Demography and Dynamics of Epidemiological Models

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What are compartmental epidemiological models?

- Well mixed, homogeneous population.
- Population is divided into compartments based on the status of the disease: susceptible, infected, infectious, recovered....
- The independent variable is time t.
- The rates of change of the size of each compartment are expressed as derivatives with respect to t of the sizes of the compartments.
- The processes of infection, recovery, etc., are deterministic.

The assumptions require large populations and then lead to systems of differential equations.

Warning.

Remember that all models are wrong; the practical question is how wrong do they have to be to not be useful.(Box and Draper)

Main concepts. Basic reproduction number

$$R_0$$

is the average number of secondary infections caused by one infectious individual in a completely susceptible population.

Basic aim of mathematical epidemiology is to determine the long term behaviour of solutions of the model and, in particular, the existence and stability of

- disease free equilibria (DFE) – equilibria of the population at which the infection ceases to persist, and
- endemic equilibria (EE) – equilibria of the population at which the disease persists.

In the model, R_0 is a combination of the parameters of the equation. Intuitively, when $R_0 < 1$, then DFE should be stable and loses the stability, when R_0 passes through $R_0 = 1$; then endemic equilibria may appear. For example,

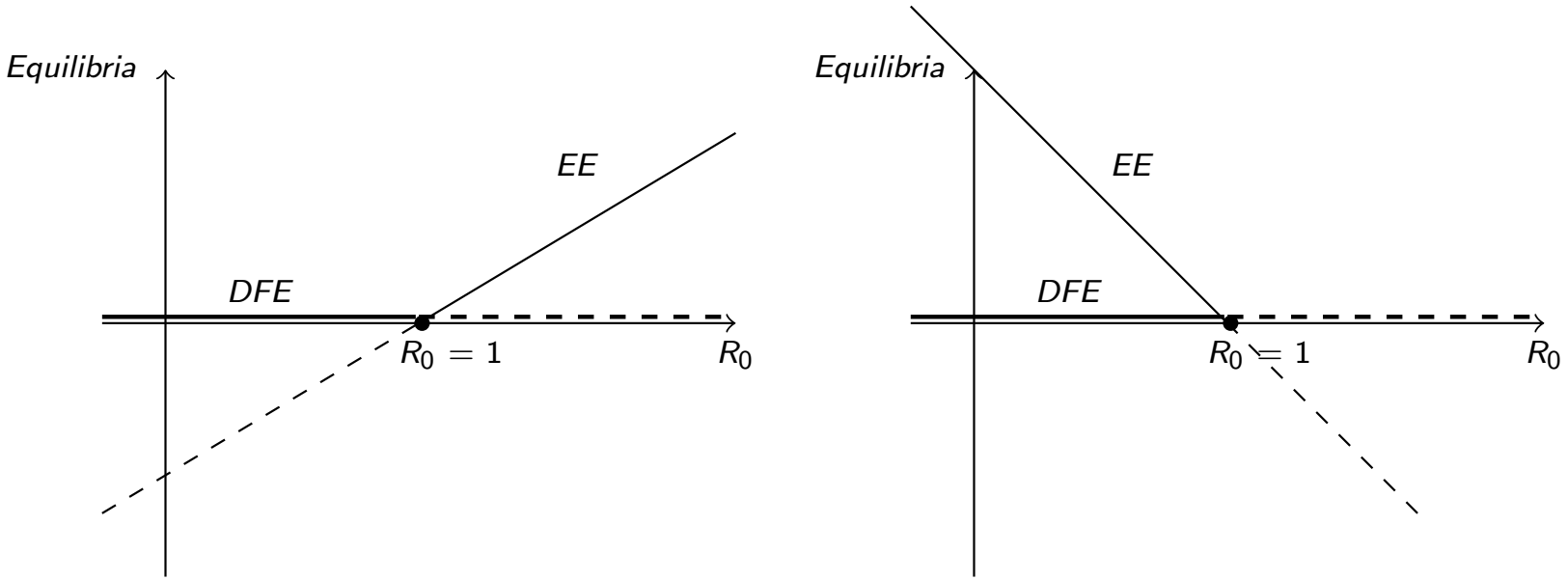

Figure: Bifurcation diagram and appearance of one stable endemic equilibrium. Forward bifurcation (left) and backward bifurcation (right).

Why and when do we need demography in epidemiological modelling?

- Diseases of duration comparable with life-span.
- Lethal diseases.
- Epidemics.
- Long-term impact of a disease on the affected population.

Basic Epidemiological Models

We begin with a simple model of a nonlethal disease in a homogeneous population divided into three classes: susceptible S, infective I and recovered R. Let us denote

$\lambda =$ the force of infection; that is, the rate at which susceptibles become infected,

$\mu =$ the death rate,

$\nu =$ the recovery rate,

$\gamma =$ the rate of immunity loss,

$B(N) =$ the total birth rate of the population.

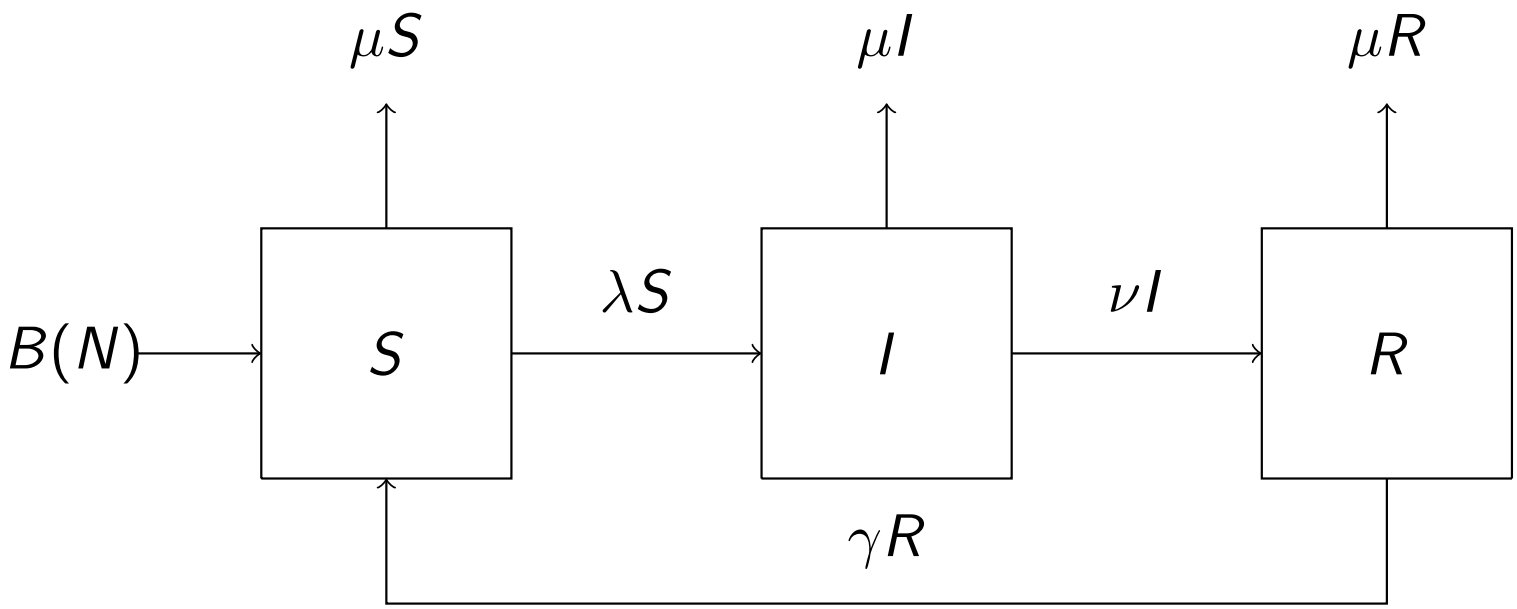

Figure: Compartments in the SIRS model with demography

On the basis of the above diagram, we build the following system of equations

$$\begin{aligned} S' &= B(N) - \lambda S + \gamma R - \mu S, \\ I' &= \lambda S - \nu I - \mu I, \\ R' &= \nu I - \gamma R - \mu R. \end{aligned} \tag{1}$$

S, I and R typically denote the number densities of, respectively, susceptibles, infectives and recovered, B is a function describing vital dynamics of the healthy population in a realistic way (here we tacitly assumed that there is no vertical transmission of the disease or permanent immunity).

Conservation laws in epidemiological modelling

If correctly written, (1) is a conservation law: adding up the equations, we see that the total population $N = S + I + R$ satisfies

$$N' = B(N) - \mu N,$$

the conservation of the population law. This is a reflection of the fact that any epidemiological model describes migrations between classes of a given population and thus the latter must satisfy the equations governing its evolution.

