DICRETE-TIME SEIS MODELS WITH EXOGENOUS RE-INFECTION AND DISPERSAL BETWEEN TWO PATCHES

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Discrete-time S-E-I-S Models With Exogenous Re-infection and Dispersal between Two Patches

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Abstract

Typically, for an epidemic to occur, infectious individuals have to generate at least one secondary infection before they die or recover ($\Re_o > 1$). A simple model is introduced where epidemics are possible when $\Re_o < 1$. Models with varying levels of complexity in the population dynamics are introduced and the question of whether or not they force or drive disease epidemic patterns is analyzed in a single and multiple patch system connected by dispersal. Interaction of this sort between patches can disrupt the initial one patch disease dynamics; for example, dispersal can cause a disease-free equilibrium where otherwise there would be none.

1 Introduction

A species dominating an isolated environment will generate demographic patterns that depend on the distribution, availability and competition for resources. Two extreme competitive behaviors observed within a species are scramble (equal distribution of resources) and contest (part of the population taking most of the resources)[6]. Populations under scramble competition (e.g. those governed by Ricker's model) may exhibit complex, possibly chaotic demographic dynamics while those under contest competition via the Verhulst model do not. In this paper we analyze the dynamics of a disease in populations with demographic patterns of various degrees of complexity.

Previous studies have addressed these questions in the presence of susceptible-infected-susceptible (S-I-S) epidemics (Castillo-Chavez and Yakubu, 2000). Here we use an adapted version of the general framework proposed by these researchers with the addition of a latent stage where individuals are asymptomatic and infected but not infectious.

Again we follow the approach of Castillo-Chavez and Yakubu (2000) and model the force of infection via a non-linear 'probability' function that depends on the prevalence of the disease. Some results are established for general probability functions while others were established for particular functional forms. Throughout and using simulations we focus on various questions including whether or not complex demographics can drive a disease as well as whether or not exogenous reinfection (the effect on disease progression of latently infected individuals who continue to interact with infectious individuals) can support epidemics when $\Re_o$ (the basic reproductive number) is less than one.

Finally, we use numerical simulations to look at the role that disease-enhanced or disease-suppressed dispersal plays in disease dynamics in a two patch system.

The paper is organized as follows: First we define the general model of our system. We then provide examples of different recruitment functions: geometric, constant and Ricker's. Stability and existence of equilibria is determined for each recruitment function and for different type forces of

infection. Local patch dynamics are studied before dispersal occurs so that we may understand the effect of dispersal on the prevalence of a disease.

2 Single Patch S-E-I-S Model

The epidemic model of Castillo-Chavez and Yakubu, is a 2-dimensional system with a recruitment function $f : [0, \infty) \to [0, \infty)$ and a function such that $G : [0, \infty) \to [0, 1]$ that represents the probability of remaining susceptible or latent (so that $1 - G$ represents the probability of becoming either latent or susceptible). The function G is a monotone decreasing function with a maximum value of 1, which occurs when there are no infecteds ($G(0) = 1$). Also, G" is always non-negative. Furthermore, we introduce a latent stage in the disease, where its probability of moving on to infective is governed by the same function G. The general system is set up in the following manner:

$$
\left.
\begin{aligned}
S_{t+1} &= f(T_t) + \gamma S_t G\left(\alpha \frac{I_t}{T_t}\right) + \gamma(1 - \delta)I_t \\
E_{t+1} &= \gamma S_t (1 - G\left(\alpha \frac{I_t}{T_t}\right)) + \gamma E_t G(\alpha \frac{I_t}{T_t}) \\
I_{t+1} &= \gamma E_t (1 - G\left(\alpha \frac{I_t}{T_t}\right)) + \delta \gamma I_t
\end{aligned}
\right\}
\tag{1}
$$

where

S_t = population of susceptibles at generation t,
E_t = population of latent at generation t,
I_t = population of infecteds at generation t,
$f(T_t)$ = recruitment at generation t,
γ = probability of survival,
α = a weight given to the proportion of infecteds on the probability
    of becoming infected,
δ = probability that an individual does not recover, and
T_t = total population at generation t, is the sum of individuals in all the
stages. Therefore,

$$
T_t = S_t + E_t + I_t.
\tag{2}
$$

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The time that an individual stays in the latent period depends on the growth of the infectious population. This leaves open the interpretation as to how this interaction occurs. In some cases, an increase in the proportion of infectives means more interactions with these and therefore a greater likelihood to develop the disease. In other cases, an increase in the number of infectives could reflect the presence of pathogens flowing in the environment.

3   Geometric recruitment μT_t

In this section, we analyze System 1 with new susceptibles joining the population at a geometric rate (that is, when the recruitment function $f(T_t) = \mu T_t$). The method for finding $\Re_0$, fixed points of the system and determining their stability can be applied to other forms of the recruitment function.

$$
\left.
\begin{array}{rcl}
S_{t+1} &=& \mu T_t + \gamma S_t G(\alpha \frac{I_t}{T_t}) + \gamma(1-\delta)I_t \\
E_{t+1} &=& \gamma S_t (1 - G(\alpha \frac{I_t}{T_t})) + \gamma E_t G(\alpha \frac{I_t}{T_t}) \\
I_{t+1} &=& \gamma E_t (1 - G(\alpha \frac{I_t}{T_t})) + \delta \gamma I_t
\end{array}
\right\} \tag{3}
$$

