

**Allelopathy in spatially distributed populations:  
A journal replication**

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Date: February 12, 2020

Word Count: 2157

This paper is a term project for the course *PBL Data Science in Ecology* with the Berry Institute, completed during the Fall and early Spring of 2019/2020. It represents a short, independent research project developed and carried out by the student under the supervision and collaboration with the instructor.

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## 1. INTRODUCTION

Classic species coexistence theory predicts that, when a group of species compete for a single limiting resource, the best or most “fit” competitor will drive all the others to extinction (Armstrong and McGehee, 1980; Levin, 1980). Yet we can frequently observe cases in nature when this is not true.

Species coexistence can occur by a number of mechanisms, including differences in species niches across space and time, source-sink and rescue effects, and nonlinear fluctuations in population densities (Hanski, 1999; Hutchinson, 1961, Loreau et al., 2003). Coexistence is often more easily achievable in spatially-explicit versions of ecological models (Hanski, 1999; Loreau et al. 2003). This is because species can find regions of the landscape that are more suitable for growth, from which individuals can disperse and help other populations recover and push themselves away from extinction.

Several studies have reported the coexistence of multiple species of *E. coli* in laboratory experiments (Durrett and Levin, 1997; Levin, 1988). For example, in a spatially structured, dynamic model, a long-term equilibrium may be sustained among three species: a colicin-sensitive (toxin-sensitive) type, a high colicin-producing type, and a “cheater” that expends less on colicin production but is resistant to colicin from other species (Durrett and Levin, 1997).

Durrett and Levin (1997) apply a theoretical model of species population growth to understand how and when *E. coli* populations are able to coexistence in lab media. According to their model, coexistence is more easily achievable in the spatially-explicit version. This is because the spatial landscape provides refugia for species that would otherwise go extinct. In this report, I analyze their 2- and 3-species non-spatial models, and then simulate the two-species model in R. I determine which parameters are most influential in determining equilibrium density.

## 2. MODEL REPLICATION

Following Durrett and Levin (1977), I analyze the 2- and 3-species models and solve for their equilibria. I then numerically investigate the behavior of the 2-species model, coding the model in R and testing which sets of initial conditions take the system to each of its equilibria. The model represents two types of bacteria that produce the toxin colicin at slightly different rates (or different toxicities) that can coexist with a third, colicin-sensitive bacteria.

### 2.1. A two-species model

As with Durrett and Levin (1977), I start with a non-spatial model of two competing species. The model assumes that both species are “well mixed”. This means that both species are evenly distributed in the landscape and interact at a constant rate. The change of the density of each species is given by the equations

$$(1) \quad \frac{du_1}{dt} = \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1$$

$$(2) \quad \frac{du_2}{dt} = \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 - \gamma u_1 u_2$$

where  $u_i$ ,  $\beta_i$ , and  $\delta_i$  represent the density, intrinsic birth rate, and natural death rate for species  $i$ . The parameter  $\gamma$  indicates the rate at which type 1 poisons type 2. In the context of the real-world system, species 1 represents the colicin-producing bacteria. Species 2 represents the colicin-sensitive bacteria.

The system of equations in (1) and (2) has three possible solutions. The first two solutions correspond to cases in which one of the two species dies out. The long-run equilibrium densities of each species can be found by setting equations (1) and (2) equal to zero. Doing so for the first species and dividing by  $u_1$  gives

$$(3) \quad \begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1 = 0 \\ \beta_1 (1 - u_1 - u_2) - \delta_1 &= 0 \end{aligned}$$

If we assume that the second species dies out, then  $u_2 = 0$  and solving (3) in terms of  $u_1$  yields the equilibrium density of species one in the absence of its competitor:

$$(4) \quad u_1^* = \frac{\beta_1 - \delta_1}{\beta_1} = 1 - \frac{\delta_1}{\beta_1}$$

Repeating the same procedure for the second species gives the equilibrium density of species two in the absence of species one:

$$(5) \quad \begin{aligned} \frac{du_2}{dt} &= \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 - \gamma u_1 u_2 = 0 \\ \beta_2 (1 - u_1 - u_2) - \delta_2 - \gamma u_1 &= 0 \\ \beta_2 (1 - u_2) - \delta_2 &= 0 \\ u_2^* &= \frac{\beta_2 - \delta_2}{\beta_2} = 1 - \frac{\delta_2}{\beta_2} \end{aligned}$$

In the absence of the competing species, the equilibrium biomass of the surviving species is determined by its natural death rate and the intrinsic birth rate. It is decreasing with the natural death rate and increasing with the intrinsic birth rate.

