The problem of global analysis

Example

$$\begin{aligned}\dot{S} &= \mu(N-S) - \beta SI/N \\ \dot{I} &= \beta SI/N - \gamma I \\ \dot{R} &= \gamma I - \mu R\end{aligned}$$

What is R_0 for this system?

Count time in units of $\tau = t/\gamma$. Let $\rho = \mu/\gamma$, $x = S/N$, $y = I/N$.

$$\begin{aligned}\dot{x} &= \rho(1-x) - R_0 xy \\ \dot{y} &= R_0 xy - y\end{aligned}$$

Global analysis

Poincare-Bendixson

Systems get trapped in two dimensions.

Bendixson-Dulac

If

$$\frac{\partial(\phi\dot{x})}{\partial x} + \frac{\partial(\phi\dot{y})}{\partial y}$$

has constant sign over a region, then there are no closed orbits wholly contained in that region (divergence theorem).

Dulac function for this system is $\phi = 1/x$

Global analysis

Lyapunov functions

The idea is to find a function V that does not increase under the dynamical flow:

$$\dot{V} = V_x \dot{x} + V_y \dot{y} \leq 0$$

First, consider the ‘epidemic’ case discussed earlier ($\rho = 0$).

$$\begin{aligned} \dot{x} &= -\beta x y \\ \dot{y} &= \beta x y - y \end{aligned}$$

We can explicitly solve for the orbits of this system:

$$\begin{aligned} dy &= (1/(\beta x) - 1) dx \\ y - y_0 &= \log(x/x_0)/\beta - (x - x_0) \end{aligned}$$

Thus the quantity $y + x - \log(x)/\beta$ is conserved over orbits.

Global analysis

Lyapunov functions

Inspired by the conserved quantity in the ‘epidemic’ case, we try the Lyapunov function

$$V = x - \bar{x}\log x + y - \bar{y}\log y$$

If we let x and y flow, we have:

$$\begin{aligned}
\dot{V} &= \dot{x}(1 - \bar{x}/x) + \dot{y}(1 - \bar{y}/y) \\
&= (\rho(1-x) - \beta x y)(\beta x - 1)/(\beta x) + (\beta x - 1)y(1 - \rho(1 - 1/\beta)/y) \\
&= \frac{-\rho(\beta x - 1)^2}{\beta x}
\end{aligned}$$

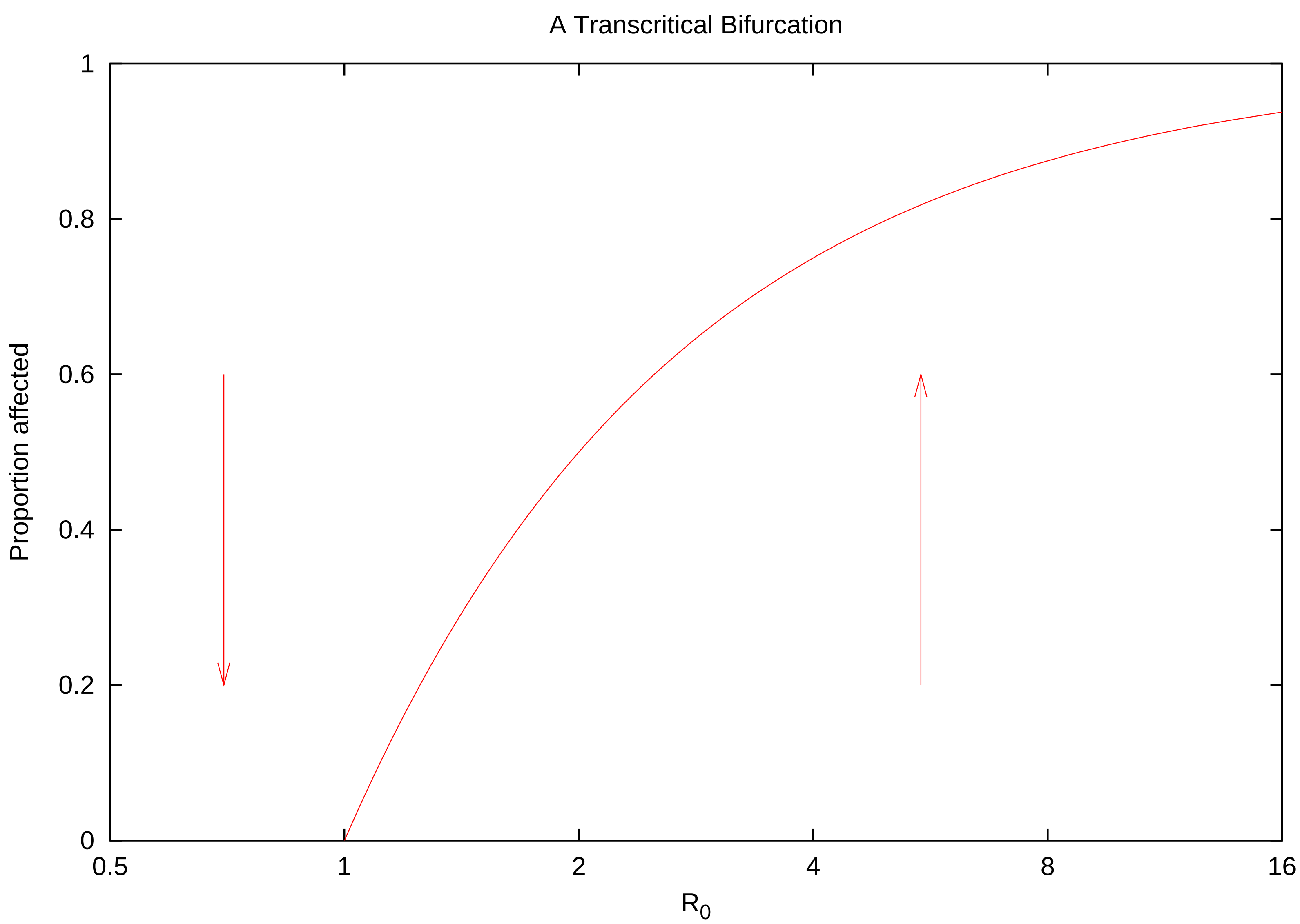
Thus V will (virtually) always decrease until it reaches the equilibrium, so the equilibrium is globally attractive, which we already knew.

Our friend the transcritical bifurcation

A bifurcation point is a point in parameter space where there is a qualitative (topological) change in the behavior of solutions of a dynamical system.

A bifurcation diagram shows changes in the behavior of a system (often the asymptotic behavior) as parameters change.

The transcritical bifurcation is very common in ecology: it is the typical way in which a species changes from going extinct in a system to invading the system.


A Transcritical Bifurcation
Proportion affected
1
0.8
0.6
0.4
0.2
0
0.5
1
2
4
8
16
R0

A multi-group model of a fatal disease

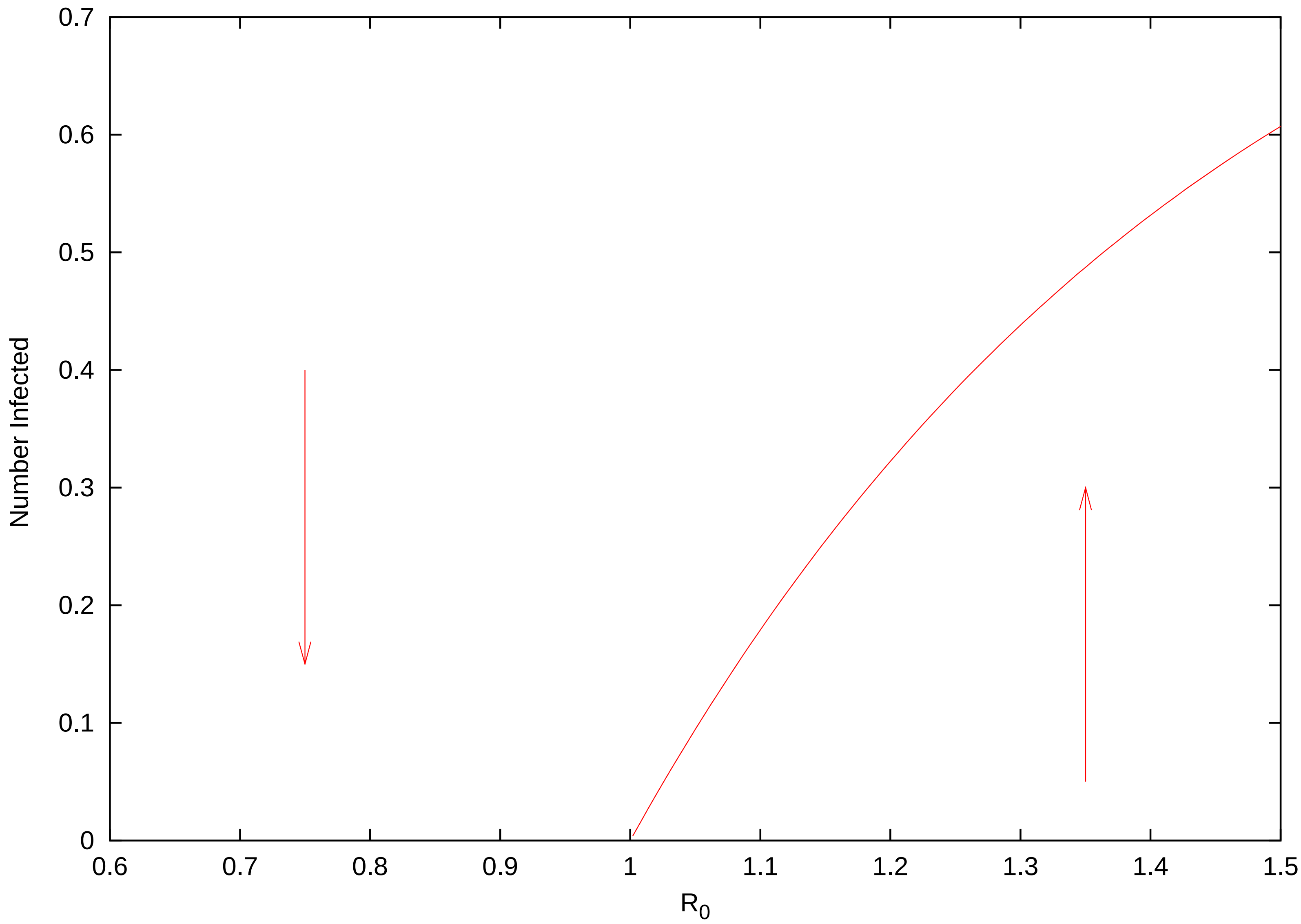
$$\begin{aligned}\dot{S}_i &= b_i - \Lambda_i S_i - \mu_i S_i \\ \dot{I}_i &= \Lambda_i S_i - \mu_i(\sigma_i + 1) I_i,\end{aligned}$$