By adding up the equations, in the system (3) we obtain

$$
\begin{aligned}
T_{t+1} &= f(T_t) + \gamma S_t + \gamma E_t + \gamma I_t \\
&= \mu T_t + \gamma(S_t + E_t + I_t) \\
&= (\mu + \gamma)T_t
\end{aligned}
$$

and by solving recursively, we obtain the following expression:

$$
T_t = (\mu+\gamma)^t T_0 \tag{4}
$$

Note that the long-term behavior of the population is determined by the rate $\mu + \gamma$. As t tends to infinity, the population goes to extinction when $\mu + \gamma$ is less than one or grows geometrically if $\mu + \gamma > 1$. Hence, we define a term $\Re_d$ (representing the basic demographic number) in the following way:

$$
\Re_d = \frac{\mu}{1 - \gamma}
$$

where $\frac{1}{1-\gamma}$ is the life expectancy (in generations per capita) and μ is the recruitment or birth rate. Hence, $\Re_d$ represents the average number of offspring that an individual will produce in its life-span. When $\Re_d < 1$, the average individual is not producing enough offspring to replace itself so the population will die out. Otherwise, when $\Re_d > 1$ the population increases geometrically. In the unlikelihood that $\Re_d = 1$ (such that $T_t = T_0$ for all t) the population will remain constant.

When $f(T_t) = \mu T_t$ System (3) is homogenous it can be written using proportions of the total population. However, it is important to emphasize that this method does not reflect the absolute demographic dynamics. Following (4), then the proportions have the following interpretation:

1. If $\mu + \gamma < 1$ then the total population will tend to zero along with S_t, E_t and I_t and the proportions will change asymptotically.

2. If $\mu + \gamma = 1$ then the value of $T_t = T_0$, so the total population remains constant. This situation is very unlikely in reality but proportions are interpretable and therefore would be an appropriate approach.

3. If $\mu + \gamma > 1$ then the total population grows geometrically. This can lead to some misinterpretation of the proportions. For example, I_t might settle to a finite equilibrium point ($I_\infty < \infty$), but if $T_\infty \to \infty$ then the proportion will tend to 0 and the behavior of I_t is not reflected.

With these precautions in mind, we can rescale the system by letting $X_t = \frac{S_t}{T_t}, Y_t = \frac{E_t}{T_t}, Z_t = \frac{I_t}{T_t}$, then

$$X_t + Y_t + Z_t = 1 \tag{5}$$

with this rescaling we obtain the new system

$$\left. \begin{array}{rcl} X_{t+1} & = & (1-q) + qX_t G(\alpha Z_t) + (1-\gamma)qZ_t, \\ Y_{t+1} & = & qX_t(1 - G(\alpha Z_t)) + Y_t qG(\alpha Z_t), \\ Z_{t+1} & = & qY_t(1 - G(\alpha Z_t)) + \delta qZ_t, \end{array} \right\} \tag{6}$$

where $q = \frac{\gamma}{(\mu+\gamma)}$ and $1 - q = \frac{\mu}{(\gamma+\mu)}$.

Using (5) we reduce (6) to a two-dimensional system.

$$
\left.
\begin{array}{rl}
Y_{t+1} = & q(1 - Y_t - Z_t)(1 - G(\alpha Z_t)) + Y_t q G(\alpha Z_t), \\
Z_{t+1} = & q Y_t(1 - G(\alpha Z_t)) + \delta q Z_t
\end{array}
\right\}
\tag{7}
$$

3.1 Disease-Free Equilibrium and $\Re_0$

Clearly, the disease-free equilibrium (DFE) of System (7) occurs when all individuals are at the susceptible stage ($X^* = 1$), that is (Y^*, Z^*) =(0,0). The local asymptotic stability of the DFE is established by applying the Jury test to the Jacobian matrix evaluated at (0,0). That is, by applying it to

$$
A = \begin{pmatrix} q & -\alpha q G'(0) \\ 0 & \delta q \end{pmatrix}.
$$

The conditions to be satisfied by matrix A for local asymptotic stability are $|trace(A)| < det(A)+1 < 2$. The second part of the inequality, $q^2\delta+1 < 2$ always holds because both q and δ are less than one. The first part of the inequality $q(1 + \delta) < 1 + q^2\delta$ is also always satisfied since,

$$
\frac{q(1+\delta)}{1+q^2\delta} < 1
$$

and we defined $q = \frac{\gamma}{\mu+\gamma}$ which when substituted into the previous inequality gives,

$$
\Re_o = \frac{\gamma\delta}{\mu+\gamma} < 1
$$

that is the fraction of old recruits that do not become infected. Note this is always true since $\delta \leq 1$ and $\frac{\gamma}{\mu+\gamma} \leq 1$, so the DFE will always be locally asymptotically stable for all values of the parameters.

3.2 Endemic Equilibria

Solving System (6) simultaneously for Y_∞ and Z_∞ will not give explicit solutions for the fixed points because G is an unknown function of Z_∞. However,

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we can prove the existence of positive solutions by looking at the roots of the non-linear equation,

$$L(Z_\infty) = M(Z_\infty) \tag{8}$$

where

$$
\begin{aligned}
L(Z_\infty) &= \frac{(1 - \delta q)}{q} Z_\infty \\
M(Z_\infty) &= q(1 - Z_\infty)(1 - G(\alpha Z_\infty))^2 - (1 - \delta q)(1 - 2G(\alpha Z_\infty))Z_\infty
\end{aligned}
$$

Every root of (8) will yield a corresponding value of Y_∞ via these values for Z_∞ are substituted into the expression:

$$Y_\infty = \frac{(1 - \delta q)Z_\infty}{q(1 - G(\alpha Z_\infty))}, \tag{9}$$

These corresponding values are the coordinates of the endemic equilibria.

