

Competition Model for Two Exotic Species and One Native Species

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Abstract

The spread of two exotic plant species and the corresponding replacement of a single native species is examined as a competition model with spatial considerations. The general model is a system of three Lotka-Volterra type nonlinear reaction-diffusion equations. The traveling wave solution is examined, giving conditions for minimum wave speed for the exotic species. The work is based on the case of Russian olive trees and tamarisks in the cottonwood woodlands of New Mexico.

1 Introduction

The consideration of spatial factors in ecological modeling has led to a variety of interesting problems in the current literature (see Neuhauser [6]). Besides better explaining the development of biological phenomena, the resulting models can lead to interesting mathematics. The specific interest here is the spread of exotic species in competition with a native species. The addition of a spatial diffusion term to the model of two interacting populations is described in Murray [5], Okubo [7] and Fife [1]. A seminal paper concerning invasive species by Okubo, et al. [8], models the spread of grey squirrels displacing red squirrels in Britain during the twentieth century. Among the key results was a minimum speed of propagation (or wave speed) for the wave front of the invasive species.

When speaking about competition, it is natural to examine the interaction between two species, and much of the literature, both biological and mathematical, has done just this. Mathematically, work has been done on generalizing the problem of multispecies competition to any number of species, though there seems to be few biological studies that examine this scenario. One situation where three species compete with each other occurs in the southwestern United States. In parts of New Mexico, native cottonwood trees have to contend with two introduced, invasive species: tamarisks (known also as saltcedar) and Russian olives. Usually only one of the two invaders is present, but there are regions where both exist (which the author can confirm personally), such as along sections of the Rio Grande in northern New Mexico. The system of equations that will be examined in this paper are based on the interaction of these three species, though many of the results can be generalized.

The governing equations are developed in Section 2, including model assumptions based on the particular species examined here. The main goal here is to find the a possible spreading for the exotics/invaders by searching for a minimum traveling wave speed. The traveling wave solution is analyzed in Section 3, leading to restrictions on the speed of propagation. Further work is detailed in Section 4.

2 Model

It is necessary to mention a few biological assumptions about the spatial nature of the population dynamics studied here before developing the system of equations. In this model, it is assumed that the native cottonwood population does not diffuse spatially; essentially it starts out in equilibrium with its environment. Additionally, the model will have the exotics out-competing cottonwood when both co-exist, something seem to be especially true in the case of Russian olive trees [4]. In some geographical regions, the cottonwoods may in fact diffuse and do not seem to be at a competitive disadvantage compared to tamarisks. There have been some studies that suggest when the environment is allowed to return to a more 'natural' state (especially with regards to flood control), that the two species will co-exist,

or the cottonwood will become the dominant species once again (see Stromberg [11], and Sher, et al. [9]). Here, however, it is assumed that the environmental factors in the relevant riparian zones are such that the tamarisk does out-compete cottonwood. In contrast, the two exotic invasive species will both be allowed to spread out spatially with neither one necessarily have a competitive advantage over the other. It should be noted that because of the semi-arid to arid climate, the three species tend to exist predominantly in riparian zones, and so analysis is confined to a single spatial direction.

2.1 Governing Equations

The development of the basic model for the spread of an invasive species is given in Shigesada and Kawasaki [10]. There are a number of different models for population growth including a diffusive term; perhaps the most commonly used for competition between species is based related to the Fisher equation [2],

$$u_t = Du_{xx} + (\varepsilon - \mu u)u \quad (1)$$

where D is the diffusion coefficient, ε the intrinsic rate of increase and μ the intra-species competition coefficient. Adding interspecies competition will give an additional term to the governing dynamics for each population under consideration. In the specific case examined here, the native species does not spread by diffusion, resulting in the following system of equations:

$$\begin{aligned} u_t &= D_1 u_{xx} + (\varepsilon_1 - \mu_{11}u - \mu_{12}v - \mu_{13}w)u \\ v_t &= D_2 v_{xx} + (\varepsilon_2 - \mu_{21}u - \mu_{22}v - \mu_{23}w)v \\ w_t &= (\varepsilon_3 - \mu_{31}u - \mu_{32}v - \mu_{33}w)w, \end{aligned} \quad (2)$$

where D_i is the diffusion rate, ε_i is the intrinsic growth rate, μ_{ij} the interaction coefficient of species j effecting species i , and the carrying capacity is ε_i/μ_{ii} . The Russian olive population is given by $u(x, t)$, tamarisk by $v(x, t)$, and cottonwood by $w(x, t)$. All parameters are taken as constants.