In contrast, recently popular fractional epidemiological models

$$\begin{aligned} D^\alpha S &= B(N) - \lambda S + \gamma R - \mu S, \\ D^\alpha I &= \lambda S - \nu I - \mu I, \\ D^\alpha R &= \nu I - \gamma R - \mu R. \end{aligned}$$

obtained simply by replacing the time derivative by its fractional counterpart, e.g., by the Caputo derivative

$${}^C D_t^\alpha f = \frac{1}{\Gamma(1-\alpha)} \int_0^t \frac{f'(\tau)}{(t-\tau)^\alpha} d\tau, \quad 0 < \alpha < 1,$$

do not make sense.

What is the meaning of

$$D^{\alpha}N = B(N) - \mu N?$$

There is a lack of physical consistency of the terms – on the RHS we have rates of change (per unit time), but the fractional derivative **is not** the rate of change.

This is not a conservation law.

So, what does the model describe?

How to model demographic processes

How not to model?

From D.J.D. Earn. A Light Introduction to Modelling Recurrent Epidemics, in: F. Brauer, P. van den Driessche & J. Wu (Eds.) Mathematical Epidemiology, Springer, 2008,

> *The timescale for substantial changes in birth rates (decades) is generally much longer than a measles epidemic (a few months), so well assume that the population size is constant (thus $B = \mu N$, so there is really only one new parameter in the above equations and we can take it to be B)*

Malthusian model. If births and death rates are constant then, denoting the net growth rate by r we obtain

$$N' = rN, \quad N(t_0) = N_0. \tag{2}$$

which has a general solution given by

$$N(t) = N_0 e^{r(t-t_0)}, \tag{3}$$

With the estimated Earth population in 1965 of 3.34 billion and the net growth rate of 2% per annum

$$N(t) = 3.34 \times 10^9 \times e^{0.02(t-1965)}. \tag{4}$$

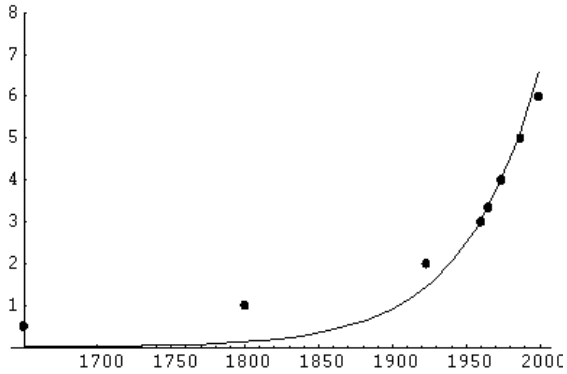

Figure: Comparison of actual population figures (points) with those obtained from equation (4).

There is a good agreement up to early 2000s. However, if we try to extrapolate this model to 2515, the population would reach approximately 200000 billion giving each of us area of $86.3\,\text{cm} \times 86.3\,\text{cm}$ to live on.

Nevertheless, the Malthusian model has its uses for short term prediction. It also provides a useful link about the death rate μ and the expected life span L of an individual.

$$L = \frac{1}{\mu}.$$

In the same way

- $1/\nu$ is the average duration of the disease,
- $1/\gamma$ is the average period of the acquired immunity.

Simplified logistic model and dangers of curve fitting. Consider

$$N' = B - \mu N. \tag{5}$$

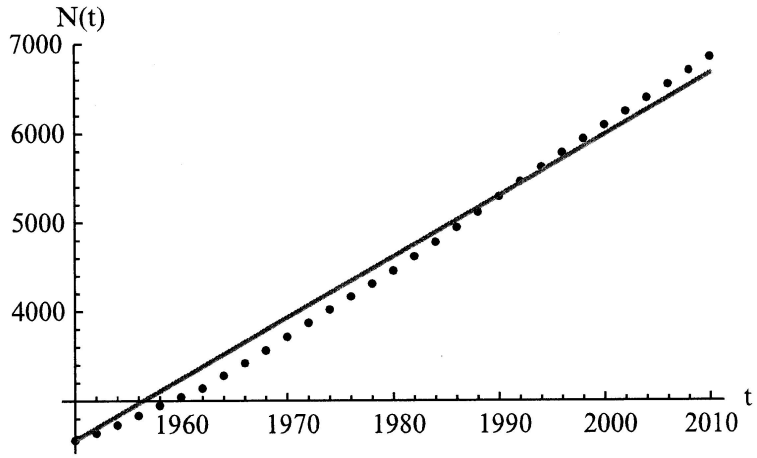

Figure: World population alongside the solution to (5) with $N(1950) = 2556.5 \times 10^6$ people. The least square error is 703 483.

However, the parameters are $B = 68.5 \times 10^6$ while $\mu = 5.54 \times 10^{-12}$.

This give the average lifespan of 1.8×10^{11} years – completely unrealistic.

Note, however, that the constant demographic terms can appear via the normalization. Consider (1) with a Malthusian growth rate

$$\begin{aligned} S' &= \alpha N - \beta S \frac{I}{N} + \gamma R - \mu S, \\ I' &= \beta S \frac{I}{N} - \nu I - \mu I, \\ R' &= \nu I - \gamma R - \mu R. \end{aligned} \tag{6}$$

and introduce $s = S/N, i = I/N, r = R/N$. Here we have

$$N' = (\alpha - \mu)N$$

$$s' = \frac{S'}{N} - \frac{S}{N^2}N' = \frac{S'}{N} - s(\alpha - \mu), \quad i' = \frac{I'}{N} - i(\alpha - \mu),$$
$$r' = \frac{R'}{N} - r(\alpha - \mu).$$

So

$$\begin{aligned} s' &= \alpha - \beta si + \gamma r - \alpha s, \\ i' &= \beta si - \nu i - \alpha i, \\ r' &= \nu i - \gamma r - \alpha r, \end{aligned} \tag{7}$$

and formally we have a system with constant total birth rate but the interpretation of terms is different. In particular

$$(s + i + r)' = \alpha - \alpha(s + i + r)$$

but $s + i + r = \frac{S}{N} + \frac{I}{N} + \frac{R}{N} = 1$, so both sides of the equation equal 0.

Logistic equation.

$$N' = rN\left(1 - \frac{N}{K}\right), \tag{8}$$

which proved to be one of the most successful models for describing a single species population. The non-equilibrium solution can be obtained by separation of variables:

$$N(t) = \frac{P(0)K}{N_0 + (K - N_0)e^{-rt}}. \tag{9}$$

This results in the famous *logistic* or *S-shaped* curve that describes saturation process.

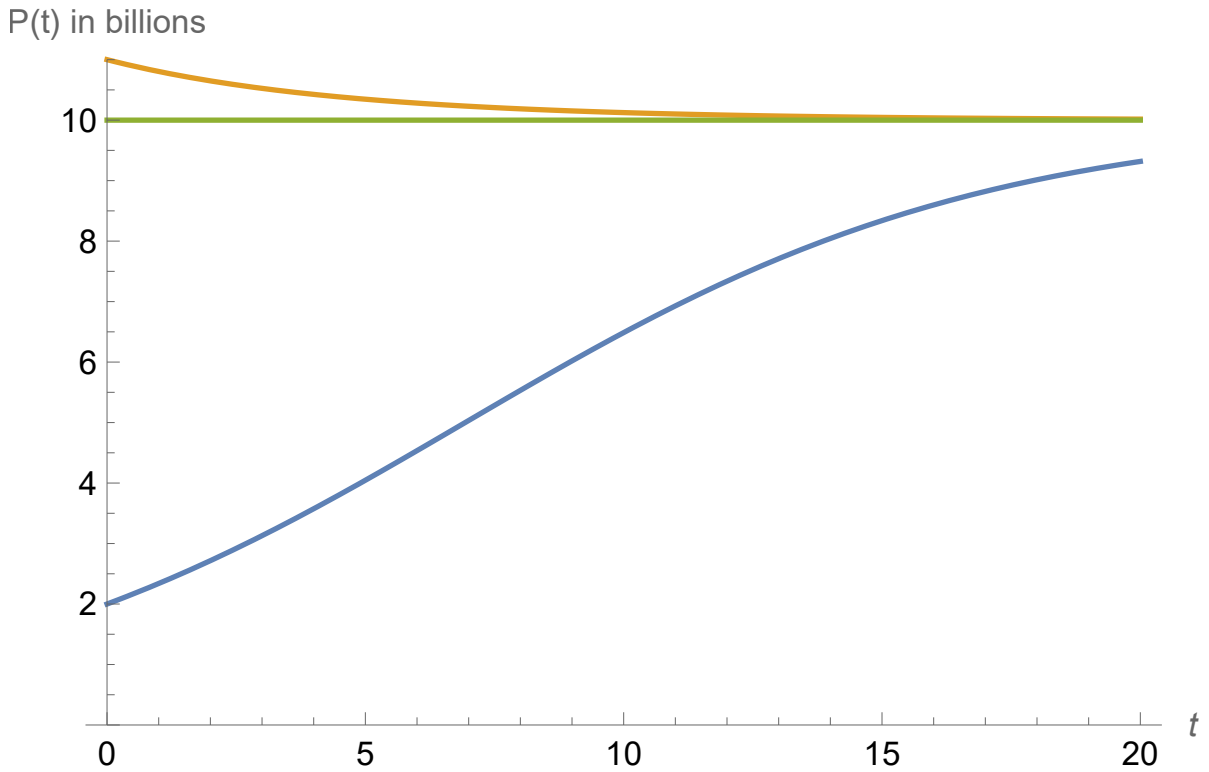

Figure: Logistic curves with $N_0 < K$ (blue line) and $N_0 > K$ (orange line) for $K = 10$ and $r = 0.02$.