where b_i is the rate that new susceptibles are recruited into group i, Λ_i is the force of infection as seen by group i, μ_i is the death rate, and σ_i represents disease-induced death.

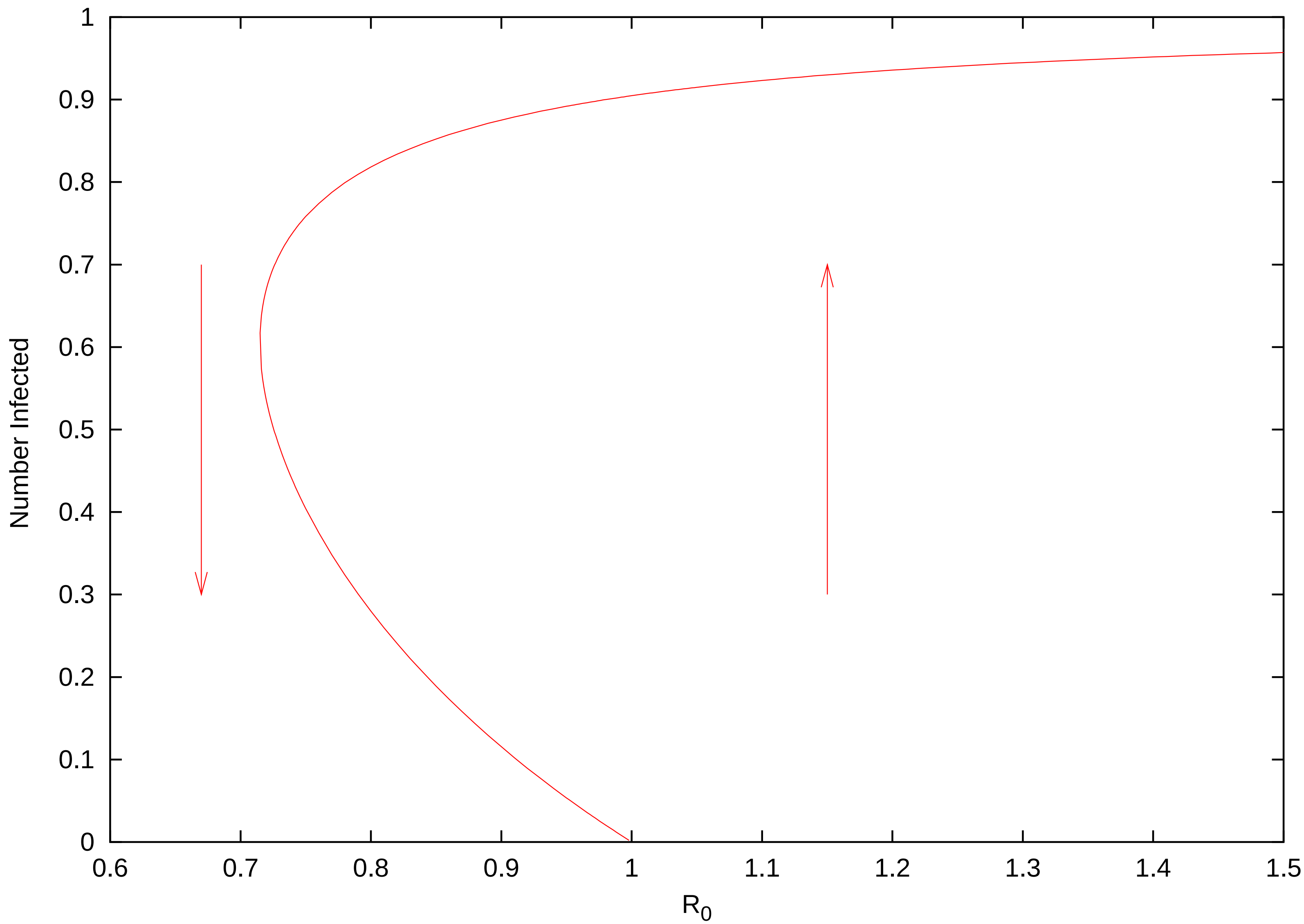
Assume mixing rates are unaffected by deaths:

$$\Lambda_i = c_i \frac{\sum_j c_j \tau_{ij} I_j}{\sum_j c_j T_j}$$

The transmission from group i to j is given by τ_{ij}.



