Competitive Exclusion in a Discrete-Time Epidemic Model with Two Competing Strains

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Abstract

In this paper, we study a Susceptible-Infected-Susceptible (S-I-S) discrete-time model with two competing strains and distinct demographic dynamics. We use two different recruitment functions to model the population demography. Discrete models are capable of generating complex dynamics. Analytic and numerical methods are used in this study to separate the impact of demography on the epidemic process. The key issues addressed in this work are those of coexistence and/or competitve exclusion of competing strains in a population with complex dynamics. The principle of competitive exclusion is the most prevalent under the assumptions of this model.

1 Introduction

In some biological systems, population growth is a discrete process and generations do not overlap. Discrete-time models are appropriate in describing the spread of infectious diseases in such discretely reproducing populations. Using a general discrete-time $S-I-S$ model with two strains, we model the dynamics of two competing strains in a population with discrete generations. The analysis, common in complex nonlinear discrete models, is carried out via a combination of simulations and analysis.

Our model arises as a particular discretization in time of the corresponding $S-I-S$ continuous time stochastic model for two competing strains. The discretization assumes the following order of the events : infection $\rightarrow$ death $\rightarrow$ recovery. In continuous time Markov chain model, the events do not follow a particular order. The corresponding continuous time Markov chain models are difficult if not impossible to analyze. Exact discretization gives rise to complex nonlinear discrete dynamical systems that are difficult to handle. If one orders the nature of the events (infections-death-recovery) then the population dynamics can be decoupled from the epidemic process, hence providing a system that is likely to yield mathematical analysis. The behaviour exhibited by stochastic population models and their deterministic analogues is not frequently the same, for more detail see Allen and Burgin [1]. They did a comparison between discrete-time stochastic models, Markov chains and deterministic models with only one strain. They found that discrete-time deterministic epidemic models generalize the form of the force of infection.

In this paper we consider two recruitment functions, constant recruitment and logistic recruitment. We analize the dynamics of the susceptible and infected populations. To be more precise we consider the long-term behaviour of each population and investigate how the demography affects them.

Our interest is the study of the dynamics of the two competing strains. We study coexistence and competitive exclusion. The principle of competitive exclusion states that no two species can forever occupy the same ecological niche. We conclude that for most parameter values, competitive exclusion occurs. Coexistence is not possible except under very special circunstances.

Castillo-Chávez, et. al. have studied competitive exclusion in a similar continuos- time model [8]. To be more specific, they studied com-

petitive exclusion in gonorrhea model, where a heterosexually active populations is exposed to two competing strains. They obtained that coexistence of these two strains is not possible except under very special circumstances. Our results, using a discrete-time model, are similar to those obtained by them.
As in their paper[8], we also study the case when we have population size asymptotically constant. Moreover, in this paper we study a more general case, demography with complex dynamics.

2 The Model

2.1 Definitions

Main Definitions

S_n	population of susceptible individuals in generation n
I_n^1	population of infected individuals with strain one in generation n
I_n^2	population of infected individuals with strain two in generation n
T_n	total population in generation n
f	recruitment function

Parameters

μ	natural death rate
γ_i	recovery rate for strain i
α_i	infection rate for strain i

2.2 Assumptions

1. The disease is not fatal.
2. All recruitments are susceptible and the recruitment function depends only on T_n
3. There are no co-infections.
4. Death, infections and recoveries are modeled as Poisson processes with rates $\mu, \alpha_i, \gamma_i (i = 1, 2)$
5. Time step is measured in generations.