In order to solve for the equilibrium biomasses when the two species coexist, we set equations (1) and (2) equal to zero and solve the system of equations simultaneously. We solve a system of two equations for two unknowns. Starting with equation (1), we solve for  $u_2$  as a function of  $u_1$  such that

$$(6) \quad \begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 (1 - u_1 - u_2) - \delta_1 u_1 = 0 \\ u_2 &= 1 - u_1 - \frac{\delta_1}{\beta_1} \end{aligned}$$

We then substitute (6) into equation (2) and solve for the equilibrium value of  $u_1$ . The result can be re-substituted back into (6) to find the equilibrium value of  $u_2$ . Doing so gives

$$\begin{aligned}
\frac{du_2}{dt} &= \beta_2 u_2 (1 - u_1 - u_2) - \delta_2 u_2 - \gamma u_1 u_2 = 0 \\
\frac{\beta_2 \delta_1}{\beta_1} - \delta_2 - \beta_1 \gamma u_1 &= 0 \\
u_1^* &= \frac{\beta_2}{\beta_1} \frac{\delta_1}{\gamma} - \frac{\delta_2}{\gamma} \\
u_2^* &= 1 - \frac{\delta_1}{\beta_1} + \frac{\delta_2}{\gamma} - \frac{\beta_2}{\beta_1} \frac{\delta_1}{\gamma}
\end{aligned}
\tag{7}$$

The equilibrium biomasses of each species depends on model parameters, including the natural birth and death rates of the opposing species. The equilibrium biomass of species 1 is increasing with the intrinsic birth rate of species 2 and the natural death rate of itself; it is decreasing with the intrinsic birth rate of itself and the natural death rate of type 2. The relationship between equilibrium biomass and the rate at which type 1 poisons type 2 is unclear. Whether it increases or decreases equilibrium biomass depends on the values of the natural death rates of each species. The equilibrium biomass of species 2 shows the same relationships to model parameters, but with different signs.

While it may seem strange that the equilibrium biomasses increase with the birth rates of the *other* species and not themselves, the reason has to do with the relative changes in growth in equations (1) and (2) with respect to the biomass of each species. For example, if we focus on equation (1), an increase in the biomass of either species will lead to a negative change in the biomass of species 1. However, relatively speaking, an increase in the biomass of species 2 will lead to a smaller negative change than the same increase in the biomass of species 1 (all else constant).

## 2.2. A three-species model

After analyzing a two-species model, Durrett and Levin (1997) investigate a three-species model. In order to be more comparable to laboratory experiments and a fully-spatial model (not analyzed here),  $u_i$  is the fraction of occupied sites of species  $i$  in the landscape. Then the change in occupied sites for each species is given by

$$(8) \quad \frac{du_1}{dt} = \beta_1 u_1 u_0 - \delta_1 u_1$$

$$(9) \quad \frac{du_2}{dt} = \beta_2 u_2 u_0 - \delta_2 u_2$$

$$(10) \quad \frac{du_3}{dt} = \beta_3 u_3 u_0 - u_3 (\delta_3 + \gamma_1 u_1 + \gamma_2 u_2)$$

where the fraction of unoccupied (empty) sites in the landscape is  $u_0 = 1 - u_1 - u_2 - u_3$ . The parameters  $\beta_i$ ,  $\delta_i$ , and  $\gamma_i$  are defined as before. The main difference between the three-

species model above and the two-species model is that in the two-species model, only one species is affected by the presence of the other species (e.g. only one species produces toxins that poison the other). In three-species model, species 1 and species 2 secrete toxin; species 3 is the only species that is affected by the direct presence of the others. All species indirectly compete for empty patches in the landscape.