Number Infected
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
R_0

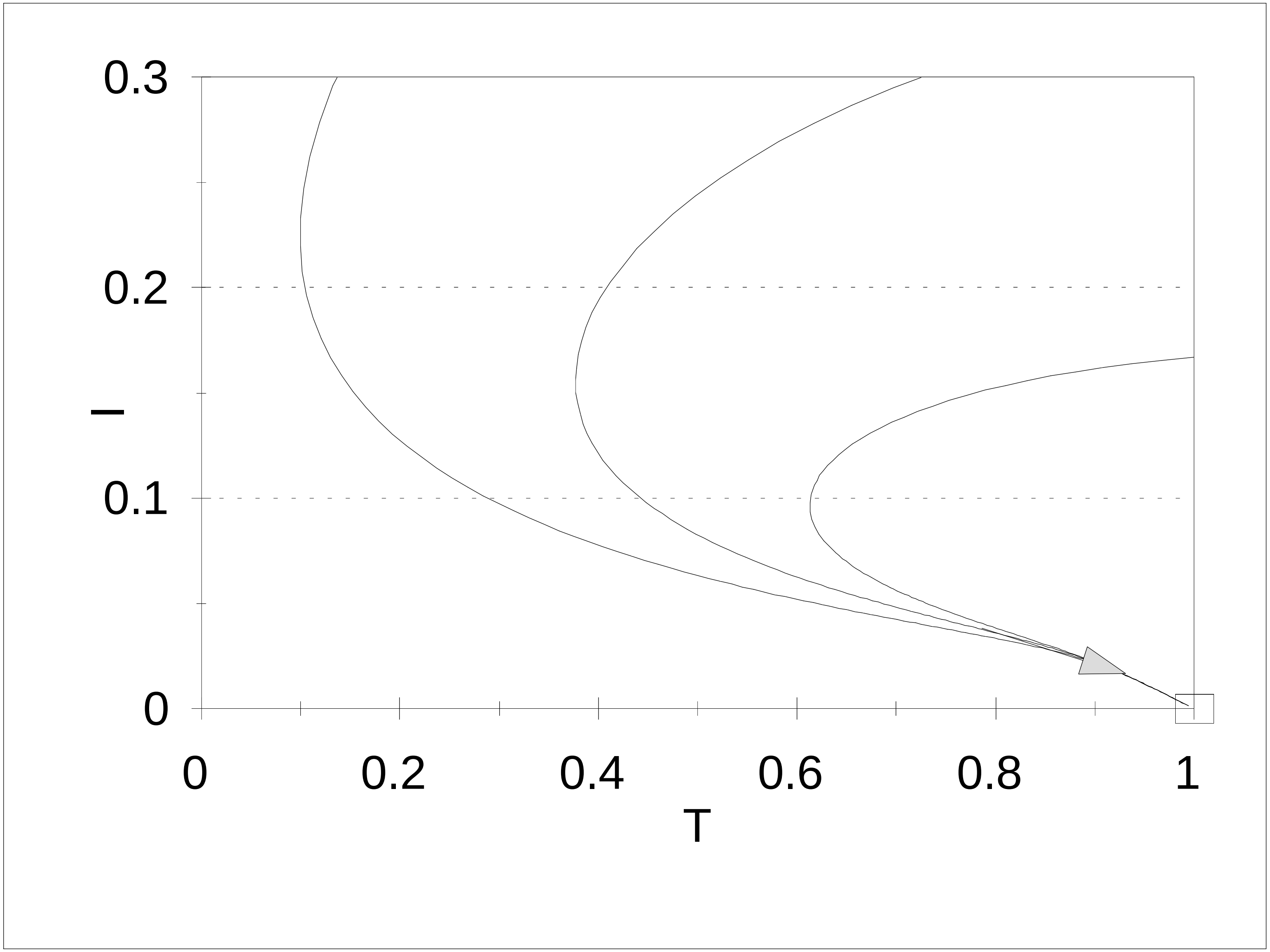

Number Infected
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
R_0

Backwards bifurcations in a multi-group model of a fatal disease

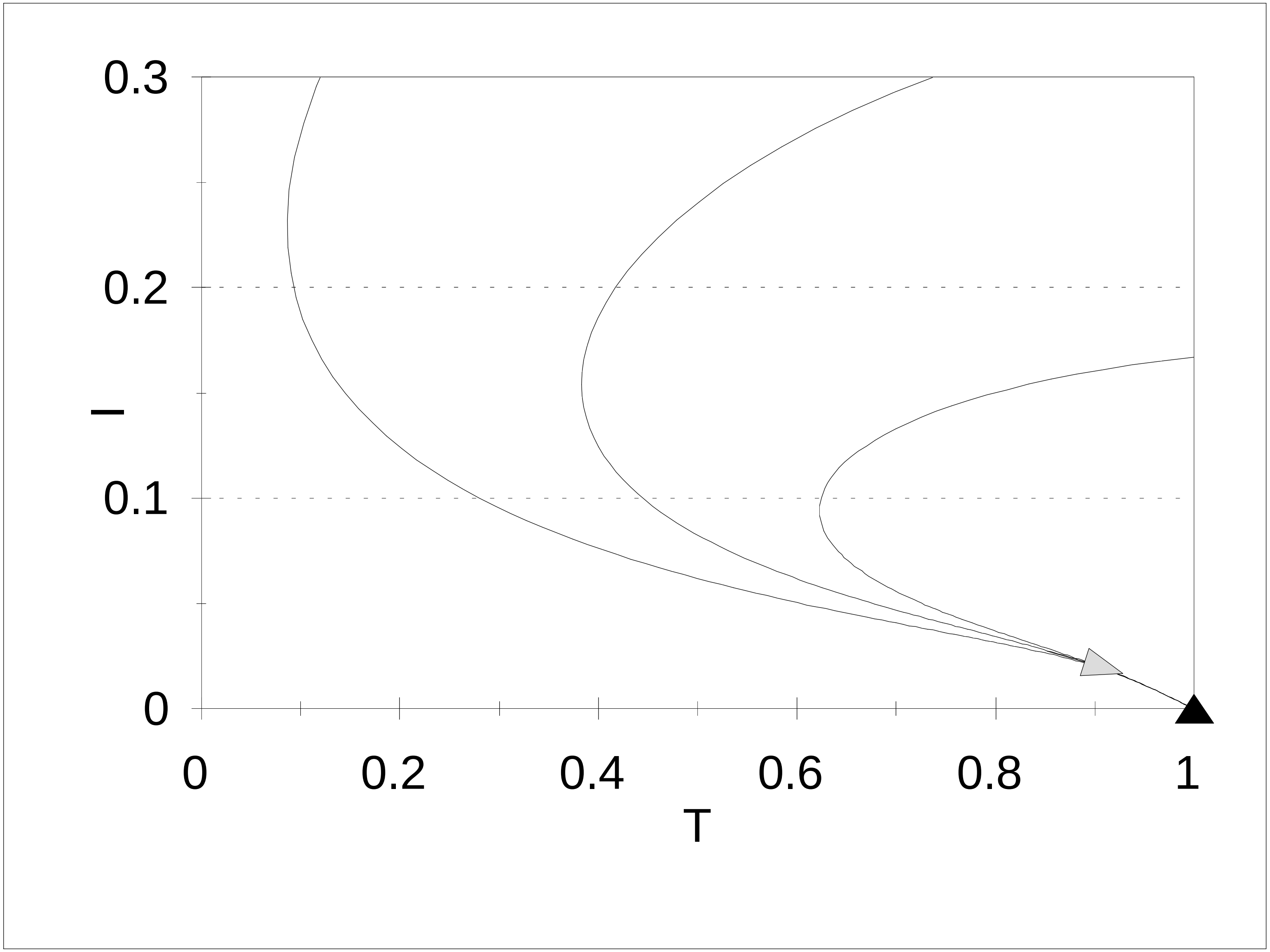
Backwards bifurcations happen precisely when the disease can invade at $R_0 = 1$. This implies that the disease helps itself by invading (the number of infections per infection increases from 1).

This can only happen if there is some mechanism to increase the reproductive number R which is stronger than the reduction in R due to reduction in the proportion of the population susceptible.

