Comparison of two mathematical models for the *Echinococcus multilocularis*-red foxes-rodents interactions

Comparación de dos modelos matemáticos para las interacciones de *Echinococcus multilocularis*-zorros rojos-roedores

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Abstract— The paper sets up two mathematical models for the *Echinococcus multilocularis*'s life cycle in the environment. Herbivores are the intermediate hosts, harboring its larval stage, while carnivores host the adults. From the wild this helminth can spill to domestic animals and thus it could be potentially harmful for humans. The models differ in the way disese transmission is modeled. Feasibility and stability of the systems' equilibria are assessed. No persistent oscillations can arise. The study of the transcritical bifurcations between the steady states provides maps that are useful for the applied ecologist for possible parasite eradication.

Keywords—Mathematical Models, Mathematical Ecology, Mathematical Epidemiology, Zoonosis, Echinococcosis

Resumen— El trabajo considera dos modelos matématicos para el ciclo de vita natural del *Echinococcus multilocularis*. Los herbivores representan los huespes intermediarios, contienen las larvas; los carnivores en vez hospitan la forma adulta. Los animales domésticos pueden assumir el parasita y en consequencia lo trasmitir a los hombres, lo que representa una menaça potential. Los modelos son differentes en quanto las transmissión del *E. multilocularis* tiene duas formulationes matématicas diferentes. La admissibilidad y la estabilidad de los equilibrios son calculadas. Las poblaciones no pueden oscillar persistentemente. Las bifurcationes transcriticas entre los equilibrios permeten a los ecologistas de determinar las maneras possibles de eliminar el helminto.

Palabras clave— Modelos Matemáticos, Ecología Matemática, Epidemiología Matemática, Zoonosis, Echinococcosis

Introduction

Echinococcus, a genus of Cestoda, is a parasitic tapeworm with a life cycle where carnivores are the definitive hosts and herbivores represent the intermediate ones. The latter harbor the larval form, while the definitive hosts harbor the adult form. Its eggs are present in contaminated food and water. Upon ingestion, the eggs proliferate in the guts and cause Echinococcosis, a zoonosis as the parasite can be transmitted from the wild to domestic animals and then to humans, for whom it is therefore potentially harmful Houston et al. (2021); Luong et al. (2018).

Echinococcus multilocularis thrives only in the northern hemisphere. It is endemic in central Europe, where its definitive host is the red fox, *Vulpes vulpes*.

The adult parasite is composed of a head and a few segments (proglottids), the last of which contains the eggs. When it is expelled into the environment, the microscopic eggs can survive for a long time even at low temperatures and especially in humid environments. The intermediate hosts get infested by ingestion of the eggs, that hatch in their stomach, with the embryos crossing the intestinal wall and reaching the liver and the lungs. The definitive host feeding on raw parasitized prey viscera gets in turn infected and develops the adult form. Thus *Echinococcus Multilocularis* has a cycle closely linked with the environment, difficult to eradicate. In natural forests the human interference is scant of absent indeed, and the main control tool is administering antibiotics to foxes. It is therefore important to understand the life cycle of this helminth in the wild, to find possibly other ways of controlling it.

In part extending the works Baudrot (2016); Baudrot et al. (2016a,b, 2018), we construct two mathematical models to study the *Echinococcus multilocularis* life cycle, in which the parasite is not explicitly built in the system. They differ only in the transmission mechanism, considering also the ideas expounded previously in Bulai and Venturino (2016).

THE MODELS

We now present two ecoepidemic models for the foxes-rodents interactions, affected by *Echinococcus multilocularis*. We must account for both animal species, but do not explicitly model the parasite. Thus the variables in consideration are the healthy foxes F, the infected, or rather carrier, foxes C, the susceptible rodents S and I, the infected rodents.

We will assume that there is no latency period in the parasites and epidemic spreading and that the transition rate from susceptibles to infected depends on the sizes of these populations. The disease transmission mechanism can be modeled in two alternative ways. First of all we can use the mass action law, good for low population densities, which produces the following equations:

$$\begin{aligned}
\frac{dF}{dt} &= r(F+C) - mF + e(k_2S + k_3I)C + ek_1FS \qquad (1)\\
&\quad -F(b_1F + b_2C) - \lambda FI - \alpha FC + \gamma_1 C,\\
\frac{dC}{dt} &= \lambda FI + \alpha FC - (m+\mu)C - C(c_1F + c_2C) - \gamma_1 C,\\
\frac{dS}{dt} &= s(S+I) - nS - S(g_1S + g_2I) - S(k_1F + k_2C)\\
&\quad -\theta SI - \beta SC + \gamma_2 I,\\
\frac{dI}{dt} &= \beta SC + \theta SI - I(n+\nu)\\
&\quad -I[(g_3S + g_4I) + (\lambda F + k_3C) + \gamma_2].
\end{aligned}$$

However, a more realistic approach is given by the standard incidence, in which the transmission rate is related to the proportion of infected in the whole population. This gives the alternative formulation

$$\begin{aligned}
\frac{dF}{dt} &= r(F+C) - mF + e(k_2S + k_3I)C + ek_1FS \qquad (2)\\
&\quad -F(b_1F + b_2C) - \lambda F\frac{I}{S+I} - \alpha F\frac{C}{F+C} + \gamma_1 C,\\
\frac{dC}{dt} &= \lambda F\frac{I}{S+I} + \alpha F\frac{C}{F+C} - (m+\mu)C\\
&\quad -C(c_1F + c_2C) - \gamma_1 C,\\
\frac{dS}{dt} &= s(S+I) - nS - S(g_1S + g_2I) - S(k_1F + k_2C)\\
&\quad -\theta S\frac{I}{S+I} - \beta S\frac{C}{F+C} + \gamma_2 I,\\
\frac{dI}{dt} &= \theta S\frac{I}{S+I} + \beta S\frac{C}{F+C} - (n+\nu)I\\
&\quad -I[(g_3S + g_4I) + (\lambda F + k_3C) + \gamma_2].
\end{aligned}$$

The first equation describes the dynamics of healthy red foxes. Both healthy and infected individuals grow with reproduction rate r due to food resources other than the rodents modeled in the system generating healthy offsprings. Thus, the parasite is not vertically transmitted. The second term contains the natural mortality rate m, then we find the infected foxes reproduction due to capture of healthy and infected rodents, at respective rates k_2 and k_3 and with conversion coefficient e. Next, the births from healthy foxes hunting of susceptible rodents at rate k_1, followed by the intraspecific competition among susceptible and infected foxes with respective rates b_1 and b_2. The new infections are accounted for in the following two terms, with rates λ and α depending on the fact that they come from the infected foxes capturing and being contaminated by an infected rodent, or by other infected foxes. Note that it is the way these two terms are formulated that distinguishes model (1) from (2). The last term denotes possible disease recovery by elimination of the parasites, at rate γ_1.

The second equation describes the dynamics of infected red foxes. They are recruited at rates λ and α from the susceptible ones, as described above, and experience natural as well as disease-induced mortality, the latter at rate μ. They further feel the intraspecific pressure due to healthy and infected individuals, at respective rates c_1 and c_2 and finally we allow them to possibly exit this class by recovery, migrating back into the susceptibles.

The third equation describes the healthy rodents dynamics. Newborns from both healthy and infected parents appear at rate s; here too vertical parasite transmission is not allowed. Natural mortality is experienced at rate n, and then the third and fourth terms contain the intra- (with rates g_1 and g_2) and interspecific (at rates k_1 and k_2) competition with both susceptible and infected individuals of both populations. The next two terms model disease transmission, at rates θ and β if respectively caused by rodents or foxes carriers. Finally the input due to recovered individuals at rate γ_2 is taken into consideration.

In the fourth equation infected rodents are recruited via parasite transmission from other infected rodents or diseased foxes. Then losses due to natural and infection-related mortality are accounted for, the latter at rate ν. Intraspecific competition models additional deaths, at respective rates g_3 and g_4 if caused by healthy or infected individuals. The damage due to foxes is then accounted for, at rate λ by susceptible ones and k_3 by carriers. Finally, individuals leave the infected class if they recover, at rate γ_2. Note that the possible administration of antibiotics can be modeled via the parameters γ_1 and γ_2.

Table 1 contains a biological interpretation of the parameters, which are all assumed to be nonnegative.

A preliminary result

We address now the boundedness of the systems solution trajectories. For both (1) and (2) define the total environmental population $A := F + C + S + I$, and add the model equations. For any $\eta > 0$, then

$$\begin{aligned}
\dot{A} + \eta A &= F(r - m + \eta) + C(r - m - \mu + \eta) \qquad (3)\\
&+S(s - n + \eta) + I(s - n - \nu + \eta) - b_1F^2 - c_2C^2 - g_1S^2\\
&-g_4I^2 - \lambda FI - FC(c_1 + b_2) - SI(g_2 + g_3)\\
&+k_1FS(e-1) + k_2CS(e-1) + k_3CI(e-1).
\end{aligned}$$

TABLE 1: SUMMARY AND INTERPRETATION OF THE PARAMETERS.