Instead of Studying the general case, we focus on a few particular cases. The following sections are the details of what was done for each example of G.

3.3 When $G\left(\alpha \frac{I_t}{T_t}\right) = 1 - \frac{I_t}{T_t}$

From the general model, we know that there exists a DFE at (1,0,0). Furthermore, reducing the system of equations to 2-dimensions and linearizing at this point determines that the value for $\Re_0 = \frac{\gamma \delta}{\mu + \gamma} < 1$ always. Hence, the DFE is always locally stable.

3.3.1 Endemic Equilibria

While we always have a locally stable DFE, we also have a coexisting EE at

$$
\left.
\begin{aligned}
Y_\infty &= \delta(\tfrac{1}{\Re_0} - 1), \\
Z_\infty &= \tfrac{1}{2} - \tfrac{\delta}{\Re_0} - \delta \pm \tfrac{1}{2}\sqrt{1 - \tfrac{4\delta^2}{\Re_0} + 4\delta^2}
\end{aligned}
\right\} \tag{10}
$$

Theorem 3.1 *Let* $G\left(\alpha \frac{I_t}{T_t}\right) = 1 - \frac{I_t}{T_t}$.

1. If $\Re_0 \geq max(\frac{4\delta^2}{1+4\delta^2}, \frac{2\delta}{2\delta+1})$ then system (3) a DFE and two EE at (10).

2. If $\Re_0 < max(\frac{4\delta^2}{1+4\delta^2}, \frac{2\delta}{2\delta+1})$ we only have the DFE.

3. If $\Re_0 = \frac{4\delta^2}{1+4\delta^2}$ and $\Re_0 \geq \frac{2\delta}{2\delta+1}$), system (3) has a DFE and only one EE at (10).

Proof
If $\Re_0 > \frac{4\delta^2}{1+4\delta^2}$ we will have $1 - 2\delta(\frac{1}{\Re_0} - 1) > 0$. Furthermore if $\Re_0 > \frac{2\delta}{2\delta+1}$ the discriminant will be positive. Hence, we will have 2EE and the DFE.
It can be quickly verified that we have the DFE only if $\Re_0 < max(\frac{4\delta^2}{1+4\delta^2}, \frac{2\delta}{2\delta+1})$.
If $\Re_0 = \frac{4\delta^2}{1+4\delta^2}$ then the discriminant is 0 and if $\Re_0 \geq \frac{2\delta}{2\delta+1}$, we have $1 - 2\delta(\frac{1}{\Re_0} - 1) > 0$. Hence both a DFE and one EE coexist.

Remark: If $\mu = \gamma$, then we will have no endemic equilibria. The proof can be easily derived from Theorem 3.1

3.3.2   Global Stability of DFE

Here we define a Lyapunov function to prove that the DFE is globally stable in the absence of an EE.

Theorem 3.2 *If* $0 < \Re_0 < \frac{2\delta}{2\delta+1}$ *then DFE is globally stable.*

Proof By Theorem (3.1), $\Re_0 < \frac{2\delta}{2\delta+1}$ implies there are no EE equilibria. Hence

$$\Re_0 < 2\delta(1 - \Re_0)$$
$$\Rightarrow \frac{1}{2} < \delta(\frac{1}{\Re_0} - 1)$$

So we can choose $a, b > 0$ such that $\frac{b}{2} < a < b\delta(\frac{1}{\Re_0} - 1)$. Let $f(Y_t, Z_t) = (Y_{t+1}, Z_{t+1})$, where f is a reproduction function of system 7 with $G(\alpha Z_t) = 1 - Z_t$. Now we construct a Lyapunov function for f.
Define $V : [0, \infty) \times [0, \infty) \to [0, \infty)$ by $V(Y_t, Z_t) = \frac{\delta}{\Re_0}(aY_t + bZ_t)$. In order to show that the DFE is globally stable, we must show that $V(f(Y_t, Z_t)) < V(Y_t, Z_t)$ for all $(Y_t, Z_t) \neq (0, 0)$.

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Let $(Y_t, Z_t) \in (0, \infty) \times (0, \infty)$

$$V(f(Y_t, Z_t)) = \frac{\delta}{\Re_0}(aY_{t+1} + bZ_{t+1})$$
$$= a(1 - Y_t - Z_t)Z_t + aY_t(1 - Z_t) + bY_tZ_t + b\delta Z_t$$
$$= (b - 2a)Z_tY_t + aZ_t - aZ_t^2 + aY_t + b\delta Z_t$$

and $b - 2a < 0$ by definition of a so,

$$V(f(Y_t, Z_t)) \leq (a + b\delta)Z_t + aY_t \tag{11}$$
$$< \frac{\delta}{\Re_0}(aY_t + bZ_t) = V(Y_t, Z_t) \tag{12}$$

Next we show that the above inequality holds when either $Y_t \neq 0$ or $Z_t \neq 0$. If $Z_t = 0$ and $Y_t \neq 0$, then by comparing the Y_t terms in (11) and (12) it is clear that

$$aY_t < \tfrac{\delta}{\Re_0}aY_t$$

is always true since $\frac{\delta}{\Re_0} > 1$.

From the choice of a and b we know that $a < \delta b(\frac{1}{\Re_0} - 1)$. Furthermore, if $Y_t = 0$ and $Z_t \neq 0$ we have:

$$(a + b\delta)Z_t < \frac{\delta}{\Re_0}bZ_t$$

Therefore, $V(f(Y_t, Z_t)) < V(Y_t, Z_t)$, and the DFE is globally stable.

