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The drift paradox in population dynamics:
Conditions for population persistence and travelling waves

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Finally, the support of my family and friends has been invaluable to me. It is safe to say that this thesis would not have been possible without the support and help of all those people.
This thesis is founded on the paper [Pachepsky], which discusses the "drift paradox": how can a population, living in a stream, survive without being washed away? Initially it was the plan to elaborate on the paper in the direction of interacting populations living together in a stream. However, when starting with a detailed study of [Pachepsky], several questions arose - some relating to mistakes or misprints, others to more mathematically oriented, eg. whether one could rigorously prove the existence of travelling waves/ population fronts.

In this master thesis the reader will therefore find elaborations in detail on mathematical results that were simply stated in [Pachepsky] without proof, or that provide corrections to results in this paper. The study of the travelling wave problem resulted in a novel approach to study the existence of a heteroclinic orbit in the three dimensional system, by considering regions in a state space and arguments for exclusion of existence of trajectories from one region to another. A graphical representation of these relations allow to draw conclusions on possible behaviours in the 3D system.
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1 Introduction

On earth there are billion of ecosystems that are the habitats of many different organisms. Lots of these ecosystems contain unidirectional water currents, very strong or weak, because of the biased downstream flow. Examples of such systems are oceans, rivers, streams, creeks but also your intestines. Comparing these systems, it is understandable that the biotic environment in streams and creeks is more conducive for growth and reproduction of aquatic organisms than oceans and rivers. But how is it possible that aquatic organisms with a low motility can persist in ecological systems like streams and creeks without being swept downstream into large rivers or oceans? In other words: How do creek and river populations avoid extinction? Without a mechanism that ensures that individuals of a population can move upstream, any small advection will ensure that the average location of the population will move downstream. So this will lead to extinction of the population in its own habitat. This phenomenon of persistence for populations subjected to continuous advection is called "the drift paradox". In this thesis we look which factors play an important role in the drift paradox and how they interact. Examples of such factors are diffusion, advection speed, domain size and growth rate.

After this problem was recognized by Hans Robert Müller in 1954 [9], many mathematicians have done research about it. They all had their own hypotheses about the mechanism of the upstream movement. Müller thought for example that adult insects balance out the downward drift of the insect larvae by flying upstream to deposit eggs, while some others thought that insects crawl back upwards using the benthos (bottom of the stream) [4].

Speirs and Gurney were the first who came up with a system which was a good but simple representation of a population residing in a small river subject to advection (stream flow) and diffusion (representing random movement). This model is as follows:

$$\frac{\partial n}{\partial t} = f(n)n + D\frac{\partial^2 n}{\partial x^2} - v\frac{\partial n}{\partial x}. \quad (1)$$

Here, $n(x,t)$ is the density of the population per unit area, $f(n)$ the local per capita growth rate of the population, $D$ the diffusion coefficient and $v$ the advection speed.

In this thesis, we examine the model proposed by [Pachepsky]. We start with extending the model of Speirs and Garney [4] by dividing the population into two interacting compartments, individuals living on the benthos and individuals drifting in the flow. We assume that the rate of entering the drift compartment is constant. Secondly, we derive necessary and sufficient conditions for persistence of the population. Next, we transform the extended model using logistic growth and travelling wave coordinates and we assume that there exists a travelling wave between the two found steady states. We do this because we will study the existence of a heteroclinic orbit between the steady states. We will
find necessary conditions with the assumption there exists a heteroclinic orbit between the steady states. Finally, we calculate the propagation speeds of the travelling waves.

1.1 Outline.

This thesis is organized as follows. In Section 2, we explain the extension of the model of Speirs and Gurney [5]. We also give a few assumptions that are applicable during this entire thesis.

In Section 3 we study persistence of the population. In Section 2 we have divided the population into two interacting compartment, individuals living on the benthos and individuals drifting in the flow. The per capita rate at which individuals in the benthic population enter the drift is given by \( \mu \). In Section 3.1 we consider the case \( \mu \geq 1 \). We start with deriving the explicit solution of \( n_b(x,t) \). Then we show in 3.1.1-3.1.4 that we will find the same condition for population persistence if we assume that \( n_b(x,0) = 0 \). With this condition we will also calculate the critical domain size with respect to the advection speed necessary for population persistence. In Section 3.2 we show that the population, irrespective of the domain length and the advection speed, will always persist for \( \mu < 1 \).

In Section 4 we consider spatial spread of the population in time. Because there is advection in our system, we need to distinguish between the propagation speed downstream (in the direction of advection) and upstream (against the advection). In Section 4.1 we consider the system, defined in Section 3, with logistic growth and we determine the steady states of the system that we obtained. In Section 4.2 we assume there exists a travelling wave between the two found steady states, a zero and a non-zero steady state. We recast the current system into travelling wave coordinates and then transform it into a system of first-order equations.

In Section 4.3 we derive necessary conditions for the existence of a heteroclinic orbit between the steady states by studying the phase portraits. From Sections 4.1 and 4.2 we found two steady states and a 3-dimensional system in which the nullclines all intersect each other. We consider the spaces that are separated by the nullclines as regions and study, with the assumption there exists a heteroclinic orbit between the steady states, through which regions an orbit must go to reach the other steady state. We split Section 4.4 up in two subsections. In Section 4.4.1 we linearise the system, found in Section 4.2, around the steady states and in Section 4.4.2 we determine the possible dimension of the stable and unstable manifolds of the steady states.

In Section 4.5 we also derive necessary conditions for the existence of a heteroclinic orbit between the steady states. Again with the assumption there exists one. But in contrast to Section 4.3, we focus in this section on the dimen-
sion of the stable and unstable manifolds. We will also determine the critical propagation speeds of the travelling waves. With the critical propagation speed we mean the transition propagation speed of the travelling waves in which we certainly know there does not exist a heteroclinic orbit and in which there could exist a heteroclinic orbit.
2 The model

We extend the system of Speirs and Gurney [5] by dividing the population into two interacting compartments, individuals living on the benthos and individuals drifting in the flow, following [Pachepsky]. We consider a population where individuals can only reproduce on the benthos and enter the water column to drift until they settle on the benthos again. Reproduction only occurs on local scale. Transfer between individuals on the benthos and in the drift are modelled Poisson processes. This means that the number of individuals on the benthos that enter the water column to drift is Poisson distributed. The same holds for individuals in the drift that settle on the benthos. The movement of an individual is expressed as a combination of advection and diffusion. We assume that the stream advection is uniform in the horizontal and vertical directions. The movement of an individual by advection represents the uniform stream flow. The movement of an individual by diffusion represents individual swimming and the heterogeneous stream flow.

We assume the domain to be the one-dimensional interval \((0, L)\), representing a stream reach. This yields the following system

\[
\begin{align*}
\frac{\partial n_d}{\partial t} &= \mu n_b - \sigma n_d + D \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x}, \\
\frac{\partial n_b}{\partial t} &= f(n_b) n_b - \mu n_b + \sigma n_d,
\end{align*}
\]

(2)

where \(x = 0\) is the top of the stream reach and \(x = L\) the end. Note that \(\mu, \sigma, v, D, f(n_b) > 0\), are described as follows

- \(n_b\) is the population density on the benthos.
- \(n_d\) is the population density in the drift.
- \(f(n_b)\) is the per capita rate of increase of the benthic population.
- \(\mu\) is the per capita rate at which individuals in the benthic population enter the drift.
- \(\sigma\) is the per capita rate at which the organisms return to benthic population from drifting.
- \(D\) is the diffusion coefficient.
- \(v\) is the advection speed.

Note that model (2) does not incorporate death for individuals drifting in the flow. If we want to add death for individuals drifting in the flow into the model, then we need to add \(-\delta n_d\) into the first equation of (2), where \(\delta\) is the death factor.
We assume no Allee effect in the population. The Allee effect is a phenomenon seen in population biology when a small population grows faster when the organisms are at high population density than it would if the population was at low density. This could come about through multiple mechanisms. In one example, you can imagine a population spread out over a large area compared to one concentrated in a small space. If the limit on reproduction is how often males and females meet, then the concentrated population will have more encounters and therefore more reproduction.

This implies in our model that the maximum per capita population growth rate is found as the population density approaches zero, \( f(0) = \max\{ f(n_b) \} \)

The boundary conditions for our model are given by

\[
\begin{align*}
vn_d(0, t) - D \left( \frac{\partial n_d}{\partial x} \right)_{x=0} &= 0, \\
n_d(L, t) &= 0,
\end{align*}
\]

for all \( t \geq 0 \). This means that no individuals enter at the top of the stream reach, and individuals in the stream cannot move beyond the top the stream. At the bottom of the stream reach, individuals that cross the boundary never come back.
3 Population persistence

In this section we derive a necessary and sufficient condition for population persistence in the model presented in the previous section, i.e. system (2). By this we mean that we will find a condition such that individuals of the population will always survive either on the benthos as in the drift. With the use of this condition we will also calculate the critical domain size with respect to the advection speed necessary for population persistence. Since the maximum per capita growth rate is at low densities, population persistence is equivalent to population growth at small densities (Lewis and Kareiva, 1993). We therefore linearize system (2) around the zero steady state and obtain conditions under which a small population grows. This linearized system is given by

\[
\frac{\partial n_d}{\partial t} = \mu n_b - \sigma n_d + D \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x},
\]

\[
\frac{\partial n_b}{\partial t} = r n_b - \mu n_b + \sigma n_d,
\]

with \(r = f(0)\). We now rescale this system by setting

\[
\tilde{t} = rt, \quad \tilde{\mu} = \frac{\mu}{r}, \quad \tilde{\sigma} = \frac{\sigma}{r}, \quad \tilde{x} = \frac{x}{\sqrt{D/r}}, \quad \tilde{v} = \frac{v}{\sqrt{Dr}}.
\]

For simplicity we drop the tildes, such that system (2) becomes

\[
\frac{\partial n_d}{\partial \tilde{t}} = \tilde{\mu} n_b - \tilde{\sigma} n_d + D \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x},
\]

\[
\frac{\partial n_b}{\partial \tilde{t}} = (1 - \tilde{\mu}) n_b + \tilde{\sigma} n_d.
\]

We will now consider the two cases \(\mu \geq 1\) and \(\mu < 1\) separately.

3.1 Population persistence for \(\mu \geq 1\)

For \(\mu \geq 1\) we have that the per capita rate at which individuals in the benthic population enter the drift is higher than the per capita rate of increase of the benthic population. So this means that the total growth rate of the benthic population at each location is negative. We will show that persistence is possible provided that the domain \(L\) is large enough with respect to the advection speed \(v\). We start with deriving expressions for \(n_b(x, t)\) and \(n_d(x, t)\) as explicit series expansions.

**Proposition 1** \(n_b(x, t)\) is given by

\[
n_b(x, t) = n_b(x, 0)e^{(1-\mu)t} + \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x, \tau) d\tau.
\]
**Proof.** We apply the variation of constants formula to (4b) and write \(n_b(x,t)\) in terms of \(n_d(x,t)\). So first we need to find the homogeneous solution, which we write as \((n_b(x,t))_h\). We get

\[
\frac{dn_b(x,t)}{dt} = (1 - \mu)n_b(x,t),
\]

\[
\int \frac{1}{(n_b(x,t))_h} dn_b(x,t) = \int (1 - \mu) dt,
\]

\[
\ln |(n_b(x,t))_h| = (1 - \mu)t + c_0,
\]

\[
(n_b(x,t))_h = c_1 e^{(1-\mu)t},
\]

with \(c_0, c_1 \in \mathbb{R}\). To find the particular solution, which we denote by \((n_b(x,t))_p\), we set \((n_b(x,t))_p = c_1(t) e^{(1-\mu)t}\). Substituting this into (4b) gives

\[
c_1'(t) e^{(1-\mu)t} + c_1(t) (1 - \mu) e^{(1-\mu)t} = c_1(t) (1 - \mu) e^{(1-\mu)t} + \sigma n_d(x,t),
\]

\[
c_1'(t) e^{(1-\mu)t} = \sigma n_d(x,t),
\]

\[
c_1'(t) = \sigma e^{(\mu-1)t} n_d(x,t),
\]

\[
c_1(t) = \sigma \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau + c_2,
\]

with \(c_2 \in \mathbb{R}\). So the particular solution becomes

\[
(n_b(x,t))_p = e^{(1-\mu)t} \left( \sigma \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau + c_2 \right)
\]

For the solution \(n_b(x,t)\) we now find

\[
n_b(x,t) = (n_b(x,t))_h + (n_b(x,t))_p,
\]

\[
= c_1 e^{(1-\mu)t} + e^{(1-\mu)t} \left( \sigma \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau + c_2 \right),
\]

\[
= c_3 e^{(1-\mu)t} + \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau,
\]

with \(c_3 = c_1 + c_2\). Because \(n_b(x,0) = c_3\) for \(t = 0\), we obtain (5). \(\square\).

At this point, [Pachepsky] simply say that without loss of generality we can assume that \(n_b(x,0) = 0\). So this means that all individuals are initially in the mobile class \(n_d\). While this does not reflect biologically realistic conditions, we will show however that this assumption is valid for deriving conditions for population persistence.

To show that without loss of generality we can assume that \(n_b(x,0) = 0\), we need to do three steps. First we show that system (4) for general initial conditions
generates the same solutions as the following system

\[
\begin{align*}
\frac{\partial \tilde{n}_d}{\partial t} &= \mu \tilde{n}_b - \sigma \tilde{n}_d + \frac{\partial^2 \tilde{n}_d}{\partial x^2} - v \frac{\partial \tilde{n}_d}{\partial x} + \mu e^{(1-\mu)t} a, \\
\frac{\partial \tilde{n}_b}{\partial t} &= (1 - \mu) \tilde{n}_b + \sigma \tilde{n}_d,
\end{align*}
\]

(6a) (6b)

with \( a = n_b(x, 0) = n_0 \) and for initial conditions \( \tilde{n}_d(x, 0) = \tilde{n}_0_d, \tilde{n}_b(x, 0) = 0 \).

Second, we determine the solutions of system (6) with \( a = 0 \) and \( a \neq 0 \) for initial conditions \( \tilde{n}_d(x, 0) = \tilde{n}_0_d, \tilde{n}_b(x, 0) = 0 \). Finally, we show that both solutions generate the same condition for population persistence which implies that we can assume \( a = n_b(x, 0) = n_0 = 0 \).

### 3.1.1 Equivalence of two initial value problems

The following proposition allows to simplify somewhat the initial conditions under which one studies persistence or extinction of the population.

**Proposition 2** Let \( t \mapsto n(x, t; n_0^d, n_0^b) \in \mathbb{R}^2 \) be the unique solution to system (4) for initial conditions \( n_d(x, 0) = n_0^d, n_b(x, 0) = n_0^b \), and \( t \mapsto \tilde{n}(x, t; n_0^d, n_0^b) \in \mathbb{R}^2 \) be the unique solution to system (6) with \( a = n_0^b \) and for initial conditions \( \tilde{n}_d(x, 0) = \tilde{n}_0_d, \tilde{n}_b(x, 0) = 0 \). Then

\[
n(x, t; n_0^d, n_0^b) = \tilde{n}(x, t; n_0^d, n_0^b) + e^{(1-\mu)t} n_0^b(x),
\]

for all \( t \geq 0 \).

**Proof.** Let us write \( n(x, t) = (n_d(x, t), n_b(x, t)) \) and \( \tilde{n}(x, t) = (\tilde{n}_d(x, t), \tilde{n}_b(x, t)) \).

Now we put

\[
\dot{n}_b(x, t) := n_b(x, t) - e^{(1-\mu)t} n_0^b(x),
\]

(7)

from which it follows that

\[
n_b(x, t) = \dot{n}_b(x, t) + e^{(1-\mu)t} n_0^b(x).
\]

(8)

Note that from (7) it follows that \( \dot{n}_b(x, 0) = n_b(x, 0) - n_0^b(x, 0) = 0 \). From (7) and (8) we find

\[
\begin{align*}
\frac{\partial n_b}{\partial t} &= \frac{\partial n_b}{\partial t} + (\mu - 1)e^{(1-\mu)t} n_0^b(x), \\
&= (1 - \mu) n_b + \sigma n_d + (\mu - 1)e^{(1-\mu)t} n_0^b(x), \\
&= (1 - \mu) (\dot{n}_b + e^{(1-\mu)t} n_0^b(x, 0)) + \sigma n_d + (\mu - 1)e^{(1-\mu)t} n_0^b(x, 0), \\
&= (1 - \mu) \dot{n}_b + \sigma n_d.
\end{align*}
\]

Note that we substituted (4b) in the second line. From (4a) and (8) we find

\[
\begin{align*}
\frac{\partial n_d}{\partial t} &= \mu (\dot{n}_b(x, t) + e^{(1-\mu)t} n_0^b(x)) - \sigma n_d + \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x}, \\
&= \mu \dot{n}_b - \sigma n_d + \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x} + \mu e^{(1-\mu)t} n_0^b(x, 0).
\end{align*}
\]

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So we obtain the following system
\[\begin{align*}
\frac{\partial n_d}{\partial t} &= \mu \hat{n}_b - \sigma n_d + \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x} + \mu e^{(1-\mu)t} n_b(x, 0), \\
\frac{\partial \hat{n}_b}{\partial t} &= (1 - \mu) \hat{n}_b + \sigma n_d.
\end{align*}\]  
(9)

with \(\hat{n}_b(x, 0) = 0\). So we conclude \((n_d(x, t), \hat{n}_b(x, t))\) satisfies system (6) with 
a = n_b(x, 0) = n^0_b and for initial conditions \(\hat{n}_d(x, 0) = \hat{n}^0_d\), \(\hat{n}_b(x, 0) = 0\). So
\[n(x, t; n^0_d, n^0_b) = \hat{n}(x, t; n^0_d, n^0_b) + e^{(1-\mu)t} n^0_b(x),\]
for all \(t \geq 0\). □

**Corollary 3.0.1** If \(0 < \mu \leq 1\), then the population persists according to model (2) for any initial condition \(n^0_b \neq 0\) (positive).