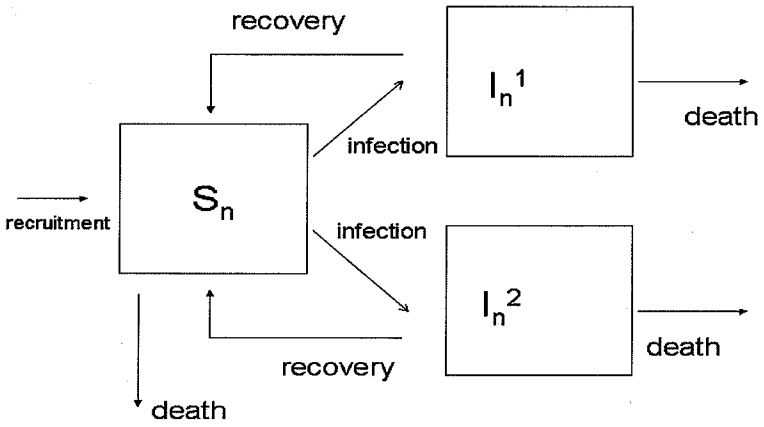

Figure 1: Flow chart to system (1).

6. The populations change only because of : births(given by the recruitment function), deaths, recovery, infection of a susceptible individual for each strain.
7. Individuals recover but do not develop permanent or temporary immunity, they are immediately susceptible.

2.3 Constructing the model

The model has the the following format:
New individuals after one generation= New borns + survivors.
Then, we have:
New susceptibles = recruitment + susceptible individuals from previous generations + recoveries(of both strains)
New infectious strain i = new type i infectious + infected individuals by strain i from previous generation.
We will model this in the following way:
$S_{n+1} = f(T_n) + S_n$ P(survival) P(not being infected) +
I_n^1P(survival)P(recovery from strain 1)+I_n^2 (survival)P(recovery from strain 2)
$I_{n+1}^i = S_n$ P(survival) P(infection with i) +I_n^1 P(survival) P(no recovery) where P( ) means, "the probability of"

2.4 Equations

By assumption (4) we have that the probability of k successful encounters is a Poisson distribution, which in general, has the form : $p(k) = \frac{e^{-\beta}\beta^k}{k!}$ where β is the parameter of the Poisson distribution. In our context, only one success is necessary. Therefore, when there are no successful encounters, the expression: $p(0) = e^{-\beta}$ represents the probability that a given event does not occur. For example, the probability that a susceptible individual does not become infective is : P(not being infected by i) $= e^{-\alpha_i I_n^i}$ and,
P(not recovering from i) $= e^{-\gamma_i I_n^i}$. Hence, P(not being infected)=
P(not being infected by 1)P(not being infected by 2) $= e^{-\alpha_1 I_n^1} e^{-\alpha_2 I_n^2}$
Now, the probability that a susceptible does become infective is given by : $1 - e^{-\alpha_i I_n^i}$.Then, P(infected by i) =
P(infected) P(infected by i | infected) $=(1 - e^{-(\alpha_1 I_n^1 + \alpha_2 I_n^2)}) \frac{\alpha_i I_n^i}{\alpha_1 I_n^1 + \alpha_2 I_n^2}$.
Therefore, the dynamic is governed by :

$$\begin{aligned} S_{n+1} &= f(T_n) + S_n e^{-\mu} e^{-(\alpha_1 I_n^1 + \alpha_2 I_n^2)} \\ &\quad + I_n^1 e^{-\mu}(1 - e^{-\gamma_1}) + I_n^2 e^{-\mu}\left(1 - e^{-\gamma_2}\right) \qquad (1a) \\ I_{n+1}^1 &= \frac{\alpha_1 S_n I_n^1}{\alpha_1 I_n^1 + \alpha_2 I_n^2} e^{-\mu}(1 - e^{-(\alpha_1 I_n^1 + \alpha_2 I_n^2)}) + I_n^1 e^{-\mu} e^{-\gamma_1} \qquad (1b) \\ I_{n+1}^2 &= \frac{\alpha_2 S_n I_n^2}{\alpha_1 I_n^1 + \alpha_2 I_n^2} e^{-\mu}(1 - e^{-(\alpha_1 I_n^1 + \alpha_2 I_n^2)}) + I_n^2 e^{-\mu} e^{-\gamma_2} \qquad (1c) \end{aligned}$$

Hence,

$$T_{n+1} = f(T_n) + T_n e^{-\mu} \qquad (2)$$

This equation is called, *the Demographic equation.* This equation tells us how the total population is changing. We will study this equation via two types of recruitment functions.