Rate	Biological interpretation
r	foxes birth on other resources
s	Rodents births
m	healthy foxes natural mortality
n	healthy rodents natural mortality
μ	foxes disease-related mortality
ν	rodents disease-related mortality
k_1	healthy foxes hunting on healthy rodents
k_2	infected foxes hunting on healthy rodents
k_3	infected foxes hunting on infected rodents
e	conversion factor of rodents into foxes
b_1	healthy foxes intraspecies competition
b_2	healthy foxes competition on infected ones
c_1	infected foxes competition on healthy ones
c_2	infected foxes intraspecies competition
g_1	healthy rodents intraspecies competition
g_2	healthy rodents competition on infected ones
g_3	infected rodents competition on healthy ones
g_4	infected rodents intraspecies competition
γ_1	infected foxes recovery
γ_2	infected rodents recovery
α	disease transmission among foxes
θ	disease transmission among rodents
λ	foxes infection by capture of infected rodents
β	healthy rodents infection by infected foxes

Then taking $e \leq 1$, observing that concave parabolae have a maximum, so that we obtain

$$F(r-m+\eta-b_1F) \leq \frac{(r-m+\eta)^2}{4b_1} = F_m,$$

$$C(r-m-\mu+\eta-c_2C) \leq \frac{(r-m-\mu+\eta)^2}{4c_2} = C_m,$$

$$S(s-n+\eta-g_1S) \leq \frac{(s-n+\eta)^2}{4g_1} = S_m,$$

$$I(s-n-\nu+\eta-g_4I) \leq \frac{(s-n-\nu+\eta)^2}{4g_4} = I_m$$

and dropping the negative terms we obtain the final estimate

$$\dot{A}+\eta A \leq F_m+C_m+S_m+I_m = D$$

from which

$$A(t) \leq \max\left\{\frac{D}{\eta}, A(0)\right\}.$$

From this, all the populations are bounded, giving a good biological ground of the models.

MASS LAW ACTION MODEL

Equilibrium points

System (1) allows the origin E_0 and the following points as equilibria:

$$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right), \quad E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right),$$

respectively feasible for

$$r \geq m \tag{4}$$

and

$$s \geq n. \tag{5}$$

Then we find the disease-free equilibrium

$$E_3 = \left(\frac{ek_1s+g_1r-ek_1n-g_1m}{b_1g_1+ek_1^2}, 0, \frac{b_1s+k_1m-b_1n-k_1r}{b_1g_1+ek_1^2}, 0\right)$$

with feasibility conditions

$$ek_1s+g_1r > ek_1n+g_1m, \quad b_1s+k_1m > b_1n+k_1r. \tag{6}$$

The next two points need a more detailed investigation, reported below: the rodents-free point $E_5 = (F_5, C_5, 0, 0)$ and the corresponding foxes-free point $E_6 = (0, 0, S_6, I_6)$. Coexistence $E_4 = (F_4, C_4, S_4, I_4)$ will instead be investigated numerically.

The rodents-free point E_5

The last two equilibrium equations of (1) are identically satisfied. From the first two we obtain the system

$$\begin{aligned} -b_1F^2 - FC(b_2+\alpha) + F(r-m) + C(r+\gamma_1) &= 0, \\ c_2C + F(c_1-\alpha) + (m+\gamma_1+\mu) &= 0, \end{aligned} \tag{7}$$

which in the (C,F) plane represents the intersection of a conic section Ω with a straight line ℓ with slope

$$\frac{c_2}{c_1-\alpha}. \tag{8}$$

Determining the line intersections with the axes, we find

$$L_1 = \left(0, \frac{m+\gamma_1+\mu}{\alpha-c_1}\right), \quad L_2 = \left(-\frac{m+\gamma_1+\mu}{c_2}, 0\right),$$

with $-(m+\gamma_1+\mu)c_2^{-1} < 0$, while $(m+\gamma_1+\mu)(\alpha-c_1)^{-1} > 0$ if and only if

$$\alpha > c_1. \tag{9}$$

In the opposite case no part of the line crosses the first quadrant, so that no feasible intersections can exist.

Assuming nondegeneracy for the conic, i.e.

$$\widetilde{\Delta} = \begin{vmatrix} -b_1 & -\frac{b_2+\alpha}{2} & \frac{r-m}{2} \\ -\frac{b_2+\alpha}{2} & 0 & \frac{r+\gamma_1}{2} \\ \frac{r-m}{2} & \frac{r+\gamma_1}{2} & 0 \end{vmatrix}$$

$$= -\frac{1}{4}(r+\gamma_1)[(b_2+\alpha)(r-m)-(r+\gamma_1)b_1] \neq 0$$

and calculating the invariant, Woods (1939)

$$\widetilde{\Gamma} = \begin{vmatrix} -b_1 & -\frac{b_2+\alpha}{2} \\ -\frac{b_2+\alpha}{2} & 0 \end{vmatrix} = -\frac{(b_2+\alpha)^2}{4} < 0$$

we find that the conic is a hyperbola. Its intersections with the axes are

$$O=(0,0), \quad P_1=\left(0,\frac{r-m}{b_1}\right).$$

To assess the slope of the hyperbola, we differentiate implicitly the conic, assuming $F=F(C)$ to get

$$r+\gamma_1-2b_1FF^{'}-(F^{'}C+F)(b_2+\alpha)+F^{'}(r-m)=0. \quad (10)$$

Evaluation at the intersections with the axes gives

$$F^{'}(O)=\frac{r+\gamma_1}{m-r}, \quad F^{'}(P_1)=\frac{r+\gamma_1}{r-m}-\frac{b_2+\alpha}{b_1}.$$

We now assess the asymptotes of Ω, recalling the asymptotes equation,

$$-b_1F^2-FC(b_2+\alpha)+F(r-m)+C(r+\gamma_1)-\frac{\widetilde{\Delta}}{\widetilde{\widetilde{\Gamma}}}=0. \quad (11)$$

Assume the form

$$F=\pi C+\sigma, \quad \pi,\sigma\in\mathbf{R} \quad (12)$$

with the coefficients to be determined. Substituting into (11), we find

$$-b_1(\pi C+\sigma)^2-(\pi C+\sigma)C(b_2+\alpha)+(\pi C+\sigma)(r-m)+C(r+\gamma_1)-\frac{\widetilde{\Delta}}{\widetilde{\widetilde{\Gamma}}}=0.$$

Dividing by C^2 and letting $C\to+\infty$, we obtain $\pi=0$, thus giving a horizontal asymptote or

$$\pi=-\frac{b_2+\alpha}{b_1}.$$

To assess the height of the horizontal asympotote, we substitute again (12), now with $\pi=0$, into (11), to get

$$-b_1\sigma^2-\sigma C(b_2+\alpha)+\sigma(r-m)+C(r+\gamma_1)-\frac{\widetilde{\Delta}}{\widetilde{\widetilde{\Gamma}}}=0,$$

from which dividing by C and again letting $C\to+\infty$, we obtain

$$\sigma=\frac{r+\gamma_1}{b_2+\alpha}>0.$$

Thus the horizontal asymptote lies above the C axis.

We can also determine the center of the hyperbola

$$C_{\text{center}}=\frac{r-m}{b_2+\alpha}-2b_1\frac{r+\gamma_1}{(b_2+\alpha)^2}, \qquad F_{\text{center}}=\frac{r+\gamma_1}{b_2+\alpha}.$$

Thus if

$$r<m, \quad (13)$$

the point P_1 lies on the negative F semiaxis, the slopes are $F^{'}(O)>0$ and $F^{'}(P_1)<0$, the center lies in the second quadrant and the hyperbola has a concave feasible branch emanating from the origin raising up to the horizontal asympotote of Ω. This is case (I).

If (4) holds instead, P_1 lies on the positive F semiaxis and $F^{'}(O)<0$. Thus

$$F^{'}(P_1)=\frac{r+\gamma_1}{r-m}-\frac{b_2+\alpha}{b_1}>0$$

if and only if the center lies in the second quadrant and

$$(r+\gamma_1)b_1>(b_2+\alpha)(r-m)>0, \quad (14)$$

giving Case (W), with a concave feasible branch emanating from P_1. In the opposite case, $F^{'}(P_1)<0$,

$$(r+\gamma_1)b_1<(b_2+\alpha)(r-m), \quad (15)$$

Case (Z), the center lies in the second quadrant and the hyperbola has a convex branch in the first one decreasing to the horizontal asymptote.

We now assess the possible intersections of the straight line ℓ with the hyperbola Ω.

In case (Z) the intersection is guaranteed if L_1 lies below P_1, namely for

$$b_1(m+\gamma_1+\mu)<(\alpha-c_1)(r-m). \quad (16)$$

Similarly, in case (W), the intersection feasibility requires in the latter case the same above condition (16), and no further additional conditions are necessary.

In case (I) the conditions (13) and (9) must be satisfied, but given that Ω has a concave branch emanating from the origin to approach the horizontal asympotote, the intersection with ℓ is either non-existent or a pair of points. This situation gives rise to a saddle-node bifurcation that is not investigated further here.