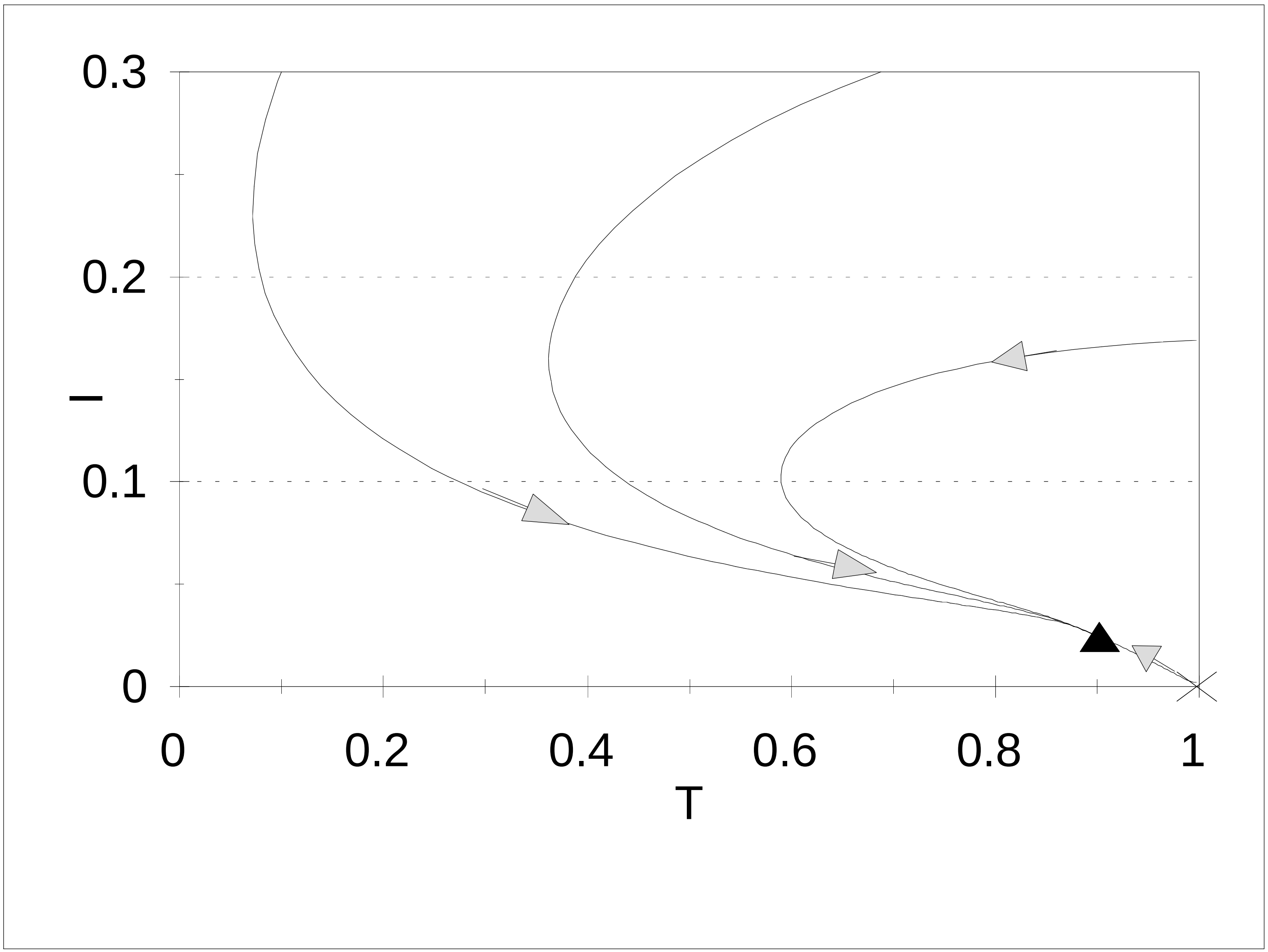
Forward bifurcation, $R_0 = 1$



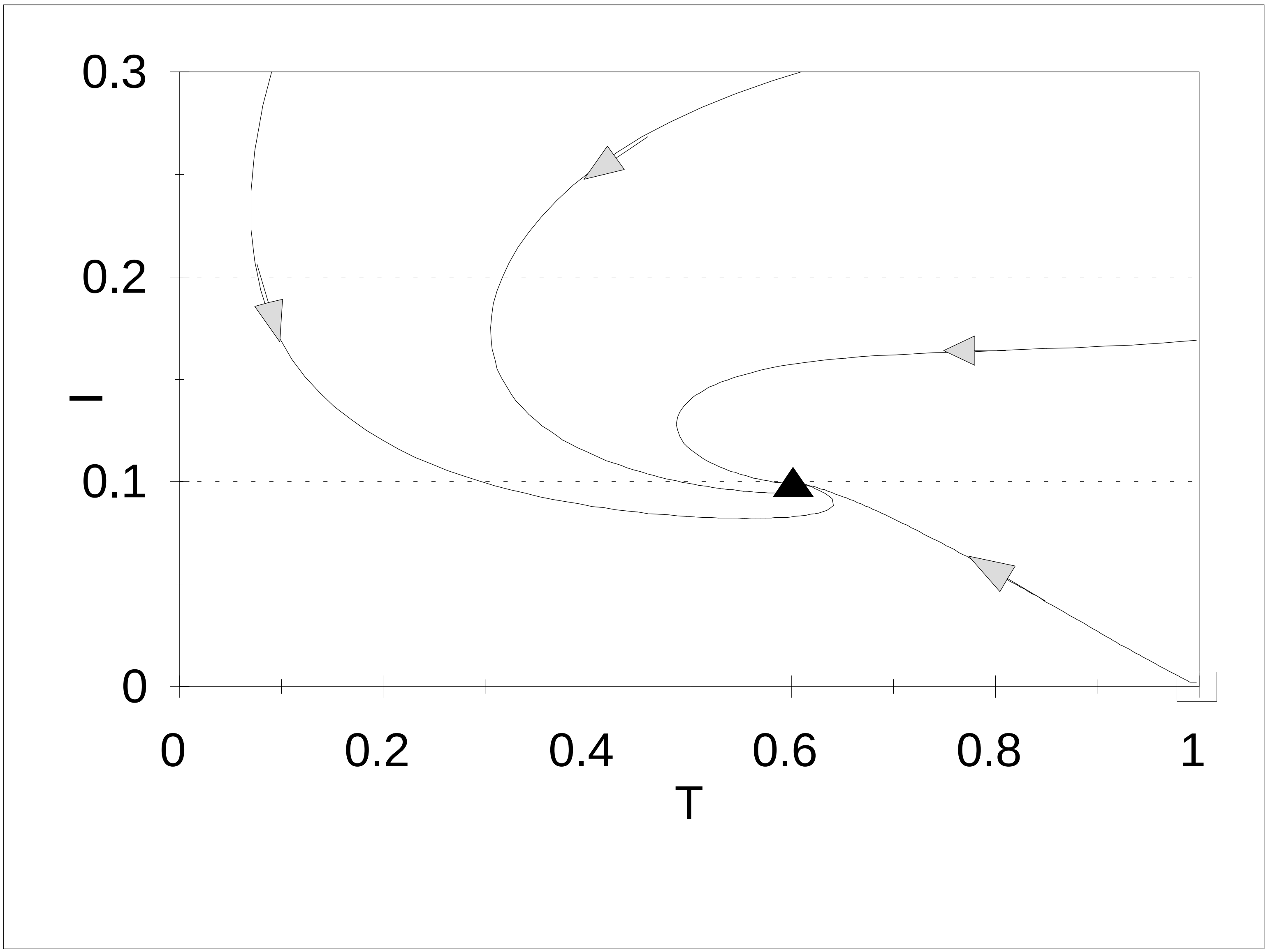
Forward bifurcation, $R_0 < 1$



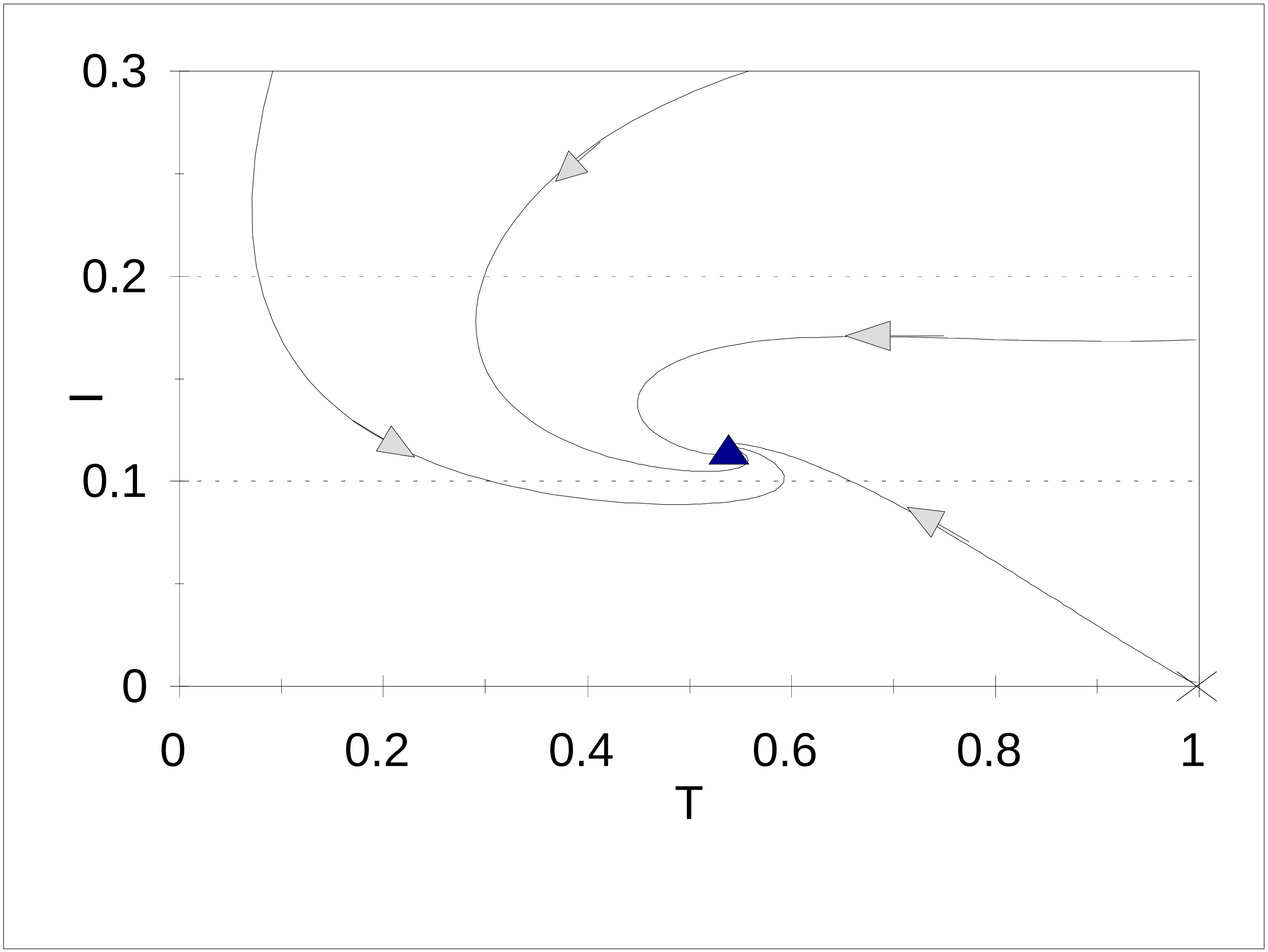
Forward bifurcation, $R_0 > 1$



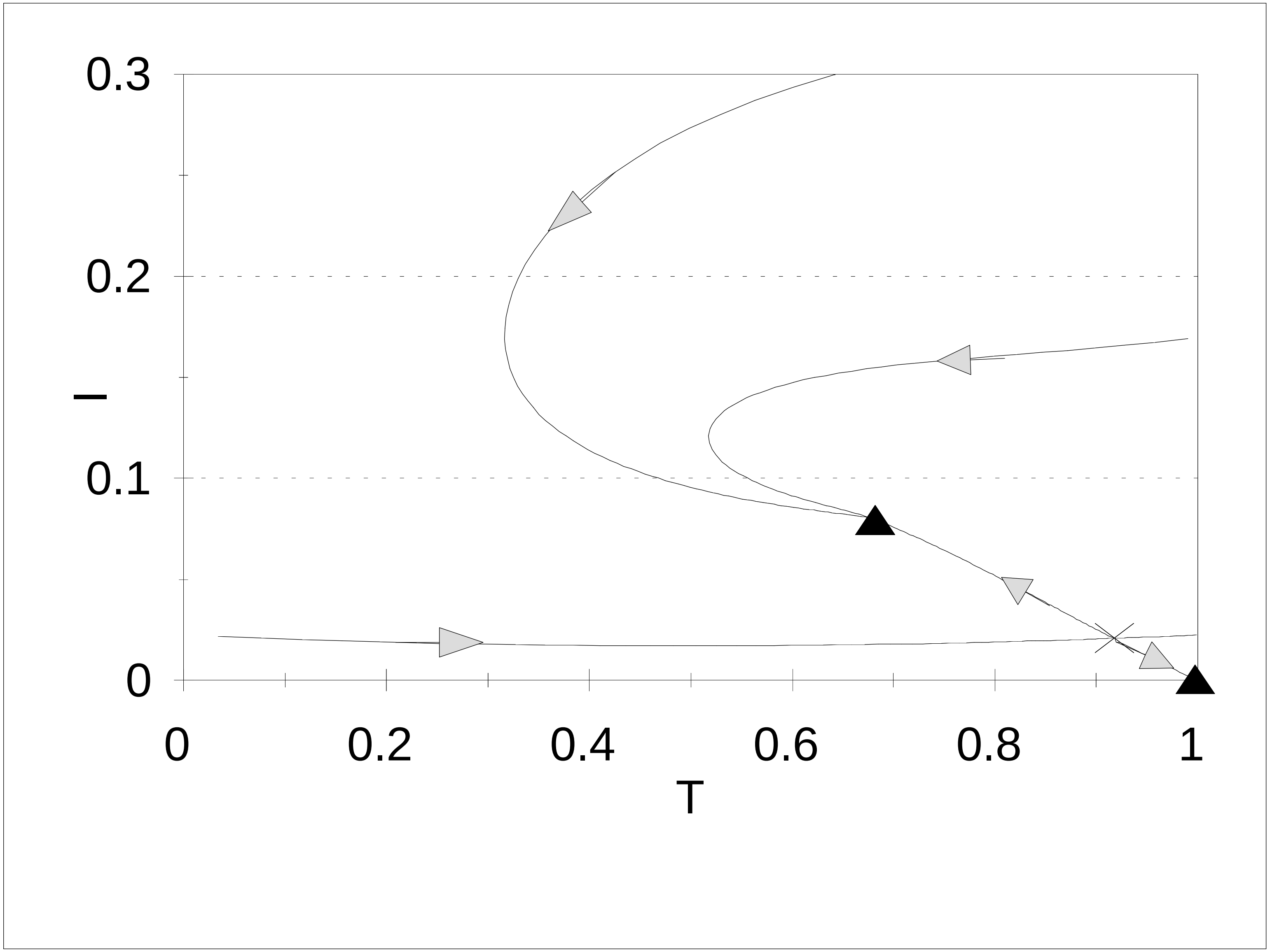
Backward bifurcation, $R_0 = 1$



Backward bifurcation, $R_0 > 1$



Backward bifurcation, $R_0 < 1$



Backwards bifurcations in a multi-group model of a fatal disease

Can only happen if the disease changes the population structure in a way that benefits its own spread.

This in turn can only happen if the groups who are most affected by the disease (a victim group) are different from those that are most effective at spreading the disease (a core group).

How realistic is this? Not so much, but it was necessary to understand the mechanism before we could think realistically about the question.