In (2) we have,

$$T_n = S_n + I_n^1 + I_n^2 \qquad (3)$$

Notice that an increase in the density of one strain leads to a decrease in the next generation. Hence, there is compeition between the two strains.

3 Dynamical Analysis

In this section we provide the stability analysis of the stationary states.

3.1 Disease-Free Equilibrium

If we have $I^1_{n+1} = I^2_{n+1} = 0$ then, model (1) reduces to:

$$T_{n+1} = f(T_n) + T_n e^{-\mu}$$

To understand the overall dynamics, we study the *Limiting equation of system* (1). First we obtain : $T_\infty = \lim_{n\to\infty} T_n$. Then we use in (3) the substitution $S_n = T_\infty - {I_n}^1 - I^2_n$ to get the following equations:

$$\begin{aligned} I^1_{n+1} &= \frac{\alpha_1 I^1_n}{\alpha_1 I^1_n + \alpha_2 I^2_n}(T_\infty - I^1_n - I^2_n)e^{-\mu}(1 - e^{-(\alpha_1 I^1_n + \alpha_2 I^2_n)}) \\ &\quad + I^1_n e^{-\mu} e^{-\gamma_1} \qquad (4a) \\ I^2_{n+1} &= \frac{\alpha_2 I^2_n}{\alpha_1 I^1_n + \alpha_2 I^2_n}(T_\infty - I^1_n - I^2_n)e^{-\mu}(1 - e^{-(\alpha_1 I^1_n + \alpha_2 I^2_n)}) \\ &\quad + I^2_n e^{-\mu} e^{-\gamma_2} \qquad (4b) \end{aligned}$$

System (4) describes the dynamic of two populations infected with the two strains. We study this system in order to infer how the populations are interacting when the total population is in equilibrium at T_∞.

Stability via linearization

Lemma. 3.1. *In system* (4), *if* $R_1 = \frac{e^{-\mu} T_\infty \alpha_1}{1 - e^{-(\mu+\gamma_1)}} < 1$ *and* $R_2 = \frac{e^{-\mu} T_\infty \alpha_2}{1 - e^{-(\mu+\gamma_2)}} < 1$, *then the equilibrium point* $(0,0)$ *is asymptotically stable*

Proof. We compute the Jacobian J of (4) evaluated at (0,0) :

$$J(0,0) = \begin{pmatrix} \frac{e^{-\mu} T_\infty \alpha_1}{1 - e^{-(\mu+\gamma_1)}} & 0 \\ 0 & \frac{e^{-\mu} T_\infty \alpha_2}{1 - e^{-(\mu+\gamma_2)}} \end{pmatrix}$$

The eigenvalues are $R_1 = \frac{e^{-\mu} T_\infty \alpha_1}{1 - e^{-(\mu+\gamma_1)}}$ and $R_2 = \frac{e^{-\mu} T_\infty \alpha_2}{1 - e^{-(\mu+\gamma_2)}}$. If both of them are less than 1 in absolute value , we know that it is a sufficient condition to ensure that the steady state is stable. □

We emphasise the fact that it is necessary for the *Limiting equation of system* (1), for T_∞ to exist. We will study the conditions for T_∞ to be positive in subsections 3.1.1 and 3.1.2.