The foxes-free point E_6

As for the previous equilibrium, for $E_6=(0,0,S_6,I_6)$ we reduce the problem to studying the feasible intersections of a conic section Θ and a straight line $\widehat{\ell}$:

$$-g_1S^2-SI(g_2+\theta)+(s-n)S+(s+\gamma_2)I=0,$$
$$(\theta-g_3)S-g_4I-(n+\nu+\gamma_2)=0.$$

The situation parallels the one of the rodents-free point. Without stating the details, we have the following results. Θ is again a hyperbola, calculating the invariants

$$\widehat{\Delta}=\begin{vmatrix} -g_1 & -\frac{g_2+\theta}{2} & \frac{s-n}{2} \\ -\frac{g_2+\theta}{2} & 0 & \frac{s+\gamma_2}{2} \\ \frac{s-n}{2} & \frac{s+\gamma_2}{2} & 0 \end{vmatrix}$$
$$=-\frac{1}{4}(s+\gamma_2)[(g_2+\theta)(s-n)-(s+\gamma_2)g_2]\neq 0,$$

assuming nondegeneracy, and

$$\widehat{\Gamma}=\begin{vmatrix} -g_1 & -\frac{g_2+\theta}{2} \\ -\frac{g_2+\theta}{2} & 0 \end{vmatrix}=-\frac{(g_2+\theta)^2}{4}<0.$$

The straight line meets the first quadrant of the $I-S$ plane only if

$$\theta>g_3, \quad (17)$$

has slope

$$\frac{g_4}{g_3-\theta}>0 \tag{18}$$

and intercepts the axes at the points

$$\widehat{L}_1=\left(0,\frac{n+\gamma_2+\nu}{\theta-g_3}\right),\quad \widehat{L}_2=\left(-\frac{n+\gamma_2+\nu}{g_4},0\right).$$

The intersections of Θ with the axes are

$$O=(0,0),\quad Q_1=\left(0,\frac{s-n}{g_1}\right)$$

and the slopes at these points

$$S^{'}(O)=\frac{s+\gamma_2}{n-s},\quad S^{'}(Q_1)=\frac{s+\gamma_2}{s-n}-\frac{g_2+\theta}{g_1}.$$

This hyperbola has a horizontal asympotote

$$S=\frac{s+\gamma_2}{g_2+\theta}>0$$

while the other one has a negative slope

$$-\frac{g_2+\theta}{g_1}<0.$$

For

$$s<n, \tag{19}$$

Θ has a concave feasible branch emanating from the origin raising up to the horizontal asympotote. This is case (II).

Instead, for (5),

$$(s+\gamma_2)g_1<(g_2+\theta)(s-n), \tag{20}$$

giving Case (X), in which the convex feasible branch approaches the horizontal asymptote decreasing from the point Q_1. In the opposite situation the feasible branch is concave and raises up from Q_1 toward the horizontal asymptote, giving Case (Y), $S^{'}(Q_1)>0$,

$$(s+\gamma_2)g_1>(g_2+\theta)(s-n)>0. \tag{21}$$

In case (X) the feasible intersection is guaranteed if the following condition holds

$$g_1(n+\gamma_2+\nu)<(\theta-g_3)(s-n). \tag{22}$$

In case (Y) instead the intersection is guaranteed again by requiring (22). Instead we note also that if (22) is not satisfied, a pair of feasible points could arise through a saddle-node bifurcation, a situation that is not further explored here.

For Case (II) a possible saddle-node bifurcation could give rise to a pair of equilibria, but this case is not examined in detail.

Table 2 summarizes these results.

TABLE 2: EQUILIBRIA OF MODEL (1)

Equilibrium point	Feasibility condition
$E_0=(0,0,0,0)$	-
$E_1=\left(\frac{r-m}{b_1},0,0,0\right)$	(4)
$E_2=\left(0,0,\frac{s-n}{g_1},0\right)$	(5)
$E_3=(F_3,0,S_3,0)$	(6)
$E_5=(F_5,C_5,0,0)$	(I): (9), (13), saddle-node; (Z): (9), (4), (15), (16); (W): (9), (4), (14), (16);
$E_6=(0,0,S_6,I_6)$	(II): (17), (19), saddle-node; (Y): (17), (5), (21), (22); (X): (17), (5), (20), (22);
$E_4=(F_4,C_4,S_4,I_4)$	numerical

Equilibria stability

The Jacobian matrix $J_{i,j}$ of the system (1) has the entries

$$J_{1,1}=ek_1S-\alpha C-b_2C-2b_1F-\lambda I-m+r,\quad J_{2,3}=0,$$
$$J_{1,2}=r+e(k_2S+k_3I)-b_2F-\alpha F+\gamma_1,\quad J_{3,1}=-k_1S,$$
$$J_{1,3}=ek_2C+ek_1F,\quad J_{2,4}=\lambda F,\quad J_{2,1}=\alpha C-c_1C+\lambda I,$$
$$J_{4,1}=-\lambda I,\quad J_{2,2}=-2c_2C+\alpha F-c_1F-m-\mu-\gamma_1,$$
$$J_{3,2}=-\beta S-k_2S,\quad J_{3,4}=-g_2S-\theta S+s+\gamma_2,$$
$$J_{3,3}=-\beta C-k_2C-k_1F-2g_1S-g_2I-\theta I-n+s,$$
$$J_{1,4}=ek_3C-\lambda F,\quad J_{4,2}=\beta S-k_3I,\quad J_{4,3}=\beta C-g_3I+\theta I,$$
$$J_{4,4}=-k_3C-\lambda F-g_3S+\theta S-2g_4I-n-\nu-\gamma_2.$$

For $E_0=(0,0,0,0)$ the eigenvalues of the Jacobian are $r-m$, $-m-\mu-\gamma_1<0$, $s-n$, $-n-\nu-\gamma_2<0$ but from (4)-(5) this point is unconditionally unstable.

At $E_1=(F_1,0,0,0)$ the eigenvalues are $-b_1F_1=m-r<0$, $-m-\mu+(\alpha-c_1)F_1-\gamma_1$, $s-n-k_1F_1$, $-n-\nu-\lambda F_1-\gamma_2<0$, so that stability is ensured by

$$\frac{(\alpha-c_1)(r-m)}{b_1}<m+\mu+\gamma_1,\quad s+\frac{k_1(m-r)}{b_1}<n. \tag{23}$$

The eigenvalues at $E_2=(0,0,S_2,0)$ are once again explicitly evaluated, $-n-\nu+S_2(\theta-g_3)-\gamma_2$, $n-s$, $r-m+ek_1S_2$, $-m-\mu-\gamma_1$, providing, after semplification from (4)-(5) the stability conditions

$$\frac{(\theta-g_3)(s-n)}{g_1}<n+\nu+\gamma_2,\quad r+\frac{ek_1(s-n)}{g_1}<m. \tag{24}$$

At $E_5=(F_5,C_5,0,0)$ the Jacobian factorizes into two minors of order two, to both of which the Routh-Hurwitz conditions apply. But the trace of one of these minors is negative,

$$-b_1F_5-c_2C_5-\frac{C_5}{F_5}(r+\gamma_1)<0, \tag{25}$$

and from the remaining ones the stability conditions are found

$$\frac{c_2(r-m)+(\alpha-c_1)(r+\gamma_1)}{2b_1c_2F_5+(m+\gamma_1+\mu)(b_2+\alpha)}<1, \tag{26}$$
$$\frac{s}{2n+F_5(k_1+\lambda)+C_5(k_2+k_3+\beta)+\nu+\gamma_2}<1,$$
$$n+k_1F_5+C_5(k_2+\beta)-s>\frac{\beta C_5(s+\gamma_2)}{n+\nu+\lambda F_5+k_3C_5+\gamma_2}.$$

The Jacobian of $E_3 = (F_3, 0, S_3, 0)$ again factorizes into the product of two minors of order two, for the first one of which the Routh-Hurwitz conditions are always satisfied, namely $b_1F_3 + g_1S_3 > 0$, $b_1g_1F_3S_3 + ek_1^2F_3S_3 > 0$. From the remaining ones, stability is ensured by

$$\frac{F_3(\alpha - c_1 - \lambda) + S_3(\theta - g_3)}{m + \mu + \gamma_1 + \gamma_2 + n + \nu} < 1, \tag{27}$$
$$[m + \mu - F_3(\alpha - c_1) + \gamma_1][n + \nu + \lambda F_3 - S_3(\theta - g_3) + \gamma_2] > \beta\lambda F_3S_3.$$

Also at $E_6 = (0, 0, S_6, I_6)$ the Jacobian factorizes into the product of two minors of order two. The trace condition of one of them holds unconditionally,

$$-g_1S_6 - \frac{I_6}{S_6}(s + \gamma_2) - g_4I_6 < 0, \tag{28}$$

while the remaining Routh-Hurwitz conditions provide the stability inequalities

$$g_4(s - n) + (\theta - g_3)(s + \gamma_2) + (n + \gamma_2 + \nu)(g_2 + \theta) > 2g_1g_4S_6, \tag{29}$$
$$r + ek_1S_6 < \lambda I_6 + \mu + \gamma_1 + 2m,$$
$$(r - m + ek_1S_6 - \lambda I_6)(-m - \mu - \gamma_1) > \lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1).$$

Table 3 summarizes the stability conditions of the equilibria of the system (1).