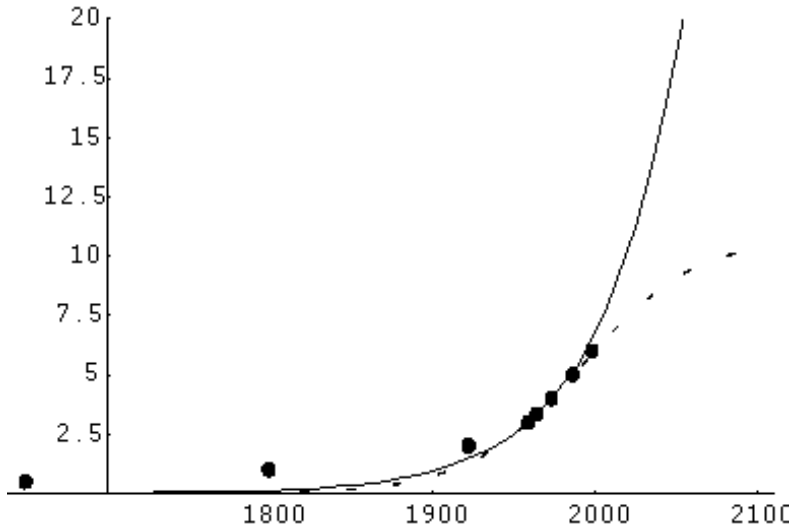

Figure: Human population on Earth with $K = 10.76$ billion and $r = 0.029$ and $N(1965) = 3.34$ billion. Observational data (points), exponential growth (solid line) and logistic growth (dashed line).

	Real	Predicted	Error	%
1790	3929000	3929000	0	0.0
1800	5308000	5336000	28000	0.5
1810	7240000	7228000	-12000	-0.2
1820	9638000	9757000	119000	1.2
1830	12866000	13109000	243000	1.9
1840	17069000	17506000	437000	2.6
1850	23192000	23192000	0	0.0
1860	31443000	30412000	-1031000	-3.3
1870	38558000	39372000	814000	2.1
1880	50156000	50177000	21000	0.0
1890	62948000	62769000	-179000	-0.3
1900	75995000	76870000	875000	1.2
1910	91972000	91972000	0	0.0
1920	105711000	107559000	1848000	1.7
1930	122775000	123124000	3498000	0.3
1940	131669000	136653000	4984000	3.8
1950	150697000	149053000	-1644000	-1.1

Table: Comparison of the actual and predicted by the logistic model population of the US.

Note, however, that the logistic model (8) can be interpreted in many ways that are relevant in epidemiological modelling. We can look at it as

$$N' = R(N)N, \tag{10}$$

which describes a population with the density dependent birth rate $R(N) = r\left(1 - \frac{N}{K}\right)$, or as

$$N' = rN - D(N)N, \tag{11}$$

where the population has a Malthusian birth rate but a density dependent death rate $D(N) = \frac{rN}{K}$.

Certainly, a combination of both is possible.

Malaria model with transmission blocking drugs

Variables	Description
S_h	susceptible humans
I_h	infectious humans
R_h	recovered humans
P_h	protected, i.e., successfully treated and noninfective humans
S_v	susceptible mosquitoes
I_v	infectious mosquitoes

Table: State variables and their description.

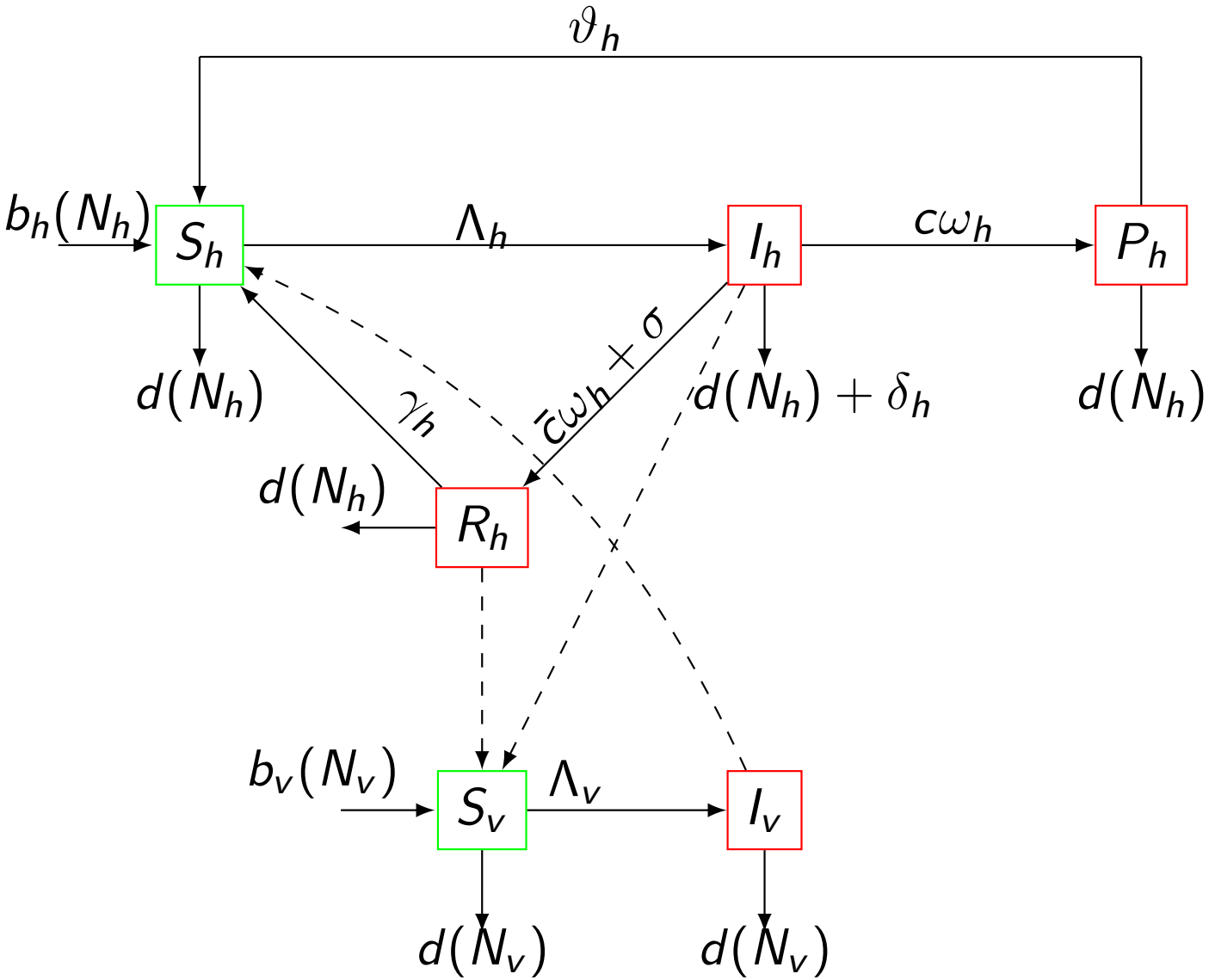

Figure: Flow diagram showing the malaria transmission dynamics.

$$
\begin{cases}
S_h' = b_h(N_h) + \gamma_h R_h + \vartheta_h P_h - \left(a\beta_{vh} \dfrac{I_v}{N_h} + d_h(N_h) \right) S_h, \\
I_h' = a\beta_{vh} \dfrac{I_v}{N_h} S_h - (\omega_h + \sigma + d_h(N_h) + \delta_h) I_h, \\
R_h' = ((1-c)\omega_h + \sigma) I_h - (\gamma_h + d_h(N_h)) R_h, \\
P_h' = c\omega_h I_h - (\vartheta_h + d_h(N_h)) P_h, \\
S_v' = b_v(N_v) - \left(a\beta_{hv} \dfrac{(I_h + \zeta_r R_h)}{N_h} + d_v(N_v) \right) S_v, \\
I_v' = a\beta_{hv} \dfrac{(I_h + \zeta_r R_h)}{N_h} S_v - d_v(N_v) I_v.
\end{cases}
\tag{12}
$$

with initial conditions $(S_h(0), I_h(0), R_h(0), P_h(0), S_v(0), I_v(0)) \gneqq 0$.