Biological Interpretation of R_i

The biological meaning of the result is that we have the conditions for the existence and stability of the disease free-equilibrium,$(S_\infty, 0, 0)$ in (1) which in terms of (4) is $(0, 0)$.
R_0 determines whether an epidemic spreads or dies out. Typical R_0 is defined as the average number of secondary infections caused by a single infective in a pool of all susceptibles. Usually it has the following form :
R_0 = (infection rate)(population size)(average duration of infection)
In our case, the conditions that we need in Lemma 3.1 have the following biological meaning:
$R_i = \alpha_i(e^{-\mu}T_\infty)(\frac{1}{1-e^{-(\mu+\gamma_i)}})$
= (infection rate per infective per generation of strain i) (Population in equilibrium(i.e. population size when there is no infection, discounted by deaths)) (average number of generations that an individual is infectious before dying or recovering).
Then, R_i = average number of effective contacts multiplied by the number of available susceptibles = average number of effective contacts.
Notice that, R_i is an infection rate per infective, i.e. number of people that an infected person infects. $R_i = \frac{e^{-\mu}T_\infty\alpha_i}{1-e^{-(\mu+\gamma_i)}} < 1$ for each $i = 1, 2$ determines extintion of the two strains of the disease.

3.1.1 Case 1. $f(T_n) = \Lambda$

This recruitment function corresponds to a constant in flow of recruits. The total population dynamics is given by

$$T_{n+1} = \Lambda + T_n e^{-\mu}$$

Hence, we can easily obtain that:

$$T_\infty = \frac{\Lambda}{1-e^{-\mu}}$$

Which is positive given that $\mu > 0$. And by Lemma 3.1, in this case,
$R_1{}^* = \frac{e^{-\mu}(\frac{\Lambda}{1-e^{-\mu}})\alpha_1}{1-e^{-(\mu+\gamma_1)}}$ and
$R_2{}^* = \frac{e^{-\mu}(\frac{\Lambda}{1-e^{-\mu}})\alpha_2}{1-e^{-(\mu+\gamma_2)}}$

3.1.2 Case 2. $f(T_n) = rT_n(1 - \frac{T_n}{k})$

In this case the total population dynamis is given by,

$$T_{n+1} = rT_n(1 - \frac{T_n}{k}) + T_n e^{-\mu} \tag{5}$$

This case correspond to contest competition, in which limited resources are distributed distributed evenly among individuals. Logistic equation is often used to describe populations with rates of growth that are decreasing, when the population is increasing.

Fixed points

•${T_n}^* = 0$

•${T_n}^{**} = \frac{k(r+e^{-\mu}-1)}{r}$, but we need $r + e^{-\mu} > 1$ in order for this fixed point to be positive, and in this case, the condition of Lemma 3.1

$${R_1}^{\diamondsuit} = \frac{e^{-\mu}k(1 - \frac{1-e^{-\mu}}{r})\alpha_1}{1 - e^{-(\mu+\gamma_1)}} < 1$$

$${R_2}^{\diamondsuit} = \frac{e^{-\mu}k(1 - \frac{1-e^{-\mu}}{r})\alpha_2}{1 - e^{-(\mu+\gamma_2)}} < 1$$

We will study the *Limiting equation* in Section 3.4.

3.2 Boundary Equilibrium

Now, if we have one of the strains missing , $I_n^2 = 0$, we get that the Limiting Equation (4) takes the form:

$$I_{n+1} = (T_\infty - I_n)e^{-\mu}(1 - e^{\alpha_1 I_n}) + I_n e^{-(\mu+\gamma)} \tag{6}$$

The following result is related to the existence and stability of $(I^*, 0)$ in (4). This kind of point is called, boundary equilibria, which exists whenever the epidemic spreads in the population. We have only one of the strains and we want to know how it is changing. This is done, by using the fact that we have total population in equilibrium at T_∞. Clearly, this analysis is applicable if we have $I_n^1 = 0$ and $I_n^2 > 0$.

Lemma. 3.2. *The limiting equation* (3.2) *has a unique positive equilibrium* I^* *that is asymptotically stable if*
$R_1^* = e^{-\mu}((T_\infty - I^*)\alpha_1 e^{-\alpha_1 I^*} - (1 - e^{-\alpha_1 I^*}) + e^{-\gamma_1}) < 1$ *and*
$R_2^* = e^{-\mu}\frac{\alpha_2}{\alpha_1 I^*}((T_\infty - I^*)(1 - e^{-\alpha_1 I^*}) + e^{-\gamma_1}) < 1.$

We do not include the proof because it has been studied in technical report [3].