3.4 When $G = e^{-\alpha \frac{I_t}{T_t}}$

As in section 3.2, the solutions for Z_∞ are all implicit, so we turn to the method for the general case (section 3) where we define the right and left sides of an equation as two functions of Z_∞. Specifically,

$$L(Z_\infty) = \frac{(1 - \delta q)}{q}Z_\infty$$
$$M(Z_\infty) = q(1 - Z_\infty)(1 - e^{-\alpha Z_\infty})^2 - (1 - \delta q)(1 - 2e^{-\alpha Z_\infty})Z_\infty$$

When we superimpose the graphs of L and M for fixed values of the parameters, we observe the existence of at least one intersection point ($Z_\infty =$
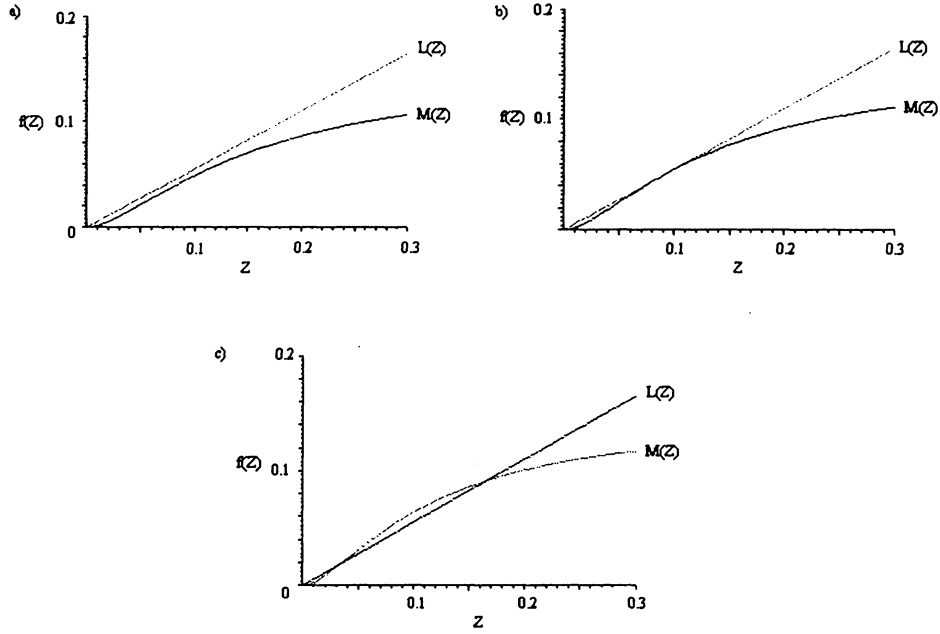
Figure 1: The graphs show $M(Z_\infty)$ and $L(Z_\infty)$ with fixed parameter values. The points where the graphs intersect will be the values we need for Z_∞. In case (a) the DFE is globally stable since it is the only intersection. Notice that in (c) there are three intersections, so for these parameters there will be coexistence. (b) shows that a threshold can be reached when $\alpha \approx 6.77$, $q = 0.5$ and $\delta = 0.9$. This threshold is where the system goes from having 1 endemic equilibrium to 2. The values for the parameters where the tangency occurs can only be approximated which is not useful when analyzing stability numerically.

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0) and at most three (see Figure 6). This implies that there can be three coexisting equilibria for the system. Numerical simulations indicate that when this is the case for G, then they will exist as a locally stable and unstable pair (in addition to DFE).

4 Limiting Systems

Up to this point we have only dealt with a homogenous system. We were able to reduce the System (3) to two dimensions by looking at proportions of the total population. If a system is not homogenous, we cannot use the same method of looking at proportions. However, if T_t reaches a limiting value as $t \to \infty$, then one can obtain a two dimensional limiting autonomous system by substituting for T_t with its limiting value. Results of Thieme and Castillo-Chavez show that this limiting system has the same qualitative dynamics for general continuous time systems, which simplifies the analysis. Furthermore, simulations show that this is the same for systems like System (3). Hence we assume that the limiting system as the same qualitative dynamics as the original system.

5 Constant Recruitment Rate Λ

In a setting where the number of individuals entering the system is constant per generation, the growth rate will be constant. Such would be the case of immigration policies that allow a limited number of individuals into a given area. Here we consider this situation by setting $f(T_t) = \Lambda$ with $G\left(\alpha \frac{I_t}{T_t}\right) = 1 - \frac{I_t}{T_t}$ in the System (1).

Given that T_{t+1} is the sum of individuals in all stages, we see that,

$$T_{t+1} = S_{t+1} + E_{t+1} + I_{t+1}, \tag{13}$$
$$= \Lambda + \gamma T_t, \tag{14}$$

or that

$$T_t = \Lambda \frac{1-\gamma^t}{1-\gamma} + \gamma^t T_0.$$

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Thus,

$$\lim_{t \to \infty} T_t = \frac{\Lambda}{1-\gamma}.$$

At the DFE, most if not all of the population will be in the susceptible class ($S_\infty = T_\infty$) so there are now infected or latent individuals. Hence, In this case the DFE will occur at the point $(S_0, E_0, I_0) = (\frac{\Lambda}{1-\gamma}, 0, 0)$.