**Corollary 3.0.2** If \(\mu > 1\), then the population persists according to model (2) if and only if \(\hat{n}(x, t; n^0_d, n^0_b)\) does not converge to 0 as \(t \to \infty\).

### 3.1.2 A series expansion for the unforced system

In the previous section we found that system (4) for general initial conditions generates essentially the same information as "forced system" (6) with \(a = n_b(x, 0) = n^0_b\) and for initial conditions \(\hat{n}_d(x, 0) = \hat{n}^0_d\), \(\hat{n}_b(x, 0) = 0\) when concerned with population persistence or extinction. As a next step we will show that assuming even that \(n_b(x, 0) = n^0_b = 0\) in system (4) yields sufficient information. This condition only holds if \(a = 0\) in system (6). In this section we derive the solution of system (6) with \(a = 0\), i.e. system (4), and for initial conditions \(\hat{n}_d(x, 0) = \hat{n}^0_d\), \(\hat{n}_b(x, 0) = 0\).

Because system (6) with \(a = 0\) is identical to system (4), we can just look at system (4) with initial conditions \(n_d(x, 0) = n^0_d\), \(n_b(x, 0) = 0\). For simplicity, we drop the tildes. Now from Lemma 5 it follows that \(n_b(x, t)\) is given by
\[n_b(x, t) = \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x, \tau) d\tau.\]
(10)

Now we have expressed the solution of \(n_b(x, t)\) in terms of \(n_d(x, t)\), we can find a rather explicit expression for the solution of \(n_d(x, t)\).

**Lemma 3.1** Put \(u(x, t) := n_d(x, t) e^{(\mu-1)t}\). Then \(u\) satisfies:
\[\frac{\partial u(x, t)}{\partial t} = \frac{\partial^2 u(x, t)}{\partial x^2} - v \frac{\partial u(x, t)}{\partial x} - \alpha u(x, t) + \mu \int_0^t u(x, \tau) d\tau,\]
(11)
with \(\alpha = \sigma - \mu + 1\).
Proof. Substituting expression (10) into (4a), one obtains
\[
\frac{\partial n_d(x,t)}{\partial t} = \mu \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau - \sigma n_d(x,t) + \frac{\partial^2 n_d(x,t)}{\partial x^2} - v \frac{\partial n_d(x,t)}{\partial x}.
\]

(12)

We now set \( u(x,t) = n_d(x,t) e^{(\mu-1)t} \), from which it follows that
\[
n_d(x,t) = u(x,t) e^{(1-\mu)t}.
\]

Substituting these expressions into (12), we find
\[
\frac{\partial u(x,t)}{\partial t} e^{(1-\mu)t} + u(x,t)(1-\mu)e^{(1-\mu)t} = \mu \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x,\tau) d\tau
\]
\[
- \sigma u(x,t)e^{(1-\mu)t} - ve^{(1-\mu)t} \frac{\partial u(x,t)}{\partial x
\]
\[
+ e^{(1-\mu)t} \frac{\partial^2 u(x,t)}{\partial x^2}.
\]

Dividing by \( e^{(1-\mu)t} \) gives
\[
\frac{\partial u(x,t)}{\partial t} + u(x,t)(1-\mu) = \mu \sigma \int_0^t u(x,\tau) d\tau - \sigma u(x,t) + \frac{\partial^2 u(x,t)}{\partial x^2} - v \frac{\partial u(x,t)}{\partial x}
\]

Setting \( \alpha = \sigma - \mu + 1 \) yields
\[
\frac{\partial u(x,t)}{\partial t} = \frac{\partial^2 u(x,t)}{\partial x^2} - v \frac{\partial u(x,t)}{\partial x} - \alpha u(x,t) + \mu \sigma \int_0^t u(x,\tau) d\tau.
\]

A series expansion for \( u(x,t) \) can now be found by separation of variables.

Lemma 3.2 A non-zero solution of the form \( U(x,t) = X(x)T(t) \) to (11) satisfies
\[
X''(x) - vX'(x) + \lambda X(x) = 0,
\]
\[
T'(t) + (\alpha + \lambda)T(t) - \mu \sigma \int_0^t T(\tau) d\tau = 0,
\]

with \( \lambda \in \mathbb{C} \).

Proof. Substituting \( u(x,t) = X(x)T(t) \) into (11) yields
\[
\frac{\partial X(x)T(t)}{\partial t} = \frac{\partial^2 X(x)T(t)}{\partial x^2} - v \frac{\partial X(x)T(t)}{\partial x} - \alpha X(x)T(t) + \mu \sigma \int_0^t X(x)T(\tau) d\tau.
\]

For \( X'(x) := \frac{dX(x)}{dx} \) and \( T'(t) := \frac{dT(t)}{dt} \) it follows that
\[
X(x)T'(t) = T(t)X''(x) - vT(t)X'(x) - \alpha X(x)T(t) + \mu \sigma X(x) \int_0^t T(\tau) d\tau.
\]
Writing all the terms of \( T(t) \) on the left-hand side and all the terms of \( X(x) \) on the right-hand side gives

\[
\frac{T'(t) + \alpha T(t) - \mu \sigma \int_0^t T(\tau)d\tau}{T(t)} = \frac{X''(x) - vX'(x)}{X(x)}.
\]

Because the left-hand side of the equation is a function with respect to \( t \) and the right-hand side a function with respect to \( x \), we must have that both functions are equal to the same constant \(-\lambda \in \mathbb{C}\) (separation constant). So, we must have

\[
\frac{X''(x) - vX'(x)}{X(x)} = -\lambda,
\]

and

\[
\frac{T'(t) + \alpha T(t) - \mu \sigma \int_0^t T(\tau)d\tau}{T(t)} = -\lambda.
\]

From these equations we obtain

\[
X''(x) - vX'(x) + \lambda X(x) = 0,
\]

and

\[
T'(t) + (\alpha + \lambda)T(t) - \mu \sigma \int_0^t T(\tau)d\tau = 0. \quad \Box
\]

Now we will determine the solutions of (13a) and (13b).

**Lemma 3.3** The general solution \( T(t) = T_\lambda(t) \) to (13b) for \( \lambda \in \mathbb{C} \) is of the form

\[
T(t) = c(m_+e^{m_+t} - m_-e^{m_-t}),
\]

with \( c \in \mathbb{C} \) and

\[
m_\pm = m_\pm(\lambda) = \frac{-(\alpha + \lambda) \pm \sqrt{(\alpha + \lambda)^2 + 4\mu\sigma}}{2}.
\]

**Proof.** Differentiating (13b) with respect to \( t \) gives

\[
T''(t) + (\alpha + \lambda)T'(t) - \mu \sigma T(t) = 0. \quad (16)
\]

Suppose that \( T(t) = ce^{mt} \) is a solution of (16), with \( c, m \in \mathbb{C} \). Substituting \( T(t) = ce^{mt} \) into (16) gives

\[
cm^2e^{mt} + c(\alpha + \lambda)me^{mt} - \mu \sigma ce^{mt} = 0.
\]

\[
ce^{mt}(m^2 + (\alpha + \lambda)m - \mu \sigma) = 0. \quad (17)
\]

From (17) we find \( m^2 + (\alpha + \lambda)m - \mu \sigma = 0 \), because \( m \) is finite. So \( T(t) = ce^{mt} \) is a solution of (16) when \( m = m_\pm(\lambda) \) given by

\[
m_\pm(\lambda) = \frac{-(\alpha + \lambda) \pm \sqrt{(\alpha + \lambda)^2 + 4\mu\sigma}}{2}.
\]
The general solution of (16) is now given by
\[ T(t) = c_1 e^{m_+ t} + c_2 e^{m_- t}, \]  
with \( c_1, c_2 \in \mathbb{C} \) arbitrary and \( m_{\pm} \) as in (15).

We now substitute this solution into (13b). We find
\[ c_1 m_+ e^{m_+ t} + c_2 m_- e^{m_- t} + (\alpha + \lambda)(c_1 e^{m_+ t} + c_2 e^{m_- t}) \]
\[ - \mu \sigma \int_0^t c_1 e^{m_+ \tau} + c_2 e^{m_- \tau} d\tau = 0. \]  
(19)

For the integral we have
\[ \int_0^t c_1 e^{m_+ \tau} + c_2 e^{m_- \tau} d\tau = \frac{c_1}{m_+} e^{m_+ t} + \frac{c_2}{m_-} e^{m_- t} - \frac{c_1}{m_+} - \frac{c_2}{m_-}. \]

So from (19) we now must have for all \( t \geq 0 \):
\[ c_1 m_+ e^{m_+ t} + c_2 m_- e^{m_- t} + (\alpha + \lambda)(c_1 e^{m_+ t} + c_2 e^{m_- t}) \]
\[ - \mu \sigma \left( \frac{c_1}{m_+} e^{m_+ t} + \frac{c_2}{m_-} e^{m_- t} - \frac{c_1}{m_+} - \frac{c_2}{m_-} \right) = 0 \]  
(20)

Since \( m_{\pm} \neq 0 \) we can divide (17) by \( m \). We find
\[ c_1 m_+ e^{m_+ t} + (\alpha + \lambda)c_1 e^{m_+ t} - \mu \sigma \frac{c_1}{m_+} e^{m_+ t} = 0, \]  
(21a)
\[ c_2 m_- e^{m_- t} + (\alpha + \lambda)c_2 e^{m_- t} - \mu \sigma \frac{c_2}{m_-} e^{m_- t} = 0. \]  
(21b)

Substituting (21a) and (21b) into (20), we obtain
\[ \frac{c_1}{m_+} + \frac{c_2}{m_-} = 0. \]  
(22)

Now we substitute (22) into the general solution (18) and we find
\[ T(t) = c_1 e^{m_+ t} - \frac{c_1 m_-}{m_+} e^{m_- t}, \]
\[ = c_3 (m_+ e^{m_+ t} - m_- e^{m_- t}), \]  
(23)

with \( c_3 = \frac{c_1}{m_+} \in \mathbb{C}. \) \( \square \)

**Remark.** The solution that we found for \( T(t) \) (see (14)) differs from the one found in [Pachepsky]. They found that \( T(t) = c_1 m_+ e^{m_+ t} + c_2 m_- e^{m_- t}. \)

We now turn to (13a) and determine the solution for \( X(x). \)

**Lemma 3.4** Let \( \lambda \in \mathbb{C} \) and \( \lambda \neq \frac{1}{4} v^2. \) The general solution of \( X(x) \) is given by:
\[ X(x) = a_1 e^{z_1 x} + a_2 e^{z_2 x}, \]  
(24)

with \( a_1, a_2 \in \mathbb{C} \) and \( z_{\pm} \in \mathbb{C} \) are the two distinct solutions to \( z^2 - vz + \lambda = 0 \).
Proof. Suppose that \( X(x) = ae^{zx} \) is a solution to (13a), with \( a, z \in \mathbb{C} \). Substituting \( X(x) = ae^{zx} \) into (13a) gives
\[
ae^{zx}(z^2 - vz + \lambda) = 0. \tag{25}
\]
From (25) it follows that \( X(x) = ae^{zx} \) is a solution to (13a) with \( a_1, a_2 \in \mathbb{C} \) and \( z_\pm \in \mathbb{C} \) the two distinct solutions to \( z^2 - vz + \lambda = 0 \). \( \square \)

If \( \lambda = \frac{1}{4}v^2 \), then \( z_+ = z_- = \frac{1}{2}v \), which implies that (13a) might have another solution.

Lemma 3.5 Let \( \lambda = \frac{1}{4}v^2 \). The general solution of \( X(x) \) is now given by:
\[
X(x) = a_1 e^{\frac{1}{2}vx} + a_2 xe^{\frac{1}{2}vx}, \tag{26}
\]
with \( a_1, a_2 \in \mathbb{C} \).

Proof. Because \( \lambda = \frac{1}{4}v^2 \), we get \( z_+ = z_- = \frac{1}{2}v \). Using the proof of Lemma (3.4) we conclude that \( X_1(x) = a_1 e^{\frac{1}{2}vx} \) is a solution to (13a). Now we suppose that \( X_2(x) = a_2 xe^{\frac{1}{2}vx} \) is also a solution to (13a). If we substitute \( X_2(x) = a_2 xe^{\frac{1}{2}vx} \) into (13a) for \( \lambda = \frac{1}{4}v^2 \), we find
\[
a_2 ve^{\frac{1}{2}vx}(1 + \frac{1}{4}vx - 1 - \frac{1}{2}vx + \frac{1}{4}vx) = 0
\]
So we conclude that \( X_2(x) = a_2 xe^{\frac{1}{2}vx} \) is indeed a solution to (13a). \( \square \)

To say something further about the solutions of \( X(x) \), we will first look to the boundary conditions. We have that \( n_d(x, t) = X(x)T(t)e^{(1-\mu)t} \). So from (3) we obtain
\[
(vX(0) - X'(0))T(t)e^{(1-\mu)t} = 0,
\]
\[
X(L)T(t)e^{(1-\mu)t} = 0.
\]
Because \( T(t) = 0 \) is the trivial solution, we must have that
\[
vX(0) - X'(0) = 0, \tag{27a}
\]
\[
X(L) = 0. \tag{27b}
\]

Lemma 3.6 If \( \lambda = \frac{1}{4}v^2 \), then the general solution (26) satisfies the boundary conditions (27a)-(27b) if and only if \( a_1 = a_2 = 0 \).

Proof. \( \Rightarrow \) If we apply the boundary conditions (27a)-(27b) to (26), we get
\[
\frac{1}{2}v a_1 - a_2 = 0, \tag{28a}
\]
\[
(a_1 + a_2 L)e^{\frac{1}{4}vL} = 0. \tag{28b}
\]
From (28a) we find \( a_2 = \frac{1}{2}v a_1 \) and from (28b) we find \( a_1 + a_2 L = 0 \). If we substitute \( a_2 = \frac{1}{2}v a_1 \) into \( a_1 + a_2 L = 0 \), we obtain \( a_1(1 + \frac{1}{2}v L) = 0 \). Note that this must hold for all different values of \( v \) and \( L \). So it implies that \( a_1 = 0 \). And from \( a_1 = 0 \), we find \( a_2 = 0 \).

\( \Leftarrow \) From \( a_1 = a_2 = 0 \), we get \( X(x) = 0 \) for all \( x \in (0,L) \). This means that the boundary conditions (27a)-(27b) are always satisfied. \( \Box \)

**Lemma 3.7** Let \( \lambda \in \mathbb{C}, \lambda \neq \frac{1}{4}v^2 \) and \( z_\pm \in \mathbb{C} \). The general solution (24) satisfies the boundary conditions (27a)-(27b) if and only if the solutions \( z_+ \) and \( z_- \) to the equation \( z^2 - vz + \lambda = 0 \) satisfy the equation

\[
z = \frac{v}{1 + e^{(2z-v)L}}.
\] (29)

**Proof:** (\( \Rightarrow \)) If we apply the boundary conditions (27a)-(27b) to (24), we find \( Ma = 0 \) with

\[
M = \begin{pmatrix}
v - z_+ & v - z_- \\
e^{z_+L} & e^{z_-L}
\end{pmatrix}
\quad \text{and} \quad
a = (a_1 \quad a_2)^\top.
\]

There exists a non-trivial solution \( a = (a_1, a_2)^\top \) if and only if \( \det(M) = 0 \). This holds if

\[
e^{z_-L}(v - z_+) - e^{z_+L}(v - z_-) = 0.
\] (30)

Multiplying with \( e^{z_-L} \) gives

\[
e^{(z_+ + z_-)L}(v - z_+) - e^{2z_+L}(v - z_-) = 0.
\] (31)

Because \( z_\pm \) are the solutions to \( z^2 - vz + \lambda = 0 \), it follows that \( z_+ + z_- = v \). Substitute this into (31), obtaining

\[
e^{vL}(v - z_+) - e^{2z_+L}z_+ = 0.
\]

Note that this equation also holds if we replace \( z_+ \) by \( z_- \). To see that, first multiply (30) by \( e^{z_-L} \) and then again use that \( z_+ + z_- = v \). So we have

\[
e^{vL}(v - z) - e^{2z_-L}z = 0,
\] (32)

with \( z = z_+ \) or \( z = z_- \). Now we find

\[
-z(e^{vL} + e^{2z_-L}) = -ve^{vL},
\]

\[
z = \frac{ve^{vL}}{e^{vL} + e^{2z_-L}},
\]

\[
z = \frac{v}{1 + e^{(2z-v)L}}.
\]

(\( \Leftarrow \)) Multiplying (29) by \( e^{vL} \) and moving all the terms to the left-hand side gives (32). Because (32) holds for both \( z_\pm \), we can just pick one, say \( z = z_+ \). For \( z = z_+ \) and knowing that \( z_+ + z_- = v \), we end up with (31). Dividing by \( e^{z_-L} \) gives (30). This means that \( X(x) \) satisfies the boundary conditions. \( \Box \)
Lemma 3.8 If $X_{\lambda}(t)$ satisfies the boundary conditions (27a)-(27b), then $\lambda = \frac{1}{4}(v^2 + y^2)$ with $y \in \mathbb{R}$. In particular, $\lambda > 0$.