TABLE 3: EQUILIBRIA STABILITY CONDITIONS OF (1)

Equilibrium	Stability conditions
$E_0 = (0, 0, 0, 0)$	unstable
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(23)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(24)
$E_3 = (F_3, 0, S_3, 0)$	(27)
$E_5 = (F_5, C_5, 0, 0)$	(26)
$E_6 = (0, 0, S_6, I_6)$	(29)
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

Equilibria verification

The previous equilibria analysis is here supported by numerical results showing that the various sets of feasibility and stability conditions are indeed not empty. In the simulations we have used values for the biological parameters borrowed from the literature Caudera et al. (2021, 2020); Viale et al. (2021), for an analogous foxes-rodents ecosystem:

$$b_1 = \log(3) - \tfrac{2}{7}, \quad e = 0{,}91, \quad g_1 = \tfrac{1}{100}\log(4{,}5) - \tfrac{4}{500},$$
$$g_2 = \tfrac{1}{100}\log(4{,}5) - \tfrac{4}{500} + 1, \quad g_4 = \tfrac{1}{100}\log(4{,}5) - \tfrac{4}{500},$$
$$k_1 = 0{,}5, \quad k_3 = 0{,}5, \quad m = \tfrac{2}{7}, \quad n = \tfrac{4}{5},$$
$$r = \log(3), \quad s = \log(4{,}5). \tag{30}$$

The remaining parameter values are hypothetical. The initial conditions are always taken as follows:

$$F(0) = 1, \quad C(0) = 0, \quad S(0) = 8, \quad I(0) = 1 \tag{31}$$

Now E_0 is attained with (30) and $m = 5$, $n = 3$, $b_2 = 0{,}1$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}15$, $\alpha = 0{,}47$, $\beta = 0{,}83$, $\gamma_1 = 0{,}23$, $\gamma_2 = 0{,}12$, $\theta = 0{,}55$, $\lambda = 0{,}67$, $\mu = 2$, $\nu = 5$.

For E_1 we need, in addition to (30), $m = 10$, $n = 3$, $r = 12$, $b_2 = 0{,}1$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}15$, $\alpha = 0{,}47$, $\beta = 0{,}83$, $\gamma_1 = 0{,}23$, $\gamma_2 = 0{,}12$, $\theta = 0{,}55$, $\lambda = 0{,}67$, $\mu = 2$, $\nu = 5$.

E_2 is obtained with the choice $m = 16$, $s = 1$, $b_2 = 0{,}2$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 6{,}91$, $\beta = 0{,}2$, $\gamma_1 = 0$, $\gamma_2 = 3$, $\theta = 0{,}2$, $\lambda = 15$, $\mu = 5$, $\nu = 5$.

For E_3 we choose $n = 0{,}01$, $s = 8$, $b_2 = 3$, $c_1 = 0{,}88$, $c_2 = 0{,}214$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 0{,}05$, $\beta = 0{,}2$, $\gamma_1 = 0{,}1$, $\gamma_2 = 3$, $\theta = 0{,}2$, $\lambda = 0{,}2$, $\mu = 0{,}22$, $\nu = 5$.

E_5 is found for $b_2 = 0{,}2$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 4$, $\beta = 0{,}2$, $\gamma_1 = 0{,}1$, $\gamma_2 = 3$, $\theta = 0{,}2$, $\lambda = 15$, $\mu = 0{,}22$, $\nu = 5$.

The parameters to attain E_6 are instead $g_2 = 0{,}2$, $g_3 = 0{,}22$, $\theta = 2$, $\gamma_2 = 0{,}1$, $\nu = 0{,}22$, $n = \frac{2}{7}$, $s = \log(3)$, $g_4 = 0{,}21$, $c_1 = 0{,}11$, $\gamma_1 = 3$, $\alpha = 0{,}2$, $\mu = 5$, $r = \log(4{,}5)$, $k_2 = 0{,}1$, $\beta = 0{,}2$, $\lambda = 15$, $e = 0{,}91$, $k_1 = 0{,}5$, $k_3 = 0{,}5$ and

$$g_1 = \log(3) - \frac{2}{7}, \quad b_1 = \frac{1}{100}\log(4{,}5) - \frac{4}{500}, \quad m = \frac{4}{5}$$
$$b_2 = \frac{1}{100}\log(4{,}5) - \frac{4}{500} + 1, \quad c_2 = \frac{1}{100}\log(4{,}5) - \frac{4}{500}.$$

The coexistence equilibrium is shown in Figure 1 together with the parameter values needed to achieve it.

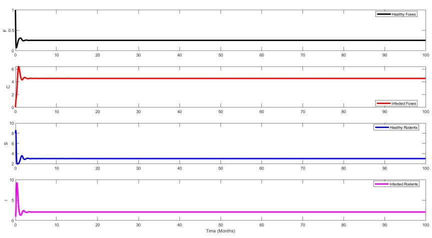

Figure 1: Coexistence equilibrium E_4 is attained for the values $s = 5$, $b_2 = 3$, $c_1 = 0{,}88$, $c_2 = 0{,}21$, $g_3 = 0{,}01$, $k_2 = 0{,}1$, $\alpha = 0{,}05$, $\beta = 0{,}2$, $\gamma_1 = 0{,}1$, $\gamma_2 = 0{,}2$, $\theta = 2$, $\lambda = 15$, $\mu = 0{,}22$, $\nu = 0{,}2$.

BIFURCATIONS

We study the bifurcations using Sotomayor's theorem, Perko (2013), applied to (1) written in shorthand as $\dot{\mathbf{x}} = \mathbf{F}(\mathbf{x})$. To this end, we need to know $D^2\mathbf{F}$ and $D^3\mathbf{F}$. To evaluate $D^2\mathbf{F}$ are necessary:

$$F^1_{F,F} = -2b_1 \quad F^1_{F,C} = -\alpha - b_2 \quad F^1_{F,S} = ek_1 \quad F^1_{F,I} = -\lambda$$
$$F^1_{C,S} = ek_2 \quad F^1_{C,I} = ek_3 \quad F^2_{F,C} = \alpha - c_1 \quad F^2_{F,I} = \lambda$$
$$F^2_{C,C} = -2c_2 \quad F^3_{F,S} = -k_1 \quad F^3_{C,S} = -\beta - k_2 \quad F^3_{S,S} = -2g_1$$
$$F^3_{S,I} = -g_2 - \theta \quad F^4_{F,I} = -\lambda \quad F^4_{C,S} = \beta \quad F^4_{C,I} = -k_3$$
$$F^4_{S,I} = -g_3 + \theta \quad F^4_{I,I} = -2g_4,$$

while all other possible combinations $F^n_{A,B}$, $A, B \in \{F, C, S, I\}$, $n \in 1, 2, 3, 4$ vanish. Hence

$$D^2\mathbf{F}^1 = \begin{pmatrix} -2b_1 & -\alpha - b_2 & ek_1 & -\lambda \\ -\alpha - b_2 & 0 & ek_2 & ek_3 \\ ek_1 & ek_2 & 0 & 0 \\ -\lambda & ek_3 & 0 & 0 \end{pmatrix}$$

$$D^2\mathbf{F}^2 = \begin{pmatrix} 0 & \alpha - c_1 & 0 & \lambda \\ \alpha - c_1 & -2c_2 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \lambda & 0 & 0 & 0 \end{pmatrix}$$

$$D^2\mathbf{F}^3 = \begin{pmatrix} 0 & 0 & -k_1 & 0 \\ 0 & 0 & -\beta - k_2 & 0 \\ -k_1 & -\beta - k_2 & -2g_1 & -g_2 - \theta \\ 0 & 0 & -g_2 - \theta & 0 \end{pmatrix}$$

$$D^2\mathbf{F}^4 = \begin{pmatrix} 0 & 0 & 0 & -\lambda \\ 0 & 0 & \beta & -k_3 \\ 0 & \beta & 0 & -g_3 + \theta \\ -\lambda & -k_3 & -g_3 + \theta & -2g_4 \end{pmatrix}$$

It is also easily found that $D^3\mathbf{F}$ is identically zero. Thus condition $\mathbf{w}^T[D^3\mathbf{F}(\mathbf{x_0}, \mu_0)(\mathbf{v},\mathbf{v},\mathbf{v})] \neq 0$ cannot be satisfied and system (1) never experiences a pitchfork bifurcation.

Bifurcations at E_0

For E_0 the Jacobian has four explicit eigenvalues, $\Lambda_1 = r - m$, $\Lambda_2 = -m - \mu - \gamma_1$, $\Lambda_3 = s - n$, $\Lambda_4 = -n - \nu - \gamma_2$.

Eigenvalue Λ_1

Take as bifurcation parameter m and let $\tilde{m} := r$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} + \mu + \gamma_1, \tilde{m} + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_0,\tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T}\mathbf{F}_m(E_0,\tilde{m}) = 0$, implying $D\mathbf{F}_m(E_0,\tilde{m})\mathbf{v} = (-1,0,0,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_0,\tilde{m})\mathbf{v}] = -(\tilde{m} + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0,\tilde{m})(\mathbf{v},\mathbf{v})] = -2b_1(\tilde{m} + \mu + \gamma_1) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_0 and E_1.