5.1 Stability of the disease free equilibrium and $\Re_o$

Unlike the previous case for recruitment, here solutions are not exponential and therefore System (1) can not be easily simplified using proportions. We can, however, work with the limiting system where the total population has reached an equilibrium state, T_∞. In order to determine when the DFE is locally stable, we perform linearization of the system in the neighborhood of the DFE, to obtain the system,

$$\begin{aligned}
E_{t+1} &= \gamma I_t + \gamma E_t \\
I_{t+1} &= \gamma \delta I_t
\end{aligned}$$

or in matrix form,

$$\begin{pmatrix} E_{t+1} \\ I_{t+1} \end{pmatrix} = \begin{pmatrix} \gamma & \gamma \\ 0 & \delta\gamma \end{pmatrix} \begin{pmatrix} E_t \\ I_t \end{pmatrix}$$

This linearized form of the system is analyzed for local stability as shown in Section 3.1. The inequality $q^2\delta + 1 < 2$ (from the Jury test) is always satisfied since $\delta\gamma^2 < 1$ is always true. Again, from the condition $|trace(A)| < det(A) + 1$ we get,

$$\begin{aligned}
\gamma(1+\delta) &< \delta\gamma^2 + 1 \text{ or that,} \\
\Rightarrow \Re_o = \delta\gamma &< 1
\end{aligned}$$

which always hols. Hence, DFE is locally asymptotically stable for all values of the parameters and $\Re_0$ is the number of individuals (in the infected state) that survive and do not become infected.

5.2 Endemic equilibria

We begin searching for endemic equilibria by letting $T_\infty = \frac{\Lambda}{1-\gamma}$, $i.\,e.$ the total population is asymptotically constant. Proceeding as in Section 3.3.1, we obtain

$$E_\infty = \gamma(T_\infty - E_\infty - I_\infty)\frac{I_\infty}{T_\infty} + \gamma E_\infty(1 - \frac{I_\infty}{T_\infty}),$$

$$I_\infty = \gamma\frac{I_\infty E_\infty}{T_\infty} + \delta\gamma I_\infty$$

Letting $Y_\infty = \frac{E_\infty}{T_\infty}$ and $Z_\infty = \frac{I_\infty}{T_\infty}$ to look at proportions of the total population allows for a simpler model that can be analyzed for equilibrium points. In this case the equilibrium points are,

$$\left.\begin{array}{rcl} Y_\infty &=& \frac{1-\delta\gamma}{\gamma} \\ Z_\infty &=& \frac{1-2Y_\infty \pm \sqrt{\gamma^2(1-2Y_\infty)^2 - 4\gamma(1-\gamma)Y_\infty}}{2\gamma} \end{array}\right\} \tag{15}$$

We utilize the same method that was used in section (3.3.1) to determine when endemic equilibria occur and stability of the equilibria. In this case we have that $1 - 2Y_\infty > 0$ if $\frac{1}{\gamma} - \frac{1}{2} < \delta < 1$. The discriminant is greater than or equal to zero whenever $\Re_0 \geq \frac{4\delta^2}{4\delta^2+1} > \frac{1}{2}$.

Again the DFE for constant recruitment is globally stable when there is the only equilibrium poi. This is proved using a similar Lyapunov function and in the same way as in (3.2) with the difference that we cannot work with proportions and therfore f and V become functions of E_t and I_t instead.

If we choose a to be $\frac{b}{2} < a < b(\frac{1}{\gamma} - \delta)$ with a,b $\in \mathbb{R}^+$ then we can define a Lyapunov function $V : [0, \infty) \times [0, \infty) \rightarrow [0, \infty)$ by $V(E_t, I_t) = \frac{\delta}{\Re_0}(aE_t + bI_t)$. DFE is globally stable when $V(f(E_t, I_t)) < V(E_t, I_t)$ for all $(E_t, I_t) \neq (0, 0)$.

6 Ricker's growth function

We now let $f(T_t) = T_t e^{r-kT_t}$ and we assume that $\lim_{t\to\infty} T_t = T_\infty$, where $T_\infty = (-\ln(1 - \gamma) + r)/k$. By simple analysis we know that T_∞ is a unique fixed point for $0 < r < 2/(1 - \gamma) + \ln(1 - \gamma)$. Hence by substituting T_∞ for T_t we obtain the following limiting system:

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$$\left.\begin{aligned}
S_{t+1} &= T_\infty(1-\gamma) + \gamma S_t(S_t + E_t)/T_\infty + (1-\delta)\gamma I_t \\
E_{t+1} &= \gamma S_t I_t/T_\infty + \gamma E_t(S_t + E_t)/T_\infty \\
I_{t+1} &= \gamma E_t I_t/T_\infty + \delta\gamma I_t
\end{aligned}\right\} \qquad (16)$$

where S_t is replaced by $T_\infty - E_t - I_t$

We linearize at the DFE ($S_t = T_\infty, 0, 0$) and we determined that $\Re_0 = \delta\gamma$, which is always less than one. Following the same method that was used in section (5.2) we obtain the same expressions of System (15). We can define a Lyapunov function that is exactly the same as that defined for the constant growth function to determine the global stability of the DFE whenever in the absence of an EE.

$$I_\infty = \frac{(T_\infty - 2E_\infty) \pm \sqrt{(T_\infty - 2E_\infty)^2 - 4(T_\infty/\gamma - T_\infty)E_\infty}}{2} \qquad (17)$$

then the EE will be stable.

