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Original Research Article

Numerical simulations of a population dynamic model describing parasite destruction in a wild type pine forest

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ABSTRACT

We consider a population dynamic model describing the growth of wild pine tree forest. This type of model incorporates the demography of the tree population (i.e. reproduction and death of trees), and also incorporates a maturation time that depends on the number of adult trees.

The goal of this article is to introduce a parasite called nematode into such a forest. Since this parasite colonizes pine trees to reproduce, it is natural to introduce a predator-prey (or consumer-resource) relationship between the trees and the parasites.

In order to investigate the behaviour of the resulting system, we will use numerical simulations, and we will introduce a parasite into a population of trees that: (1) is not oscillating around the positive equilibrium; (2) has some damped oscillations; (3) has some undamped oscillations. This will correspond to three scenarios for parameter values. As one may expect, this will lead to complex dynamics, since we combine the oscillations produced by the predator-prey system with the oscillations coming from the demographic properties of the prey.

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1. Introduction

Pine wilt disease (PWD) is one of the most serious disease of pine species in all over the world. The pathogenic agent of PWD is the pine wood nematode (PWN) *Bursaphelenchus xylophilus*, and it is transmitted from tree to tree by a species of insect *Monochamus*. This PWN is a native nematode species in North America. It was first introduced in Japan in the early 20th century and spreaded into other Asian countries (China, Korea, etc.) in the 1980s. In 1999, it was first detected in Portugal (Mota et al., 1999) and its only insect vector in this region was *Monochamus galloprovincialis* (Sousa et al., 2001, 2002). In 2008, with the detection of this PWN in other areas of Portugal and even on Madeira Island, the entire territory of Portugal was affected (Rodrigues, 2008). PWD also spreads into other European countries due to the wood transportation. For more information about the spread of PWD in Europe and in the world, we refer in addition to Mota et al. (2009); Mota and Vieira (2008); Vicente et al. (2012) and the references therein.

In this paper we consider the population of nematode, which is a parasite spreading into a wild pine tree forest. This means that we totally neglect the way the nematode spreads in between the pine trees, namely the insect vector *Monochamus galloprovincialis*. The life cycle of nematode is very short (around 4 days). In comparison, the pine tree's life cycle is rather slow. Therefore it makes sense to use instantaneous production of new nematodes when pine trees are degraded by nematodes and serve as a resource to produce new nematodes. We refer to Koutroumpa (2007) for more information about the biology of nematode.

There have been some attempts to build a model to describe the dynamics in the pine-nematode community (Gruffudd et al., 2016 and the references therein). In this paper, in order to describe the relationship between pine trees and nematodes, we will use a predator-prey system which goes back to Lotka (1925) and Volterra (1927, 1928) in the early 20th century. More generally speaking, the class of system we have in mind is the so-called consumer-resource model which attracts a lot of interests in ecology during the last four decades. We refer to Holland and DeAngelis (2009, 2010); Lafferty et al., (2015); MacArthur (1972); May (1972); Rosenzweig and MacArthur (1963) and the references therein for a nice overview on this subject. Let $A(t)$ be the number of adult pine trees, and $I(t)$ be the number of nematodes. We consider a simplified

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model for the population dynamics of pine trees and nematodes

$$\begin{cases} \dfrac{dA(t)}{dt} = (\beta - \mu_A)A(t) - \underbrace{\dfrac{\gamma_A I(t)A(t)}{1+\kappa A(t)}}_{\text{pine tree destruction}}, \\ \dfrac{dI(t)}{dt} = \left(\underbrace{\dfrac{\varepsilon\chi\gamma_A A(t)}{1+\kappa A(t)}}_{\text{production of new nematodes}} - \mu_I\right) I(t), \end{cases} \tag{1.1}$$

where $\beta > 0$ is the birth rate of trees, $\mu_A > 0$ is the natural mortality of adult trees, $\gamma_A > 0$ is the number of adult trees consumed per nematode per unit time, $\kappa \geqslant 0$ is interpreted as a constant handling time for each prey captured (Accolla, 2015; Dawes and Souza, 2013; Kazarinoff and Driessche, 1978), $\varepsilon > 0$ is the conversion efficiency from tree biomass to nematode biomass, $\chi > 0$ is the birth rate of nematodes, $\mu_I > 0$ is the natural mortality of nematodes.

One may observe that the special case $\kappa = 0$ of system (1.1) corresponds to the classical Lotka-Volterra model, while the case $\kappa > 0$ corresponds to the Holling's type II functional response (Holling, 1959a, 1959b). In the article we will investigate both cases for κ.

In order to incorporate the vital dynamics of the population of trees, we need to add a limitation of the growth of trees due to the competition for light. This can be achieved by using the so-called size-structured models. We refer to Magal and Zhang (2017a); Smith (1993, 1994); Webb (2008) for a nice survey on this topic. In Magal and Zhang (2017a) a comparison of size-structured model with a forest computer simulator has been successfully done, and the model considered takes the following form

$$\begin{cases} \partial_t u(t,s) + f(A(t))\partial_s u(t,s) = -\mu(s)u(t,s), \text{ for } t \geqslant 0, s \geqslant s_-, \\ f(A(t))u(t,s_-) = \beta A(t), \text{ for } t \geqslant 0 \end{cases} \tag{1.2}$$

with the initial distribution of trees

$$u(0,.) = u_0(.) \in L^1(0,+\infty),$$

where $s_- > 0$ is the minimal size of juvenile trees and $s \mapsto u(t,s)$ is the density of population of trees of size s at time t, which means that for each $s_2 \geqslant s_1 \geqslant s_-$,

$$\int_{s1}^{s2} u(t,s)ds$$

is the number of trees of size in between s_1 and s_2 at time t. Therefore the total number of trees in the population is

$$U(t) = \int_{s_-}^{+\infty} u(t,s)ds.$$

We assume that the number of adult and juvenile trees are respectively given by

$$A(t) := \int_{s^*}^{+\infty} u(t,s)ds \text{ and } J(t) := \int_{s_-}^{s^*} u(t,s)ds$$

where $s^* > s_-$ is the size of maturity for trees, namely the minimal size of adult trees.