The time derivatives of the total human population $N_h(t)$ and mosquitoes $N_v(t)$ can be obtained by adding the first fourth, (respectively, the last two), equations, of system (12):

$$\begin{cases} N_h' = b_h(N_h) - d_h(N_h)N_h - \delta_h I_h, \\ N_v' = b_v(N_v) - d_v(N_v)N_v. \end{cases} \tag{13}$$

Therefore often we will find it advantageous to work with the following version of (12)

$$\begin{cases} N_h' = b_h(N_h) - d_h(N_h)N_h - \delta_h I_h, \\ I_h' = A_h \dfrac{I_v}{N_h}(N_h - I_h - R_h - P_h) - g_i(N_h)I_h, \\ R_h' = f_r I_h - g_r(N_h)R_h, \\ P_h' = c\omega_h I_h - g_p(N_h)P_h, \\ N_v' = b_v(N_v) - d_v(N_v)N_v, \\ I_v' = A_v \dfrac{(I_h + \zeta_r R_h)}{N_h}(N_v - I_v) - d_v(N_v)I_v. \end{cases} \tag{14}$$

We consider four demographic models for the human population

a) Malthusian growth,

$$b_h(N_h) = \pi_h N_h, \quad d_h(N_h) = \mu_{1h}.$$

b) Simplified logistic growth,

$$b_h(N_h) = \lambda_h, \quad d_h(N_h) = \mu_{1h}.$$

c) Logistic growth — density dependent birth rate,

$$b_h(N_h) = rN_h\left(1 - \frac{N_h}{K}\right), \quad d_h(N_h) = \mu_{1h}.$$

d) Logistic growth — density dependent death rate,

$$b_h(N_h) = \pi_h N_h, \quad d_h(N_h) = \mu_{1h} + \mu_{2h}N_h.$$

Disease free equilibrium points

Disease free equilibria (DFE) are positive equilibria of the form

$$\mathcal{E}^0 = \left(N_h^0, 0, 0, 0, N_v^0, 0\right)$$

where $\left(N_h^0, N_v^0\right)$ are positive equilibria of (13) with $I_h = 0$, that is,

$$\begin{cases} b_h(N_h) - d_h(N_h)N_h = 0 \\ b_v(N_v) - d_v(N_v)N_v = 0. \end{cases} \tag{15}$$

Under certain assumptions there is a unique DFE. However, this is not a rule.

Endemic equilibrium points

We solve for $EEP = (N_h^*, I_h^*, R_h^*, P_h^*, N_v^*, I_v^*)$ the following system:

$$\begin{cases} b_h(N_h) - d_h(N_h)N_h - \delta_h I_h = 0, \\ A_h \dfrac{I_v}{N_h} S_h - g_i(N_h) I_h = 0, \\ f_r I_h - g_r(N_h) R_h = 0, \\ c\omega_h I_h - g_p(N_h) P_h = 0, \\ A_v \dfrac{(I_h + \zeta_r R_h)}{N_h} S_v - d_v^0 I_v = 0. \end{cases}$$

where $S_h = N_h - I_h - R_h - P_h$ and $S_v = N_v - I_v = N_v^0 - I_v$, N_v^0 being the only nontrivial solution to $b_v(N_v^0) - d_v(N_v^0)N_v^0 = 0$.

Denoting $b_h^* = b_h(N_h^*), d_h^* = d_h(N_h^*), g_i^* = g_i(N_h^*), g_r^* = g_r(N_h^*)$ and $g_p^* = g_p(N_h^*)$. We obtain

$$R_h^* = \frac{f_r}{g_r^*} I_h^*,$$

$$P_h^* = \frac{c\omega_h}{g_p^*} I_h^*,$$

$$I_v^* = \frac{A_v \left(1 + \frac{\xi_r f_r}{g_r^*}\right) I_h^* N_v^0}{A_v \left(1 + \frac{\xi_r f_r}{g_r^*}\right) I_h^* + d_v^0 N_h^*}.$$

Returning to the equation for I_h^* and introducing the notation

$$\begin{aligned} G_r &= 1 + \frac{\xi_r f_r}{g_r} \\ F_r &= 1 + \frac{f_r}{g_r} + \frac{c\omega_h}{g_p}, \end{aligned} \tag{16}$$

with G_r^* and F_r^* obtained from (16) with $g_r = g_r^*$ and $g_p = g_p^*$, we obtain

$$I_h^* = \frac{g_i^* d_v^0 N_h^* \left(A_h A_v G_r^* N_v^0 - g_i^* d_v^0 N_h^*\right)}{A_v G_r^* \left(A_h F_r^* N_v^0 + g_i^* N_h^*\right)}. \tag{17}$$

Finally, we must find positive N_h^* satisfying

$$b_h(N_h^*) - d_h(N_h^*)N_h^* - \delta_h \frac{g_i^* d_v^0 N_h^* \left(A_h A_v G_r^* N_v^0 - g_i^* d_v^0 N_h^*\right)}{A_v G_r^* \left(A_h F_r^* N_v^0 + g_i^* N_h^*\right)} = 0. \tag{18}$$

Malthusian growth rate

1. Problems

1. Is there a DFE?

a) If $r_h = \pi_h - \mu_{1h} < 0$, then N_h, even without the disease, converges to zero, so DFE is (human) extinction equilibrium.

b) If $r_h = 0$, then the population equation is

$$N_h' = -\delta_h I_h$$

and thus DFE is given by

$$(N_h(0), 0, 0, 0, N_v^0, 0)$$

but this is a family of non-isolated equilibria – no linearization theorem available.

c) If $r_h > 0$, then there is no DFE – the disease free population grows exponentially.

What is R_0 here?

What can be done?

Lemma 1

The number of infectives I_h and hence the numbers of recovered R_h and protected P_h remain bounded independently of r_h and $N_h(0)$.

Proof. The second equation in (14) yields

$$I_h' \leq A_h I_{v,\max} - g_i I_h,$$

where we used the assumption on the vector's demography to claim that $\max_{t\geq 0} I_v(t) =: I_{v,\max} \leq \max_{t\geq 0} N_v(t) =: N_{v,\max} < \infty$, independent of r_h and $N_h(0)$, and the fact that $g_i(N_h) =: g_i$ is independent of N_h.

Hence

$$I_h(t) \leq e^{-g_i t} I_h(0) + \frac{A_h I_{v,\max}}{g^i}(1 - e^{-g_i t}) \leq \max\left\{ I_h(0), \frac{A_h N_{v,\max}}{g^i} \right\}. \tag{19}$$

Thus

$$\max_{t \geq 0} I_h(t) =: I_{h,\max} < \infty$$

for a constant $I_{h,\max}$ independent of r_h and $N_h(0)$ and the statement for I_h is proved.

The statement for R_h and P_h follows from (14), as the relevant equations are linear in the respective variables. □

Proposition 1

If $r_h = 0$, then $I_h(t) \to 0$ as $t \to \infty$ and, moreover,

$$\int_0^\infty I_h(s)ds \leq \frac{N_h(0)}{\delta_h}.$$

Proof. If we take $N = S_h + I_h + R_h + P_h$ as a Lyapunov function for (12), we obtain

$$N' = -\delta_h I_h.$$

Since, by Lemma 1, the trajectories are bounded, LaSalle's principle shows that all positive trajectories converge to the largest invariant set contained in $\{(S_h, I_h, R_h, P_h, S_v, I_v) \in \mathbb{R}^6_+ \ : \ I_h = 0\}$ and hence $I_h(t) \to 0$ as $t \to \infty$. □

Corollary 2

There is no globally stable equilibrium for (14) *if* $r_h > 0$.