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7 Backward bifurcation: coexistence of a DFE and an EE

As stated before, if the basic reproductive number ($\mathfrak{R}_0$) is less than one, then essentially an individual will on average cause less than one secondary infection before dying or recovering. Hence the disease that is present in the susceptible population will eventually die out. However, in all the examples we have shown of System (1), $\mathfrak{R}_0 < 1$ always (so the DFE is locally stable) and yet the disease can prevail, implying that the fate of an epidemic will depend on its initial conditions. Previous studies in continuous time show that the backward bifurcation phenomena is a result of exogenous re-infection. The case seems to be same for discrete time systems. The appearance of an
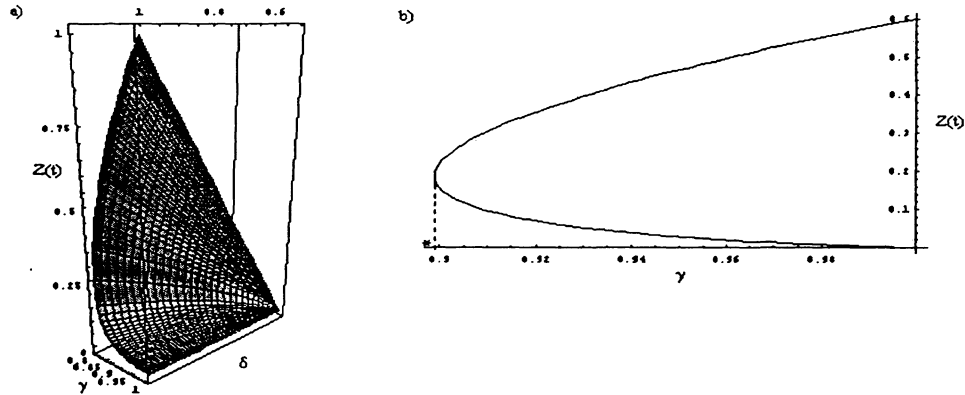
Figure 2: Shows the number of equilibria according to the values of δ and γ. (a) is the graph of (10) as a function of its parameters. Recall that this expression for Z_∞ was obtained with $G = 1 - \frac{I_t}{T_t}$. If we fix the value for one of the parameters we get a projection that looks like (b). This second function was done by fixing $\delta = 0.8$. The value pointed out in the diagram (*) is similar to $\mathfrak{R}_m$ in that passing that value of γ will result in the appearance of a second endemic equilibrium. Wherever there are two equilibria, the lower one will always be the unstable one due to the stable nature of the DFE.

endemic equilibrium (EE) occurs at a value of $\mathfrak{R}_0$ (called $\mathfrak{R}_m$). Beyond $\mathfrak{R}_m$, the equilibrium point splits into two separate steady states, one stable and the other unstable (see Figure 2). For values of $\mathfrak{R}_0$ close to one, the presence of only few infected individuals may cause an epidemic whereas for values of $\mathfrak{R}_0$ close to $\mathfrak{R}_m$ an epidemic will only thrive if there are many infecteds in

the system. This has further biological implications that are discussed later in the paper.

8 Dispersal Models

We allowed dispersal of susceptibles between two patches (see figure 3) in the same fashion Hastings showed in 1993 [4]. The movement of susceptible individuals $\hat{S}$ is modeled in the following manner:

$$
\begin{aligned}
S_{t+1}^1 &= f_1(\bar{S}_t^1(1 - D_1) + \bar{S}_t^2 D_2, E_t^1, I_t^1) \\
E_{t+1}^1 &= f_2(\bar{S}_t^1(1 - D_1) + \bar{S}_t^2 D_2, E_t^1, I_t^1) \\
I_{t+1}^1 &= f_3(\bar{S}_t^1(1 - D_1) + \bar{S}_t^2 D_2, E_t^1, I_t^1) \\
S_{t+1}^2 &= h_1(\bar{S}_t^2(1 - D_2) + \bar{S}_t^1 D_1, E_t^2, I_t^2) \\
E_{t+1}^2 &= h_2(\bar{S}_t^2(1 - D_2) + \bar{S}_t^1 D_1, E_t^2, I_t^2) \\
I_{t+1}^2 &= h_3(\bar{S}_t^2(1 - D_2) + \bar{S}_t^1 D_1, E_t^2, I_t^2)
\end{aligned}
$$

where $\bar{S}$ represents the population of susceptibles before dispersal. D_1 and D_2 represent the probability of dispersal out of patch 1 and patch 2 respectively and $0 < D_1, D_2 < 1$.
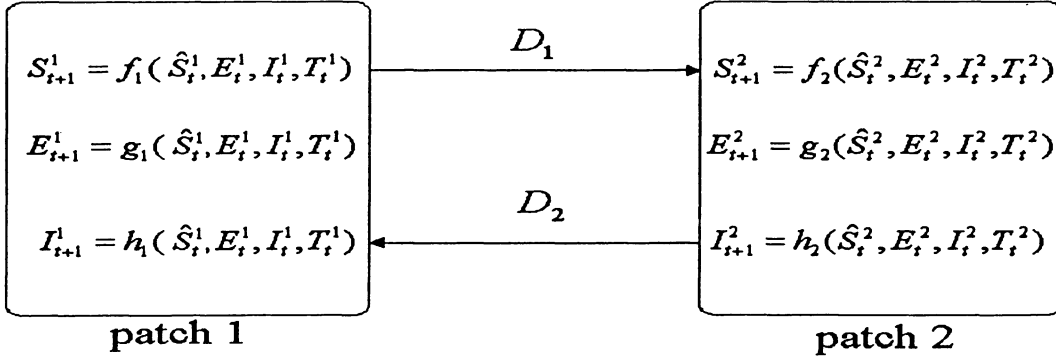

