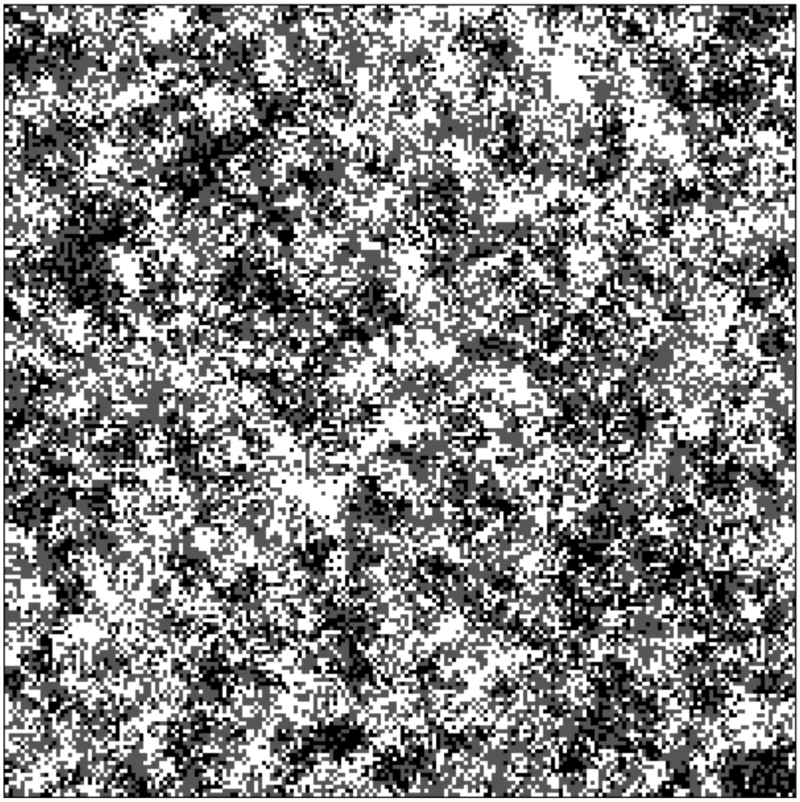

Figure 4: Picture of the range 2 process on the 200×200 square with periodic boundary conditions at time 50 and starting from a Bernoulli product measure. Black sites refer to hosts of type 1 associated with a symbiont, grey sites to unassociated hosts of type 1, and white sites to unassociated hosts of type 2. The parameters are equal to $\gamma_1 = 1$, $\gamma_2 = 1.5$ and $\gamma_3 = 1.15$.