As with the two-species model, I solve for the equilibrium fraction of sites occupied by each species in the absence of the other species. I set each equation in (8)-(10) equal to zero and then set the fraction of sites occupied by the competing species equal to zero. Then

$$(11) \quad u_i^* = 1 - \frac{\delta_i}{\beta_i}$$

Like the two-species model, in the absence of competing species, the long-run fraction of occupied sites by species  $i$  is determined by the ratio of its birth and death rates. The equilibrium fraction of occupied sites decreases with the death rate and increases with the birth rate.

Solving for the long-run equilibria where all species coexist is more difficult than in the two-species system. We set all equations in (8)-(10) equal to zero and solve the system of three equations for three unknowns. Doing so gives

$$\begin{aligned} \frac{du_1}{dt} &= \beta_1 u_1 u_0 - \delta_1 u_1 = 0 \\ \beta_1 (1 - u_1 - u_2 - u_3) - \delta_1 &= 0 \end{aligned}$$

$$(12) \quad u_1 = 1 - u_2 - u_3 - \frac{\delta_1}{\beta_1}$$

$$\begin{aligned} \frac{du_2}{dt} &= \beta_2 u_2 u_0 - \delta_2 u_2 = 0 \\ \beta_2 (1 - u_1 - u_2 - u_3) - \delta_2 &= 0 \\ \beta_2 \left( 1 - \left( 1 - u_2 - u_3 - \frac{\delta_1}{\beta_1} \right) - u_2 - u_3 \right) - \delta_2 &= 0 \end{aligned}$$

$$(13) \quad \frac{\beta_2 \delta_2}{\beta_1} - \delta_2 = 0 \rightarrow u_2^* = 0$$

$$\begin{aligned} \frac{du_3}{dt} &= \beta_3 u_3 u_0 - u_3 (\delta_3 + \gamma_1 u_1 + \gamma_2 u_2) = 0 \\ \beta_3 \left( 1 - u_3 - \frac{\delta_1}{\beta_1} \right) - \delta_3 - \gamma_1 \left( 1 - u_3 - \frac{\delta_1}{\beta_1} \right) &= 0 \end{aligned}$$

$$(14) \quad u_3^* = \frac{\beta_1 (\gamma_1 + \delta_3) - \delta_1 (\gamma_1 + \beta_3)}{\beta_1 \gamma_1}$$

Finally, substituting (13) and (14) into (12) and simplifying gives the equilibrium number of patches occupied by species 1 such that,

$$u_1^* = 1 - \left[ \frac{\beta_1(\gamma_1 + \delta_3) - \delta_1(\gamma_1 + \beta_3)}{\beta_1\gamma_1} \right] - \frac{\delta_1}{\beta_1}$$

$$(15) \quad u_1^* = \frac{\delta_1\beta_3 - \beta_1\delta_3}{\beta_1\gamma_1}$$

Given the construction of the model, coexistence of all three species is not possible. The third species always survives, while the first or second goes extinct. (Whether it is the first or second depends on the ordering of solving the system of equations. If the first species is extirpated, then the equilibrium occupancy of species two will resemble (15) but with its growth, death, and interaction terms.) The reason for this is that all species indirectly compete for available patches, with species 1 and 2 being more dominant and one of those two driving the other to extinction. Species 3, which is directly, negatively affected by the presence of species 1 or 2, exists at a low population size. The resulting proportion of occupied patches by the two surviving species depends on the relative combinations of growth, death, and interaction terms.

### 2.3. Numerical simulations

I simulated the two-species system from equations (1)-(2) using a first-order Euler approximation with a step size of 0.1. Simulations were run with sufficient time for each system to reach its long-term equilibrium. All parameter values were set according to Durrett and Levin (1997).

In my numerical simulations, coexistence was not possible. Even if we start close to the coexistence equilibrium, eventually at least one of the species in the system dies out (Figure 1). The effects of competition for empty sites and toxin secretion are strong enough to always lead to the extinction of one species. Lowering the effect of toxin secretion increases the time of coexistence; turning toxin secretion off leads to the most efficient species (in terms of balancing growth and death) to eventually dominate.