Eigenvalue Λ_3

Take as bifurcation parameter n and let $\tilde{n} := s$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0,0,1,0)^T$, $\mathbf{w} = (0,0,\tilde{n} + \nu + \gamma_2, \tilde{n} + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_0,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T}\mathbf{F}_n(E_0,\tilde{n}) = 0$, implying $D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v} = (0,0,-1,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_0,\tilde{n})\mathbf{v}] = -(\tilde{n} + \nu + \gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0,\tilde{n})(\mathbf{v},\mathbf{v})] = -2g_1(\tilde{n} + \nu + \gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_0 and E_2.

Bifurcations at E_1

For E_1 the Jacobian has four explicit eigenvalues, $\Lambda_1 = m - r$, $\Lambda_2 = -m - \mu + (\alpha - c_1)F_1 - \gamma_1$, $\Lambda_3 = s - n - k_1F_1$, $\Lambda_4 = -n - \nu - \lambda F_1 - \gamma_2$.

Eigenvalue Λ_2

Take as bifurcation parameter m and let

$$\tilde{m} := \frac{(\alpha - c_1)r - b_1(\mu + \gamma_1)}{b_1 - c_1 + \alpha},$$

feasible for $(\alpha - c_1)r > b_1(\mu + \gamma_1)$ with $\alpha > c_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (r - F_1(b_2 + \alpha) + \gamma_1, b_1F_1, 0, 0)^T$, $\mathbf{w} = (0, n + \nu + \lambda F_1 + \gamma_2, 0, \lambda F_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1,\tilde{m}) = (-F_1,0,0,0)$, for which $\mathbf{w^T}\mathbf{F}_m(E_1,\tilde{m}) = 0$, implying $D\mathbf{F}_m(E_1,\tilde{m})\mathbf{v} = (-r + F_1(b_2 + \alpha) - \gamma_1, -b_1F_1, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_1,\tilde{m})\mathbf{v}] = -b_1F_1(n + \nu + \lambda F_1 + \gamma_2) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_1,\tilde{m})(\mathbf{v},\mathbf{v})] = (n + \nu + \lambda F_1 + \gamma_2)2b_1F_1((\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) - c_2b_1F_1)$. Now if $(\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) \neq c_2b_1F_1$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_5.

Eigenvalue Λ_2

Taking instead as bifurcation parameter μ and let $\tilde{\mu} := -m - \gamma_1 + F_1(\alpha - c_1)$, feasible for $F_1(\alpha - c_1) > m + \gamma_1$ with $\alpha > c_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (r - F_1(b_2 + \alpha) + \gamma_1, b_1F_1, 0, 0)^T$, $\mathbf{w} = (0, n + \nu + \lambda F_1 + \gamma_2, 0, \lambda F_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_1,\tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w^T}\mathbf{F}_\mu(E_1,\tilde{\mu}) = 0$, implying $D\mathbf{F}_\mu(E_1,\tilde{\mu})\mathbf{v} = (0, -b_1F_1, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\mu(E_1,\tilde{\mu})\mathbf{v}] = -b_1F_1(n + \nu + \lambda F_1 + \gamma_2) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_1,\tilde{\mu})(\mathbf{v},\mathbf{v})] = (n + \nu + \lambda F_1 + \gamma_2)2b_1F_1((\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) - c_2b_1F_1)$. Now if $(\alpha - c_1)(r - F_1(b_2 + \alpha) + \gamma_1) \neq c_2b_1F_1$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_1 and E_5.

Eigenvalue Λ_3

Take as bifurcation parameter n and let $\tilde{n} := s - k_1F_1$, feasible for $s > k_1F_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_1, 0, b_1F_1, 0)^T$, $\mathbf{w} = (0, 0, s - F_1(k_1 - \lambda) + \nu + \gamma_2, s + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_1,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T}\mathbf{F}_n(E_1,\tilde{n}) = 0$, implying $D\mathbf{F}_n(E_1,\tilde{n})\mathbf{v} = (0,0,-b_1F_1,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_1,\tilde{n})\mathbf{v}] = -b_1F_1(s - F_1(k_1 - \lambda) + \nu + \gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1,\tilde{n})(\mathbf{v},\mathbf{v})] = -2b_1F_1^2(ek_1^2 + b_1g_1)(s - F_1(k_1 - \lambda) + \nu + \gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_1 and E_3.

Bifurcations at E_2

For E_2 the Jacobian has four explicit eigenvalues, $\Lambda_1 = n - s$, $\Lambda_2 = -n - \nu + S_2(\theta - g_3) - \gamma_2$, $\Lambda_3 = r - m + ek_1S_2$, $\Lambda_4 = -m - \mu - \gamma_1$.

Eigenvalue Λ_2

Take as bifurcation parameter n and let

$$\tilde{n} := \frac{(\theta - g_3)s - g_1(\gamma_2 + \nu)}{g_1 - g_3 + \theta}),$$

feasible for $(\theta - g_3)s > g_1(\gamma_2 + \nu)$ with $\theta > g_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - S_2(g_2 + \theta) + \gamma_2, g_1S_2)^T$, $\mathbf{w} = (0, \beta S_2, 0, m + \mu + \gamma_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2,\tilde{n}) = (0,0,-S_2,0)$, for which $\mathbf{w^T}\mathbf{F}_n(E_2,\tilde{n}) = 0$, implying $D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v} = (0,0,S_2(g_2 + \theta) - s - \gamma_2, -g_1S_2)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_2,\tilde{n})\mathbf{v}] = -g_1S_2(m + \mu + \gamma_1) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_2,\tilde{n})(\mathbf{v},\mathbf{v})] = 2g_1S_2(m + \mu + \gamma_1)((\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) - g_1g_4S_2)$. Now if $(\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) \neq g_1g_4S_2$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_6.

Eigenvalue Λ_2

Take as bifurcation parameter ν and let $\tilde{\nu} := -n + S_2(\theta - g_3) - \gamma_2$, feasible for $S_2(\theta - g_3) > n + \gamma_2$ with $\theta > g_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - S_2(g_2 + \theta) + \gamma_2, g_1 S_2)^T$, $\mathbf{w} = (0, \beta S_2, 0, m + \mu + \gamma_1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_2, \tilde{\nu}) = \mathbf{0}$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_\nu(E_2, \tilde{\nu}) = 0$, implying $D\mathbf{F}_\nu(E_2, \tilde{\nu})\mathbf{v} = (0, 0, 0, -g_1 S_2)^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_\nu(E_2, \tilde{\nu})\mathbf{v}] = -g_1 S_2(m + \mu + \gamma_1) \neq 0$. Further, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{\nu})(\mathbf{v}, \mathbf{v})] = 2g_1 S_2(m + \mu + \gamma_1)((\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) - g_1 g_4 S_2)$. Now if $(\theta - g_3)(s - S_2(g_2 + \theta) + \gamma_2) \neq g_1 g_4 S_2$ a transcritical bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$, between E_2 and E_6.

Eigenvalue Λ_3

Take as bifurcation parameter m and let $\tilde{m} := r + ek_1 S_2$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (g_1 S_2, 0, -k_1 S_2, 0)^T$, $\mathbf{w} = (r + ek_1 S_2 + \mu + \gamma_1, r + ek_2 S_2 + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_2, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_m(E_2, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v} = (-g_1 S_2, 0, 0, 0)^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v}] = -g_1 S_2(r + ek_1 S_2 + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2g_1 S_2^2(r + ek_1 S_2 + \mu + \gamma_1)(b_1 g_1 + ek_1^2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_2 and E_3.

Bifurcations at E_3

At E_3 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = \frac{1}{2}\Big[\pm\sqrt{b_1^2 F_3^2 + g_1^2 S_3^2 - 2b_1 g_1 F_3 S_3 - 4ek_1^2 F_3 S_3} - b_1 F_3 - g_1 S_3\Big],$$

$$\Lambda_{B_{1,2}} = \frac{1}{2}\Big[-F_3(c_1 - \alpha + \lambda) - S_3(g_3 - \theta) \pm \sqrt{\Delta} - m - n - \gamma_1 - \gamma_2 - \mu - \nu\Big],$$

where

$$\Delta = [\gamma_1 + \gamma_2 + \mu + \nu + F_3(c_1 - \alpha + \lambda) + S_3(g_3 - \theta)]^2 + m + n - 4\{[-m - \mu + F_3(\alpha - c_1) - \gamma_1][-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2] - \beta\lambda F_3 S_3\}$$