Proof. From (29) we find

$$e^{(2z-v)L} = \frac{v-z}{z}. \quad (33)$$

For $\omega = 2z - v$, we find $z = \frac{1}{2}v + \frac{i}{2}\omega$. If we substitute this into (33), we obtain

$$e^{\omega L} = \frac{v - \frac{1}{2}v - \frac{i}{2}\omega}{\frac{1}{2}v + \frac{i}{2}\omega} = \frac{v - \omega}{v + \omega}. \quad (34)$$

Now we substitute $\omega = x + iy$, $x, y \in \mathbb{R}$, into the right-hand side of (34). We obtain

$$\theta = \frac{v - w}{v + w} \quad \frac{v - x - iy}{v + x + iy} = \frac{v - x - iy}{v + x + iy}, \quad \frac{v + x - iy}{v + x - iy} = \frac{v^2 - x^2 - y^2 - 2v iy}{(v + x)^2 + y^2}. \quad (35)$$

For the modulus squared of $\theta$ we get

$$|\theta|^2 = \frac{(v^2 - x^2 - y^2)^2 + 4v^2y^2}{((v + x)^2 + y^2)^2},$$

$$= \frac{v^4 - 2v^2(x^2 + y^2) + (x^2 + y^2)^2 + 4v^2y^2}{(v + x)^4 + 2y^2(v + x)^2 + y^4},$$

$$= \frac{v^4 + x^4 + y^4 - 2v^2x^2 + 2v^2y^2 + 2x^2y^2}{(v + x)^4 + 2y^2(v + x)^2 + y^4},$$

$$= \frac{(v + x)^4 - 8v^2x^2 - 4v^3x - 4v^2x^3 + 2v^2y^2 + 2x^2y^2 + y^4}{(v + x)^4 + 2y^2(v + x)^2 + y^4},$$

$$= \frac{(v + x)^4 + 2y^2(v + x)^2 + y^4 - 4vxy^2 - 8v^2x^2 - 4v^3x - 4v^2x^3}{(v + x)^4 + 2y^2(v + x)^2 + y^4},$$

$$= \frac{(v + x)^4 + 2y^2(v + x)^2 + y^4 - 4vxy(v + x)^2 + y^2}{(v + x)^4 + 2y^2(v + x)^2 + y^4}. \quad (35)$$

And for the modulus squared of $e^{\omega L}$ we find

$$|e^{\omega L}|^2 = |e^{(x+iy)L}|^2,$$

$$= |e^{Lx}(|\cos(Ly) + i \sin(Ly))|^2,$$

$$= e^{2Lx}. \quad (36)$$

So if $x > 0$, then $|\theta|^2 < 1$, while $|e^{\omega L}|^2 > 1$. And if $x < 0$, then $|\theta|^2 > 1$, while $|e^{\omega L}|^2 < 1$. This means that there cannot be a solution with $x \neq 0$. For $x = 0$, we have $|\theta|^2 = |e^{\omega L}|^2 = 1$. So a solution may exists for $\omega = iy$, $y \in \mathbb{R}$. From this we find $z = \frac{1}{2}(v + iy)$, $y \in \mathbb{R}$. Let $y_\pm$ be the $y$ corresponding to $z_\pm$. Because $v = z_+ + z_- = v + \frac{i}{2}(y_+ + y_-)$, we must have $y_+ = -y_-$. This implies $z_+ = \bar{z}_-$. Now from $z_+ z_- = \lambda$, we obtain $\lambda = \frac{1}{4}(v^2 + y^2) \in \mathbb{R}_{>0}$. □
If $\lambda = \frac{1}{4}v^2$, only the trivial solution satisfies the boundary conditions (Lemma 3.6). So we know that $\lambda > \frac{1}{4}v^2 > 0$. We can now look at the solution of $X(x)$ in more detail.

**Lemma 3.9** Let $\lambda > \frac{1}{4}v^2$. Applying the boundary conditions (27a)-(27b) to (24) gives

$$\frac{\sqrt{4\lambda - v^2}}{v} + \tan\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) = 0.$$  \hspace{1cm} (37)

**Proof.** Because $z_{\pm}$ are complex for $\lambda > \frac{1}{4}v^2$, we obtain from (24),

$$X(x) = a_1 e^{+\sqrt{4\lambda - v^2}x} + a_2 e^{-\sqrt{4\lambda - v^2}x},$$

$$= a_1 e^{\frac{x}{2}\sqrt{4\lambda - v^2}} \left( \cos\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right) + i \sin\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right) \right)$$

$$+ a_2 e^{\frac{x}{2}\sqrt{4\lambda - v^2}} \left( \cos\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right) - i \sin\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right) \right),$$

$$= a_3 e^{\frac{x}{2}\sqrt{4\lambda - v^2}} \cos\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right) + a_4 e^{\frac{x}{2}\sqrt{4\lambda - v^2}} \sin\left(\frac{x}{2}\sqrt{4\lambda - v^2}\right),$$ \hspace{1cm} (38)

with $a_3 = a_1 + a_2$ and $a_4 = i(a_1 - a_2)$, both in $\mathbb{C}$.

Applying the boundary conditions for $X(x)$ to (38) yields

$$e^{\frac{x}{2}} (a_3 \cos\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) + a_4 \sin\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right)) = 0.$$  \hspace{1cm} (39)

and

$$\frac{1}{2} a_4 \sqrt{4\lambda - v^2} - a_3 v = 0.$$  \hspace{1cm} (40)

From (40) we find $a_3 = \frac{a_4 \sqrt{4\lambda - v^2}}{v}$. Substituting this into (39) yields

$$a_4 e^{\frac{x}{2}} \left(\frac{\sqrt{4\lambda - v^2}}{v} \cos\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) + \sin\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right)\right) = 0,$$

$$\frac{\sqrt{4\lambda - v^2}}{v} \cos\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) + \sin\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) = 0,$$

$$\frac{\sqrt{4\lambda - v^2}}{v} + \tan\left(\frac{L}{2}\sqrt{4\lambda - v^2}\right) = 0. \hspace{3.5cm} \square$$

**Lemma 3.10** There exists a strictly increasing sequence $\lambda_n = \lambda_n(v, L) > 0$, $n \in \mathbb{N}$, such that $\lambda > 0$ is a solution to (37) if and only if $\lambda = \lambda_n$ for some $n$.

**Proof.** ($\Rightarrow$) First we put $x = \sqrt{4\lambda - v^2} > 0$, such that (37) becomes

$$\tan\left(\frac{L}{2}x\right) = -\frac{1}{v}x.$$  \hspace{1cm} (41)
Figure 1 shows a plot of \( \tan(\frac{L}{2}x) \). We note that the vertical asymptotes of \( \tan(\frac{L}{2}x) \) are at \( \frac{L}{2}x = \frac{1}{2} \pi + k \pi, \ k \in \mathbb{Z} \). That is, \( x = \frac{2}{L}(\frac{1}{2} \pi + k \pi) = \frac{2k+1}{2} \pi, \ k \in \mathbb{Z} \). We also have that \( -\frac{1}{v} x \) is a decreasing line through 0 because \( v > 0 \). So on each interval \( (\frac{2k+1}{2} \pi, \frac{2(k+1)+1}{2} \pi) \), we have exactly one intersection point with the line \( y = -\frac{1}{v} x \). This gives \( x_1, x_2, ..., \) with \( 0 < x_1 < x_2 < ... \) and we find

\[
\lambda_n = \lambda_n(v, L) = \frac{1}{4}(x_n^2 + v^2) > 0, \quad n = 1, 2, 3, ...
\]  

(\( \Leftarrow \) We have argued that each solution \( \lambda \) to (37) is such that the associated \( x \) solves (41). Hence, \( \lambda \) is of the form (42) for some \( n \). On the other hand, \( \lambda \) of the form (42) has \( x_n \) satisfying (41). So (37) holds. \( \square \)

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{\( \tan(\frac{L}{2}x) = -\frac{1}{v} x \) for \( L = 2 \) and \( v = 3 \frac{1}{3} \).}
\end{figure}

Corresponding to each \( \lambda_n \) we have \( m_{\pm}(\lambda_n) = m_{\pm,n} \). So now we can write the solution for \( u(x,t) \) and therefore for \( n_d(x,t) \).

**Proposition 3** The solution \( n_d(x,t) \) is given by

\[
n_d(x,t) = \sum_{n=1}^{\infty} \left[ a_{4,n} \left( \frac{\sqrt{4\lambda_n - v^2}}{v} \cos\left(\frac{x}{2} \sqrt{4\lambda_n - v^2}\right) + e^{\frac{\pi}{2} x} \sin\left(\frac{x}{2} \sqrt{4\lambda_n - v^2}\right) \right) \right]
\times \left[ c_{3,n} \left( m_{+,n} e^{(m_{+,n} + 1 - \mu) t} - m_{-,n} e^{(m_{-,n} + 1 - \mu) t} \right) \right].
\]  

\]  

(43)
Proof.

\[ n_d(x, t) = \sum_{n=1}^{\infty} X_n(x) T_n(t) e^{(1-\nu)t}, \]

\[ = \sum_{n=1}^{\infty} \left[ a_{3,n} e^{\frac{x}{\nu} \cos(\frac{x}{2} \sqrt{4v^2 - 4\lambda n})} + a_{4,n} e^{\frac{x}{\nu} \sin(\frac{x}{2} \sqrt{4v^2 - 4\lambda n})} \right] \]

\[ \times \left[ c_{3,n} \left( m_{+,n} e^{(m_+,n+1-\lambda)t} - m_{-,n} e^{(m_-,n+1-\lambda)t} \right) \right], \]

\[ \sum_{n=1}^{\infty} \left[ a_{4,n} \left( \frac{\sqrt{4\lambda_n - \nu^2}}{\nu} e^{\frac{x}{\nu} \cos(\frac{x}{2} \sqrt{4\lambda_n - \nu^2})} \right) \right] \]

\[ \times \left[ c_{3,n} \left( m_{+,n} e^{(m_+,n+1-\lambda)t} - m_{-,n} e^{(m_-,n+1-\lambda)t} \right) \right]. \]

3.1.3 A series expansion for the forced system

So now we have convenient expressions for the solutions \( \tilde{n}_d(x,t) \) and \( \tilde{n}_b(x,t) \) for system (6) with \( a = 0 \), we can also determine the expressions for the solutions to system (6) with \( a = n_b(x,0) = n_0^b \).

Let \( S_t \) be the solution operator for system (4). In fact, if \( \tilde{U}_0 = (\tilde{n}_d^0, 0)^\top \) then \( S_t[\tilde{U}_0] \) are the found solutions in the previous section. The solution of system (6) for \( a \neq 0 \) is now given by

\[ \tilde{U}(x,t) = S_t[\tilde{U}_0] + \mu \int_0^t S_{t-s}[e^{(1-\nu)s}n_b(x,0)e_1]ds, \]

with \( \tilde{U}(x,t) = (\tilde{n}_d(x,t), \tilde{n}_b(x,t))^\top \). Writing \( \tilde{U}(x,t) \) as two components, we obtain

\[ \tilde{n}_d(x,t) = (S_t[\tilde{U}_0])_1 + \mu \int_0^t (S_{t-s}[e^{(1-\nu)s}n_b(x,0)e_1])_1 ds, \]

\[ \tilde{n}_b(x,t) = (S_t[\tilde{U}_0])_2 + \mu \int_0^t (S_{t-s}[e^{(1-\nu)s}n_b(x,0)e_1])_2 ds. \]

Note that from the previous section we already found \( (S_t[\tilde{U}_0])_1 \) and \( (S_t[\tilde{U}_0])_2 \). For \( (S_t[\tilde{U}_0])_1 \) we found:

\[ (S_t[\tilde{U}_0])_1 = \sum_{n=1}^{\infty} A_n(x) \left( m_{+,n} e^{(m_+,n+1-\lambda)t} - m_{-,n} e^{(m_-,n+1-\lambda)t} \right), \]

with

\[ A_n(x) = a_{4,n} c_{3,n} \left( \frac{\sqrt{4\lambda_n - \nu^2}}{\nu} e^{\frac{x}{\nu} \cos(\frac{x}{2} \sqrt{4\lambda_n - \nu^2})} \right). \]
Moreover, for $(S_t[U_0])_2$ we found (see (10)):

$$(S_t[U_0])_2 = \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} n_d(x, \tau) d\tau,$$

$$= \sigma e^{(1-\mu)t} \int_0^t e^{(\mu-1)\tau} \sum_{n=1}^{\infty} A_n(x) \left( m_{m,n} e^{(m_{m,n}+1-\mu)\tau} - m_{-m,n} e^{(m_{-m,n}+1-\mu)\tau} \right) d\tau,$$

$$= \sigma e^{(1-\mu)t} \int_0^t \sum_{n=1}^{\infty} A_n(x) \left( m_{m,n} e^{m_{m,n}\tau} - m_{-m,n} e^{m_{-m,n}\tau} \right) d\tau,$$

$$= \sigma e^{(1-\mu)t} \sum_{n=1}^{\infty} A_n(x) \int_0^t m_{m,n} e^{m_{m,n}\tau} - m_{-m,n} e^{m_{-m,n}\tau} d\tau,$$

$$= \sigma \sum_{n=1}^{\infty} A_n(x) \left( e^{(m_{m,n}+1-\mu)t} - e^{(m_{-m,n}+1-\mu)t} \right). \quad (46)$$

To determine $\mu \int_0^t \left( S_{t-s} \left[ e^{(1-n)s} n_b(x, 0) \bar{e}_1 \right] \right) ds$, we note that $S_t[n_b(x, 0)\bar{e}_1]$ has the same form as $S_t[n_d(x, 0)\bar{e}_1]$. So $(S_t[n_b(x, 0)\bar{e}_1])_1$ has the same form as (43) but with different coefficients. This is because the coefficients now depend on $n_b(x, 0)$ instead of $n_d(x, 0)$. We find

$$\mu \int_0^t S_{t-s} \left[ e^{(1-\mu)s} n_b(x, 0) \bar{e}_1 \right] ds = \mu \int_0^t e^{(1-\mu)s} S_{t-s} \left[ n_b(x, 0) \bar{e}_1 \right] ds,$$

$$= \int_0^t e^{(1-\mu)s} \sum_{n=1}^{\infty} B_n(x) \left( m_{m,n} e^{(m_{m,n}+1-\mu)(t-s)} - m_{-m,n} e^{(m_{-m,n}+1-\mu)(t-s)} \right) ds,$$

$$= \sum_{n=1}^{\infty} B_n(x) \left( m_{m,n} e^{(m_{m,n}+1-\mu)t} \int_0^t e^{-m_{m,n}s} ds - m_{-m,n} e^{(m_{-m,n}+1-\mu)t} \int_0^t e^{-m_{-m,n}s} ds \right),$$

$$= \sum_{n=1}^{\infty} B_n(x) \left( e^{(m_{m,n}+1-\mu)t} - e^{(m_{-m,n}+1-\mu)t} \right), \quad (47)$$

with

$$B_n(x) = \tilde{c}_{3,n} \tilde{a}_{4,n} \left( \sqrt{4\lambda_n - v^2} e^{x} \cos \left( \frac{x}{2} \sqrt{4\lambda_n - v^2} \right) + e^{x} \sin \left( \frac{x}{2} \sqrt{4\lambda_n - v^2} \right) \right).$$

To determine $\mu \int_0^t \left( S_{t-s} \left[ e^{(1-n)s} n_b(x, 0) \bar{e}_1 \right] \right) ds$, we note that $S_t[n_b(x, 0)\bar{e}_1]$ has the same form as $S_t[n_d(x, 0)\bar{e}_1]$. So $(S_t[n_b(x, 0)\bar{e}_1])_2$ has the same form as (10) but with different coefficients. With the use of (46) we find
\[
\mu \int_0^t S_{t-s} \left[ e^{(1-\mu)s} n_b(x,0) \vec{e}_1 \right] ds = \mu \int_0^t e^{(1-\mu)s} S_{t-s} \left[ n_b(x,0) \vec{e}_1 \right] ds,
\]

\[
= \mu \int_0^t e^{(1-\mu)s} \sigma e^{(1-\mu)(t-s)} \int_0^{t-s} e^{(\mu-1)\tau} n_d(x,\tau) d\tau ds,
\]

\[
= \mu \sigma \int_0^t e^{(1-\mu)s} e^{(1-\mu)(t-s)} \int_0^{t-s} \sum_{n=1}^{\infty} B_n(x) \left( m_{+n} e^{m_{+n}\tau} - m_{-n} e^{m_{-n}\tau} \right) d\tau ds,
\]

\[
= \mu \sigma \int_0^t e^{(1-\mu)s} \sum_{n=1}^{\infty} B_n(x) \left( e^{m_{+n}(t-s)} - e^{m_{-n}(t-s)} \right) ds,
\]

\[
= \mu \sigma e^{(1-\mu)t} \sum_{n=1}^{\infty} B_n(x) \int_0^t e^{m_{+n}(t-s)} - e^{m_{-n}(t-s)} ds,
\]

\[
= \mu \sigma e^{(1-\mu)t} \sum_{n=1}^{\infty} B_n(x) \left( \frac{1}{m_{+n}} (1 - e^{m_{+n}t}) - \frac{1}{m_{-n}} (1 - e^{m_{-n}t}) \right)
\]

\[
= \mu \sigma \sum_{n=1}^{\infty} B_n(x) \left( \frac{1}{m_{+n}} (e^{(1-\mu)t} - e^{(m_{+n}+1-\mu)t}) - \frac{1}{m_{-n}} (e^{(1-\mu)t} - e^{(m_{-n}+1-\mu)t}) \right)
\]

(48)

3.1.4 Condition for population persistence

Because we have found the solutions of the forced and unforced systems, we can now look for which values of the parameters the population persists and when it goes extinct for \( t \to \infty \). This leads to the condition for persistence. Note that if \( \mu \leq 1 \) there is population persistence (Corollary 3.0.1). The interesting case is \( \mu > 1 \).