Moreover, to describe the fact that the more adult trees there are, the less light is left to juvenile trees to grow, we assume that the growth speed depends on the number of adults, namely

$$f(A(t)) := \frac{\alpha}{1+\delta A(t)},$$

where $\alpha > 0$ and $\delta > 0$ are parameters that will be determined later on.

The full model combining both the parasite destruction and the vital dynamics of the population of tree is the following

$$\begin{cases} \partial_t u(t,s) + f(A(t))\partial_s u(t,s) = -\left[\mu(s) + \dfrac{\gamma(s)I(t)}{1+\kappa A(t)}\right]u(t,s), \\ \text{for } s \geqslant s_-, t \geqslant 0, f(A(t))u(t,s_-) = \beta A(t), \text{ for } t \geqslant 0, \dfrac{dI(t)}{dt} \\ \qquad = \dfrac{\varepsilon\chi}{1+\kappa A(t)} \displaystyle\int_{s_-}^{+\infty} \gamma(s)u(t,s)ds I(t) \\ \qquad - \mu_I I(t), \text{ for } t \geqslant 0, \end{cases} \tag{1.3}$$

with the initial distributions

$$u(0,.) = u_0(.) \in L^1(0,+\infty);\ I(0) = I_0 \geqslant 0.$$

In system (1.3) $\mu(s) > 0$ is the mortality of trees of size s and $\gamma(s) \geqslant 0$ is the number of trees of size s consumed per nematode per unit time. We assume for simplicity that

$$\mu(s) = \begin{cases} \mu_A > 0, \text{ if } s \geqslant s^*, \\ \mu_J > 0, \text{ if } s < s^*, \end{cases} \gamma(s) = \begin{cases} \gamma_A \geqslant 0, \text{ if } s \geqslant s^*, \\ \gamma_J \geqslant 0, \text{ if } s < s^*. \end{cases}$$

As is described in Appendix A (see also Magal and Zhang, 2017a; Smith, 1993, 1994), we can transform system (1.3) into the following state-dependent delay differential equations

$$\begin{cases} \dfrac{dA(t)}{dt} = f(A(t))\dfrac{\beta A(t-\tau(t))}{f(A(t-\tau(t)))} e^{-\mu_J \tau(t) - \gamma_J \int_{t-\tau(t)}^{t} \frac{I(l)}{1+\kappa A(l)} dl} - \mu_A A(t) - \dfrac{\gamma_A I(t)A(t)}{1+\kappa A(t)}, \\ \int_{t-\tau(t)}^{t} f(A(\sigma))d\sigma = s^* - s_-, \\ \dfrac{dI(t)}{dt} = \left[\dfrac{\varepsilon\chi}{1+\kappa A(t)}(\gamma_A A(t) + \gamma_J J(t)) - \mu_I\right] I(t), \end{cases} \tag{1.4}$$

with the initial distributions

$$A(t) = A_0(t) \geqslant 0, \forall t \in (-\infty, 0] \downarrow\ \tau(0) = \tau_0 \geqslant 0 \downarrow\ I(0) = I_0 \geqslant 0.$$

In system (1.4), the function $\tau(t)$ describes the time needed by a tree to grow to the maturity size s^* at time t from the minimal size s_-. Namely $\tau(t)$ the time needed for a tree to become mature at time t. Then we must have $\tau_0 \geqslant 0$ the initial length of maturation satisfying

$$\int_{-\tau_0}^{0} f(A_0(\sigma))d\sigma = s^* - s_-,$$

and the second equation of (1.4) is equivalent to

$$\int_{t-\tau(t)}^{t} f(A(\sigma))d\sigma = \int_{-\tau_0}^{0} f(A_0(\sigma))d\sigma,$$

where the initial value $\tau(0) = \tau_0$ is derived. Therefore we can fix either $\tau(t)$ at time $t = 0$, or equivalently $s^* - s_-$, which is the difference between the size of maturity s^* and the size at birth s_-. A detailed explanation will also be found in Appendix A.

In the following we will assume for simplicity that $\gamma_A > 0$ and $\gamma_J = 0$. Therefore in this article we consider the following model

$$\begin{cases} \dfrac{dA(t)}{dt} = f(A(t))\dfrac{\beta A(t-\tau(t))}{f(A(t-\tau(t)))} e^{-\mu_J \tau(t)} - \mu_A A(t) - \dfrac{\gamma_A I(t)A(t)}{1+\kappa A(t)}, \\ \int_{t-\tau(t)}^{t} f(A(\sigma))d\sigma = \int_{-\tau_0}^{0} f(A_0(\sigma))d\sigma, \\ \dfrac{dI(t)}{dt} = \left(\dfrac{\varepsilon\chi\gamma_A A(t)}{1+\kappa A(t)} - \mu_I\right) I(t) \end{cases} \tag{1.5}$$

with the initial distributions

$$A(t) = A_0(t) \geqslant 0, \forall t \in (-\infty, 0] \downarrow\ \tau(0) = \tau_0 \geqslant 0 \downarrow\ I(0) = I_0 \geqslant 0.$$

The first basic fact about system (1.5) is that when $I_0 = 0$ then

$$I(t) = 0, \forall t \geqslant 0.$$

Therefore $I_0 = 0$ corresponds to the model without parasite, namely Eq. (1.2).

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