3 Traveling Waves

The traveling wave solution for (2) should give insight as to the spreading speed for the invasive species, given appropriate initial conditions. This type of solution also can give some insight to the qualitative nature of the solution, such as whether or not there are oscillations and when then could occur. There are a number of books which discuss how to find a traveling wave solution, such as Volpert, et al. [12], and Murray [5], the latter of which focuses on the development for biological applications.

A new space-time independent variable is defined as $z = x - ct$. Then we have $u(x, t) = U(z)$ and similarly for v and w . Using the chain rule, the system (2) then becomes the system of ordinary differential equations

$$\begin{aligned} D_1 U'' - cU' - (\varepsilon_1 - \mu_{11}U - \mu_{12}V - \mu_{13}W)U &= 0 \\ D_2 V'' - cV' - (\varepsilon_2 - \mu_{21}U - \mu_{22}V - \mu_{23}W)V &= 0 \\ -cW' - (\varepsilon_3 - \mu_{31}U - \mu_{32}V - \mu_{33}W)W &= 0. \end{aligned} \quad (3)$$

Converting this into a system of first order equations allows for five-dimensional phase space analysis:

$$\begin{aligned} U' &= \phi \\ \phi' &= -(\varepsilon_1 - \mu_{11}U - \mu_{12}V - \mu_{13}W)U \\ V' &= \psi \\ \psi' &= -(\varepsilon_2 - \mu_{21}U - \mu_{22}V - \mu_{23}W)V \\ W' &= -(\varepsilon_3 - \mu_{31}U - \mu_{32}V - \mu_{33}W)W. \end{aligned} \quad (4)$$

The phase space analysis yields eight singular states:

$$(0, 0, 0, 0, 0)$$

$$\begin{aligned}
& \left(\frac{\varepsilon_1}{\mu_{11}}, 0, 0, 0, 0 \right) \\
& \left(0, \frac{\varepsilon_2}{\mu_{22}}, 0, 0, 0 \right) \\
& \left(0, 0, \frac{\varepsilon_3}{\mu_{33}}, 0, 0 \right) \\
& \left(\frac{\varepsilon_2\mu_{12} - \varepsilon_1\mu_{22}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}, \frac{\varepsilon_2\mu_{11} - \varepsilon_1\mu_{21}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}, 0, 0, 0 \right) \\
& \left(\frac{\varepsilon_3\mu_{13} - \varepsilon_1\mu_{33}}{\mu_{11}\mu_{33} - \mu_{13}\mu_{31}}, 0, \frac{\varepsilon_3\mu_{11} - \varepsilon_1\mu_{31}}{\mu_{11}\mu_{33} - \mu_{13}\mu_{31}}, 0, 0 \right) \\
& \left(0, \frac{\varepsilon_3\mu_{23} - \varepsilon_2\mu_{33}}{\mu_{22}\mu_{33} - \mu_{23}\mu_{32}}, \frac{\varepsilon_3\mu_{22} - \varepsilon_2\mu_{32}}{\mu_{22}\mu_{33} - \mu_{23}\mu_{32}}, 0, 0 \right) \\
& \left(\frac{-\left(\varepsilon_1\mu_{32}\mu_{23} - \varepsilon_1\mu_{22}\mu_{33} + \mu_{12}\varepsilon_2\mu_{33} - \mu_{12}\mu_{23}\varepsilon_3 + \mu_{13}\mu_{22}\varepsilon_3 - \mu_{13}\mu_{32}\varepsilon_2\right)}{-\mu_{11}\mu_{32}\mu_{23} - \mu_{21}\mu_{12}\mu_{33} + \mu_{11}\mu_{22}\mu_{33} - \mu_{22}\mu_{31}\mu_{13} + \mu_{31}\mu_{12}\mu_{23} + \mu_{32}\mu_{21}\mu_{13}}, \right. \\
& \quad \frac{\mu_{11}\varepsilon_2\mu_{33} - \mu_{11}\mu_{23}\varepsilon_3 + \mu_{21}\mu_{13}\varepsilon_3 - \varepsilon_2\mu_{31}\mu_{13} + \mu_{23}\mu_{31}\varepsilon_1 - \mu_{21}\varepsilon_1\mu_{33}}{-\mu_{11}\mu_{32}\mu_{23} - \mu_{21}\mu_{12}\mu_{33} + \mu_{11}\mu_{22}\mu_{33} - \mu_{22}\mu_{31}\mu_{13} + \mu_{31}\mu_{12}\mu_{23} + \mu_{32}\mu_{21}\mu_{13}}, \\
& \quad \left. \frac{-\left(-\mu_{11}\mu_{22}\varepsilon_3 + \mu_{11}\mu_{32}\varepsilon_2 - \mu_{32}\mu_{21}\varepsilon_1 + \mu_{21}\mu_{12}\varepsilon_3 - \mu_{31}\mu_{12}\varepsilon_2 + \mu_{22}\mu_{31}\varepsilon_1\right)}{-\mu_{11}\mu_{32}\mu_{23} - \mu_{21}\mu_{12}\mu_{33} + \mu_{11}\mu_{22}\mu_{33} - \mu_{22}\mu_{31}\mu_{13} + \mu_{31}\mu_{12}\mu_{23} + \mu_{32}\mu_{21}\mu_{13}}, 0, 0 \right),
\end{aligned}$$