## 3. DISCUSSION

In this paper, I reproduced the analytical results of the two- and three-species bacteria models of Durrett and Levin (1997). In the two-species model, I found that the equilibrium densities were determined by ratios between the intrinsic birth rate, natural death rate and interaction rate. There exists a coexistence equilibrium, but I was unable to attain this in numerical simulations. In the three-species model, coexistence of all three species was not possible. For the two remaining species, the resulting proportion of occupied patches at equilibrium depended on the relative growth, death, and the interaction parameters.

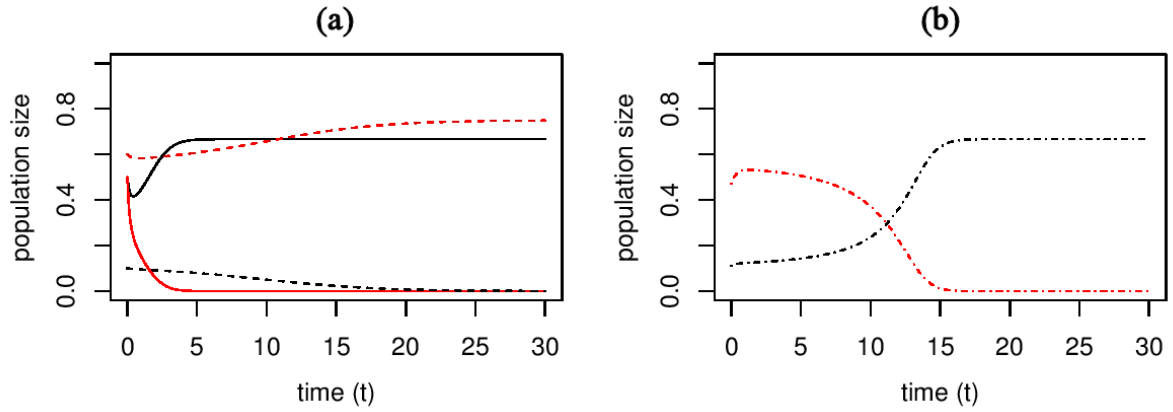


Figure 1. Numerical simulations for the two-species model. Line color indicates species 1 (black) and species 2 (red). Line style shows paired trajectories of each species over different initial conditions (solid, dashed, dot-dashed). In (b), initial conditions were set close to the coexistence equilibrium. Model parameters are:  $\alpha_1 = 3$ ,  $\alpha_2 = 4$ ,  $\delta_1 = 1$ ,  $\delta_2 = 1$ , and  $\gamma = 3$ .

According to Durrett and Levin (1997), two types of bacteria that produce colicin at slightly different rates (or with different toxicities) can coexist in the long-term with a third, colicin-sensitive, type. The reason why they can coexist is largely because they exist in a spatially-structured environment: colicin-producing bacteria find refugia where they can persist at low densities and invade regions where the other species dominate. Colicin-producing bacteria can then partially regulate populations of colicin-sensitive types by imposing additional mortality, the level of which is determined by the cost of producing colicin. There are regions of the landscape where colicin production is advantageous, and other regions where it is not.

However, as demonstrated, in the non-spatial model coexistence was not possible. There is a tradeoff between the costs and benefits of colicin production, and the model does not allow a mix of regions or times when colicin production is advantageous or disadvantageous. It is either one or the other. In a spatial environment, parts of the landscape may favor the production of colicin while other parts may not, which favors the coexistence of both colicin-producing and colicin-sensitive species across the entire landscape (Levin, 1988).

When it comes to reality, these results show that space can be important if we need to manage a group or groups of species. Space can provide refugia where they can persist and grow and prevent one species from being too dominant. This idea is true for preserving a single species like the checkerspot butterfly or snowshoe hare (Griffin and Mills, 2009; Harrison et al., 1988) or groups of individual species (Loreau et al., 2003). For an endangered species, if we have populations that are isolated from each other, we could try to increase the connectivity between them with corridors between habitat patches to decrease the probability of extinction or help population recover. If we wanted to increase overall biodiversity, then we could manage the landscape to increase the number of microhabitats, providing different environmental conditions that could be advantageous for a more diverse set of species.

#### 4. REFERENCES

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