For the following theorem, note that the sequence of positive real numbers \( \lambda_n = \lambda_n(v, L) \) is introduced in Lemma 3.10.
Theorem 3.11 If $\mu > 1$, then the population persists if and only if $\lambda_1(v, L) < \frac{\sigma}{\mu - 1}$.

Proof. ($\Rightarrow$) For system (6) with $a = 0$ we see in (43) that $n_d \to 0$ for $t \to \infty$ if $m_{+,n} + 1 - \mu < 0$ and $m_{-,n} + 1 - \mu < 0$ for all $n$. Because $m_{-,n} < m_{+,n}$, the only condition for extinction of the population will be $m_{+,n} + 1 - \mu < 0$. For system (6) with $a \neq 0$ we see in (47) that we also find the condition $m_{+,n} + 1 - \mu < 0$ for population extinction (see Corollary (3.0.2)). Note that we find the same condition if we look to the population on the benthos.

Lemma 3.12 $m_+(\lambda)$ is a decreasing function of $\lambda$ on $(0, \infty)$.

Proof. Differentiating $m_+$ with respect to $\lambda$ gives

$$m'_+(\lambda) = \frac{1}{2} + \frac{\alpha + \lambda}{2\sqrt{(\alpha + \lambda)^2 + 4\mu\sigma}}.$$  

Because $\mu, \sigma > 0$ we have $\sqrt{(\alpha + \lambda)^2 + 4\mu\sigma} > \alpha + \lambda$. And because $2\sqrt{(\alpha + \lambda)^2 + 4\mu\sigma} > 0$, we get $m'_+ < 0$. So $m_+$ is a decreasing function for $\lambda > 0$. □

This means that $n_d \to 0$ for $t \to \infty$ if and only if $m_{+,1} + 1 - \mu < 0$. We get

$$\frac{-(\alpha + \lambda_1) + \sqrt{(\alpha + \lambda_1)^2 + 4\mu\sigma}}{2} + 1 - \mu < 0,$$

$$\frac{-(\alpha + \lambda_1) + \sqrt{(\alpha + \lambda_1)^2 + 4\mu\sigma} + 2 - 2\mu}{2} < 0.$$  

That is

$$2(\mu - 1) + \alpha + \lambda_1 > \sqrt{(\alpha + \lambda_1)^2 + 4\mu\sigma}. \quad (49)$$

Now we first show that $2(\mu - 1) + \alpha + \lambda_1 > 0$. We have

$$2(\mu - 1) + \alpha + \lambda_1 > 0,$$

$$\lambda_1 > 2(1 - \mu) - \alpha,$$

$$> 1 - (\mu + \sigma).$$

And because $\mu + \sigma > 1$ we have that $\lambda_1 > 1 - (\mu + \sigma)$ is always satisfied. So now squaring both sides in (49) yields

$$4(\mu - 1)^2 + (\alpha + \lambda_1)^2 + 4(\mu - 1)(\alpha + \lambda_1) > (\alpha + \lambda_1)^2 + 4\mu\sigma,$$

$$(\mu - 1)^2 + (\mu - 1)(\alpha + \lambda_1) > \mu\sigma,$$

$$\alpha + \lambda_1 > \frac{\mu\sigma - (\mu - 1)^2}{\mu - 1},$$

$$\lambda_1 > \frac{\mu\sigma - (\mu - 1)^2 - \alpha(\mu - 1)}{\mu - 1}.  \quad 28$$
And because $\alpha = \sigma - \mu + 1$, we find that $n_d \to 0$ for $t \to \infty$ if
\[
\lambda_1(v, L) > \frac{\mu \sigma - (\mu - 1)^2 - (\sigma - \mu + 1)(\mu - 1)}{\mu - 1} = \frac{\sigma}{\mu - 1}.
\]
So we conclude that a population only persists when
\[
\lambda_1(v, L) < \frac{\sigma}{\mu - 1}. \quad (50)
\]
($\Leftarrow$) We can immediately conclude that $n_d \to 0$ for $t \to \infty$ if $\lambda_1(v, L) > \frac{\sigma}{\mu - 1}$.
So this implies that the population persists if $\lambda_1(v, L) > \frac{\sigma}{\mu - 1}$. $\square$

Now we know the necessary condition for population persistence, we can look to the relationship between the domain size and the advection speed such that the population persists or goes extinct.

**Corollary 3.12.1** The population persists if
\[
L > L^* = \frac{2}{\sqrt{\frac{4\sigma}{\mu - 1} - v^2}} \left[ \pi + \arctan \left( -\frac{1}{v} \sqrt{\frac{4\sigma}{\mu - 1} - v^2} \right) \right]. \quad (51)
\]

**Proof.** From (37) we find
\[
\tan \left( \frac{L}{2} \sqrt{4\lambda_1 - v^2} \right) = -\frac{\sqrt{4\lambda_1 - v^2}}{v},
\]
\[
\frac{L}{2} \sqrt{4\lambda_1 - v^2} = k\pi + \arctan \left( -\frac{1}{v} \sqrt{4\lambda_1 - v^2} \right), \quad (52a)
\]
\[
L = \frac{2}{\sqrt{4\lambda_1 - v^2}} \left[ k\pi + \arctan \left( -\frac{1}{v} \sqrt{4\lambda_1 - v^2} \right) \right]. \quad (52b)
\]
Note that in (52a) we had to add $k\pi, k \in \mathbb{Z}_{\geq 1}$, because the period of $\tan(x)$ is $\pi$ and $\frac{L}{2} \sqrt{4\lambda_1 - v^2} > 0$ and $-\frac{1}{v} \sqrt{4\lambda_1 - v^2} < 0$. Now from (52b), we see that $L$ can be as large as possible. But because we want to find the critical length $L^*$, we need the smallest $L$ that satisfies (52a). Because $\lim_{x \to -\infty} \arctan(x) = -\frac{1}{2} \pi$, it implies that $k = 1$. Now from (50) we find for the critical length
\[
L^* = \frac{2}{\sqrt{\frac{4\sigma}{\mu - 1} - v^2}} \left[ \pi + \arctan \left( -\frac{1}{v} \sqrt{\frac{4\sigma}{\mu - 1} - v^2} \right) \right]. \quad (53)
\]
Note that $L^*$ becomes larger when $\lambda_1$ becomes smaller. So this means that the population persists for $L > L^*$. $\square$

**Remark.** In [Pachepsky] the term $\pi$ within the brackets in (51) is missing.

**Corollary 3.12.2** If $v \geq v^* := 2 \sqrt{\frac{\sigma}{\mu - 1}}$, the population cannot persist on a domain of any size.
Proof. We have that $L^*$ is an increasing function with respect to $v$. This can be found by differentiating $L^*$ with respect to $v$. Intuitions, this can also be concluded by imagining that a population with faster advection, will require a larger domain size to persist. But since $\arctan(x)$ is a bounded function, we have that $L^*$ tends to infinity if $\frac{4\sigma}{\mu-1} - v^2$ goes to $0$. In other words

$$L^* \to \infty \quad \text{for} \quad v \uparrow v^* = 2\sqrt{\frac{\sigma}{\mu-1}}.$$  

**Corollary 3.12.3** The population persist if $1 \leq \mu < \mu^* := 1 + \frac{4\sigma}{9\pi^2 + v^2}.$

**Proof.** From (42), we know that $\lambda_1 \in \left(\frac{1}{4}(\frac{\sigma^2}{L^2} + v^2), \frac{1}{4}(\frac{9\pi^2}{L^2} + v^2)\right)$. So this implies that if $\frac{1}{4}(\frac{9\pi^2}{L^2} + v^2) < \frac{\sigma}{\mu-1}$, the population persists, according to Theorem 3.11. We find that the population persists for

$$\mu < \mu^* = \frac{4\sigma}{9\pi^2 + v^2} + 1.$$  

Remark. We see that $\frac{\sigma}{\mu-1} \to \infty$ for $\mu \downarrow 1$, which implies that for given domain size $L$, condition (50) is always satisfied for $\mu$ sufficient close to $1$. Furthermore, we note that $v^* \to \infty$ for $\mu \to 1$. So this means that the population will always persist for $\mu \downarrow 1$.

### 3.2 Population persistence for $\mu < 1$

For $\mu < 1$ we have that the per capita rate of increase of the benthic population is higher than the per capita rate at which individuals in the benthic population enter the drift. So this means that the population will always persist because the total growth rate of the benthic population at each location is positive. We will show that this is mathematically also correct.

**Lemma 3.13** $n_d(x,t)$ is non-negative for non-negative initial values.

**Proof.** We will show that the maximum principle holds for (4a). Suppose that $n_d(x,t)$ first crosses from positive to negative at time $t_0$ and at point $x_0$. And suppose that $n_d(x,t)$ has a non-degenerate minimum at $x_0$. Then we get $\frac{\partial n_d}{\partial x}(x_0,t_0) = 0$ and $\frac{\partial^2 n_d}{\partial x^2}(x_0,t_0) > 0$. Hence, from (4a) we get $\frac{\partial n_d}{\partial t}(x_0,t_0) > 0$. So $n_d(x,t)$ cannot evolve forward in time into the region $n_d(x,t) < 0$. □

Now we will look at the dynamics of the benthic population, $n_b(x,t)$.

**Lemma 3.14** $n_b(x,t) \geq 0$ for $t \geq 0$. 

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Proof. From (4b) and Lemma 3.13 we obtain
\[
\frac{\partial n_b}{\partial t} = (1 - \mu)n_b + \sigma n_d \geq (1 - \mu)n_b,
\]
(54)

From (54) we obtain
\[
\frac{\partial n_b}{\partial t} - (1 - \mu)n_b = q, \quad q \in \mathbb{R}_{\geq 0}
\]
(55)

For the homogeneous solution we find \((n_b(x,t))_h = ce^{(1-\mu)t}, \) with \(c \in \mathbb{C}\). And for the particular solution we find \((n_b(x,t))_p = \frac{q}{\mu - 1}\). So we find
\[
n_b(x,t) = ce^{(1-\mu)t} + \frac{q}{\mu - 1}, \quad q \in \mathbb{R}_{\geq 0}.
\]

And because we assume that \(n_b(x,0) = 0\), we get \(c = \frac{q}{1 - \mu}\). So the solution becomes
\[
n_b(x,t) = \frac{q}{1 - \mu}(e^{(1-\mu)t} - 1), \quad q \in \mathbb{R}_{\geq 0}.
\]

We note that \(e^{(1-\mu)t} > 1\) for \(0 < \mu < 1\). Thus, we conclude that \(n_b(x, t) \geq 0\) for \(t \geq 0\). \(\square\)

We can also show this by using Grönwall's Inequality. A version of Grönwall's Inequality is as follows [13]:

**Theorem 3.15 (Grönwall's inequality [13])** Let \(I\) denote an interval on the real line of the form \([a, \infty)\) or \([a, b]\) or \([a, b)\) with \(a < b\). Let \(\beta\) and \(u\) be real-valued continuous functions defined on \(I\). If \(u\) is differentiable in the interior \(I^0\) of \(I\) (the interval \(I\) without the end points \(a\) and possibly \(b\)) and satisfies the differential inequality
\[
u'(t) \leq \beta(t)u(t), \quad t \in I^0,
\]
then \(u\) is bounded by the solution of the corresponding differential equation \(y'(t) = \beta(t)y(t)\):
\[
u(t) \leq u(a)e^\int_a^t \beta(s)ds,
\]
for all \(t \in I\).

**Lemma 3.16** \(n_b(x,t) \geq 0\) for \(t \geq 0\) using Grönwall's Inequality.

**Proof.** We have
\[
\frac{d}{dt}n_b \geq (1 - \mu)n_b,
\]
consequently, \(\frac{d}{dt}n_b - (1 - \mu)n_b \geq 0\). Multiplying by the positive "integrating factor" \(e^{-\int_0^t(1-\mu)ds} = e^{(\mu-1)t}\) gives
\[
e^{(\mu-1)t}\left(\frac{d}{dt}n_b - (1 - \mu)n_b\right) = \frac{d}{dt}(n_be^{(\mu-1)t}) \geq 0.
\]
Integrating this inequality finally implies
\[
n_b e^{(\mu - 1)t} \geq c.
\] (56)

So we find \( n_b(x, t) \geq ce^{(1-\mu)t} \). From \( n_b(x, 0) = 0 \), we get \( c = 0 \). So we conclude that \( n_b(x, t) \geq 0 \) for \( t \geq 0 \).

We conclude that the population on the benthos, irrespective of the domain length and the advection speed, will always persist at small densities. We also showed that the population grows at least exponentially in this case.
4 Persistence or extinction through a moving population front

In the previous section, we derived necessary and sufficient conditions for system (2) such that the population will persist or go extinct. In this section we consider spatial spread of the population in time, in particular by means of a fixed front in population density that is moving up or downwards. When we introduce advection into the system, we need to distinguish between the propagation speed downstream (in the direction of advection) and upstream (against the advection). With increasing advection, the propagation speed downstream increases, whereas the propagation speed upstream decreases.

Before we can determine the up- and downstream propagation speed, we recast the system in travelling wave coordinates and then transform it into a system of first-order equations. This system is three dimensional. The existence of a travelling wave is equivalent to the existence of a heteroclinic orbit between the steady states of this system. [Pachepsky] did not provide necessary and sufficient conditions for the existence of the travelling waves, only necessary conditions. In this section we make an analysis that goes beyond the results obtained by [Pachepsky]. However, the three dimensionality of the system in the end prevented us from obtaining a full characterisation of existence of travelling waves as well.

Next we assume there exist a travelling wave between the found steady states and determine by phase portrait necessary conditions there actually could exist one. Then we linearize the system around the steady states, which informs us about the dimensions of the stable and unstable manifolds of the steady states.

4.1 Idealized model equations and homogeneous steady states

We consider system (2) with logistic growth with carrying capacity $K$ and intrinsic growth rate $r$, that is

$$f(n_b)n_b = rn_b(1 - \frac{n_b}{K}).$$

In order to arrive at a system similar to (4), we set $\tilde{n}_d = \frac{n_d}{K}$ and $\tilde{n}_b = \frac{n_b}{K}$. We find

$$\frac{\partial \tilde{n}_d}{\partial t} = \frac{1}{K} \frac{\partial n_d}{\partial t},$$

$$= \frac{1}{K} (\mu n_b - \sigma n_d + \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x}),$$

$$= \mu \tilde{n}_b - \sigma \tilde{n}_d + \frac{\partial^2 \tilde{n}_d}{\partial x^2} - v \frac{\partial \tilde{n}_d}{\partial x}. $$

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For $\partial \tilde{n}_b/\partial t$ we obtain

$$\frac{\partial \tilde{n}_b}{\partial t} = \frac{1}{K} \frac{\partial n_b}{\partial t},$$

$$= \frac{1}{K} \left[ r n_b \left( 1 - \frac{n_b}{K} \right) - \mu n_b + \sigma n_d \right],$$

$$= r \left( \tilde{n}_b - \tilde{n}_b^2 \right) - \mu \tilde{n}_b + \sigma \tilde{n}_d,$$

$$= r \tilde{n}_b \left( 1 - \tilde{n}_b \right) - \mu \tilde{n}_b + \sigma \tilde{n}_d.$$

Now we drop the tildes for convenience, and obtain

$$\frac{\partial n_d}{\partial t} = \mu n_b - \sigma n_d + \frac{\partial^2 n_d}{\partial x^2} - v \frac{\partial n_d}{\partial x}, \quad (57a)$$

$$\frac{\partial n_b}{\partial t} = r n_b \left( 1 - n_b \right) - \mu n_b + \sigma n_d. \quad (57b)$$

We are going to study travelling waves in (57), defined on the infinite domain $\mathbb{R}$ (instead of $(0, L)$, as before). One should interpret this change of domain as an idealisation of travelling population fronts in the finite domain. In the latter, one cannot expect fronts moving at fixed speed, with fixed shape. Near the boundary, propagation and shape must change substantially.