Proof. Since $I_h(t) \leq I_{h,\max}$, $t \geq 0$, we have

$$N_h' = r_h N_h - \delta_h I_h \geq r_h N_h - \delta_h I_{h,\max}$$

and

$$N_h(t) \geq e^{r_h t}\left(N_h(0) - \frac{\delta_h I_{h,\max}}{r_h}\right) + \frac{\delta_h I_{h,\max}}{r_h}.$$

Hence, the population will tend to infinity if we take sufficiently large initial population $N_h(0)$. □

Proposition 2

If $\delta_h < r_h$, then $I_v(t) \to 0$ as $t \to \infty$.

Proof. Denoting $\eta = r_h - \delta_h$, we have

$$N_h \geq N_h(0)e^{\eta t}.$$

Consider the last equation in (14), written as

$$I_v' = A_v \frac{(I_h + \zeta_r R_h)}{N_h} N_v - \left(A_v \frac{(I_h + \zeta_r R_h)}{N_h} + \mu_v \right) I_v$$

Hence, using Lemma 1 and the boundedness of N_v, we have

$$I_v' \leq Ke^{-\eta t} - \mu_v I_v$$

for some constant K.

Hence, integrating as before,

$$I_v(t) \leq e^{-\mu_v t} I_v(0) + \frac{K}{\mu_v - \eta} \left(e^{-\eta t} - e^{-\mu_v t} \right)$$

with an obvious modification if $\eta = \mu_v$. □

Corollary 3

Under assumptions of Proposition 2, $I_h(t) \to 0$ as $t \to \infty$.

Proof. Writing the second equation of (14) as

$$I_h' \leq A_h I_v - g_i I_h,$$

we obtain

$$I_h(t) \leq e^{-g_i t} I_h(0) + \frac{e^{-g_i t}}{A_h} \int_0^t e^{g_i s} I_v(s) ds.$$

The thesis follows either by direct substitution or L'Hôspital's rule.

Potential endemic equilibria. If $\delta_h > r_h$, then the disease can result in a stabilization of the population as (18) yields

$$r_h N_h^* - \delta_h \frac{g_i d_v^0 N_h^* \left(A_h A_v G_r^* N_v^0 - g_i d_v^0 N_h^*\right)}{A_v G_r^* \left(A_h F_r^* N_v^0 + g_i N_h^*\right)} = 0, \qquad (20)$$

which, if $N_h^* > 0$, gives

$$N_h^* = \frac{A_h A_v G_r^* N_v^0 (\delta_h - r_h F_r^*)}{g_i (A_h G_r^* r_h + \delta_h d_v^0)}.$$

We see that $N_h^* > 0$ provided $\delta_h > r_h \left(1 + \frac{f_r}{g_r^*} + \frac{c\omega_h}{g_p^*}\right)$ so, in particular, δ_h must be bigger than r_h, which is consistent with Corollary 3.

- if $r_h = \pi_h - \mu_{1h} > \delta_h$, then there is no asymptotically stable equilibrium for the whole system (14) as the population is growing unboundedly, however, the numbers of infective hosts and vectors (and hence of recovered and protected humans) tend to zero;
- if $r_h = 0$ and $\delta_h > 0$, then the disease goes extinct but we do not know whether also the population vanishes or there are survivors;
- if $0 < r_h \ll \delta_h$, then there exists finite population in balance with the disease. It is not GAS, but is it at least locally stable?

A simplified example. Consider the following SIS model with balanced malthusian growth

$$\begin{cases} S' = \mu N + \gamma I - \beta \dfrac{SI}{N} - \mu S = (\mu + \gamma) I - \beta \dfrac{SI}{N}, \\ I' = \beta \dfrac{SI}{N} - (\gamma + \mu + \delta) I, \end{cases} \tag{21}$$

where $N = S + I$. Here, we have

$$N' = -\delta I.$$

As in Proposition 1, $\lim_{t \to \infty} I(t) = 0$. But, does the disease end because the population gets wiped out, or there are survivors?

The isoclines are

- $S' = 0$ if and only if $I = 0$ or

$$I(\mu + \gamma) - (\beta - \mu - \gamma)S = 0 \quad \Rightarrow \quad I = \left(\frac{\beta}{\mu + \gamma} - 1\right) S,$$

and

- $I' = 0$ if and only if $I = 0$ or

$$I(\mu+\gamma+\delta)-(\beta-\mu-\gamma-\delta)S = 0 \quad \Rightarrow \quad I = \left(\frac{\beta}{\mu + \gamma + \delta} - 1\right) S.$$

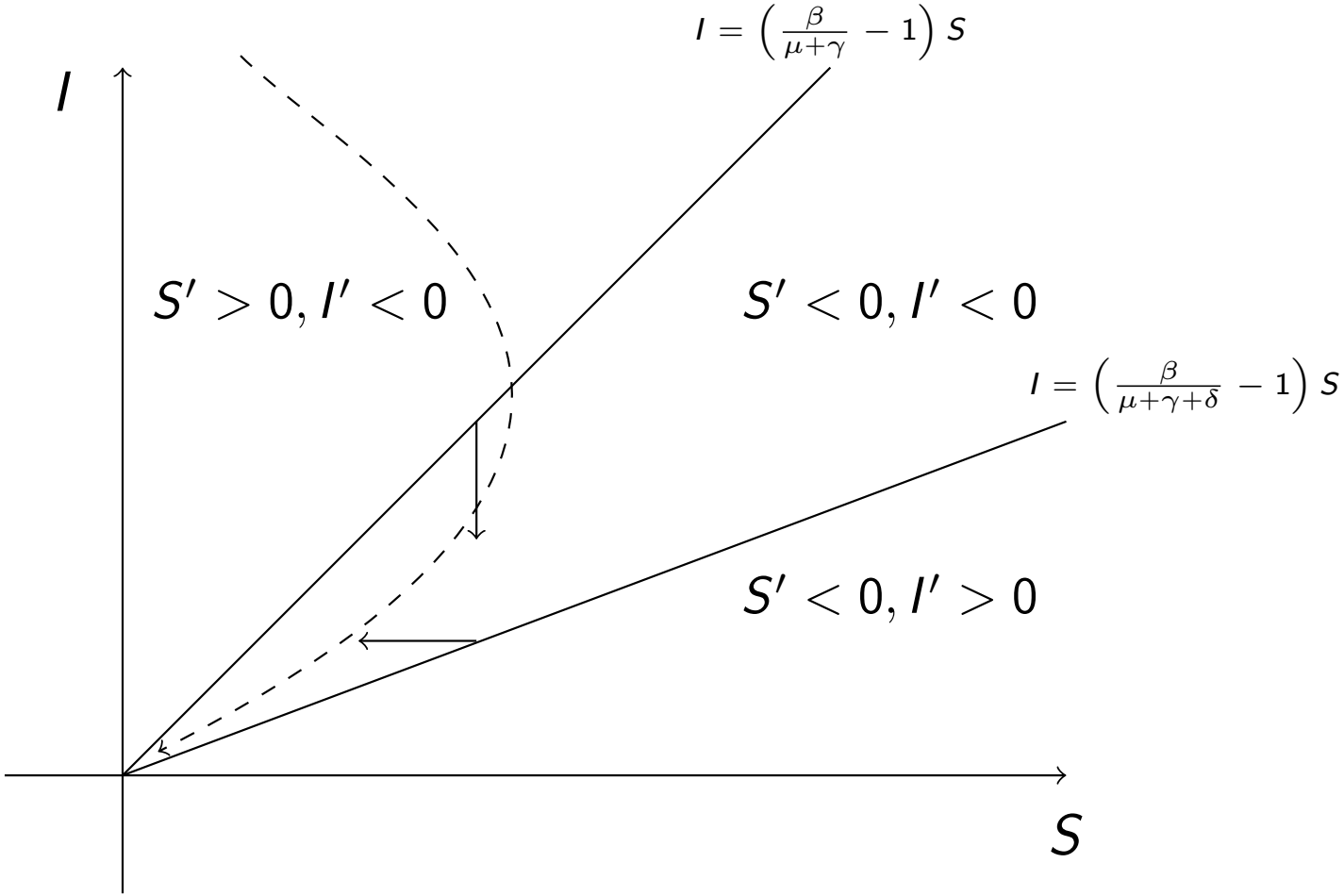

Figure: Isoclines of (21) with $\frac{\beta}{\mu+\gamma} > \frac{\beta}{\mu+\gamma+\delta} > 1$.