Figure 3: General local dynamics and dispersal between patches. S_{t+1}^i, E_{t+1}^i and I_{t+1}^i (for $i = 1, 2$) represent the functions mentioned previously where i is the patch number. $\hat{S}$ represents the dynamics of susceptibles when these move between patches, following the dynamics shown in (18) and (18).
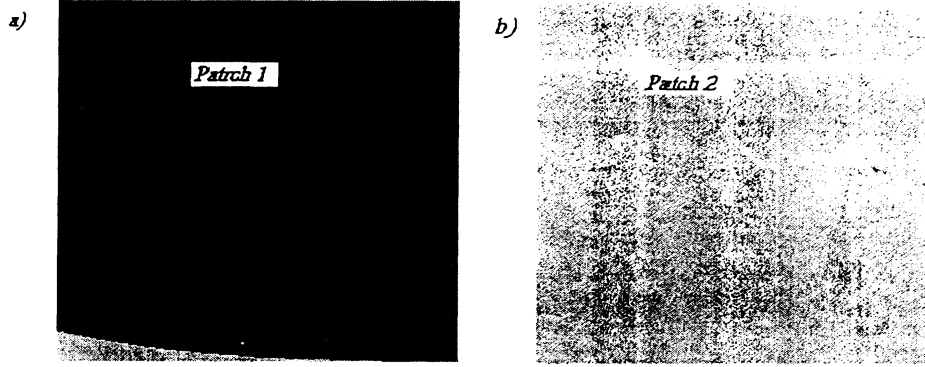
Figure 4: Basin of attraction for a two patch system with geometric recruitment. a) The darker area represents the basin of intial conditions where the point will eventually reach an endemic equilibrium. The lighter area is basin for the DFE. b)Basin of attraction for the DFE in patch 2.

We show various scenarios with various levels of dispersal. For simplicity, throughout this section, when we mention equilibria and refer only to the EE's, we imply the coexistence of the DFE since $\Re_0$ is always less than one. We compare the patterns that arise in a patch, before and after dispersal. Here we discuss only the drastic, more interesting cases for each recruitment function, but the behaviour we describe could occur only for a given set of parameters.

8.0.1 Case1: Geometric Recruitment

We begin by exploring the long-term behaviour when both patches have geometric recruitment and infection probability is governed by $G = 1 - \frac{I_t}{T_t}$.
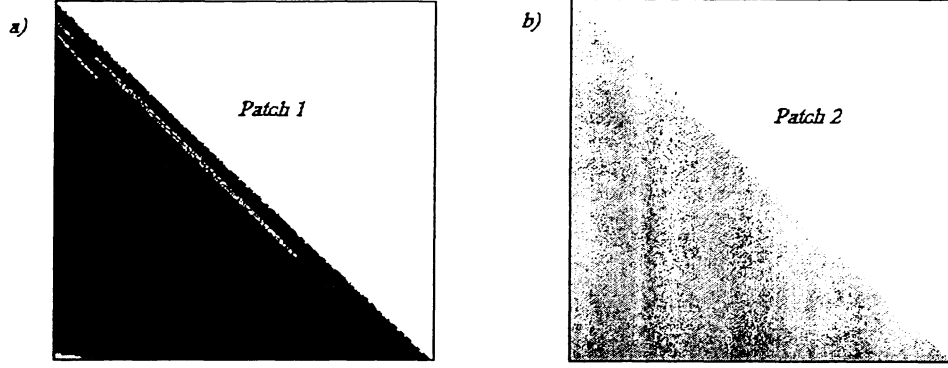
Figure 5: Basin of attraction for a two patch system with constant recruitment. a)Basin of attraction for patch 1 after dispersal. The darker area represents the basin of initial conditions where the point will eventually enter the chaotic attractor. Initial values in the lighter area will go to the DFE; b)Basin of attraction for patch 2 after dispersal. Note that here the DFE is globally stable. The top half in both cases is discarded because we use proportions so we can only look at the points where $X_\infty + Y_\infty + Z_\infty = 1$.

We start out with only one attractor in each patch. Hence, both patches have a DFE only. After allowing dispersal between the two patches, patch 1 has two attractors. This particular case is very interesting since an increase in dispersal caused an empidemic even though both patches were disease free.

8.0.2 case2: Constant Recruitment

The second example we consider constant growth for the recruitment function, with $G(\frac{I_t}{T_t}) = 1 - \frac{I_t}{T_t}$. We assume that the total population has reached an asymptotically stable steady state (T_∞).

A single patch with this recruitment function initially shows very predictable and ordinary dynamics. However, introducing dispersal between two patches of this same type will cause significant changes in the dynamics so that the demographics will not reflect the behaviour of the disease.

In a system where both patches begin with endemic equilibria, dispersal will cause one patch to lose its endemic attractor and the other patch to retain it. However, the endemic attractor in this second patch changes in
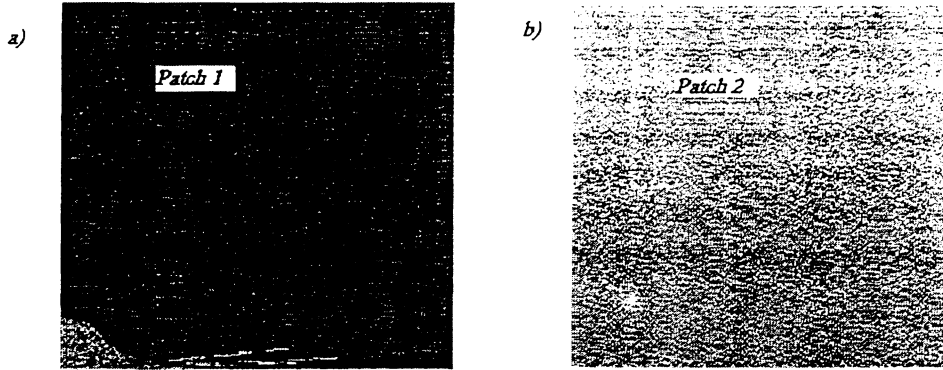
18