where the points correspond to (U, V, W, ϕ, ψ) . These are the same as the steady states for the spatial independent version of (2), except for the presence of ϕ and ψ , which are found to be zero at every point listed above.

A traveling wave solution should go from an unstable steady state to a stable one. Here we want to examine what happens when two new species enter an environment where an existing species already is present, which corresponds to the boundary conditions

$$U(-\infty) = 0, \quad V(-\infty) = 0, \quad W(-\infty) = \frac{\varepsilon_3}{\mu_{33}}$$

$$U(\infty) = \frac{\varepsilon_2\mu_{12} - \varepsilon_1\mu_{22}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}, \quad V(\infty) = \frac{\varepsilon_2\mu_{11} - \varepsilon_1\mu_{21}}{\mu_{11}\mu_{22} - \mu_{12}\mu_{21}}, \quad W(\infty) = 0. \quad (5)$$

The boundary value problem under considerations is thus (4) and (5). Linearizing the system about the point $(0, 0, \frac{\varepsilon_3}{\mu_{33}}, 0, 0)$, i.e. the steady state where $U = 0$, $V = 0$ and $W = \varepsilon_3/\mu_{33}$, the eigenvalues are found to be

$$\begin{aligned}
\lambda_1 &= \frac{\varepsilon_3}{c}, \\
\lambda_2, \lambda_3 &= \frac{1 - \mu_{33} \pm \sqrt{\mu_{33}^2 c^2 - 4\mu_{33}^2 D_2 \varepsilon_2 + 4\mu_{33} D_2 \mu_{23} \varepsilon_3}}{2\mu_{33} D_2}, \\
\lambda_4, \lambda_5 &= \frac{1 - \mu_{33} \pm \sqrt{\mu_{33}^2 c^2 - 4\mu_{33}^2 D_1 \varepsilon_1 + 4\mu_{33} D_1 \mu_{13} \varepsilon_3}}{2\mu_{33} D_1}.
\end{aligned}$$

The point around which the system was linearized corresponds to the wave front for the traveling wave, representing the point where a small number of invaders enter the ecological system. In the region around the wave front there is a requirement that the solution is not oscillatory, since this would correspond to a biologically impossible situation (i.e., negative invasive populations). This is overcome by imposing the conditions

$$c \geq 2\sqrt{\varepsilon_1 D_1 \left(1 - \frac{\varepsilon_3 \mu_{13}}{\varepsilon_1 \mu_{33}}\right)}, \quad (6)$$

$$c \geq 2\sqrt{\varepsilon_2 D_2 \left(1 - \frac{\varepsilon_3 \mu_{23}}{\varepsilon_2 \mu_{33}}\right)}, \quad (7)$$

with U , V , and W all non-negative. Thus there is a minimum wave speed c^* , the exact value of which depends on which of the two conditions above is larger. These conditions assume that the two species were introduced at the same time and place. The minimum wave speed for two species competition is very similar:

$$c \geq 2\sqrt{\varepsilon_1 D_1 \left(1 - \frac{\varepsilon_3 \mu_{13}}{\varepsilon_1 \mu_{33}}\right)}. \quad (8)$$

Okubo, et al. [8] found that the minimum wave speed (8) closely corresponds to the actually spreading speed calculated with reasonable parameter values. This case is further discussed in Shigesada and Kawasaki [10].

4 Comments and Future Directions

The minimum speed of propagation was found for the two exotic species, assuming that they were introduced at the same time and place into the ecological community. Since the two exotics used in the specific model here were both introduced to New Mexico in the late 19th century, it would be interesting to see how accurately the real spreading speed matches the theoretical ones given above, perhaps through numerical simulations.

One concern comes from a paper by Hosono [3], who showed that the minimum wave speed found for the two species model does not correspond to a valid spreading speed for all parameter values. There is no corresponding property for multispecies competition. Further work needs to be done in this direction.

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