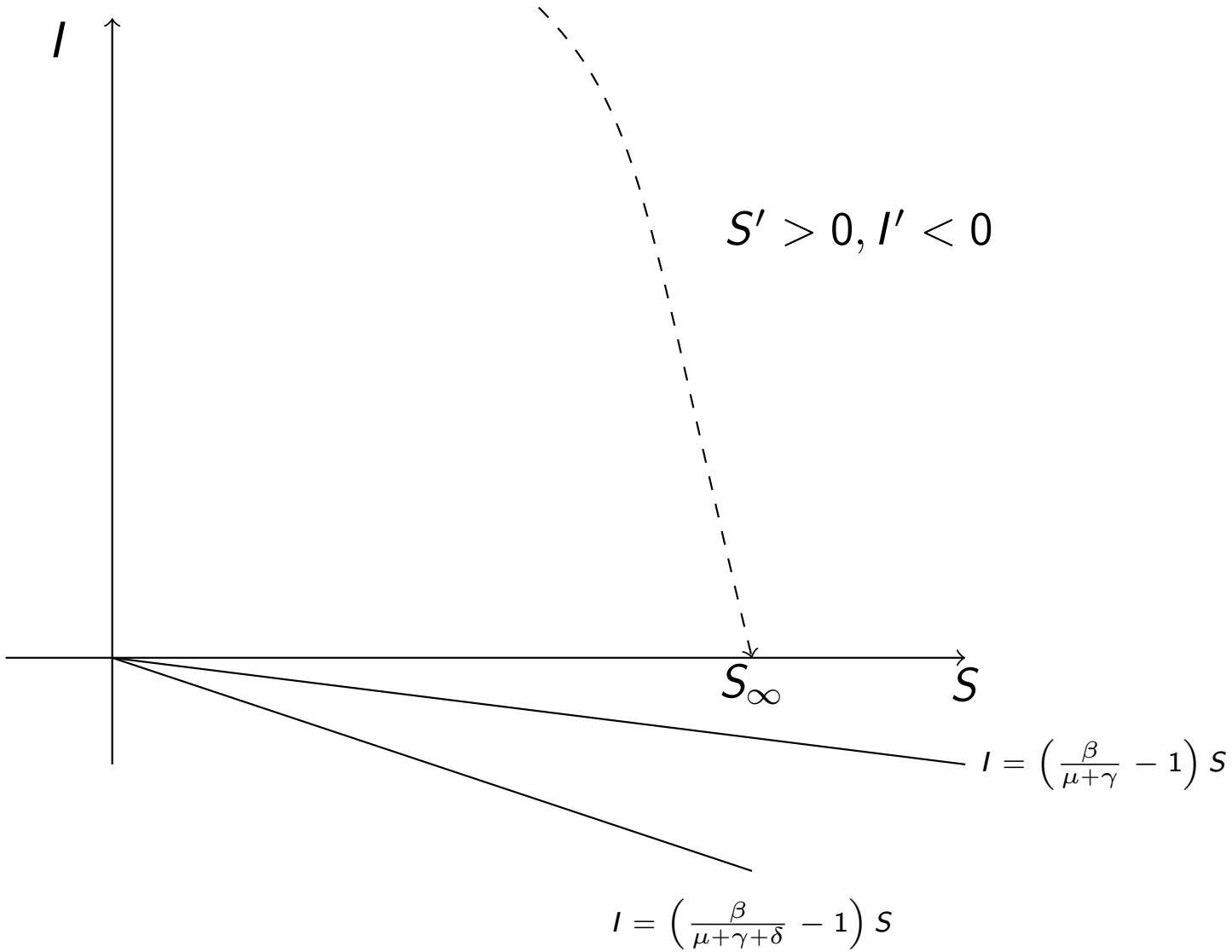

Figure: Isoclines of (21) with $\frac{\beta}{\mu+\gamma+\delta} < \frac{\beta}{\mu+\gamma} < 1$.

Demography with single isolated steady state. In cases b)–d), system (12) has a unique nontrivial DFE given by $\mathscr{E}^0 = \left(N_h^0, 0, 0, 0, N_v^0, 0\right)$, where N_h^0 and N_v^0 are the equilibria of the host's and vector's populations without the disease. Then, in each case, the basic reproduction number, R_0, evaluated at $\mathscr{E}^0$ is given by

$$R_0 = \sqrt{\frac{A_h A_v N_v^0 \left(g_r^0 + f_r \xi_r\right)}{N_h^0 d_v^0 g_i^0 g_r^0}} = \sqrt{\frac{A_h A_v N_v^0 G_r^0}{N_h^0 d_v^0 g_i^0}}, \qquad (22)$$

where, as before,

$g_i^0 = g_i(N_h^0), g_r^0 = g_r(N_h^0), g_p^0 = g_p(N_h^0), d_v^0 = d_v(N_v^0)$ and, similarly to (16), $G_r^0 = 1 + \frac{\xi_r f_r}{g_r^0}$.

Cases b) i c) — $d_h(N_h) = \mu_{1h}$. Here $g_i^* = g_i^0 =: g_i, g_r^* = g_r^0 =: g_r, g_p^* = g_p^0 =: g_p, G_r^* = G_r^0 =: G_r, F_r^* = F_r^0 =: F_r$ are independent of the population. Then (17) can be written as

$$I_h^* = \frac{N_h^* \left(A_h N_v^0 c_1 - g_i^0 d_v^0 N_h^*\right)}{c_0 + c_1 g_i^0 N_h^*}. \tag{23}$$

where

$$c_0 = A_h A_v N_v^0 G_r F_r = R_0^2 N_h^0 d_v^0 g_i F_r$$

$$c_1 = A_v F_r = R_0^2 \frac{N_h^0 d_v^0 g_i}{A_h N_v^0}.$$

Case b) — $b_h(N) = \lambda_h$. In this case, recognizing that $\lambda_h = N_h^0 \mu_{1h}$, (18) can be written as

$$\mu_{1h} N_h^0 - \mu_{1h} N_h^* - \delta_h \frac{N_h^* \left(A_h N_v^0 c_1 - g_i^0 d_v^0 N_h^* \right)}{c_0 + c_1 g_i^0 N_h^*} = 0. \tag{24}$$

Since we are interested in solutions N_h^* satisfying $0 < N_h^* \leq N_h^0$, it is convenient to make the substitution

$$N_h^* = \frac{N_h^0}{x+1} \Leftrightarrow x = \frac{N_h^0}{N_h^*} - 1,$$

as then the solution $x = 0$ will correspond to DFE and positive solutions will correspond to $N_h^* < N_h^0$.

Then (24) can be written as

$$\Phi(R_0, x) := x^2 + \alpha(\kappa - 1)x + \alpha(R_0^{-2} - 1) = 0,$$

where

$$\kappa = \frac{\mu_{1h}}{\delta_h}\left(F_r + \frac{N_h^0 g_i}{A_h N_v^0}\right),$$
$$\alpha = \frac{\delta_h}{\mu_h F_r}.$$

Importantly, we can see that there are free parameters in R_0^2, namely A_v, d_v^0 and ξ_r, which do not appear in the coefficients of the equation and thus we can change R_0^2 without altering the other coefficients.

Interlude—a simple version of Castillo-Chavez–Song theorem. As we have seen, in many cases the bifurcation question reduces to finding positive solution to the equation

$$\Phi(R_0, x) = 0$$

for R_0 in some neighbourhood of $R_0 = 1$, given that

$$\Phi(1, 0) = 0.$$

If such solutions occur for $R_0 > 1$, then we have a forward bifurcation, if for $R_0 < 1$, then we talk about a backward bifurcation.

We assume Φ is a differentiable function. The crucial assumption is that

$$\left.\frac{\partial \Phi}{\partial x}\right|_{R_0=1, x=0} \neq 0.$$

In particular, it ensures that the solution is isolated. Implicit Function Theorem gives the existence of a unique differentiable function $R_0 \mapsto x(R_0)$ in some neighbourhood of $R_0 = 1$ such that $x(1) = 0$ and

$$\Phi(R_0, x(R_0)) \equiv 0.$$

We differentiate this equation implicitly with respect to R_0,

$$\frac{\partial \Phi}{\partial R_0} + \frac{\partial \Phi}{\partial x}\frac{dx}{dR_0} \equiv 0,$$

hence

$$\frac{dx}{dR_0} = -\frac{\dfrac{\partial \Phi}{\partial R_0}}{\dfrac{\partial \Phi}{\partial x}}.$$

Since all functions above are continuous, their signs in some neighbourhood of $R_0 = 1$ and $x = 0$ are determined by that at $R_0 = 1, x = 0$. Therefore

- There is a backward bifurcation at $R_0 = 1$ if $\left.\frac{dx}{dR_0}\right|_{R_0=1} < 0$, that is,

$$\frac{\left.\frac{\partial \Phi}{\partial R_0}\right|_{R_0=1,x=0}}{\left.\frac{\partial \Phi}{\partial x}\right|_{R_0=1,x=0}} > 0.$$

- There is a forward bifurcation at R_0 if $\left.\frac{dx}{dR_0}\right|_{R_0=1} > 0$, that is,

$$\frac{\left.\frac{\partial \Phi}{\partial R_0}\right|_{R_0=1,x=0}}{\left.\frac{\partial \Phi}{\partial x}\right|_{R_0=1,x=0}} < 0.$$

See R.Ouifki, J.B., *Epidemiological models with quadratic equation for endemic equilibriaa bifurcation atlas*. Math. Methods Appl. Sci. 43 (2020), no. 18, 1041310429.