Figure 6: Basin of attraction for a two patch system with Ricker's growth function after dispersal. a) Basin of attraction for patch 1. The darker area represents the basin of intial conditions where the point will eventually enter the stable period 8 cycle. The lighter area is the basin for the DFE. b)Basin of attraction for the DFE in patch 2.

nature to become chaotic. This is a clear example where the demographic dynamics have no influence on the dynamics of a disease since the local patch dynamics are very simple but after dispersal is allowed the dynamics become very complex.

8.0.3 case:3 Ricker's Equation, with $G = e^{-\alpha \frac{I_t}{T_t}}$

Finally, we analyze the beviour of the system when the patches are governed by Ricker's equation with $G = e^{-\alpha \frac{I_t}{T_t}}$ and r in a chaotic region.
For this case we see the opposite effect of dispersal on the attractors as in the previous case. Patch 1 had a chaotic attractor for the EE, patch 2 had a DFE only. After dispersal we no longer had a chaotic attractor but a stable period 8 cycle. Again we show evidence that dispersal can change the nature of an attractor. Patch 2 remained with a DFE only.

9 Conclusions

The fact that there exists a backward bifurcation in the single and two patch dynamics is the result of both a latent stage in the system and controlling

the movement of individuals from the latent stage to the infectious stage. In a system where the latent stage is present and its flow to stage I_t is constant, the coexistence is lost so there will either be a DFE or an EE but not both (González, Sáenz and Sánchez, 2000) simultaneously. A possible explanation for this is that latency period creates a reservoir of potential infectious individuals that will be 'exploited' when the proportion of infecteds reaches the appropriate value.

Tuberculosis is an example of a disease where an individual may acquire partial immunity to initial infection (therefore be in the latency period) but may develop the active disease with re-infection [1]. A reservoir of latents can also be created in examples of vaccination where only a portion of a population is vaccinated and the effect of the vaccine wears out with time. The speed at which the immunity is lost will determine if coexistence occurs in the system [5].

On the other hand, the restrictions for $\Re_0$ so that there exists an endemic equilibrium (greater than one-half) suggests that regardless of the portion of latents in the system, if $\Re_0 < \frac{1}{2}$ the endemic equilibrium will not occur. Further more if there is no endemic state, then the DFE will show global stability.

Coexistence of this sort has important evolutionary implications since the destiny of a given population (or disease in this case) will depend not only on the population strategy but also on the initial conditions, that is, going back to the origin or emergence of the population.

The effect of the demographical dynamics on the disease dynamics is not clearly marked. The geometric and constant recruitment functions have similar effects on the disease since they exhibit the same properties for $\Re_0$ and coexistence of EE and DFE are possible. For Ricker's equation with appropriate values of the parameters, coexistence also occurs but the endemic attractor exhibits chaotic behaviour. This reflects the chaotic nature of a population governed by Ricker's dynamics with suitable parameter values. On the other hand, when local demographics follow constant recruitment and dispersal is introduced, the disease will enter a chaotic attractor (coexisting with the DFE), implying no effect of the population dynamics on the disease. Further studies using other demographic regimes such as Verhulst dynamics should exhibit this sort of behaviour.

Dispersal between patches showed to generally work against the disease. When both patches begin with an EE, there will always be a set of parameters for which the EE in one of the patches will collapse except when the recruitment into the system follows geometric growth. This usually occurs with an increment in the dispersal between patches suggesting that the more movement between the patches, the higher the probability of the patch of becoming disease-free.

In the case where dispersal is zero and both patches only have a DFE, then the geometric recruitment is the only one where an EE appears with dispersal. This means that for a population with geometric growth carrying a disease that follows our model then the movement of infecteds is not necessary to push the epidemic to an equilibrium. The effect of the movement of latent or infected individuals between patches, could be substantial in the arisal of EE's where they originally did not exist.

If one patch has local dynamics such that there is a DFE and the other shows coexistence, the effects of dispersal change depending on the recruitment function. For constant recruitment, the EE is lost and the whole system becomes disease-free. The Ricker's recruitment causes one of the patches to remain as a DFE, whereas the other patch shows coexistence with an endemic chaotic attractor. Geometric recruiment doesn't affect the local patch dynamics.

Numerical explorations of the basins of attraction with different parameters are by far the most time-consuming because of the numerous parameters in the system. In order to facilitate the simulations, we made some simplifying assumptions. We assumed that a probability of dispersal greater than 0.7 would not be realistic since in a given population it is rare that most of the individuals disperse. Also, it is important to note that our observations are only for fixed parameter values, hence any conjectures made may not hold for different values, because there is a lot to explore in this sense. We leave this topic as future work. Moreover, in this case we only allow dispersal of the susceptible portion so further studies should concentrate on the movement of the infecteds or latents, depending on the nature of the disease.

Clearly, the possibilities for this kind of study are still open since there are

still many numerical explorations to be done not only with these examples but with many others. The use of computer packages like Dynamics and others of the sort are clearly very useful and can help visualize and explain behaviour that otherwise would be unpredictable.

10   Acknowledgements

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