The conditions of Lemma 3.2 in terms of the Limiting Equation and the R_i that we have already found can be rewritten in the following statment:

Limiting equation has a unique stable positive boundary equilibrium $(I^* > 0, 0)$, *provided that* $R_1 > R_2 > 1$ *or* $R_1 > 1 > R_2$.

This equilibrium is the result of competition between the two strains. The value of the reproductive number R_i, again, determines the stability of this point. If $R_1 > R_2 > 1$, then $(I^* > 0, 0)$ will be stable and $(0, I^{**} < 0)$ unstable. There is only one stable equilibrium, corresponding to the largest R_i.

3.3 Endemic Equilibrium

In this section, we obtain a necessary and sufficient condition for the existence of the endemic equilibrium in (4), that is, we are looking for the coexistence of the two strains. A necessary condition for this, will be $R_1 > 1$ and $R_2 > 1$ (see Lemma 3.1).

Lemma. 3.3. *A necessary condition for the endemic equilibrium in* (4) *to exist is* $R_1 = R_2$.

Proof. If exists (I^{1*}, I^{2*}) this endemic equilibrium , we must have that:

$$\begin{aligned} I^{i*} &= \frac{\alpha_i I^{i*}}{\alpha_1 I^{*1} + \alpha_2 I^{*2}} (T_\infty - I^{*1} - I^{*2}) e^{-\mu} \left(1 - e^{-(\alpha_1 I^{*1} + \alpha_2 I^{*2})}\right) \\ &\quad + I^{i*} e^{-(\mu+\gamma_i)} \end{aligned} \tag{7}$$

But, if $I^{1*} > 0, I^{2*} > 0$, we can divide by I^{i*} and get :

$$(1 - e^{-(\mu+\gamma_i)}) = \frac{\alpha_i}{\alpha_1 I^{*1} + \alpha_2 I^{*2}} (T_\infty - I^{*1} - I^{*2}) e^{-\mu} (1 - e^{-(\alpha_1 I^{*1} + \alpha_2 I^{*2})})$$

Hence,

$$e^{\mu}(1 - e^{-(\mu+\gamma_i)}) = \frac{\alpha_i}{\alpha_1 I^{*1} + \alpha_2 I^{*2}} (T_\infty - I^{*1} - I^{*2}) (1 - e^{-(\alpha_1 I^{*1} + \alpha_2 I^{*1})})$$

with $i = 1, 2$. Then we can divide both equations, and we will have

$$\frac{1 - e^{-(\mu+\gamma_1)}}{1 - e^{-(\mu+\gamma_2)}} = \frac{\alpha_1}{\alpha_2}$$

which is equivalent to:

$$\frac{\alpha_2}{1-e^{-(\mu+\gamma_2)}} = \frac{\alpha_1}{1-e^{-(\mu+\gamma_1)}} \tag{8}$$

Hence, we have that it is necessary that,

$$R_1 = R_2$$

□

Thus, coexistence of both strains is biologically unlikely. For most parameter values there is no coexistence of the two competing strains.

3.4 Demographic equation

As we saw in Section 3.1 our demographic equation is:

$$T_{n+1} = f(T_n) + T_n e^{-\mu}$$

In this section, we show how the dynamics of the total population changes when we change $f(T_n)$, the recruitment function.

3.4.1 Case 1. $f(T_n) = \Lambda$

Here,

$$T_{n+1} = \Lambda + T_n e^{-\mu}$$

Hence, we can easily obtain that:

$$T_\infty = \frac{\Lambda}{1-e^{-\mu}}$$

Further results can be found in [3].