Returning to the model, we see that

- $\Phi(1,0) = 0$,
- $\left.\frac{\partial \Phi(R_0,x)}{\partial x}\right|_{R_0=1,x=0} = \alpha(\kappa - 1)$.

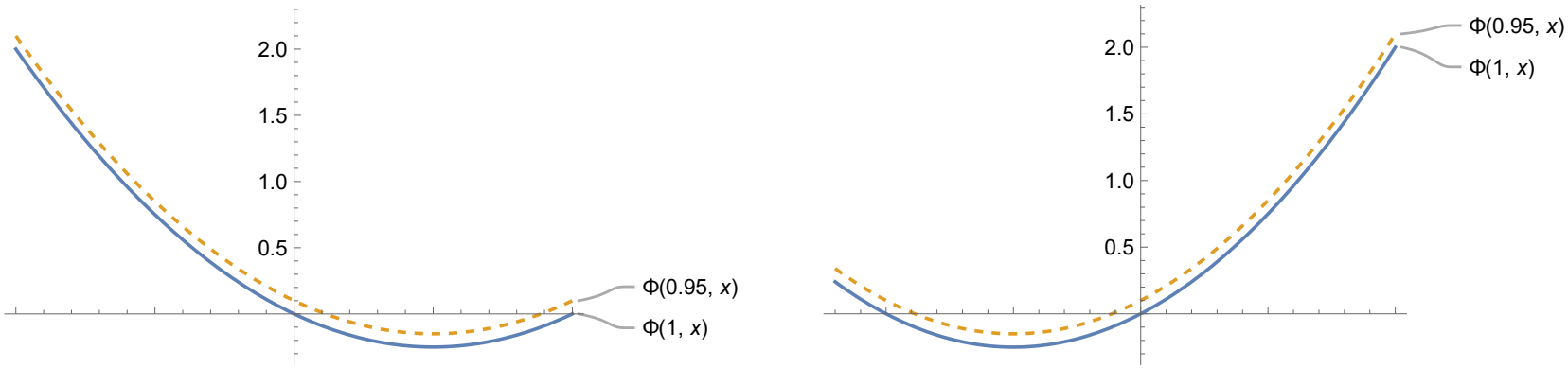

Figure: Graphs of $\Phi(1,x)$ with $\kappa < 1$ (left) and $\kappa > 1$ (right).

We see that a small decrease in R_0 from $R_0 = 1$ results in an emergence of another endemic equilibrium, and hence a backward bifurcation, if

$$\kappa = \frac{\mu_{1h}}{\delta_h}\left(1 + \frac{f_r}{g_r} + \frac{c\omega_h}{g_p} + \frac{N_h^0 g_i}{A_h N_v^0}\right) < 1.$$

In particular, there is no backward bifurcation if $\mu_{1h} > \delta_h$, that is, for small disease induced death rates.

Case c) — $b_h(N_h) = rN_h\left(1 - \frac{N_h}{K}\right)$. In this case, taking into account $N_h^* > 0$, we can write (18) as

$$(r - \mu_{1h}) - \frac{rN_h^*}{K} - \delta_h \frac{\left(A_h N_v^0 c_1 - g_i^0 d_v^0 N_h^*\right)}{c_0 + c_1 g_i^0 N_h^*} = 0, \qquad (25)$$

which we transform to

$$(N_h^*)^2 + N_h^*\left(\beta - N_h^0 - \frac{\alpha}{R_0^2}\right) + N_h^0(\alpha - \beta) = 0,$$

where, using $\eta := r - \mu_{1h} = \frac{rN_h^0}{K}$,

$$\alpha = \frac{\delta_h A_h N_v^0}{\eta g_i}$$

$$\beta = \frac{F_r A_h N_v^0}{g_i}.$$

As before, we make the substitution

$$N_h^* = \frac{N_h^0}{x+1} \Leftrightarrow x = \frac{N_h^0}{N_h^*} - 1$$

to obtain

$$\Psi(R_0, x) := x^2 + x\frac{\beta + N_h^0 + \alpha\left(\frac{1}{R_0^2} - 2\right)}{\beta - \alpha} + \frac{\alpha}{\beta - \alpha}\left(\frac{1}{R_0^2} - 1\right) = 0.$$

As before, the parameters A_v, d_v and ξ_r do not appear in R_0^2 and

- $\Psi(1, 0) = 0$,
- $\left.\frac{\partial \Psi(R_0,x)}{\partial x}\right|_{R_0=1,x=0} = 1 + \frac{N_h^0}{\beta-\alpha}$.

Now,

$$\beta - \alpha = \frac{A_h N_v^0}{g_i} \left(\frac{r - \mu_{1h} - \delta_h}{r - \mu_{1h}} + \frac{f_r}{g_r} + \frac{c\omega_h}{g_p} \right)$$

and we have three cases (we ignore $\beta - \alpha = 0$ or $1 + \frac{N_h^0}{\beta - \alpha} = 0$):

i) $\beta - \alpha > 0$ (and hence $1 + \frac{N_h^0}{\beta - \alpha} > 0$),

ii) $\beta - \alpha < 0$ but $1 + \frac{N_h^0}{\beta - \alpha} > 0$,

iii) $1 + \frac{N_h^0}{\beta - \alpha} < 0$ (and hence $\beta - \alpha < 0$).

Let us write

$$\Psi(R_0, x) = x^2 + b(R_0)x + c(R_0) = 0,$$

where

$$b(R_0) := \frac{\beta + N_h^0 + \alpha\left(\frac{1}{R_0^2} - 2\right)}{\beta - \alpha}$$

$$c(R_0) := \frac{\alpha}{\beta - \alpha}\left(\frac{1}{R_0^2} - 1\right).$$

In some neighbourhood of $R_0 = 1$, both b and c are decreasing functions of R_0 in case i) and increasing in case iii), whereas b is decreasing and c is increasing in case ii).