Mechanisms for backwards bifurcations in disease models

- Disease-induced changes in population structure
- Behavioral changes
- Interactions between level of infection and immune reactions

Calculating the sign of the transcritical bifurcation

In one dimension:

$$\dot{x} = f(x, \mu)x.$$

This is a typical ecological formulation, as opposed to the more generic formulation for most other areas of dynamics — $\dot{x} = f(x, \mu)$. It is the *per capita* nature of the equation that leads to the ubiquity of the transcritical bifurcation.

Bifurcation when $f(0, \hat{\mu}) = 0$. Sign given by

$$\frac{\partial}{\partial x} f(0, \hat{\mu})$$

Calculating the sign of the transcritical bifurcation

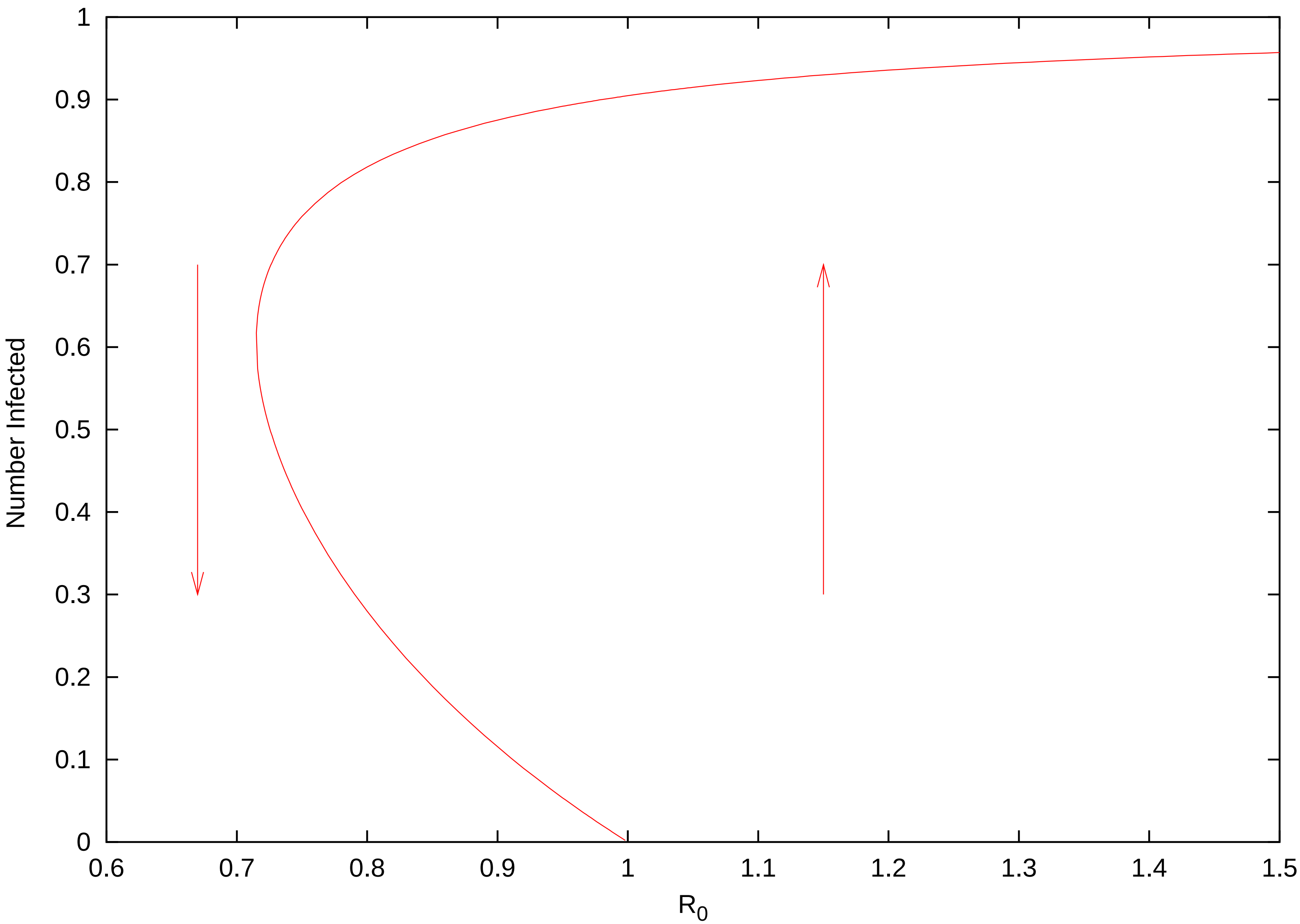
In multiple dimensions:

$$\dot{Y} = F(Y, \mu)Y.$$

Transcritical bifurcation when $F(0, \hat{\mu})$ has single, simple zero eigenvector. The criterion is similar to the 1-d case:

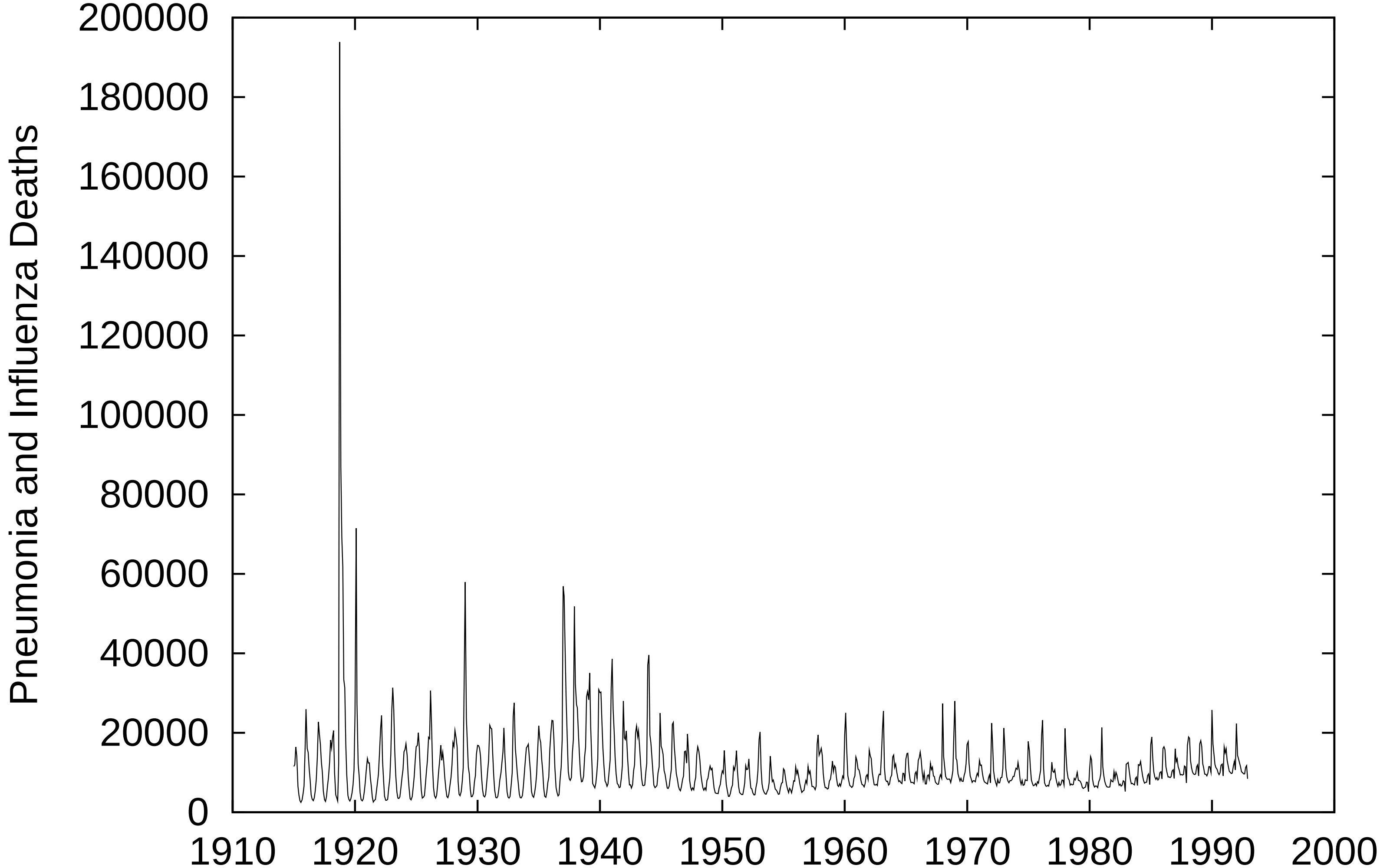
$$W \frac{\partial F(\varepsilon V)}{\partial \varepsilon}(0, \hat{\mu})V.$$

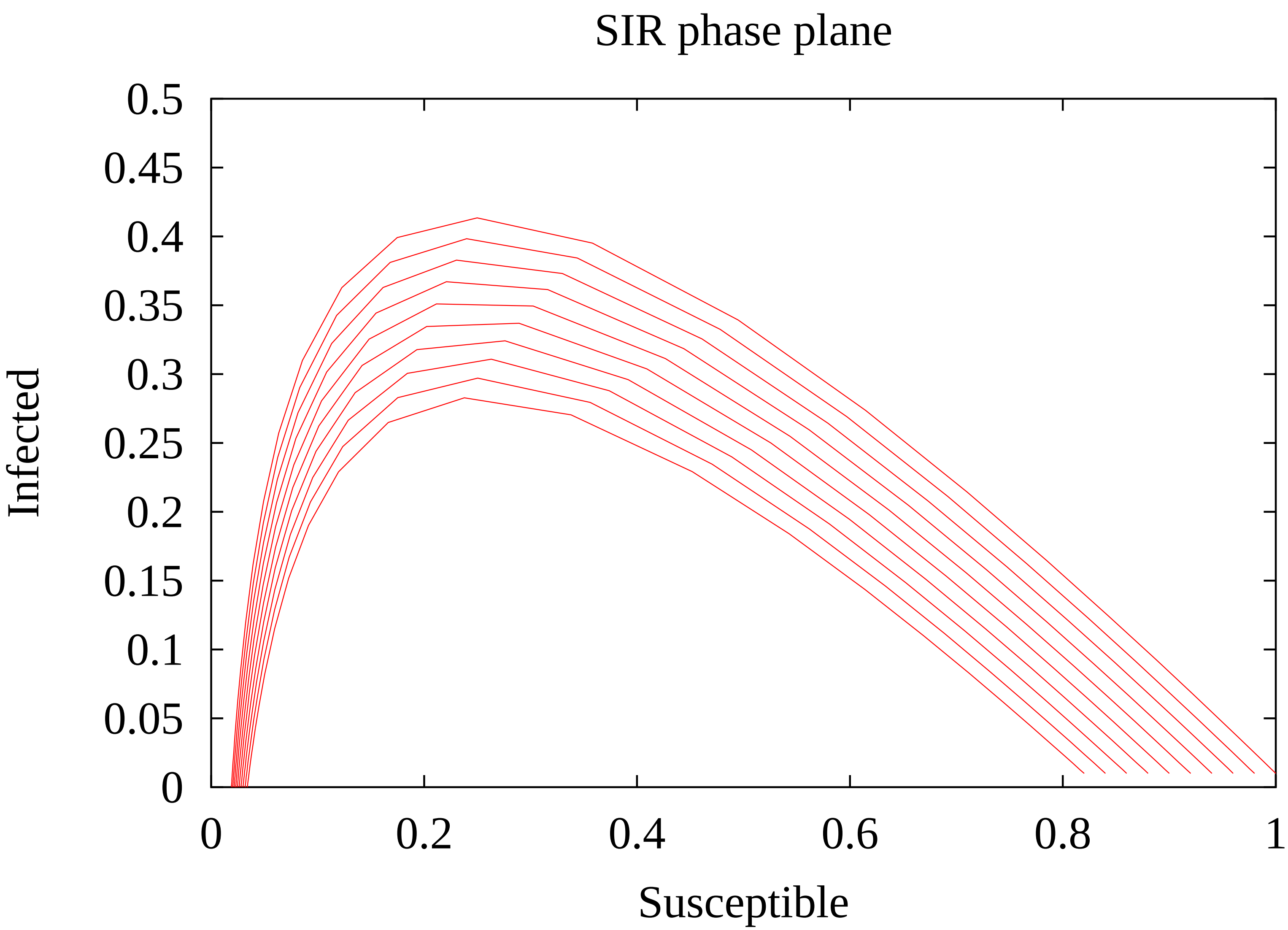
where V and W are the dominant eigenvectors.

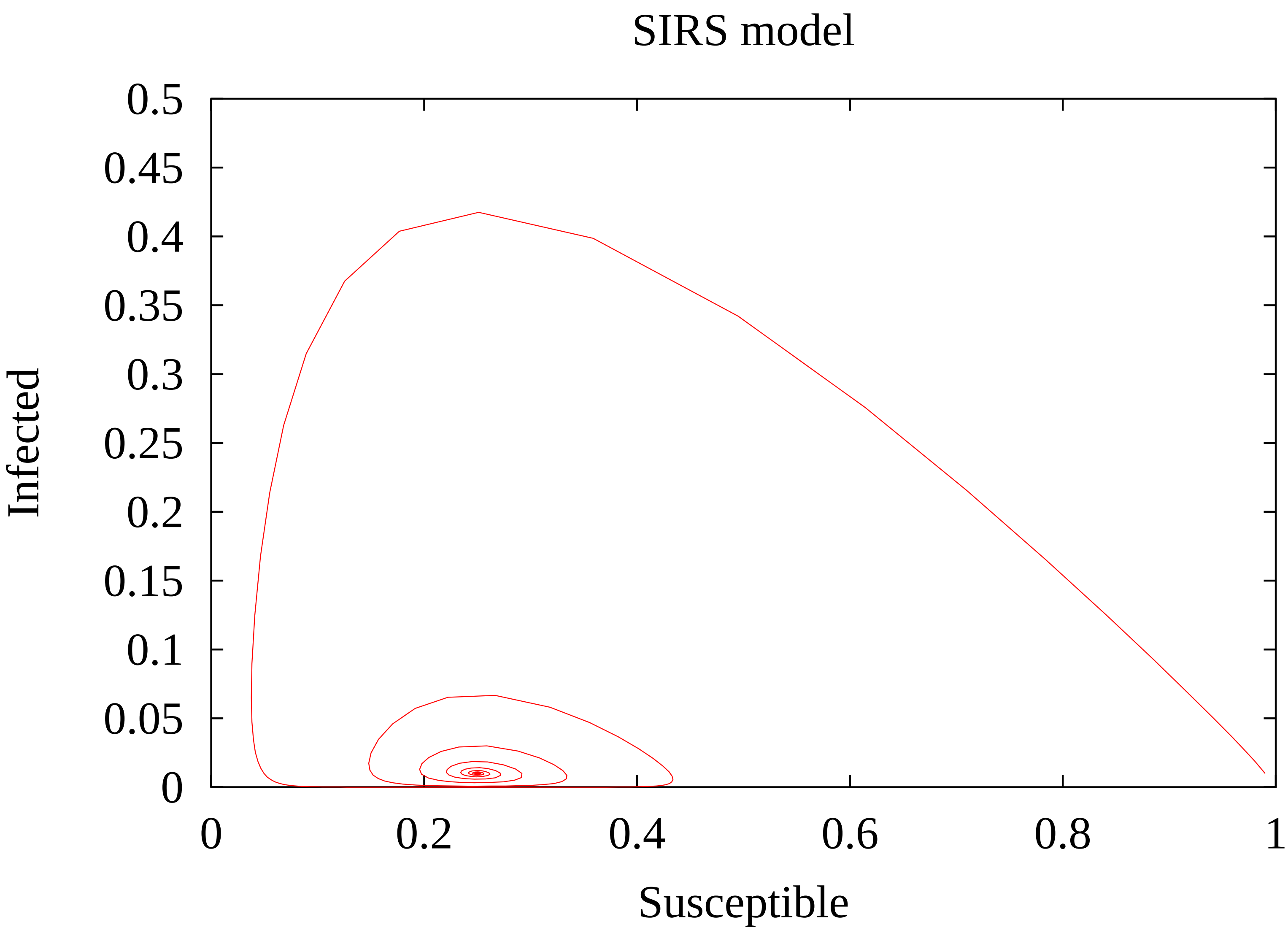


Number Infected
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.6
0.7
0.8
0.9
1
1.1
1.2
1.3
1.4
1.5
R0

US Monthly Mortality




SIR phase plane
Infected
Susceptible
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
0
0.2
0.4
0.6
0.8
1


SIRS model
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Infected
0
0.2
0.4
0.6
0.8
1
Susceptible

In search of the Hopf bifurcation

Transcritical and saddle-node occur when a single eigenvalue travels through 0.