3.4.2 Case 2. $f(T_n) = rT_n(1 - \frac{T_n}{k})$

In this case,

$$T_{n+1} = rT_n(1 - \frac{T_n}{k}) + T_n e^{-\mu}. \tag{9}$$

Equilibria and Stability

In this section, we consider equation (9) as a one-dimensional difference equation. We now study the equilibria and their stability.
If $e^{-\mu} + r < 1, T_0 = 0$ is stable and T^* does not exist. See Section 3.1.2.
If $2 - e^{-\mu} - r > 1, T^* = \frac{k(r+e^{-\mu}-1)}{r}$ exists and it is stable.

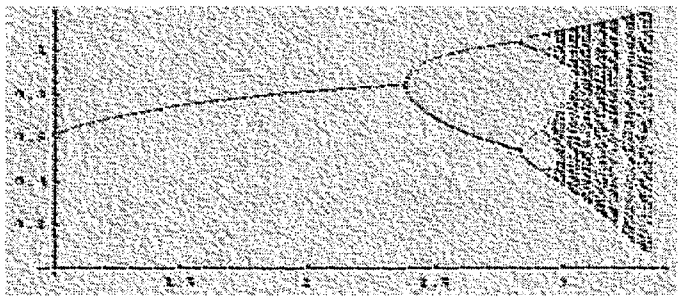

Figure 2: Bifurcation Diagram to equation (9) with $\mu = 0.5$ and $k = 1$

We compute the period-2 points. To compute the period 2 points, we solve the equation $T_{n+2} = T_n$, the period 2 points are:

$T^{**} = \frac{e^{-\mu}k(1+e^{\mu}+e^{\mu}r-\sqrt{1-2e^{\mu}-3e^{2\mu}+2e^{\mu}r-2e^{2\mu}r+e^{2\mu}r^2)}}{2r}$ and
$T^{***} = \frac{e^{-\mu}k(1+e^{\mu}+e^{\mu}r+\sqrt{1-2e^{\mu}-3e^{2\mu}+2e^{\mu}r-2e^{2\mu}r+e^{2\mu}r^2)}}{2r}$.

The conditions for T^{**} and T^{***} to be positive are :
$1 + e^{2\mu}(r^2e^{\mu} - 2re^{\mu} - 3e^{\mu}) + e^{\mu}(2r - 2) > 0$ and
$4e^{\mu}(1 + e^{\mu} + e^{\mu}r) > 0$.

The reproduction function of (9) is : $f(T) = rT(1 - \frac{T}{k}) + Te^{-\mu}$.

In order to test the stability of this periodic solution, we must compute $(f^2)'(T)$ and substitute T^{**} and T^{***} in $(f^2)'(T)$ (where $f^2(T)$ means $f(f(T))$). In the next section, we use a bifurcation diagram to provide a geometric analysis.

3.5 Numerical Analysis

In general, numerical simulations provided us a general knowledge about the things that we found via analytic results. In particular in Section 3.4, we studied via numerical simulations, how the Demographic Function affects to the total population. Our analysis in the last section provided us ranges for the parameters for numerical simulations.We executed several simulations for distinct values of r, bifurcation parameter in equation (9).

Figure 2 is the complemental analysis to the last section,shows that the positive fixed point of (9) undergoes period doubling bifurcation

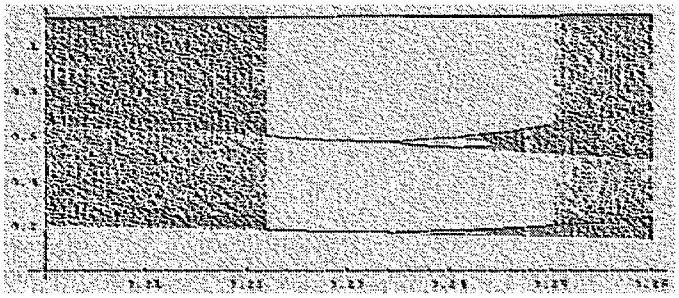

Figure 3: Period 3 region in the Logistic Demographic Function.