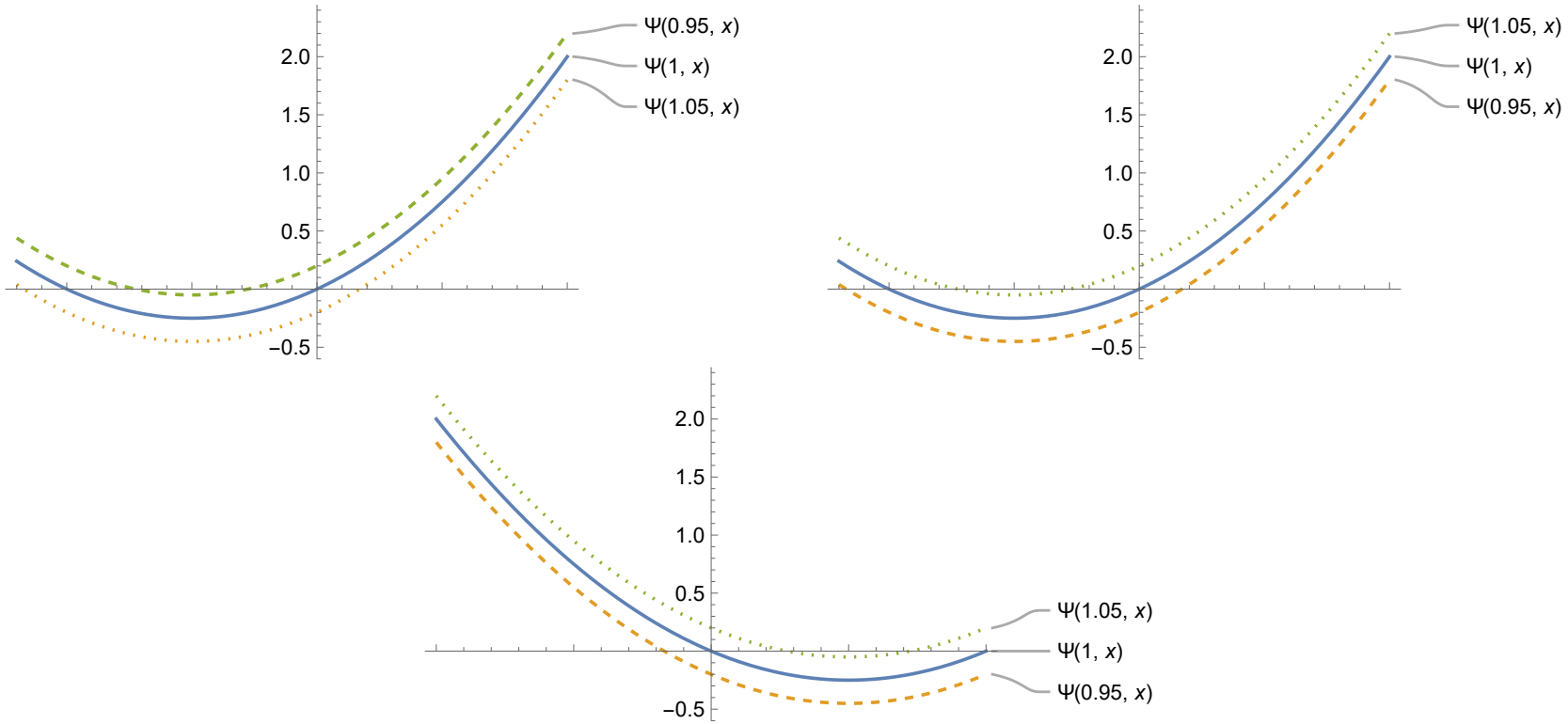

Figure: Graphs of case i) (upper left), ii) (upper right) and iii) (bottom)

We see that at $R_0 = 1$ there is a forward bifurcation in case i), a single backward bifurcation in case ii) and double forward/single backward bifurcation in case iii).

We observe that, assuming a logistic growth of the disease free population, that is, $r - \mu_{1h} > 0$, cases ii) and iii) would require a large δ_h to make $\beta - \alpha < 0$. Hence, typically, for small δ_h, we do not have backward bifurcation in this scenario, as in the previous one.

Bifurcation atlas

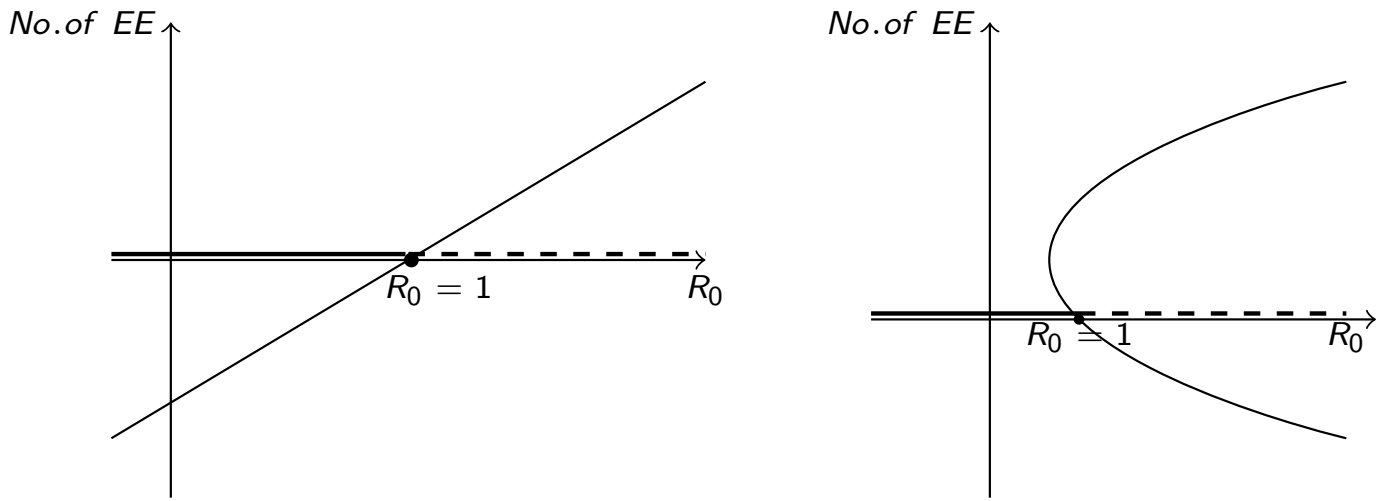

Figure: Structure of endemic equilibria in the case of simplified logistic growth. Forward bifurcation ($\kappa > 1$, left) and backward bifurcation ($\kappa < 1$, right).

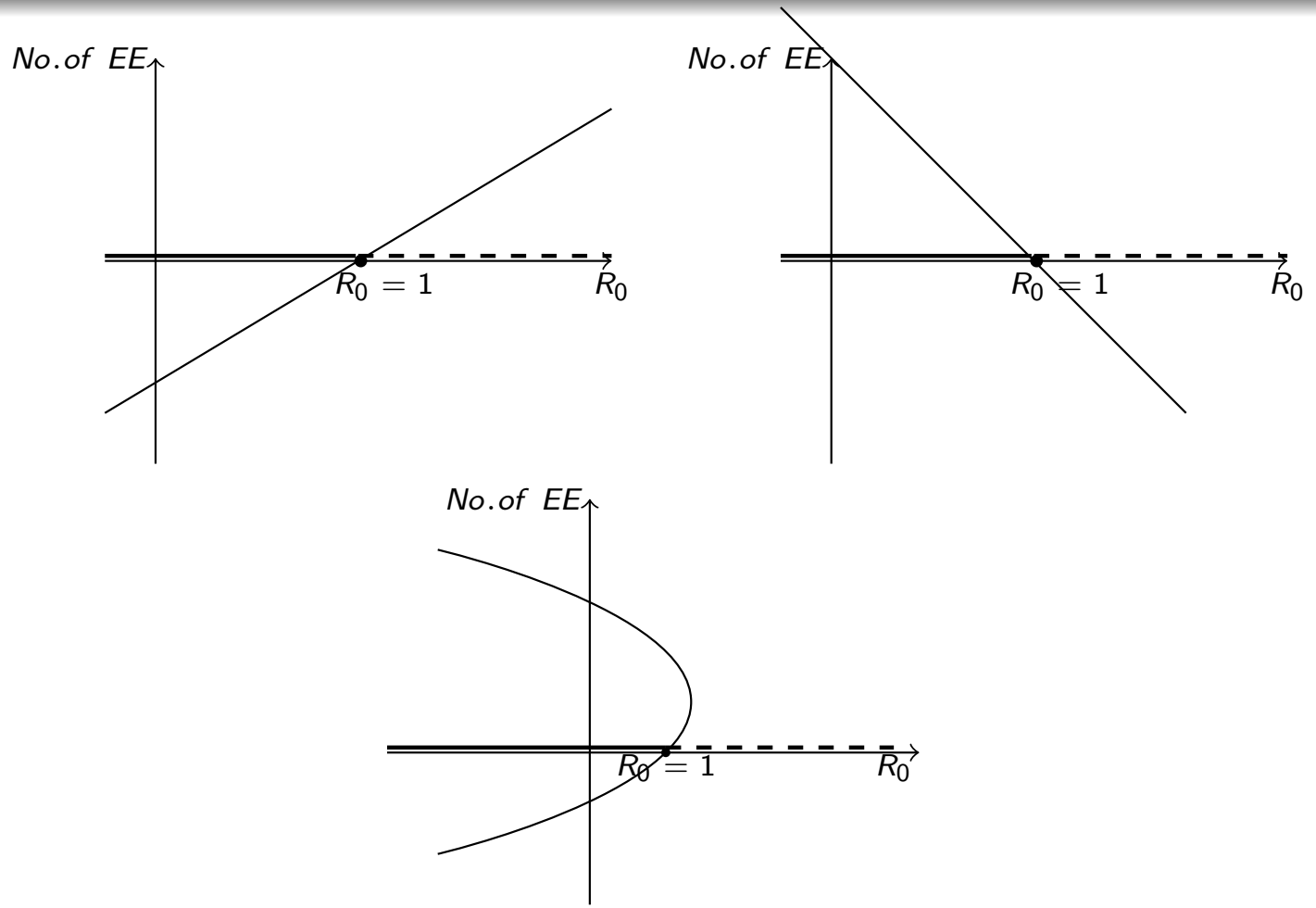

Figure: Structure of endemic equilibria in the case of logistic growth. Single forward bifurcation (case i), top left), single backward (case ii), top right), double forward (case iii), bottom).