For the travelling wave problem, we are interested in the spatially homogeneous steady states of (57), i.e. $n_d(x, t) = n_d^* \in \mathbb{R}_{>0}$ and $n_b(x, t) = n_b^* \in \mathbb{R}_{>0}$. From (57a) we find $n_d = \frac{\mu}{\sigma} n_b$ and then from (57b) we get $r n_b \left( 1 - n_b \right) = 0$. This implies that $n_b = 0$ or $n_b = 1$. For $n_b = 0$ we find $n_d = 0$ and for $n_b = 1$ we find $n_d = \frac{\mu}{\sigma}$. So the spatially homogeneous steady states of system (57) are given by

$$(n_{b_0}, n_{d_0}) = (0, 0) \quad \text{and} \quad (n_{b_1}, n_{d_1}) = (1, \frac{\mu}{\sigma}).$$

### 4.2 Travelling wave equations

Now assume that there exists a travelling wave connecting the two spatially homogeneous steady states. This means that there is a solution of (57) of the form $(n_b, n_d)(x, t) = (N_b, N_d)(x - ct) = (N_b, N_d)(z)$, for some fixed $c \in \mathbb{R}$, the wave propagation speed. Substitution of this specific solution into (57) yields

$$-c N'_d = \mu N_b - \sigma N_d - v N'_d + N''_d, \quad (58)$$

$$-c N'_b = N_b \left( 1 - N_b \right) - \mu N_b + \sigma N_d.$$

Note that the prime stands for the derivative with respect to $z$. System (58) is equivalent to

$$N'_b = \frac{N^2_b}{c} + \frac{(\mu - 1) N_b}{c} - \frac{\sigma}{c} N_d, \quad \text{for} \quad N'_d = M, \quad N'_d = M - \mu N_b + \sigma N_d + (v - c) M. \quad (59)$$

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Note that the steady states are now given by
\[ x^*_0 := (N_{b_0}, N_{d_0}, M_0) = (0, 0, 0) \quad \text{and} \quad x^*_1 := (N_{b_1}, N_{d_1}, M_1) = (1, \frac{\mu}{\sigma}, 0). \]

To find the behaviour at \( \pm \infty \) of for \( N_b, N_d \) and \( M = N'_d \), we need to take into account the fact that we have two types of waves, the upstream and the downstream facing wave. For the upstream facing wave (see Figure 2), we have the following boundary conditions at \( z = \pm \infty \)
\[ N_b(\infty) = 1, \quad N_d(\infty) = \frac{\mu}{\sigma}, \quad M(\infty) = 0, \]
\[ N_b(-\infty) = 0, \quad N_d(-\infty) = 0, \quad M(-\infty) = 0. \]

In Figure 2 we see that the upstream facing wave with wave propagation speed \( c < 0 \) will imply population spread. This means that the population will persist. For a wave propagation speed \( c > 0 \), we see that the population goes extinct.

For a downstream facing wave (see Figure 3), we have the following boundary conditions
\[ N_b(\infty) = 0, \quad N_d(\infty) = 0, \quad M(\infty) = 0, \]
\[ N_b(-\infty) = 1, \quad N_d(-\infty) = \frac{\mu}{\sigma}, \quad M(-\infty) = 0. \]
In Figure 3 we see that the downstream facing wave with a positive wave propagation speed will imply population spread and persistence, while for a negative wave propagation speed the population goes extinct.

To summarise:

**Proposition 4** A travelling wave solution to (57) exists if and only if the three dimensional system (59) for some \( c \neq 0 \) admits a heteroclinic orbit connecting the steady states \( x_0^* \) and \( x_1^* \).

<table>
<thead>
<tr>
<th></th>
<th>( c &lt; 0 )</th>
<th>( c &gt; 0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Upstream facing wave</td>
<td>from ( x_0 ) to ( x_1 ) (pers.)</td>
<td>from ( x_0 ) to ( x_1 ) (ext.)</td>
</tr>
<tr>
<td>Downstream facing wave</td>
<td>from ( x_1 ) to ( x_0 ) (ext.)</td>
<td>from ( x_1 ) to ( x_0 ) (pers.)</td>
</tr>
</tbody>
</table>

**Table 1:** Population persistence and extinction for different values of the propagation speed \( c \) for the up- and downstream facing waves.

### 4.3 Necessary conditions for the existence of a heteroclinic orbit by analysing the phase portraits.

To get conditions for the up- and downstream propagation speed \( c^* \) of the travelling waves, we first need to understand that both steady states can only be connected if there exists a heteroclinic orbit between them. In this section we will study the phase portraits of system (59) to see for which values of the parameters there could exist a heteroclinic orbit between the steady states.

The analysis and presentation that we provide in this section does not appear in [Pachepsky]. It is new as for as we could see in the literature.

The first step is to find the nullclines of system (59). From \( N_b' = 0 \), \( N_d' = 0 \) and \( M' = 0 \) we find

\[
\begin{align*}
n_b = 1/n_d = \frac{\nu}{\sigma} \\
c < 0 \quad \rightarrow \quad c > 0 \\
t \rightarrow -\infty \\
n_b = 0/n_d = 0 \\
t \rightarrow \infty
\end{align*}
\]
• $N_b$-nullcline: parabolic cylinder $N_d = \frac{1}{\sigma} N_b (N_b + \mu - 1)$.
• $N_d$-nullcline: plane $M = 0$.
• $M$-nullcline: plane $-\mu N_b + \sigma N_d + (v - c) M = 0$.

Biologically relevant solutions are only there for which $N_b, N_d \in \mathbb{R}_{\geq 0}$. To make a sketch (see Figure 4) of how the nullclines are located in the space

$$S = \{(N_b, N_d, M) | N_b \geq 0, N_d \geq 0, M \in \mathbb{R}\},$$

we need to look more specific to the equations of these nullclines.

From $N_b' = 0$ we see that the location where the parabolic cylinder intersects the plane $N_d = 0$ in $S$ depends on $\mu$. From $N_d = 0$ we get $N_b = 1 - \mu$. So for $\mu < 1$ we have $N_b = 1 - \mu > 0$ and for $\mu \geq 1$ we get $N_b = 0$ because $N_b \geq 0$. To see how the plane $M' = 0$ is located in the space $S$, we will study the normal vector of this plane. The normal vector of the plane $-\mu N_b + \sigma N_d + (v - c) M = 0$ is given by $\vec{n} = (-\mu, \sigma, v - c)$. So the $N_b$-component of $\vec{n}$ is always negative and the $N_d$-component always positive. For the $M$-component of $\vec{n}$ we have that it can only be positive if $v > c$. So we always have $v - c > 0$ for $c < 0$, but if $c > 0$ we must have $v > c$ for $v - c > 0$. For $v = c$ we get the plane $N_d = \frac{\mu}{\sigma} N_b$ which does not depend on $M$ any more. Note that this also means that for $M = 0$ we get the line $N_d = \frac{\mu}{\sigma} N_b$. 

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(a) $v - c > 0$ and $\mu \geq 1$.

(b) $v - c > 0$ and $\mu < 1$.

(c) $v - c < 0$ and $\mu \geq 1$.

(d) $v - c < 0$ and $\mu < 1$.

**Figure 4:** Location of the nullclines for the travelling wave equations.

The $N_b$-nullcline is the parabolic cylinder (orange) and the $M$-nullcline is the plane (green). The $N_d$-nullcline is the plane $M = 0$, i.e. the ($N_b$, $N_d$)-coordinate plane. The bold lines lie in the respective surfaces and have $M \geq 0$. For the $N_b$-nullcline (orange), the parabolic intersection curve with the plane $M = 0$ is shown. Note that $x_0^* = (0, 0, 0)$ and $x_1^* = (1, \frac{\mu}{c}, 0)$ are the steady states.

Because the nullclines separate the relevant part of space $S$ in different domains of $\mathbb{R}^3$, we consider these domains as regions. Note that we find $2^3 = 8$ different regions because all the nullclines intersect each other. The regions are denoted by the Roman letters $A$ to $H$. In the following definitions, 'above (or below) the
parabolic cylinder’ refers to a larger (or smaller) $N_d$-coordinate, while 'above (or below) the plane $M'=0$’ refers to a larger (or smaller) $M$-coordinate.

- $A$: The region above $(v - c \geq 0)$ or below $(v - c < 0)$ the plane $M' = 0$ and above the parabolic cylinder $N'_b = 0$ for $M > 0$.

- $B$: The region below $(v - c \geq 0)$ or above $(v - c < 0)$ the plane $M' = 0$ and above the parabolic cylinder $N'_b = 0$ for $M > 0$.

- $C$: The region below $(v - c \geq 0)$ or above $(v - c < 0)$ the plane $M' = 0$ and below the parabolic cylinder $N'_b = 0$ for $M > 0$.

- $D$: The region above $(v - c \geq 0)$ or below $(v - c < 0)$ the plane $M' = 0$ and above the parabolic cylinder $N'_b = 0$ for $M < 0$.

- $E$: The region below $(v - c \geq 0)$ or above $(v - c < 0)$ the plane $M' = 0$ and above the parabolic cylinder $N'_b = 0$ for $M < 0$.

- $F$: The region below $(v - c \geq 0)$ or above $(v - c < 0)$ the plane $M' = 0$ and below the parabolic cylinder $N'_b = 0$ for $M < 0$.

- $G$: The region above $(v - c \geq 0)$ or below $(v - c < 0)$ the plane $M' = 0$ and below the parabolic cylinder $N'_b = 0$ for $M > 0$.

- $H$: The region above $(v - c \geq 0)$ or below $(v - c < 0)$ the plane $M' = 0$ and below the parabolic cylinder $N'_b = 0$ for $M < 0$.

In Figure 4 we see that the form of the regions will change as $\mu$ changes from $\mu \geq 1$ to $\mu < 1$. Their geometric location will stay the same for $\mu \geq 1$ as for $\mu < 1$ however.

**Remark.** The definitions of the regions are such that the normal vector $\vec{n}$ of the plane $M' = 0$ points into regions $A, D, G$ and $H$, and out of regions $B, C, E$ and $F$. When $c$ changes from $v - c > 0$ to $v - c < 0$, the direction of changes from pointing upwards to pointing downwards and the location of e.g. $A$ and $B$ changes accordingly. Be aware of this phenomenon when reading the subsequent parts.

To get a better visual view of the location of the regions, in Figure 4 we sketched the regions in a 2D-sketch for $M = -\epsilon < 0$, $M = 0$ and $M = \epsilon > 0$ for the case $v - c > 0$ and $\mu \geq 1$. Note that $\epsilon$ is small.
Figure 4: The location of the regions when intersected with the planes $M = -\epsilon < 0$, $M = 0$ and $M = \epsilon > 0$. The figure is drawn for $v - c \geq 0$, $\mu \geq 1$.

Now we exactly know what the location of every different region is, we can continue with finding the possible heteroclinic orbits. From now on we will consider the cases $c < 0$, $c > 0$ separately. We start with $c < 0$.

In Table 2 we show the signs of $N'_b$, $N'_d$ and $M'$ for $c < 0$ in every different region.
Table 2: The signs of $N'_b$, $N'_d$ and $M'$ for $c < 0$ in every region.

<table>
<thead>
<tr>
<th>Regions</th>
<th>Sign</th>
<th>$N'_b$</th>
<th>$N'_d$</th>
<th>$M'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>−</td>
<td>+</td>
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<tr>
<td>D</td>
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<tr>
<td>E</td>
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<td>−</td>
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<tr>
<td>F</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td></td>
</tr>
<tr>
<td>G</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>H</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td></td>
</tr>
</tbody>
</table>

Proposition 5 Let $c < 0$ and $\mu \geq 1$. There does not exist a heteroclinic orbit from $x^*_1$ to $x^*_0$, through $S$.

Proof. Suppose, for the sake of contradiction, there exists a heteroclinic orbit from $x^*_1$ to $x^*_0$. Then there exist an orbit $\phi(t) : \mathbb{R} \to \mathbb{R}^3(= (N'_b, N'_d, M))$ with $\phi(t) \to x^*_0$ as $t \to \infty$ and $\phi(t) \to x^*_1$ as $t \to -\infty$. It is only possible for $\phi(t)$ to arrive in $x^*_0$ through the regions $A, B, C, D, E$ and $F$ because these are the only regions that are connected with $x^*_0$, in the sense that $x^*_0$ lies in their closure.

In $A$, $B$ and $C$ we have $M > 0$. This means that $N'_d > 0$. So $\phi(t)$ can never reach $x^*_0$ because the $N'_d$-component of $\phi(t)$ will always become more positive. In $D$ and $E$, the orbit will move in the direction of the parabolic cylinder $N'_b = 0$ because $N'_b > 0$. So $\phi(t)$ can also not arrive in $x^*_0$ through $D$ and $E$ because $N'_b$-component of $\phi(t)$ will always become more positive. So the only possible option for the orbit to arrive in $x^*_0$ that is left is through $F$. But in $F$ we have $M' < 0$. And because $M < 0$, the $M$-component of the orbit will always become more negative which means that $\phi(t)$ can also never reach $x^*_0$ through $F$. So we have found a contradiction that there exists a heteroclinic orbit from $x^*_1$ to $x^*_0$.

Proposition 6 Let $c < 0$ and $\mu < 1$. There does not exist a heteroclinic orbit from $x^*_1$ to $x^*_0$, through $S$.

Proof. The intersection points of the parabolic cylinder $N'_b = 0$ with the plane $N'_d = 0$ are given by $(N'_b, N'_d, M) = (0, 0, M)$ and $(N'_b, N'_d, M) = (1 - \mu, 0, M)$, $M \in \mathbb{R}$. Note that $1 - \mu > 0$. We have that $N'_b > 0$ above $N'_b = 0$ and $N'_b < 0$ below $N'_b = 0$. This means that the $N'_b$-component of an orbit that starts in $x^*_1$ can never become less than $1 - \mu$ without crossing the plane $N'_d = 0$, see Figure 5. So an orbit that starts in $x^*_1$ can never reach $x^*_0$ through $S$. 

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Figure 5: Partial phase portrait for $c < 0$ and $\mu < 1$, at some level $M = M_0 \in \mathbb{R}$. Quantitatively, the situation is the same for each $M_0$.

**Proposition 7** Let $c < 0$. If there exists a heteroclinic orbit from $x_0^*$ to $x_1^*$, then this orbit moves from $x_0^*$ to $A$ to $B$ to $x_1^*$ possibly with multiple switches between $A$ and $B$.

**Proof.** Suppose there exists a heteroclinic orbit from $x_0^*$ to $x_1^*$. Then there exists an orbit $\gamma(t) : \mathbb{R} \rightarrow \mathbb{R}^3(= (N_b, N_d, M))$ with $\gamma(t) \rightarrow x_1^*$ as $t \rightarrow \infty$ and $\gamma(t) \rightarrow x_0^*$ as $t \rightarrow -\infty$. Because all the regions are connected to $x_1^*$, it is possible for $\gamma(t)$ to arrive in $x_1^*$ through all these regions, in principle.

**Lemma 4.1** Let $c < 0$. An orbit cannot reach $x_1^*$ through $A$, $E$, $F$ or $G$.

**Proof.** In $A$ and $G$ we have $M' > 0$. And because $M > 0$, the $M$-component of an orbit will always become more positive. So an orbit can never reach $x_1^*$ through $A$ or $G$. In $E$ and $F$ we have $M' < 0$. And because $M < 0$, the $M$-component of an orbit will always become more negative. So an orbit can also never reach $x_1^*$ through $E$ and $F$.

**Lemma 4.2** Let $c < 0$. An orbit can only leave $x_0^*$ through $A$.

**Proof.** The only possible regions for an orbit to leave $x_0^*$ are $A$, $B$, $C$, $D$, $E$ and $F$, since these regions are connected to $x_0^*$. In $A$ we have $N'_b > 0$, $N'_d > 0$ and $M' > 0$ which implies that an orbit could leave $x_0^*$ through $A$. In $B$ and $C$ we have $M' < 0$, while $M > 0$. So an orbit starting from $x_0^*$ and entering into $B$ or $C$ cannot have increasing $M$-component, as it should. So an orbit can not leave $x_0^*$ through $B$ or $C$. In $D$, $E$ and $F$ we have $M < 0$, which means that $N'_d < 0$. So the $N_d$-component can never become positive for an orbit starting from $x_0^*$ and entering into $D$, $E$ or $F$. This means that an orbit can also not leave $x_0^*$ through $D$, $E$ and $F$. So we conclude that the orbit can only leave $x_0^*$ through $A$. □
From Lemma 4.1 and Lemma 4.2 we find that $\gamma(t)$ leaves $x_0^*$ through $A$ and that it reaches $x_1^*$ through $B, C, D$ or $H$. Because we certainly know that $\gamma(t)$ moves into $A$, we will look what happens with the orbit in $A$.

**Lemma 4.3** Let $c < 0$. An orbit in $A$ can only move out of $A$ if it crosses the plane $M' = 0$.

**Proof.** In $A$ we have $M > 0$, $N'_b > 0$, $N'_d > 0$ and $M' > 0$, see Table 2. So the only possible way for an orbit to leave $A$ is to cross the $N_b$-nullcline, that is the parabolic cylinder, or the plane $M' = 0$. But on the parabolic cylinder, on the boundary of $A$, the vectorfield points into $A$ since for $M > 0$ we have $N'_d > 0$ and $M' > 0$ on this $N_b$-nullcline. □

So after $\gamma(t)$ moves into $A$, it has to cross the plane $M' = 0$ at least once. But what happens on this plane? Because the orbit is still above the $N_b$-nullcline and $N_d$-nullcline, we get $N'_b > 0$ and $N'_d > 0$. This means that after $\gamma(t)$ reaches the plane $M' = 0$, it can move into $B$ or $A$ again.

**Lemma 4.4** Let $S^0 := (N^0_b, N^0_d, M^0)$ be a point where an orbit reaches the plane $M' = 0$, $\bar{n}$ the normal vector of $M' = 0$ and $\rho = -\mu \left( \frac{(N^0_b)^2}{c} + \frac{(\mu - 1)N^0_b}{c} - \frac{2}{c} N^0_d \right) + \sigma M^0$.