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter m and getting $\tilde{m}$ from $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) - \beta\lambda F_3 S_3 = 0$, feasible for $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) < \beta\lambda F_3 S_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1 F_3, \lambda F_3, b_1 F_3, \tilde{m} + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1 S_3, \beta F_3, ek_1 F_3, \tilde{m} + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_3, \tilde{m}) = (-F_3, 0, 0, 0)$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_m(E_3, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v} = (-ek_1 F_3, -\lambda F_3, 0, 0)^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v}] = -ek_1 g_1 F_3 S_3 - \beta\lambda F_3 S_3 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{m})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter n and getting $\tilde{n}$ from $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) - \beta\lambda F_3 S_3 = 0$, feasible for $(-m - \mu + F_3(\alpha - c_1) - \gamma_1)(-n - \nu - \lambda F_3 + S_3(\theta - g_3) - \gamma_2) < \beta\lambda F_3 S_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1 F_3, \lambda F_3, b_1 F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1 S_3, \beta F_3, ek_1 F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_3, \tilde{n}) = (0, 0, -S_3, 0)$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_n(E_3, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v} = (0, 0, -b_1 F_3, -(m + \mu + \gamma_1 + F_3(c_1 - \alpha)))^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v}] = -eb_1 k_1 F_3^2 - (m + \mu + \gamma_1 + F_3(c_1 - \alpha))^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter μ and let

$$\tilde{\mu} = -m + F_3(\alpha - c_1) - \gamma_1 + \frac{\beta\lambda F_3 S_3}{n + \nu + \lambda F_3 + S_3(g_3 + \theta) + \gamma_2},$$

feasible for

$$F_3(\alpha - c_1) + \frac{\beta\lambda F_3 S_3}{n + \nu + \lambda F_3 + S_3(g_3 + \theta) + \gamma_2} > m + \gamma_1.$$

The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1 F_3, \lambda F_3, b_1 F_3, m + \tilde{\mu} + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1 S_3, \beta F_3, ek_1 F_3, m + \tilde{\mu} + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_3, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_\mu(E_3, \tilde{\mu}) = 0$, implying $D\mathbf{F}_\mu(E_3, \tilde{\mu})\mathbf{v} = (0, -\lambda F_3, 0, 0)^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_\mu(E_3, \tilde{\mu})\mathbf{v}] = -\beta\lambda F_3 S_3 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{\mu})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter ν and let

$$\tilde{\nu} = -n - \lambda F_3 + S_3(\theta - g_3) - \gamma_2 + \frac{\beta\lambda F_3 S_3}{m + \mu + F_3(c_1 - \alpha) + \gamma_1},$$

feasible for

$$S_3(\theta - g_3) + \frac{\beta\lambda F_3 S_3}{m + \mu + F_3(c_1 - \alpha) + \gamma_1} > n + \gamma_2 + \lambda F_3.$$

The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1 F_3, \lambda F_3, b_1 F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$, $\mathbf{w} = (g_1 S_3, \beta F_3, ek_1 F_3, m + \mu + \gamma_1 + F_3(c_1 - \alpha))^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_3, \tilde{\nu}) = \mathbf{0}$, for which $\mathbf{w}^\mathbf{T}\mathbf{F}_\nu(E_3, \tilde{\nu}) = 0$, implying $D\mathbf{F}_\nu(E_3, \tilde{\nu})\mathbf{v} = (0, 0, 0, -(m + \mu + \gamma_1 + F_3(c_1 - \alpha)))^T$ and therefore $\mathbf{w}^\mathbf{T}[D\mathbf{F}_\nu(E_3, \tilde{\nu})\mathbf{v}] = -(m + \mu + \gamma_1 + F_3(c_1 - \alpha))^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{\nu})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$, between E_3 and E_4.

Bifurcations at E_5

For E_5 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = \frac{r - m - 2b_1 F_5 - C_5(b_2 + \alpha) - c_2 C_5 \pm \sqrt{\Delta_A}}{2},$$

$$\Lambda_{B_{1,2}} = \frac{1}{2}[s - 2n - k_1F_5 - C_5(k_2+\beta) \\ -\nu - \lambda F_5 - k_3C_5 - \gamma_2 \pm \sqrt{\Delta_B}]$$

where

$$\begin{aligned}\Delta_A = [r - m - 2b_1F_5 - C_5(b_2+\alpha) - c_2C_5]^2 \\ +4[c_2C_5(r - m - 2b_1F_5 - C_5(b_2+\alpha)] \\ +C_5(\alpha - c_1)[r - F_5(b_2+\alpha)+\gamma_1)]; \\ \Delta_B = [s - n - k_1F_5 - C_5(k_2+\beta) - n - \nu - \lambda F_5 - k_3C_5 - \gamma_2]^2 \\ -4\{[s - n - k_1F_5 - C_5(k_2+\beta)][-n - \nu - \lambda F_5 - k_3C_5 - \gamma_2) \\ -\beta C_5(s+\gamma_2)\}.\end{aligned}$$

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter m and getting $\tilde{m}$ from $c_2(r - m - 2b_1F_5 - C_5(b_2+\alpha)) + (\alpha - c_1)(r - F_5(b_2+\alpha)+\gamma_1) = 0$, feasible for $r+\gamma_1 > F_5(b_2+\alpha)$ with $\alpha > c_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, 0, 0)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2+\alpha)+\gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_5,\tilde{m}) = (-F_5, -C_5, 0, 0)^T$, for which $\mathbf{w^T F}_m(E_5,\tilde{m}) = -C_5(c_2F_5 + r - F_5(b_2+\alpha)+\gamma_1) \neq 0$, implying $D\mathbf{F}_m(E_5,\tilde{m})\mathbf{v} = (-c_2, c_1 - \alpha, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_5,\tilde{m})\mathbf{v}] = -c_2^2C_5 + (c_1 - \alpha)(r - F_5(b_2+\alpha)+\gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_5,\tilde{m})(\mathbf{v},\mathbf{v})] = -2c_2^2C_5(b_1c_2 + (\alpha+b_2)(\alpha - c_1)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $m = \tilde{m}$.

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter μ and getting $\tilde{\mu}$ from $c_2(r - m - 2b_1F_5 - C_5(b_2+\alpha)) + (\alpha - c_1)(r - F_5(b_2+\alpha)+\gamma_1) = 0$, feasible for $r+\gamma_1 > F_5(b_2+\alpha)$ with $\alpha > c_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, 0, 0)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2+\alpha)+\gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_5,\tilde{\mu}) = (0, -C_5, 0, 0)^T$, for which $\mathbf{w^T F}_\mu(E_5,\tilde{\mu}) = -C_5(r - F_5(b_2+\alpha)+\gamma_1) \neq 0$, implying $D\mathbf{F}_\mu(E_5,\tilde{\mu})\mathbf{v} = (0, c_1 - \alpha, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\mu(E_5,\tilde{\mu})\mathbf{v}] = (c_1 - \alpha)(r - F_5(b_2+\alpha)+\gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_5,\tilde{\mu})(\mathbf{v},\mathbf{v})] = -2c_2^2C_5(b_1c_2 + (\alpha+b_2)(\alpha - c_1)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter n and getting $\tilde{n}$ from $(s - n - k_1F_5 - C_5(k_2+\beta))(-n - \nu - \lambda F_5 - k_3C_5 - \gamma_2) - \beta C_5(s+\gamma_2) = 0$, feasible for $s < n + k_1F_5 + C_5(k_2+\beta)$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, s+\gamma_2, \tilde{n} + k_1F_5 + C_5(k_2+\beta) - s)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2+\alpha)+\gamma_1, \beta C_5, \tilde{n} + k_1F_5 + C_5(k_2+\beta) - s)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_5,\tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_5,\tilde{n}) = 0$, implying $D\mathbf{F}_n(E_5,\tilde{n})\mathbf{v} = (0, 0, -(s+\gamma_2), -(\tilde{n} + k_1F_5 + C_5(k_2+\beta) - s))^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_5,\tilde{n})\mathbf{v}] = -(s+\gamma_2)\beta C_5 - (\tilde{n} + k_1F_5 + C_5(k_2+\beta) - s)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_5,\tilde{n})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_5 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter ν and getting $\tilde{\nu}$ from $(s - n - k_1F_5 - C_5(k_2+\beta))(-n - \nu - \lambda F_5 - k_3C_5 - \gamma_2) - \beta C_5(s+\gamma_2) = 0$, feasible for $s < n + k_1F_5 + C_5(k_2+\beta)$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (c_2, \alpha - c_1, s+\gamma_2, n + k_1F_5 + C_5(k_2+\beta) - s)^T$, $\mathbf{w} = (c_2C_5, r - F_5(b_2+\alpha)+\gamma_1, \beta C_5, n + k_1F_5 + C_5(k_2+\beta) - s)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_5,\tilde{\nu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\nu(E_5,\tilde{\nu}) = 0$, implying $D\mathbf{F}_\nu(E_5,\tilde{\nu})\mathbf{v} = (0, 0, 0, -(n + k_1F_5 + C_5(k_2+\beta) - s))^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\nu(E_5,\tilde{\nu})\mathbf{v}] = -(n + k_1F_5 + C_5(k_2+\beta) - s)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_5,\tilde{\nu})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$, between E_5 and E_4.