The next simplest thing that can happen is a Hopf bifurcation, where a pair of complex eigenvalues crosses the imaginary axis. The ‘forward’ Hopf bifurcation leads to local, cyclic behavior. The ‘backward’ Hopf bifurcation leads to non-local behavior.

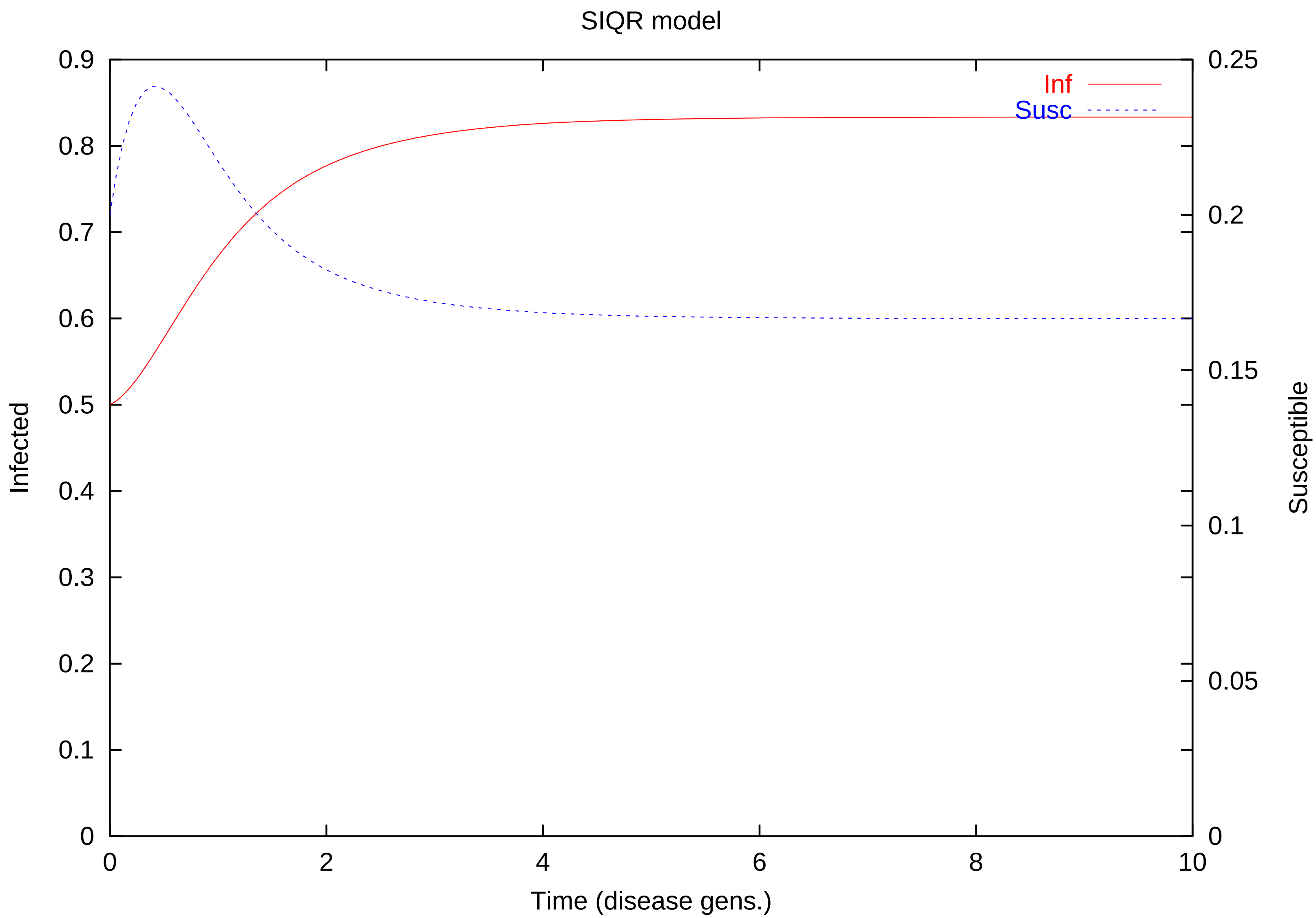
In search of the Hopf bifurcation (making disease models oscillate)

- Stochasticity (demographic, parametric)
- External forcing
- Time delays
- Discrete-time models