1. If $\rho > 0$, then an orbit in $S^0$ is pointing in the direction of the same side of the plane as $\bar{n}$ does.

2. If $\rho < 0$, then an orbit in $S^0$ is pointing in the direction of the other side of the plane as $\bar{n}$ does.

3. If $\rho = 0$, then there is no conclusion.

**Proof.** Suppose that an orbit reaches the plane $M' = 0$. The tangent vector $\vec{r}$ of this orbit in $S^0$ is parallel to the $(N_b, N_d)$-plane because $M' = 0$. This tangent vector is given by $\vec{r} = (r_1, r_2, 0)$ with $r_1 = N'_b$ and $r_2 = N'_d = M^0$. For the normal vector of the plane $M' = 0$ we have $\bar{n} = (-\mu, \sigma, v - c)$. Figure 5a and 5b show that if the angle between both vectors is less than $\frac{1}{2} \pi$, then $\vec{r}$ is pointing in the direction of the same side of the plane as $\bar{n}$ does. If the angle between both vectors is greater than $\frac{1}{2} \pi$, then $\vec{r}$ is pointing in the direction of the other side of the plane as $\bar{n}$ does. The angle between $\vec{r}$ and $\bar{n}$ can be found by the following formula,

$$\cos(\alpha) = \frac{\langle \bar{n}, \vec{r} \rangle}{\|\bar{n}\| \cdot \|\vec{r}\|}.$$
Note that \( \cos(\alpha) > 0 \) for \( \alpha < \frac{1}{2} \pi \) and \( \cos(\alpha) < 0 \) for \( \alpha > \frac{1}{2} \pi \). Furthermore, we have that \( ||\vec{n}|| \cdot ||\vec{r}|| > 0 \). So we only need to look to the sign of \( \langle \vec{n}, \vec{r} \rangle \). We find

\[
\langle \vec{n}, \vec{r} \rangle = -\mu r_1 + \sigma r_2,
\]

\[
= -\mu r_1 + \sigma M^0,
\]

\[
= -\mu \left( \frac{(N_0^b)^2}{c} + \frac{(\mu - 1)N_0^{bc}}{c} - \frac{\sigma c N_0^{bd}}{c} \right) + \sigma M^0.
\]

So we conclude that if \( -\mu \left( \frac{(N_0^b)^2}{c} + \frac{(\mu - 1)N_0^{bc}}{c} - \frac{\sigma c N_0^{bd}}{c} \right) + \sigma M^0 > 0 \), then the orbit in \( S^0 \) is pointing in the direction of the same side of the plane as \( \vec{n} \) does. And if \( -\mu \left( \frac{(N_0^b)^2}{c} + \frac{(\mu - 1)N_0^{bc}}{c} - \frac{\sigma c N_0^{bd}}{c} \right) + \sigma M^0 < 0 \), then the orbit in \( S^0 \) is pointing in the direction of the same side of the plane as \( \vec{n} \) does. Note that for \( -\mu \left( \frac{(N_0^b)^2}{c} + \frac{(\mu - 1)N_0^{bc}}{c} - \frac{\sigma c N_0^{bd}}{c} \right) + \sigma M^0 = 0 \) we get Figure 5c and 5d. From these figures we see that we cannot conclude which side of the plane the orbit will go. \( \square \)

**Figure 5:** Direction of the tangent vector \( \vec{r} \) for \( \rho > 0 \), \( \rho < 0 \) and \( \rho = 0 \).
Because $v - c > 0$ for $c < 0$ we conclude that after $\gamma(t)$ reaches the plane $M' = 0$, it will move into $A$ if $-\mu \left( \frac{(N_b^0)^2}{c} + \frac{(\mu-1)N_b^0}{c} - \frac{\sigma}{c} N_d^0 \right) + \sigma M^0 > 0$ or into $B$ if $-\mu \left( \frac{(N_b^0)^2}{c} + \frac{(\mu-1)N_b^0}{c} - \frac{\sigma}{c} N_d^0 \right) + \sigma M^0 < 0$. Note that $\gamma(t)$ could have multiple touching events with the plane $M' = 0$ before it reaches a point where it may cross the plane.

**Lemma 4.5** An orbit in $B$ can only reach $x_1^*$ if it reaches $x_1^*$ through $B$ with possible multiple crossing events with $A$.

**Proof.** In $B$ we have $M > 0$, $N_b' > 0$, $N_d' > 0$ and $M' < 0$. This means that we have the following possible options for an orbit in $B$ (see Figure 6).

1. The orbit reaches the $N_b$-nullcline (the parabolic cylinder; orange).
2. The orbit reaches the plane $M' = 0$ (the upper plane; green).
3. The orbit reaches the plane $M = 0$ (the lower horizontal plane; white).
4. The orbit reaches the $N_b$-nullcline and the plane $M = 0$ at the same time.
5. The orbit reaches the planes $M' = 0$ and $M = 0$ at the same time.
6. The orbit reaches $x_1^*$.

![Figure 6: Case $c < 0$ and $\mu < 1$.](image)

The region $B$ is the wedge-like shape enclosed by the green plane ($M' = 0$), the orange parabolic cylinder ($N_b' = 0$) and the ($N_b, N_d$)-coordinate plane (horizontal white plane).

Suppose an orbit reaches the $N_b$-nullcline. On this $N_b$-nullcline we have $N_b' > 0$ and $M' < 0$ because $M > 0$. This means that the orbit will move into $B$ again. If an orbit reaches the plane $M' = 0$, then we have found that the orbit points into $A$ or $B$. If it points into $A$, the orbit can come back in $B$ or it will stay in $A$ forever. The third option is that the orbit reaches the plane $M = 0$. Because the orbit is below the plane $M' = 0$, we have $M' < 0$. This means that the orbit will move into $E$. This cannot give a heteroclinic orbit because the orbit will eventually move out of $S$, according to Lemma 4.6.

**Lemma 4.6** Let $c < 0$. An orbit starting in $F$ will leave $S$. An orbit starting in $E$ will move into $F'$.  

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Proof. In $E$ we have $M < 0$, $N'_b > 0$, $N'_d < 0$ and $M' < 0$. This means that the orbit eventually will reach the $N_b$-nullcline after which it will move into $F$. But because $M$ becomes more negative in $F$, the orbit eventually will cross the plane $N_d = 0$. So this leads to no biologically relevant solutions. □

If an orbit reaches the $N_b$-nullcline and the plane $M = 0$ at the same time, we get that the $M$-component of the orbit becomes more negative which implies that it will move into $F$. And in $F$, we saw that we get no biologically relevant solutions eventually. The last option is that an orbit reaches the planes $M' = 0$ and $M = 0$ at the same time. If this happens, then the orbit stays on the plane $M = 0$ in the beginning because $N'_b > 0$. Then it will move into $E$ because $M'$ becomes negative. This will lead to no biologically relevant solutions according to Lemma 4.6. So we conclude that an orbit in $B$ can only reach $x^*_1$ if it reaches $x^*_1$ through $B$ with possible multiple crossing events with $A$. □

A schematic representation of the possible paths of an orbit that starts in $x^*_0$, is given in Figure 7.

![Figure 7: Representation of the possible paths of an orbit that starts in $x^*_0$ for the case $c < 0$.](image)
Note that the circles stand for regions and the squares for steady states. Also notice that n.b.r.s stands for ‘no biologically relevant solutions’ and that this is the region where $N_b < 0$ or $N_d < 0$. To define the straight arrows, let $X$ be a region with $x_0 \in X$, $x(t;x_0)$ the solution which starts at $x_0$ and $\tau X(x_0) = \inf\{t > 0 | x(t,x_0) \in X^c\}$, i.e. the time in which the solution touches a nullcline for the first time. If $\inf\{t > 0 | x(t,x_0) \in X^c\} = \emptyset$, then $\tau X(x_0) = -\infty$ by definition. Now we can define the straight arrows. If there exists an arrow between $X$ and itself, then there exists $x_0 \in X$ such that $x(t,x_0) \in X$ for all $t \geq 0$. Let $Y$ be another region. If there exists an straight arrow from $X$ to $Y$, then there exists a $x_0 \in X$ such that $x(t,x_0) \in Y$ for $t > \tau X(x_0)$ and $t - \tau X(x_0)$ sufficiently small. A dotted arrow means that an orbit will move from the steady state into the indicated region or that there is an orbit starting in that region converging to the steady state.

So looking at the graph in Figure 7, we conclude that if there exists a heteroclinic orbit from $x^*_0$ to $x^*_1$ for $c < 0$, then this orbit moves from $x^*_0$ to $A$ to $B$ to $x^*_1$ possibly with multiple switches between $A$ and $B$. □

Now we will look if there also could exist a heteroclinic orbit for $c > 0$. Note that for $c > 0$ we have two cases: $0 < c < v$ and $c > v$. But because of the definitions we used for the regions $A$ to $H$, the conclusions stay the same for both of the cases.

Because c is positive, we have that $N'_b$ will be negative in the regions above the parabolic cylinder $N'_b = 0$ and positive in the regions below, see Table 3.

<table>
<thead>
<tr>
<th>Regions</th>
<th>Sign</th>
<th>$N'_b$</th>
<th>$N'_d$</th>
<th>$M'$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>$-$</td>
<td>$+$</td>
<td>$+$</td>
<td></td>
</tr>
<tr>
<td>$B$</td>
<td>$-$</td>
<td>$+$</td>
<td>$-$</td>
<td></td>
</tr>
<tr>
<td>$C$</td>
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<td>$+$</td>
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<td>$G$</td>
<td>$+$</td>
<td>$+$</td>
<td>$+$</td>
<td></td>
</tr>
<tr>
<td>$H$</td>
<td>$+$</td>
<td>$-$</td>
<td>$+$</td>
<td></td>
</tr>
</tbody>
</table>

**Table 3:** The signs of $N'_b$, $N'_d$ and $M'$ in every region for $c > 0$.

**Proposition 8** Let $c > 0$ and $\mu \geq 1$. There does not exist a heteroclinic orbit from $x^*_0$ to $x^*_1$ in $S$.

**Proof.** Suppose, for the sake of contradiction, there exists a heteroclinic orbit from $x^*_0$ to $x^*_1$. Then there exist an orbit $\phi(t) : \mathbb{R} \to \mathbb{R}^3(= (N_b, N_d, M))$ with $\phi(t) \to x^*_1$ as $t \to \infty$ and $\phi(t) \to x^*_0$ as $t \to -\infty$. It is only possible for $\phi(t)$ to
leave \( x^*_0 \) through the regions \( A, B, C, D, E \) or \( F \).

In \( A, B, D \) and \( E \) we have \( N'_b < 0 \). Because \( \phi(t) \) starts in \( x^*_0 \), the \( N_b \)-component of the orbit can never become positive in these regions. So \( \phi(t) \) cannot leave \( x^*_0 \) through \( A, B, D \) and \( E \). In \( C \) we have \( M' < 0 \). So the \( M \)-component of the orbit can never become positive which means that \( \phi(t) \) can also never leave \( x^*_0 \) through \( C \). The last option to leave \( x^*_0 \) is through \( F \). But in \( F \) we have that \( N'_d < 0 \). So the \( N_b \)-component of \( \phi(t) \) can never become positive, which implies that the orbit can also not leave \( x^*_0 \) through \( F \). So we have found a contradiction that there exists a heteroclinic orbit from \( x^*_0 \) to \( x^*_1 \) contained in \( S \). \( \square \)

**Proposition 9** Let \( c > 0 \) and \( \mu < 1 \). There does not exist a heteroclinic orbit from \( x^*_0 \) to \( x^*_1 \) in \( S \).

**Proof**: The intersection points of the parabolic cylinder \( N'_b = 0 \) with the plane \( N_d = 0 \) are given by \((N_b, N_d, M) = (0, 0, M)\) and \((N_b, N_d, M) = (1 - \mu, 0, M)\). Note that \( 1 - \mu > 0 \). We have that \( N'_b < 0 \) above \( N'_b = 0 \) and \( N'_b > 0 \) below \( N'_b = 0 \). This means that the \( N_b \)-component of an orbit that starts in \( x^*_0 \) can never become greater than 0 without getting a negative \( N_d \)-component, see Figure 8. So an orbit that starts in \( x^*_0 \) can never reach \( x^*_1 \) which means there does not exist a heteroclinic orbit from \( x^*_0 \) to \( x^*_1 \). \( \square \)

**Figure 8**: Partial phase portrait for \( c > 0 \) and \( \mu < 1 \), on a plane \( M = M_0 \), \( M_0 \in \mathbb{R} \). For each \( M_0 \in \mathbb{R} \) the situation is quantitatively similar.

**Lemma 4.7** Let \( c > 0 \). If there exists a heteroclinic orbit from \( x^*_1 \) to \( x^*_0 \), then this orbit moves from \( x^*_1 \) to \( E \) to \( D \) to \( x^*_0 \) possibly with multiple switches between \( E \) and \( D \).
Proof. Suppose there exists a heteroclinic orbit from $x_1^*$ to $x_0^*$. Then there exists an orbit $\gamma(t) : \mathbb{R} \to \mathbb{R}^3(=\{N_b,N_d,M\})$ with $\gamma(t) \to x_0^*$ as $t \to \infty$ and $\gamma(t) \to x_1^*$ as $t \to -\infty$. It is only possible for $\gamma(t)$ to reach $x_0^*$ through $A, B, C, D, E$ and $F$.

Lemma 4.8 Let $c > 0$. An orbit can only reach $x_0^*$ through $D$.

Proof. In $A, B$ and $C$ we have $M > 0$. This means that $N_b^d > 0$. So an orbit in $A, B$ or $C$ can never reach $x_0^*$ because the $N_d$-component of the orbit will always become more positive. In $D$ we have $N_b^d < 0, N_d^d < 0$ and $M' > 0$ which means that all the components of the orbit are pointing in the direction of $x_0^*$. So an orbit could reach $x_0^*$ through $D$. In $E$ we have $M < 0$ and $M' < 0$. So an orbit can never reach $x_0^*$ through $E$ because the $M$-component becomes more negative. It is also not possible to reach $x_0^*$ through $F$ because in $F$ we have $N_b^d > 0$ which means that the $N_b$-component becomes more positive. So we conclude that an orbit can only reach $x_0^*$ through $D$. ∎

Lemma 4.9 Let $c > 0$. An orbit that reaches $x_0^*$, cannot leave $x_1^*$ through $A, B, C, D, F, G$ or $H$.

Proof. In $A$ we have $M' > 0$, $N_b^d < 0$ and $N_d^d > 0$. This implies that for $v - c \geq 0$, an orbit eventually will cross the plane $N_b = 0$. So this leads to no biologically relevant solutions. For $v - c < 0$, an orbit can also reach the plane $M' = 0$. Because $M > 0$ and the orbit is still above $N_b^d = 0$, we get $N_d^d < 0$ and $N_d^d > 0$. So after the orbit reaches the plane $M' = 0$, it will move into $A$ again. And because $N_b^d$ stays negative, it will also lead to no biologically relevant solutions. In $B$ and $C$ we have $M' < 0$, which implies that the $M$-component of an orbit that starts in $x_1^*$ never becomes positive. So it is impossible for an orbit to leave $x_1^*$ through $B$ or $C$. An orbit can also not leave $x_1^*$ through $D$ or $H$ because there we have $M' > 0$. So the $M$-component never becomes negative. In $F$ we have $M < 0$, $N_b^d > 0$, $N_d^d < 0$ and $M' < 0$. This means that the orbit eventually will cross the the plane $N_d = 0$ for $v - c \geq 0$. So this leads to no biologically relevant solutions. For $v - c < 0$, an orbit can also reach the plane $M' = 0$. Because $M < 0$ and the orbit is still below $N_b^d = 0$, we get $N_d^d > 0$ and $N_d^d < 0$. So after the orbit reaches the plane $M' = 0$, it will move into $F$ again. And because $N_b^d$ stays negative, it will also lead to no biologically relevant solutions. In $G$ we have $M > 0$, $N_b^d > 0$, $N_d^d > 0$ and $M' > 0$. So the only possible way for an orbit to leave $G$ is through the $N_b$-nullcline or $M$-nullcline.

Suppose that an orbit in $G$ reaches the $N_b$-nullcline. On this nullcline we have $N_b^d > 0$ and $M' > 0$. This means that the orbit will move into $A$ what leads to no biologically relevant solutions. Now suppose that an orbit in $G$ reaches the $M$-nullcline. On this nullcline we have $N_b^d > 0$ and $N_d^d > 0$. So from here, the orbit can move into $C$ or $G$ again. Suppose the orbit will move into $C$. In $C$ we have $M > 0$, $N_b^d > 0$, $N_d^d > 0$ and $M' < 0$. This means that the orbit can only leave $C$ through the $M$-nullcline or $N_b$-nullcline. We found that the orbit will move into $C$ or $G$ after it reaches the $M$-nullcline. So suppose it reaches
the $N_b$-nullcline. On this nullcline we have $N_b' > 0$ and $M' < 0$ which means that the orbit will move into $F$. And we found that this leads to no biologically relevant solutions. So we conclude that an orbit that could reach $x_0^*$, can not leave $x_0^*$ through $A, B, C, D, F, G$ or $H$. □.

From Propositions 4.8 and 4.9 it follows that $\gamma(t)$ must leave $x_1^*$ through $E$ and that it reaches $x_0^*$ through $D$. Now we will look what happens with an orbit in $E$.

**Proposition 10** Let $c > 0$. An orbit in $E$ can only reach $D$ if it crosses the plane $M' = 0$ from $E$.

**Proof.** In $E$ we have $M < 0, N_b' < 0, N_d' < 0$ and $M' < 0$. This means that an orbit can only leave $E$ if it reaches the $N_b$-nullcline or the plane $M' = 0$. On the $N_b$-nullcline, we have $N_b' < 0$ and $M' < 0$. So the orbit will move into $F$. And we found that this leads to no biologically relevant solutions. On the $M$-nullcline, we have $N_d' < 0$ and $N_b' < 0$. So on this nullcline, an orbit will move into $D$ or $E$ again. Note that for $v - c \geq 0$, an orbit needs to reach the plane $M' = 0$ before $N_b$ becomes negative. We conclude that an orbit in $E$ can only reach $D$ if it crosses the plane $M' = 0$ from $E$. □.