Bifurcations at E_6

For E_6 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = \frac{r - 2m + ek_1S_6 - \lambda I_6 - \mu - \gamma_1 \pm \sqrt{\Delta_A}}{2}$$

$$\Lambda_{B_{1,2}} = \frac{s - n - 2g_1S_6 - I_6(g_2+\theta) - g_4I_6 \pm \sqrt{\Delta_B}}{2}$$

where

$$\begin{aligned}\Delta_A = (r - 2m + ek_1S_6 - \lambda I_6 - \mu - \gamma_1)^2 \\ -4[(r - m + ek_1S_6 - \lambda I_6)(-m - \mu - \gamma_1) \\ -\lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1)] \\ \Delta_B = (s - n - 2g_1S_6 - I_6(g_2+\theta) - g_4I_6)^2 \\ -4\{-g_4I_6[s - n - 2g_1S_6 - I_6(g_2+\theta)] \\ -I_6(\theta - g_3)[s - S_6(g_2+\theta)+\gamma_2]\}\end{aligned}$$

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter m and getting $\tilde{m}$ from $(r - m + ek_1S_6 - \lambda I_6)(m+\mu+\gamma_1) + \lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1) = 0$, feasible for $r + ek_1S_6 < m + \lambda I_6$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (\tilde{m} + \mu + \gamma_1, \lambda I_6, g_4, \theta - g_3)^T$, $\mathbf{w} = (\tilde{m} + \mu + \gamma_1, r + ek_2S_6 + ek_3I_6 + \gamma_1, g_4I_6, s - S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_6,\tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T F}_m(E_6,\tilde{m}) = 0$, implying $D\mathbf{F}_m(E_6,\tilde{m})\mathbf{v} = (-(\tilde{m}+\mu+\gamma_1), -\lambda I_6, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_6,\tilde{m})\mathbf{v}] = -(\tilde{m}+\mu+\gamma_1)^2 - \lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1) \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{m})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_6 and E_4.

Eigenvalue $\Lambda_{A_{1,2}}$

Take as bifurcation parameter μ and getting $\tilde{\mu}$ from $(r - m + ek_1S_6 - \lambda I_6)(m+\mu+\gamma_1) + \lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1) = 0$, feasible for $r + ek_1S_6 < m + \lambda I_6$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (m + \mu + \gamma_1, \lambda I_6, g_4, \theta - g_3)^T$, $\mathbf{w} = (m + \mu + \gamma_1, r + ek_2S_6 + ek_3I_6 + \gamma_1, g_4I_6, s - S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_6,\tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\mu(E_6,\tilde{\mu}) = 0$, implying $D\mathbf{F}_\mu(E_6,\tilde{\mu})\mathbf{v} = (0, -\lambda I_6, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\mu(E_6,\tilde{\mu})\mathbf{v}] = -\lambda I_6(r + ek_2S_6 + ek_3I_6 + \gamma_1) \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{\mu})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_6 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter n and getting $\tilde{n}$ from $g_4(s - n - 2g_1S_6 - I_6(g_2+\theta)) + (\theta - g_3)(s - S_6(g_2+\theta)+\gamma_2) = 0$, feasible for $s+\gamma_2 > S_6(g_2+\theta)$ with $\theta > g_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0,0,g_4,\theta - g_3)^T$, $\mathbf{w} = (0,0,g_4I_6, s - S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_6,\tilde{n}) = (0,0,-S_6,-I_6)^T$, for which $\mathbf{w^T F}_n(E_6,\tilde{n}) = -I_6(g_4S_6 + s - S_6(g_2+\theta)+\gamma_2) \neq 0$, implying $D\mathbf{F}_n(E_6,\tilde{n})\mathbf{v} = (0,0,-g_4,g_3-\theta)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_6,\tilde{n})\mathbf{v}] = -(g_4^2I_6 + (s - S_6(g_2+\theta)+\gamma_2)(\theta - g_3)) \neq 0$. Also $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{n})(\mathbf{v},\mathbf{v})] = -2g_4^2I_6(g_1g_4 + (g_2+\theta)(\theta - g_3)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $n = \tilde{n}$.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter ν and getting $\tilde{\nu}$ from $g_4(s - n - 2g_1S_6 - I_6(g_2+\theta)) + (\theta - g_3)(s - S_6(g_2+\theta)+\gamma_2) = 0$, feasible for $s+\gamma_2 > S_6(g_2+\theta)$ with $\theta > g_3$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0,0,g_4,\theta - g_3)^T$, $\mathbf{w} = (0,0,g_4I_6, s - S_6(g_2+\theta)+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_6,\tilde{\nu}) = (0,0,0,-I_6)^T$, for which $\mathbf{w^T F}_\nu(E_6,\tilde{\nu}) = -I_6(s - S_6(g_2+\theta)+\gamma_2) \neq 0$, implying $D\mathbf{F}_\nu(E_6,\tilde{\nu})\mathbf{v} = (0,0,0,g_3-\theta)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\nu(E_6,\tilde{\nu})\mathbf{v}] = (g_3-\theta)(s - S_6(g_2+\theta)+\gamma_2) \neq 0$. Also $\mathbf{w}^T[D^2\mathbf{F}(E_6,\tilde{\nu})(\mathbf{v},\mathbf{v})] = -2g_4^2I_6(g_1g_4 + (g_2+\theta)(\theta - g_3)) \neq 0$. Hence a saddle-node bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$.

Tables 4 and 5 summarize the findings respectively for saddle-node and transcritical bifurcations. Figure 2 instead shows their mutual relationships graphically.

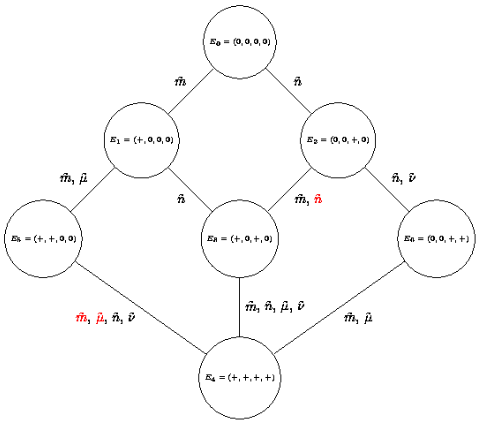

Figure 2: Transcritical bifurcations representation of model (1); in red those numerically found.

TABLE 4: POSSIBLE SADDLE-NODE BIFURCATIONS OF MODEL (1).

Eq.	Eigenvalue	Threshold
E_5	$\Lambda_{A_{1,2}} = 0$	$m = \tilde{m}$
	$\Lambda_{A_{1,2}} = 0$	$\mu = \tilde{\mu}$
E_6	$\Lambda_{B_{1,2}} = 0$	$n = \tilde{n}$
	$\Lambda_{B_{1,2}} = 0$	$\nu = \tilde{\nu}$

TABLE 5: POSSIBLE TRANSCRITICAL BIFURCATIONS OF MODEL (1). NA MEANS THAT SOTOMAYOR'S THEOREM IS NOT APPLICABLE.

Eq.	Eigenvalue	Threshold
$E_0 - E_1$	$\Lambda_1 = 0$	$m = \tilde{m}$
$E_0 - E_2$	$\Lambda_3 = 0$	$n = \tilde{n}$
$E_1 - E_0$	$\Lambda_1 = 0$	$m = \tilde{m}$
$E_1 - E_5$	$\Lambda_2 = 0$	$m = \tilde{m}$
$E_1 - E_5$	$\Lambda_2 = 0$	$\mu = \tilde{\mu}$
E_1(NA)	$\Lambda_3 = 0$	$m = \tilde{m}$
$E_1 - E_3$	$\Lambda_3 = 0$	$n = \tilde{n}$
$E_2 - E_0$	$\Lambda_1 = 0$	$n = \tilde{n}$
$E_2 - E_6$	$\Lambda_2 = 0$	$n = \tilde{n}$
$E_2 - E_6$	$\Lambda_2 = 0$	$\nu = \tilde{\nu}$
$E_2 - E_3$	$\Lambda_3 = 0$	$m = \tilde{m}$
$E_2 - E_3$(NA)	$\Lambda_3 = 0$	$n = \tilde{n}$
$E_5 - E_4$(NA)	$\Lambda_{B_{1,2}} = 0$	$m = \tilde{m}$
$E_5 - E_4$	$\Lambda_{B_{1,2}} = 0$	$n = \tilde{n}$
$E_5 - E_4$(NA)	$\Lambda_{B_{1,2}} = 0$	$\mu = \tilde{\mu}$
$E_5 - E_4$	$\Lambda_{B_{1,2}} = 0$	$\nu = \tilde{\nu}$
$E_3 - E_4$	$\Lambda_{B_{1,2}} = 0$	$m = \tilde{m}$
$E_3 - E_4$	$\Lambda_{B_{1,2}} = 0$	$n = \tilde{n}$
$E_3 - E_4$	$\Lambda_{B_{1,2}} = 0$	$\mu = \tilde{\mu}$
$E_3 - E_4$	$\Lambda_{B_{1,2}} = 0$	$\nu = \tilde{\nu}$
$E_6 - E_4$	$\Lambda_{A_{1,2}} = 0$	$m = \tilde{m}$
$E_6 - E_4$(NA)	$\Lambda_{A_{1,2}} = 0$	$n = \tilde{n}$
$E_6 - E_4$	$\Lambda_{A_{1,2}} = 0$	$\mu = \tilde{\mu}$
$E_6 - E_4$(NA)	$\Lambda_{A_{1,2}} = 0$	$\nu = \tilde{\nu}$

Non-existence of Hopf bifurcations

The points E_0, E_1, E_2 have only real eigenvalues, thus Hopf bifurcations cannot arise.