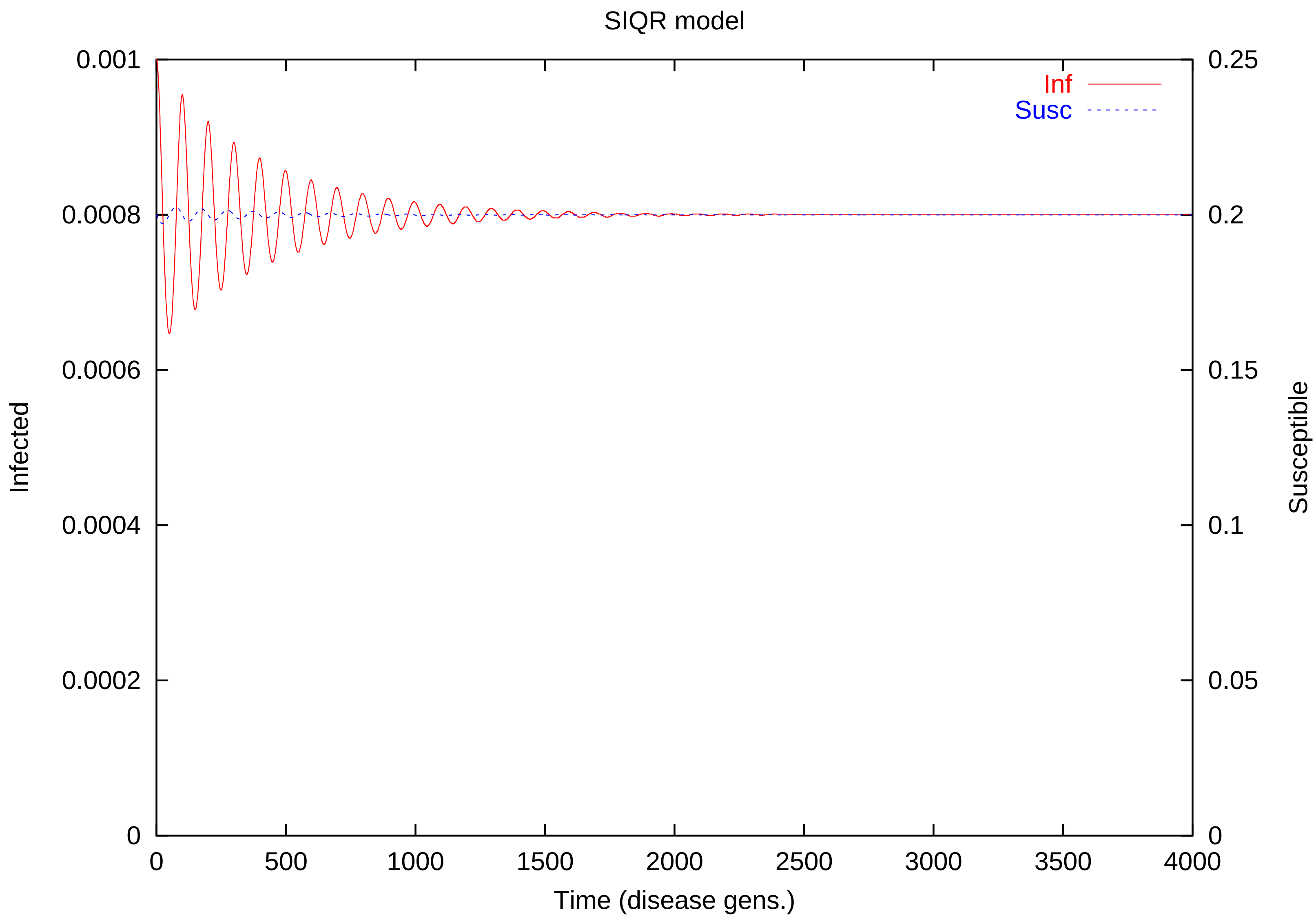
Quarantine measles model

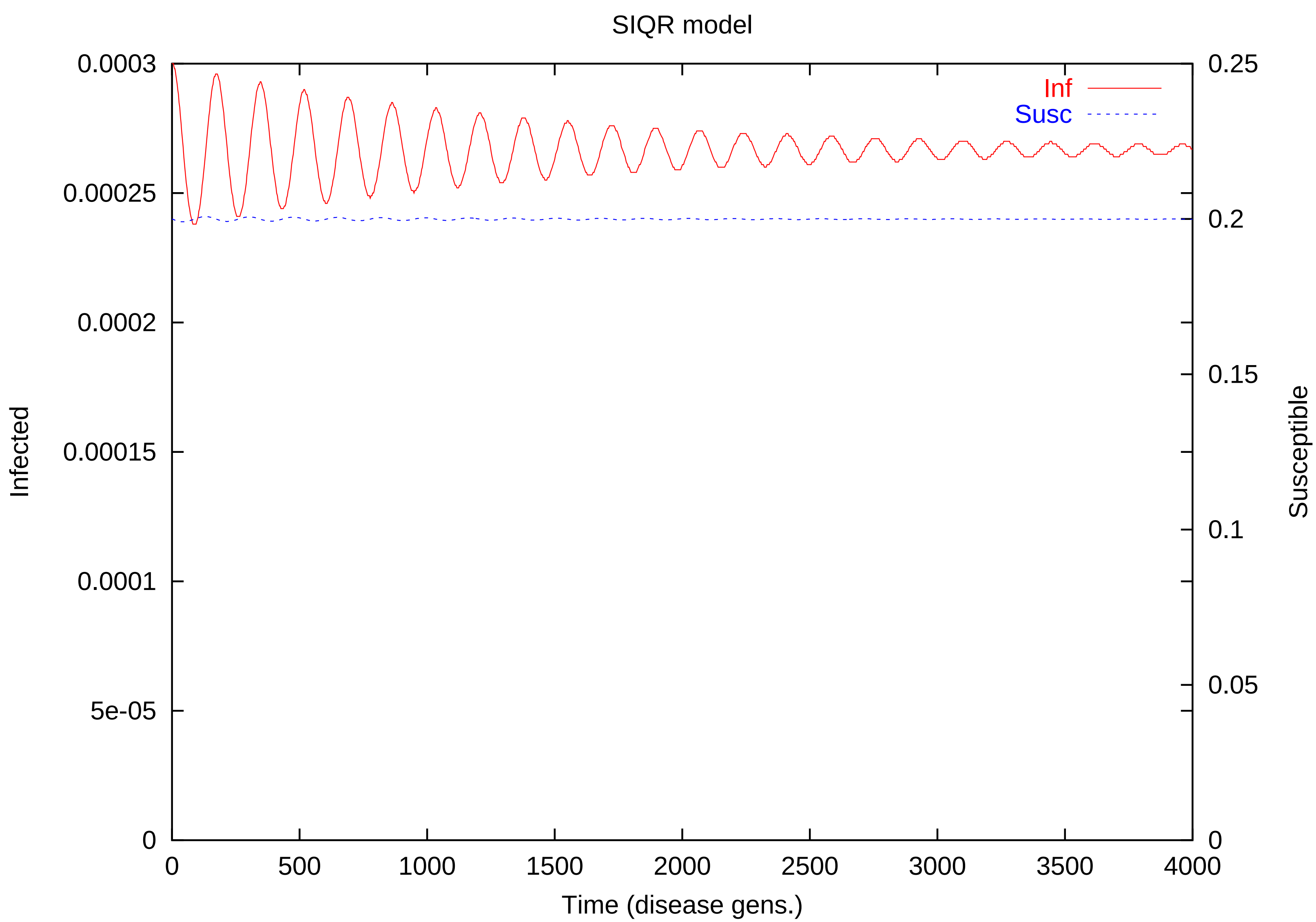
$$\begin{aligned}\dot{S} &= \mu(N - S) - \beta SI/N \\ \dot{I} &= \beta SI/N - \gamma I \\ \dot{Q} &= \gamma I - \phi Q\end{aligned}$$

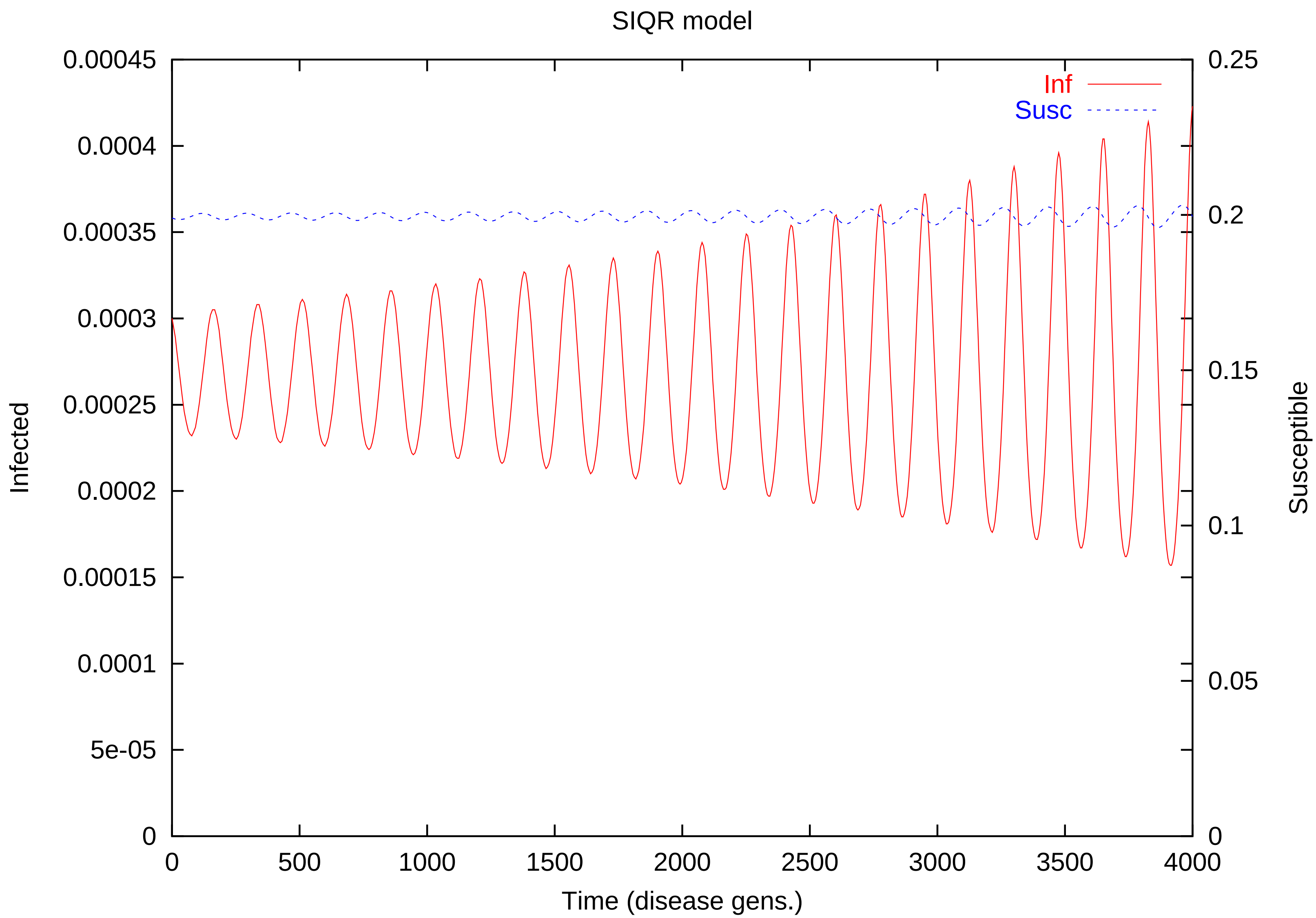
Trick: $N = S + I + R$, so that when children are quarantined, others compensate by mixing more with remaining ones.



SIQR model
Inf
Susc
Infected
Susceptible
Time (disease gens.)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0.05
0.15
0.25
2
4
6
8
10


SIQR model
Inf
Susc
0.001
0.0008
0.0006
0.0004
0.0002
0
Infected
0.25
0.2
0.15
0.1
0.05
0
Susceptible
0
500
1000
1500
2000
2500
3000
3500
4000
Time (disease gens.)


SIQR model
Inf
Susc
Infected
Susceptible
Time (disease gens.)
0.0003
0.00025
0.0002
0.00015
0.0001
5e-05
0
0.25
0.2
0.15
0.1
0.05
0
500
1000
1500
2000
2500
3000
3500
4000


SIQR model
Inf
Susc
Infected
Susceptible
Time (disease gens.)
0.00045
0.0004
0.00035
0.0003
0.00025
0.0002
0.00015
0.0001
5e-05
0
0.25
0.2
0.15
0.1
0.05
0
500
1000
1500
2000
2500
3000
3500
4000