So after $\gamma(t)$ moves into $E$, it has to cross the plane $M' = 0$ at least once to get into $D$. The conditions that $\gamma(t)$ crosses the plane $M' = 0$ can be found in Lemma 4.4. Note that $\gamma(t)$ could have multiple touching events with the plane $M' = 0$ before it reaches a point where it will cross the plane.

**Proposition 11** Let $c > 0$. An orbit in $D$ can only reach $x_0^*$ if it reaches $x_0^*$ through $D$ with possible multiple crossing events with $E$.

**Proof.** In $D$ we have $M < 0, N_b' < 0, N_d' < 0$ and $M' > 0$. This means that we have the following possible options for an orbit in $D$.

1. The orbit reaches the plane $M' = 0$.
2. The orbit reaches the plane $M = 0$.
3. The orbit reaches the plane $M' = 0$ and the plane $M = 0$ at the same time.
4. The orbit reaches the plane $N_b = 0$ without reaching $x_0^*$.
5. The orbit reaches $x_0^*$

Suppose an orbit reaches the plane $M' = 0$. On this plane, we found that an orbit will move into $E$ or $D$ again. If it points into $E$, then we have seen that it will return to $D$ or it will lead to no biologically relevant solutions. On the plane $M = 0$, we have $N_b' < 0$ and $M' > 0$. So an orbit that reaches the plane $M = 0$ from $D$ will move into $A$. And here we found that it can never reach $x_0^*$ again. The third option is that an orbit reaches the planes $M' = 0$ and
\(M = 0\) at the same time. Then we find that the orbit will also move into \(A\) because first we only get \(N'_b < 0\) and then also \(M' > 0\). If an orbit reaches the plane \(N_b = 0\), then we get no biologically relevant solutions because on this plane we have \(N'_b < 0\). So we conclude that an orbit in \(D\) can only reach \(x^*_0\) if it reaches \(x^*_0\) through \(D\) with possible multiple crossing events with \(E\). □

A schematic representation of the possible paths of an orbit that starts in \(x^*_1\), is given in Figure 9.

\[\text{Figure 9: Representation of the possible paths of an orbit that starts in } x^*_1 \text{ for the case } c > 0.\]
So looking to Figure 9 we conclude that if there exists a heteroclinic orbit from $x^*_1$ to $x^*_0$ for $c > 0$, then this orbit moves from $x^*_1$ to $E$ to $D$ to $x^*_0$ possibly with multiple switches between $E$ and $D$. □

Conclusion: From Propositions 5, 6, 8 and 9 it seems that extinction is not realized by means of “washout”, nor a downwards moving extinction front nor an upwards moving extinction front (see Table 1). The decay of the population seems to be more complicated.

4.4 Dimensionality of the stable and unstable manifolds.

In Section 4.3 we have seen that there could only exist a heteroclinic orbit from $x^*_0$ to $x^*_1$ for $c < 0$ and from $x^*_1$ to $x^*_0$ for $c > 0$. The conclusion of the previous section does not imply that there exists a heteroclinic orbit for any $c$ indicated. A necessary condition for the existence of a heteroclinic orbit is that one steady state must have a non-trivial unstable manifold and the other one a non-trivial stable manifold. These should ‘point’ into the right region, as analysed in the previous section. In this section we will analyse the stability of the steady states after which we can determine the possible dimension of the stable and unstable manifolds. In this we follow [Pachepsky], but elaborate substantially in detail on the exposition provided there.

4.4.1 Linear stability analysis.

To analyse the stability of the both steady states, we first linearize system (59) around both steady states and then we determine the characteristic polynomials to find the eigenvalues.

Lemma 4.10 Linearization around $x^*_0 = (0, 0, 0)$ yields the characteristic polynomial

$$ P_0(\lambda) = A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4, \quad (60) $$

where

$$ A_1 = -1, $$
$$ A_2 = \frac{\mu - 1}{c} + v - c, $$
$$ A_3 = (\mu - 1)(1 - \frac{v}{c}) + \sigma, $$
$$ A_4 = \frac{\sigma}{c}. $$

Proof. The Jacobian $D f(N_b, N_d, M)$ of the right-hand side of (59) is given by

$$ D f(N_b, N_d, M) = \begin{pmatrix} \frac{2N_b + \mu - 1}{c} & -\frac{\sigma}{c} & 0 \\ 0 & 0 & 1 \\ -\mu & \sigma & v - c \end{pmatrix}. $$

Substituting $x^*_0 = (0, 0, 0)$ gives

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\[
Df(0,0,0) = \begin{pmatrix}
\frac{\mu-1}{c} & -\frac{\sigma}{c} & 0 \\
0 & 0 & 1 \\
-\mu & \sigma & v-c
\end{pmatrix}.
\]

For the characteristic polynomial \( P_0(\lambda) \), we obtain

\[
P_0(\lambda) = \det (Df(0,0,0) - \lambda I),
\]

\[
= - \lambda(v-c-\lambda)\left(\frac{\mu-1}{c} - \lambda\right) + \frac{\sigma \mu}{c} - \sigma\left(\frac{\mu-1}{c} - \lambda\right),
\]

\[
= \frac{v(1-\mu)}{c} \lambda + v\lambda^2 + (\mu-1)\lambda - c\lambda^2 + \frac{\mu-1}{c} \lambda^2 - \lambda^3 + \frac{\sigma \mu}{c} + \frac{\sigma(1-\mu)}{c} + \sigma \lambda,
\]

\[
= -\lambda^3 + \left(\frac{\mu-1}{c} + v - c\right)\lambda^2 + ((\mu-1)(1-v)+\sigma)\lambda + \frac{\sigma}{c}.
\]

\[\square\]

**Lemma 4.11** Linearization around \( x^*_1 = (1, \frac{\mu}{\sigma}, 0) \) yields the characteristic polynomial

\[
P_1(\lambda) = B_1 \lambda^3 + B_2 \lambda^2 + B_3 \lambda + B_4,
\]

where

\[
B_1 = -1,
\]

\[
B_2 = \frac{\mu+1}{c} + v - c,
\]

\[
B_3 = (\mu+1)(1-v) + \sigma,
\]

\[
B_4 = -\frac{\sigma}{c}.
\]

**Proof.** The Jacobian \( Df(N_b, N_d, M) \) for \( x^*_1 = (1, \frac{\mu}{\sigma}, 0) \) is given by

\[
Df(1, \frac{\mu}{\sigma}, 0) = \begin{pmatrix}
\frac{\mu+1}{c} & -\frac{\sigma}{c} & 0 \\
0 & 0 & 1 \\
-\mu & \sigma & v-c
\end{pmatrix}.
\]

For the characteristic polynomial, we obtain

\[
P_1(\lambda) = \det (Df(1, \frac{\mu}{\sigma}, 0) - \lambda I),
\]

\[
= - \lambda(v-c-\lambda)\left(\frac{\mu+1}{c} - \lambda\right) + \frac{\sigma \mu}{c} - \sigma\left(\frac{\mu+1}{c} - \lambda\right),
\]

\[
= - \frac{v(\mu+1)}{c} \lambda + v\lambda^2 + (\mu+1)\lambda - c\lambda^2 + \frac{\mu+1}{c} \lambda^2 - \lambda^3 + \frac{\sigma \mu}{c} - \frac{\sigma(\mu+1)}{c} + \sigma \lambda,
\]

\[
= -\lambda^3 + \left(\frac{\mu+1}{c} + v - c\right)\lambda^2 + ((\mu+1)(1-v)+\sigma)\lambda + \frac{\sigma}{c}.
\]

\[\square\]

### 4.4.2 Dimensionality of the stable and unstable manifolds.

To determine the possible number of positive and negative real roots of \( P_0(\lambda) = 0 \) and \( P_1(\lambda) = 0 \), we will use Descarte’s Rule of Signs (see Theorem 4.12, [2]). We consider the cases \( c < 0 \) and \( c > 0 \) separately.
Theorem 4.12 (Descarte’s rule of signs, [2]) If the terms of a single-variable polynomial with real coefficients are ordered by descending variable exponent, then the number of positive roots of the polynomial is either equal to the number of sign differences between nonzero coefficients, or is less than it by an even number. The number of negative roots is the number of sign changes after multiplying the coefficients of odd-power terms by -1, or fewer than it by an even number.

The case \( c < 0 \).

First we will look to the possible dimensions of the stable and unstable manifolds of the zero steady state. Using Descartes rule of signs, we need to look to the sign changes of the coefficients of \( P_0(\lambda) \) and \( P_0(-\lambda) \). In \( P_0(\lambda) \) we have that \( A_1 < 0, A_2 > 0 \) and \( A_4 < 0 \) for \( \mu < 1 \). For \( \mu > 1 \) we have that \( A_1 < 0, A_3 > 0 \) and \( A_4 < 0 \). And for \( \mu = 1 \) we have that \( A_1 < 0, A_2 > 0, A_3 > 0 \) and \( A_4 < 0 \). This means that the coefficients of \( P_0(\lambda) \) always have two sign changes. So \( P_0(\lambda) = 0 \) has zero or two positive real roots. For \( P_0(-\lambda) \) we have

\[
P_0(-\lambda) = -A_1\lambda^3 + A_2\lambda^2 - A_3\lambda + A_4. \tag{62}
\]

We see that \( -A_1 > 0, A_2 > 0 \) and \( A_4 < 0 \) for \( \mu < 1 \). For \( \mu > 1 \) we have \( -A_1 > 0, -A_3 < 0 \) and \( A_4 < 0 \). And for \( \mu = 1 \) we have \( -A_1 > 0, A_2 > 0, -A_3 < 0 \) and \( A_4 < 0 \). This implies that \( P_0(-\lambda) = 0 \) has exactly one positive real root, which means that \( P_0(\lambda) = 0 \) has exactly one negative real root. Now there are two possible cases,

1. \( P_0(\lambda) = 0 \) has two positive real roots and one negative real root.

2. \( P_0(\lambda) = 0 \) has one negative real root and two conjugated non-real roots, both with either Re > 0 or Re < 0.

We know that if \( P_0(\lambda) = 0 \) has two complex roots, the real part of these roots has the same sign because non-real roots of a polynomial with real coefficients must occur in conjugate pairs. Now we know all the possible roots of \( P_0(\lambda) = 0 \), we conclude that the possible dimension of the stable manifold of the zero steady state, \( W^s_0 \), is 1 or 3. For the unstable manifold \( W^u_0 \) we have that the possible dimension is 2 or 0, respectively.

Now we will determine the possible dimensions of the stable and unstable manifolds of the non-zero steady state. In \( P_1(\lambda) \), we have that \( B_1 < 0, B_3 > 0 \) and \( B_4 > 0 \). This means that \( P_1(\lambda) = 0 \) has exactly one positive real root. For \( P_1(-\lambda) \) we have

\[
P_1(-\lambda) = -B_1\lambda^3 + B_2\lambda^2 - B_3\lambda + B_4. \tag{63}
\]

We see that \( -B_1 > 0, -B_3 < 0 \) and \( B_4 > 0 \). This implies that \( P_1(-\lambda) = 0 \) has zero or two positive real roots, which means that \( P_1(\lambda) = 0 \) has zero or two negative real roots. Now there are again two possible cases,
1. $P_1(\lambda) = 0$ has one positive real root and two negative real roots.

2. $P_1(\lambda) = 0$ has one positive real root and two conjugated non-real roots, both with either $Re > 0$ or $Re < 0$.

So we conclude that $\dim(W^s_1) = 0$ or $2$ and $\dim(W^u_1) = 3$ or $1$, respectively.

The case $c > 0$.

In $P_0(\lambda)$, we have that $A_1 < 0$ and $A_4 > 0$ (For $\mu = 1$ we also have $A_3 > 0$). This means that $P_0(\lambda) = 0$ has one or three positive real roots. In $P_0(-\lambda)$, we have that $-A_1 > 0$ and $A_4 > 0$ (For $\mu = 1$ we also have $-A_3 < 0$) This implies that $P_0(-\lambda) = 0$ has zero or two positive real roots, which means that $P_0(\lambda) = 0$ has zero or two negative real roots. Now there are three possible cases,

1. $P_0(\lambda) = 0$ has three positive real roots.
2. $P_0(\lambda) = 0$ has one positive real root and two negative real roots.
3. $P_0(\lambda) = 0$ has one positive real root and two conjugated non-real roots, both with either $Re > 0$ or $Re < 0$.

So we conclude that $\dim(W^s_0) = 0$ or $2$ and $\dim(W^u_0) = 3$ or $1$, respectively.

In $P_1(\lambda)$, we have that $B_1 < 0$ and $B_4 < 0$. This means that $P_1(\lambda) = 0$ has zero or two positive real roots. In $P_1(-\lambda)$, we have that $-B_1 > 0$ and $B_4 < 0$. This implies that $P_1(-\lambda) = 0$ has one or three positive real roots, which means that $P_1(\lambda) = 0$ has one or three negative real roots. Now there are again three possible cases,

1. $P_1(\lambda) = 0$ has three negative real roots.
2. $P_1(\lambda) = 0$ has two positive real roots and one negative real root.
3. $P_1(\lambda) = 0$ has one negative real root and two conjugated non-real roots, both with either $Re > 0$ or $Re < 0$.

So we conclude that $\dim(W^s_1) = 1$ or $3$ and $\dim(W^u_1) = 2$ or $0$, respectively.

A summary of the results on dimensions of the stable and unstable manifold of $x^*_0$ and $x^*_1$ are given in Tables 4 and 5.

<table>
<thead>
<tr>
<th></th>
<th>$c &lt; 0$</th>
<th>$c &gt; 0$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\dim(W^s_0)$</td>
<td>1 or 3</td>
<td>0 or 2</td>
</tr>
<tr>
<td>$\dim(W^u_0)$</td>
<td>2 or 0</td>
<td>3 or 1</td>
</tr>
</tbody>
</table>

**Table 4:** The possible dimensions of the stable and unstable manifold of $x^*_0$.  

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4.5 The propagation speeds and necessary conditions for the existence of a heteroclinic orbit by analysing the dimensionality of the manifolds.

For the existence of a heteroclinic orbit connecting the steady states $x^*_0$ and $x^*_1$, it is necessary that one steady state has an unstable manifold and the other one a stable manifold. However, this does not prove the existence of a heteroclinic orbit. It only says that it could be possible there exists one. In this section we only provide necessary conditions for the existence of a heteroclinic orbit, based on consideration of the dimensionality of stable and unstable manifolds. In this we follow [Pachepsky] essentially, but elaborate on their exposition.

In the previous section we saw that $P_0(\lambda)$ always has one negative real root for $c < 0$. We also saw that $P_1(\lambda)$ always has one positive real root for $c < 0$. So there is no obstruction to the existence of a heteroclinic orbit starting from the non-zero steady state to the zero steady state because both manifolds have dimension of at least one.

Note that $P_0(\lambda)$ and $P_1(\lambda)$ both could have non-real roots. For the unstable manifold of the non-zero steady state this will not give any problems but for the stable manifold of the zero steady state it will. The approach of the orbit to the steady states would be oscillatory what in the case of the zero steady state will lead to negative solutions. So this would not give a biologically relevant solution.

Now we know that it could be possible there is a heteroclinic orbit starting from the non-zero steady state to the zero steady state for $c < 0$, we also would like to find conditions on the propagation speed such that there exists a heteroclinic orbit starting from the zero steady state to the non-zero steady state for $c < 0$.

**Proposition 12** Let $c < 0$. If there exists an upstream travelling wave from $x^*_0$
to $x_1^+$ with speed $c$, then $R^0_+(c) > 0$ and $R^1_-(c) < 0$, where

$$R^0_+(c) = -(\lambda^0_+)^3 + A_2(\lambda^0_+)^2 + A_3\lambda^0_+ + A_4,$$

$$\lambda^0_+ = \frac{A_2 + \sqrt{A_2^2 + 3A_3}}{3},$$

and

$$R^1_-(c) = -(\lambda^1_-)^3 + B_2(\lambda^1_-)^2 + B_3\lambda^1_- + B_4,$$

$$\lambda^1_- = \frac{B_2 - \sqrt{B_2^2 + 3B_3}}{3}.$$

**Proof.** To make it possible to have a heteroclinic orbit from the zero steady state to the non-zero steady state, we need that $P_0(\lambda)$ has at least one real positive root and $P_1$ at least one root with $Re < 0$ (it is allowed that the orbit oscillates around the non-zero steady state). We will first look to the roots of $P_0(\lambda)$.

From the previous section we see that the only case in which we for certain know that $P_0(\lambda)$ has at least one positive real root is the case where $P_0(\lambda)$ has two positive real roots and one negative real root. The transition point between zero or two positive real roots is exactly when the local maximum of $P_0(\lambda)$ is a positive real root, see Figure 10. This means that $P'_0(\lambda) = 0$ and $P_0(\lambda) = 0$ for $\lambda > 0$.

![Figure 10: The shape of $P_0(\lambda)$ when its two roots switch from complex to real.](image)

From $P'_0(\lambda) = 0$ we find

$$-3\lambda^2 + 2A_2\lambda + A_3 = 0.$$  \hfill (66)

With the abc-formula we find that the solutions to (66) are

$$\lambda^0_\pm = \frac{A_2 \pm \sqrt{A_2^2 + 3A_3}}{3}.$$  \hfill (67)
Note that $\lambda_0^+$ is a function of $c$.