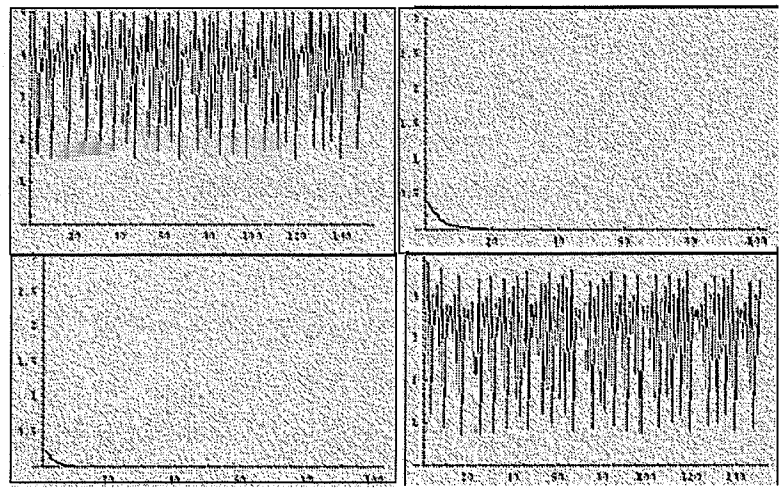

Figure 4: These are the iterates of T_n, I_n and S_n respectively. $R_1 < 1, R_2 < 1, K = 1$ and $r = 3.3$

as r is varied($x - axis$). So, in this case Limiting equation will not work.

The next graph shows the region where we have period 3. The presence of a period 3 orbit in a one-dimensional discrete model implies chaos [7].

The figure above shows Mutual Exclusion.

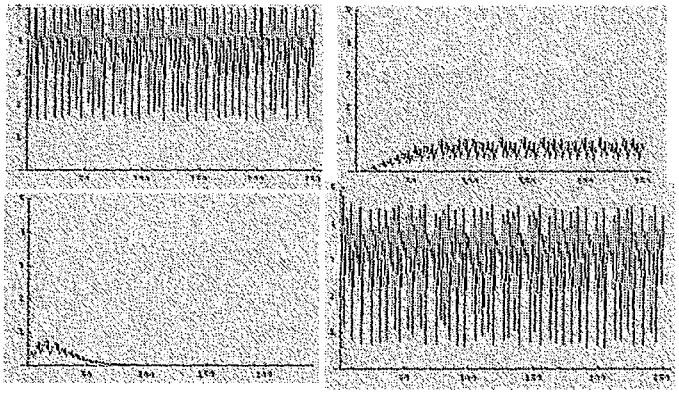

Figure 5: T_n, I_n^1, I_n^2 and S_n respectively. $R_1 > R_2, R_1 > 1, K = 1$ and $r = 2.9$

As we can see the total population T_n persists chaotically(Figure 3) but the two strains ultimately go extinct(next two) due to the chaotic behavior of T_n for certain values of the parameter r. The infection does not persist for any of the strain. The population of Susceptible(fourth graph) also has the chaotic behaviour given by the demographic function.
Now, we consider another example.

This example is very interesting(Fig. 5), because it show how show the demographic function weakly affects the other dynamics. In this example, the demographic is chaotic(see Fig 2). All the dynamics are related. The total population is chaotic, one of the strains is oscillating, the other one dissapears and the susceptible population is also chaotic. Thus, competitive exclusion ocurrs with a chaotic demographic function.

In the following figure we show how the Demographic Function affects the behaviour of the other populations. In this case we have coexistence.

The figure in the next page, is an example of the case when we have multiple endemic equilibrium points. The analysis for this case has not being completed. Castillo-Chávez , et. al.[8], , found that if the conditions of Lemma 3.3 holds, there exists a *continuum of equilibria.*

to understand the mechanisms involved in the case when we have co-existence.

5 Acknowledgements

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