We have that $P_0'(\lambda)$ has one positive and one negative real root. Here $\lambda_0^+$ is the positive real root which corresponds to the local maximum of $P_0(\lambda)$ and $\lambda_0^-$ the negative real root which corresponds to the local minimum of $P_0$. Note that $P_0(\lambda)$ has exactly one real positive root if $P_0(\lambda_0^+) = 0$. So we conclude that if $P_0(\lambda_0^+) > 0$, then $P_0(\lambda)$ has two positive real roots. So for $P_0(\lambda_0^+) > 0$, the dimension of the unstable manifold of the zero steady state is two.

For the propagation speed, we know that $P_0(\lambda_0^+)$ is a function of $c$. We define $R_0(c) := P_0(\lambda_0^+)$. The critical propagation speed $c^*_0$ can then be found by solving the equation,

$$R_0'(c^*_0) = -3\lambda_0^+ \lambda_0^+ + 2B_2 + A_3\lambda_0^+ + A_4 = 0.$$ (68)

This means that for all values of $c$ with $c < 0$ and $R_0'(c) > 0$, it could be possible there is an upstream travelling wave starting starting from the zero steady state.

For $P_1(\lambda)$, we need at least one root with $Re < 0$. The only case in which we certainly know we have at least one root with $Re < 0$ is the case where $P_1(\lambda) = 0$ has one positive real root and two negative real roots. The transition point between zero negative real roots and two negative real roots is exactly when the local minimum of $P_1(\lambda)$ is a negative real root, see Figure 11. This means that $P_1'(\lambda) = 0$ and $P_1(\lambda) = 0$ for $\lambda < 0$.

![Figure 11](image)

**Figure 11:** The shape of $P_1(\lambda)$ when it’s two roots switch from complex to real.

From $P_1'(\lambda) = 0$ we find

$$-3\lambda^2 + 2B_2\lambda + B_3 = 0.$$ (69)

With the abc-formula we find that the solutions to (69) are

$$\lambda_1^\pm = \frac{B_2 \pm \sqrt{B_2^2 + 3B_3}}{3}.$$ (70)
Note that $\lambda^1_\pm$ is a function of $c$.

We have that $P_1^\prime(\lambda)$ has one positive and one negative real root. Here $\lambda^1_-$ is the negative real root which corresponds to the local minimum of $P_1(\lambda)$ and $\lambda^1_+$ the positive real root which corresponds to the local maximum of $P_1$. Note that $P_1(\lambda)$ has exactly one negative real root if $P_1(\lambda^1_-) = 0$. So we conclude that if $P_1(\lambda^1_+) < 0$, then $P_1$ has two negative real roots. So for $P_1(\lambda^1_-) < 0$, the dimension of the stable manifold of the non-zero steady state is two.

For the propagation speed, we know that $P_1(\lambda^1_-)$ is a function of $c$. We define $R^1_-(c) := P_1(\lambda^1_-(c))$. The critical propagation speed $c^*_1$ can then be found by solving the equation,

$$R^1_-(c^*_1) = -(\lambda^1_-)^3 + B_2(\lambda^1_-)^2 + B_3\lambda^1_- + B_4 = 0. \quad (71)$$

This means that for all values of $c$ with $c < 0$ and $R^1_-(c) < 0$, it could be possible there is an upstream travelling wave to the non-zero steady state. □

**Remark.** The critical speeds $c^*_0$ and $c^*_1$ defined in (68) and (71) provide bounds on possible wave propagation speeds $c$ that these need to satisfy. One cannot conclude of course that for $c$ that satisfy the bounds, there exists a heteroclinic orbit.

In the previous section we also saw that $P_0(\lambda)$ always has at least one positive real root and $P_1(\lambda)$ always has at least one negative real root for $c > 0$. So there is no obstruction to the existence of a heteroclinic orbit starting from the zero steady state to the non-zero steady state from dimensionality consideration because both manifolds have dimension of at least one.

Now we know that it could be possible there is a heteroclinic orbit starting from the zero steady state to the non-zero steady state for $c > 0$, we also want to find conditions on the propagation speed in this case, similar to the ones established before.

**Proposition 13** Let $c > 0$. If there exists a downstream travelling wave from $x^*_1$ to $x^*_0$ with speed $c$, then $R^0_-(c) < 0$ and $R^1_+(c) > 0$, with

$$R^0_-(c) = -(\lambda^0_-)^3 + A_2(\lambda^0_-)^2 + A_3\lambda^0_- + A_4,$$

$$\lambda^0_- = A_2 - \sqrt{A_2^2 + 3A_3},$$

and

$$R^1_+(c) = -(\lambda^1_+)^3 + B_2(\lambda^1_+)^2 + B_3\lambda^1_+ + B_4,$$

$$\lambda^1_+ = B_2 + \sqrt{B_2^2 + 3B_3}.$$
Proof. To make it possible to have a heteroclinic orbit from the non-zero steady state to the zero steady state, we need that \( P_0(\lambda) \) has at least one negative real root and \( P_1(\lambda) \) at least one root with \( \Re > 0 \).

The only case that we know for sure we have at least one negative real root is the case where \( P_0(\lambda) = 0 \) has one positive real root and two negative real roots. The transition point between zero or two negative real roots is exactly when the local minimum of \( P_0(\lambda) \) is a negative real root, see Figure 12. This means that \( P_0'(\lambda) = 0 \) and \( P_0(\lambda) = 0 \) for \( \lambda < 0 \).

![Figure 12: The shape of \( P_0(\lambda) \) when its two roots switch from complex to real.](image)

From \( P_0'(\lambda) = 0 \) we find the same solutions as in (69). Here \( \lambda^0_- \) is the negative real root which corresponds to the local minimum of \( P_0(\lambda) \) and \( \lambda^0_+ \) the positive real root which corresponds to the local maximum of \( P_0(\lambda) \). Note that \( P_0(\lambda) \) has exactly one negative real root if \( P_0(\lambda^0_-) = 0 \). So we conclude that if \( P_0(\lambda^0_-) < 0 \), then \( P_0(\lambda) \) has two negative real roots. So for \( P_0(\lambda_-) < 0 \), the dimension of the stable manifold of the zero steady state is two.

For the propagation speed, we know that \( P_0(\lambda^0_-) \) is a function of \( c \). We define \( R_0(c) := P_0(\lambda^0_-(c)) \). The critical propagation speed \( c_0^0 \) can then be found by solving the equation,

\[
R_0(c_0^0) = -(\lambda^0_-)^3 + A_2(\lambda^0_-)^2 + A_4\lambda^0_- + A_4 = 0.
\]

This means that for all values of \( c \) with \( c > 0 \) and \( R_0(c) < 0 \), it could be possible there is a downstream travelling wave to the zero steady state.

For \( P_1(\lambda) \), we need at least one root with \( \Re > 0 \). The only case in which we certainly know we have at least one root with \( \Re > 0 \) is the case where \( P_1(\lambda) = 0 \) has two positive real roots and one negative real root. The transition point between zero positive real roots and two positive real roots is exactly when the local maximum of \( P_1(\lambda) \) is a positive real root, see Figure 13. This means that \( P_1'(\lambda) = 0 \) and \( P_1(\lambda) = 0 \) for \( \lambda > 0 \).

From \( P_1'(\lambda) = 0 \) we find the same solutions as in (70). Here \( \lambda_{1+} \) is the positive
real root which corresponds to the local maximum of $P_1(\lambda)$ and $\lambda^1_+$ the negative real root which corresponds to the local minimum of $P_1(\lambda)$. Note that $P_1(\lambda)$ has exactly one positive real root if $P_1(\lambda^1_+) = 0$. So we conclude that if $P_1(\lambda^1_+) > 0$, then $P_1(\lambda)$ has two positive real roots. So for $P_1(\lambda^1_+) > 0$, the dimension of the unstable manifold of the non-zero steady state is two.

For the propagation speed, we know that $P_1(\lambda^1_+)$ is a function of $c$. We define $R_1^1(c) := P_1(\lambda^1_+)(c)$ The critical propagation speed $c^*_1$ can then be found by solving the equation,

$$R_1^1(c^*_1) = - (\lambda^1_+)^3 + B_2(\lambda^1_+)^2 + B_3\lambda^1_+ + B_4 = 0.$$  

This means that for all values of $c$ with $c > 0$ and $R_1^1(c) > 0$, it could be possible there is a downstream travelling wave starting from non-zero steady state. □

We would like to see how $c^*_0$ and $c^*_1$ depend on $v$ (and $L$) such that one may obtain conditions that exclude a propagation speed $c$ that satisfies the conditions of Proposition 12 (for $c < 0$) and Proposition 13 (for $c > 0$), this excluding a travelling wave solution. To that end we have:

**Proposition 14** $R_1^0(c)$ is given by

$$R_1^0(c) = \lambda^0_+ \left(\frac{2}{9}A_2^2 + \frac{2}{3}A_3\right) + \frac{1}{9}A_2A_3 + A_4.$$  

**Proof.** Because $\lambda^0_+$ satisfies (66), we find

$$(\lambda^0_+)^2 = \frac{2}{3}A_2\lambda^0_+ + \frac{1}{3}A_3.$$  \hspace{1cm} (72)
Substituting (72) into (64) yields

\[ R_0^+ (c) = - (\lambda_0^+)^3 + A_2 (\lambda_0^+)^2 + A_3 \lambda_0^+ + A_4, \]
\[ = - \lambda_0^+ \left( \frac{2}{3} A_2 \lambda_0^+ + \frac{1}{3} A_3 \right) + A_2 \left( \frac{2}{3} A_2 \lambda_0^+ + \frac{1}{3} A_3 \right) + A_3 \lambda_0^+ + A_4, \]
\[ = - \frac{2}{3} A_2 (\lambda_0^+)^2 - \frac{1}{3} A_3 \lambda_0^+ + \frac{2}{3} A_2^2 \lambda_0^+ + \frac{1}{3} A_2 A_3 + A_3 \lambda_0^+ + A_4, \]
\[ = - \frac{2}{3} A_2 (\frac{2}{3} A_2 \lambda_0^+ + \frac{1}{3} A_3) + \frac{2}{3} A_3 \lambda_0^+ + \frac{2}{3} A_2^2 \lambda_0^+ + \frac{1}{3} A_2 A_3 + A_4, \]
\[ = - \frac{4}{9} A_2^2 \lambda_0^+ - \frac{2}{9} A_2 A_3 + \frac{2}{3} A_3 \lambda_0^+ + \frac{2}{3} A_2^2 \lambda_0^+ + \frac{1}{3} A_2 A_3 + A_4, \]
\[ = \frac{2}{9} A_2^2 \lambda_0^+ + \frac{2}{3} A_3 \lambda_0^+ + \frac{1}{9} A_2 A_3 + A_4, \]
\[ = \lambda_0^+ \left( \frac{2}{9} A_2^2 + \frac{2}{3} A_3 \right) + \frac{1}{9} A_2 A_3 + A_4. \]

Note that the calculations for determining \( R_0^+(c) \), \( R_1^+(c) \) and \( R_1^-(c) \) are almost exactly the same. We find

\[ R_0^-(c) = \lambda_0^+ \left( \frac{2}{9} A_2^2 + \frac{2}{3} A_3 \right) + \frac{1}{9} A_2 A_3 + A_4, \]
\[ R_1^+(c) = \lambda_1^+ \left( \frac{2}{9} B_2^2 + \frac{2}{3} B_3 \right) + \frac{1}{9} B_2 B_3 + B_4, \]
\[ R_1^-(c) = \lambda_1^+ \left( \frac{2}{9} B_2^2 + \frac{2}{3} B_3 \right) + \frac{1}{9} B_2 B_3 + B_4. \]

Unfortunately, the expressions for the \( R_1^+(c) \) are such that they do not provide much insight into exclusion of travelling wave solutions. It should be noted that in [Pachepsky] for a very particular choice of parameters (\( \mu = 0.8, \sigma = 0.8 \)), \( c_0^* \) and \( c_1^* \) are numerically solved, providing an indication of the range in which propagation speeds should be in that particular case. Generally results seem hard to obtain (analytically) though.
5 Conclusions

In this thesis we studied a model for a population residing in a stream or small river, subject to advection (stream flow) and diffusion (representing random movement). The individuals of the population can live on the benthos or drift in the flow, while reproduction can only occur on the benthos.

For the case $\mu < 1$ we showed that persistence of the population is always guaranteed, irrespective of the domain length and the advection speed, because the total growth rate of the benthic population at each location is always positive.

For the case $\mu \geq 1$, we first derived a necessary condition for persistence of the population. We found that this condition is given by

$$\lambda_1(v, L) < \frac{\sigma}{\mu - 1}.$$  

For $\mu \geq 1$ we also calculated that persistence is possible provided that the domain $L$ is large enough with respect to the advection speed $v$. This condition is given by

$$L > L^* = \frac{2}{\sqrt{\frac{4\sigma}{\mu - 1} - v^2}} \left[ \pi + \arctan \left( -\frac{1}{v} \sqrt{\frac{4\sigma}{\mu - 1} - v^2} \right) \right].$$

This critical length contains the additional term $\pi$ that is missing in [Pachepsky]. We also found, that for any $L$, the population will persist provided $\mu \geq 1$ sufficiently close to 1.

In the next section we considered spatial spread of the population in time, by means of a travelling population front. In mathematically terms this means considering the existence of a travelling wave solution to an idealized model defined on $\mathbb{R}$ instead of the original model on $(0, L)$. The considerations were limited to a logistic growth model for the population on the benthos.

We distinguished between the propagation speed downstream and upstream because with increasing advection the propagation speed downstream increases, whereas the propagation speed upstream decreases. Before we determined the up- and downstream propagations speeds, we recast the three dimensional system into travelling wave coordinates and then transformed it into a system of first-order equations, see (59).

Next we assumed there exists a travelling wave between the found steady states and we determined by phase portrait analyse necessary conditions there actually could exist one. Because all the nullclines of the 3-dimensional found system intersect each other, we ended up with eight different regions which we denoted by $A$ to $H$. We found that if there exists a heteroclinic orbit from the
zero-steady state to the non-zero steady state, then \( c < 0 \) and this orbit moves from the zero steady state to \( A \) to \( B \) to the non-zero steady state possibly with multiple switches between \( A \) and \( B \), see Figure 7. We also found that if there exists a heteroclinic orbit from the non-zero steady state to zero steady state, then \( c > 0 \) and this orbit moves from the non-zero steady state to \( E \) to \( D \) to the zero steady state possibly with multiple switches between \( E \) and \( D \), see Figure 9. The dimensionality of the problem prevented as from providing sufficient conditions for the existence of travelling waves, though. In [Pachepsky], the aspect of existence is not treated either. We obtained a more detailed view of how the heteroclinic orbits need to run through the biologically relevant part of state space.

We also found that extinction is not realized by means of "washout", nor a downwards moving extinction front nor an upwards moving extinction front (see Table 1). The decay of the population seems to be more complicated.

Then we linearized the system around the steady states, which informed us about the stability of the manifolds around the steady states. The characteristic polynomials belonging to the zero and non-zero steady state are given by

\[
P_0(\lambda) = -\lambda^3 + \left( \frac{\mu - 1}{c} + v - c \right) \lambda^2 + \left( (\mu - 1)(1 - \frac{v}{c}) + \sigma \right) \lambda + \frac{\sigma}{c},
\]

and

\[
P_1(\lambda) = -\lambda^3 + \left( \frac{\mu + 1}{c} + v - c \right) \lambda^2 + \left( (\mu + 1)(1 - \frac{v}{c}) + \sigma \right) \lambda - \frac{\sigma}{c}.
\]

With the use of these polynomials and Descarte’s rule of Signs we determined the possible dimensionality of the stable and unstable manifolds of the steady states, see Table 4 and Table 5.

In the last part of this thesis we determined conditions on the propagation speed of the travelling wave that necessarily need to hold if the wave exists. This provides further necessary conditions for the existence of a heteroclinic orbit between the steady states. We found that if there exists an upstream travelling wave with speed \( c < 0 \) starting from the zero steady state to the non-zero steady state, then \( R_0^\pm(c) > 0 \) and \( R_1^\pm(c) < 0 \). And if there exists a downstream travelling wave with speed \( c > 0 \) starting from the non-zero steady state to the zero steady state, then \( R_0^\pm(c) < 0 \) and \( R_1^\pm(c) > 0 \). Where \( R_0^\pm(c) \) and \( R_1^\pm(c) \) are given by

\[
R_0^\pm(c) = \lambda_\pm^0 \left( \frac{2}{9} A_2^2 + \frac{2}{3} A_3 \right) + \frac{1}{9} A_2 A_3 + A_4,
\]

\[
R_1^\pm(c) = \lambda_\pm^1 \left( \frac{2}{9} B_2^2 + \frac{2}{3} B_3 \right) + \frac{1}{9} B_2 B_3 + B_4,
\]

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where

\[ \lambda_0^\pm = \frac{A_2 \pm \sqrt{A_2^2 + 3A_3}}{3}, \]

\[ \lambda_1^\pm = \frac{B_2 \pm \sqrt{B_2^2 + 3B_3}}{3}, \]

and with \( A_2, A_3, B_2 \) and \( B_3 \) as in (60) and (61). The critical propagation speed for the upstream travelling wave can be found by solving the equations \( R_0^1 (c_0^*) = 0 \) and \( R_1^1 (c_1^*) = 0 \). And for the downstream travelling wave \( R_0^0 (c_0^*) = 0 \) and \( R_1^1 (c_1^*) = 0 \).
References


\[ \mu \in \sigma \text{ en } \mu^*(\sigma) \]