For equilibrium E_3, the trace of the first quadratic into which the characteristic equation factorizes is $b_1F_3 + g_1S_3$ which cannot vanish. The trace of the second quadratic, from (27) can be rewritten as

$$S_3(g_3 - \theta) = -[m + n + \gamma_1 + \gamma_2 + \mu + \nu + F_3(c_1 - \alpha + \lambda)]$$

and substitution into the determinant inequality, the second one in (27), produces a condition that cannot be satisfied as well:

$$-(m + \mu + F_3(c_1 - \alpha) + \gamma_1)^2 - \beta\lambda F_3S_3 > 0.$$

At E_5 again factorization occurs. It is already known that the first quadratic has a negative trace, (25), so that purely imaginary eigenvalues cannot arise. For the second one, the determinant condition, i.e. the last inequality in (26), implies

$$s - n - k_1F_5 - C_5(k_2 + \beta) < 0$$

and substitution into the trace inequality, the second one in (26), leads to

$$s - 2n - k_1F_5 - C_5(k_2 + \beta) - \nu - \lambda F_5 - k_3C_5 - \gamma_2 < 0$$

thereby preventing the trace from vanishing.

Similar considerations hold for E_6. One trace is negative, (28). The determinant of the second quadratic, last inequality of (29), implies

$$r - m + ek_1S_6 - \lambda I_6 < 0$$

and using this result in the trace inequality we find that the latter is strictly negative and therefore cannot vanish:

$$r - 2m + ek_1 S_6 - \lambda I_6 - \mu - \gamma_1 < 0.$$

STANDARD INCIDENCE MODEL

Equilibrium points

Note that for the equilibria evaluation, the standard incidences vanish when both populations vanish, as the numerators are quadratic terms, while the denominators are linear just functions.

The possible equilibria for (2) are the origin, E_0, E_1, E_2 and E_3, the very same points found in the model (1). Now, their feasibility conditions are therefore (4), (5) and (6).

We now investigate the rodents-free equilibrium $E_5 = (F_5, C_5, 0, 0)$. Summing the two equilibrium equations and rearranging the second one we obtain the following two conic sections:

$$\begin{aligned}\Psi(C,F) : b_1F^2 + c_2C^2 + (b_2+c_1)FC + F(m-r)\\ +C(m+\mu-r) = 0,\\ \Phi(C,F) : c_1F^2 + c_2C^2 + (c_1+c_2)FC\\ +(m-\alpha+\gamma_1+\mu)F + (m+\gamma_1+\mu)C = 0.\end{aligned}$$

Both the conics go through the origin.

The invariant $b_1c_2 - (b_2+c_1)^2 4^{-1}$ of Ψ is not decisive to assess its nature, and thus we look for intersections with the axes,

$$O = (0,0), \quad Q_1^* = \left(0, \frac{r-m}{b_1}\right), \quad Q_2^* = \left(\frac{r-m-\mu}{c_2}, 0\right)$$

Differentiating implicitly and evaluating at the three previous points we get

$$\begin{aligned}F'(O) &= \frac{m+\mu-r}{r-m},\\ F'(Q_1^*) &= -\frac{b_1(m+\mu-r)+(r-m)(b_2+c_1)}{b_1(r-m)},\\ F'(Q_2^*) &= \frac{c_2(m+\mu-r)}{c_2(m-r)+(b_2+c_1)(r-m-\mu)}.\end{aligned}$$

Thus we have four cases:

- Case (A):
$$r > m, \quad m+\mu > r. \tag{32}$$
Q_1^* lies on the positive F-axis, Q_2^* lies on the negative C-axis, $F'(O) > 0$, $F'(Q_1^*) < 0$, $F'(Q_2^*)$ could be of either sign.

- Case (B):
$$r > m, \quad m+\mu < r. \tag{33}$$
Q_1^* lies on the positive F-axis, Q_2^* lies on the positive C-axis, $F'(O) < 0$.

- Case (C):
$$r < m, \quad m+\mu > r. \tag{34}$$
Q_1^* lies on the negative F-axis, Q_2^* lies on the negative C-axis and $F'(O) < 0$.

- Case (D):
$$r < m, \quad m+\mu < r. \tag{35}$$
Q_1^* lies on the negative F-axis, Q_2^* lies on the positive C-axis, $F'(O) > 0$, $F'(Q_1^*) < 0$, $F'(Q_2^*) < 0$. However the inequalities (35) are contradictory and this situation therefore cannot arise.

This means that in Case (A) we can have either ellipses, for which there is an arc that lies in the first quadrant, or hyperbolae. In the latter situation, the origin and the two points Q_1^* and Q_2^* must all lie on the same branch. Therefore, the ellipse and hyperbola configurations are in these cases topologically equivalent. Therefore in Case (A) the arc joining the origin and Q_1^* lies in the first quadrant, independently of the type of the conic section.

In Case (B), if the three points are on the same branch of the conic, the latter can be an ellipse, and then the concave arc joining Q_1^* and Q_2^* is feasible, or a hyperbola, and the very same arc is again feasible and concave. In this case however there could be also two arcs in the first quadrant emanating respectively from each intersection Q_1^* and Q_2^*. If Q_1^* and Q_2^* lie on the same branch again the arc joining them is feasible, but convex in this case. The other possible arrangements of O, Q_1^* and Q_2^* on different branches of the hyperbola Ψ lead to impossible configurations, in view of the signs of the slopes at these points.

Case (C) gives rise to a feasible arc only in one situation. Indeed, if the three points, O, Q_1^* and Q_2^* belong to the same branch of the conic, be it an ellipse or a hyperbola, the arc on which they lie does not meet the first quadrant, but the other one is entirely feasible. If two of them lie on the same branch of the hyperbola, they must be Q_1^* and Q_2^*, because in the other two cases the slope at the origin would be positive; the arc joining Q_1^* and Q_2^* is concave and does not intersect the first quadrant.

For the second conic Φ the invariant is negative, $-(c_2 - c_1)^2 4^{-1} < 0$ showing that it is a hyperbola. Its intersections with the axes are the origin O and

$$P_1^* = \left(0, -\frac{m-\alpha+\gamma_1+\mu}{c_1}\right), \quad P_2^* = \left(-\frac{m+\gamma_1+\mu}{c_2}, 0\right)$$

Note that the abscissa of P_2^* is negative. Differentiating implicitly at the above points we find

$$\begin{aligned}F'(O) &= \frac{m+\gamma_1+\mu}{\alpha-m-\gamma_1-\mu},\\ F'(P_1^*) &= \frac{\alpha}{m-\alpha+\gamma_1+\mu} - \frac{c_2}{c_1},\\ F'(P_2^*) &= -c_2\frac{m+\gamma_1+\mu}{c_1(m+\gamma_1+\mu)+c_2\alpha} < 0.\end{aligned} \tag{36}$$

Thus for

$$\alpha > \gamma_1 + m + \mu \tag{37}$$

the height of the point P_1^* is positive, $F'(O) > 0$, $F'(P_1^*) < 0$ and $F'(P_2^*) < 0$. Now if the three points, O, P_1^* and P_2^* are on the same branch of the hyperbola, the arc joining O and P_1^* lies in the first quadrant. The three configurations for which two points are on the same branch, are incompatible with the sign of $F'(O)$ or $F'(P_1^*)$.

On the other hand for

$$\alpha < \gamma_1 + m + \mu \tag{38}$$

P_1^* has negative height and $F'(O) < 0$. If O, P_1^* and P_2^* lie on the same branch of the hyperbola, it must be unfeasible, the remaining one lies entirely in the first quadrant. However, in this case the derivative at P_2^* would be positive, which gives a contradiction with what found above, (36). The configurations for which two points lie on the same branch are incompatible with the sign of the derivative at the origin, except when the arc joins P_1^* and P_2^*; but in such case both branches of the hyperbola are unfeasible. In summary, thus, this situation cannot arise.

We now need to find the conditions leading to possible intersections of Ψ and Φ in the first quadrant.

For (32) and (37), the intersection depends on the combination of heights and slopes at the origin, namely it is necessary that either one of the following pairs is satisfied:

$$\frac{\alpha-m-\gamma_1-\mu}{c_1} > \frac{r-m}{b_1}, \quad \frac{m+\gamma_1+\mu}{\alpha-m-\gamma_1-\mu} > \frac{m+\mu-r}{r-m}; \tag{39}$$
$$\frac{\alpha-m-\gamma_1-\mu}{c_1} < \frac{r-m}{b_1}, \quad \frac{m+\gamma_1+\mu}{\alpha-m-\gamma_1-\mu} < \frac{m+\mu-r}{r-m}.$$

For (33) and (37), the intersection is always guaranteed if the heights of the points on the F axis are properly arranged, namely

$$\frac{\alpha-m-\gamma_1-\mu}{c_1} > \frac{r-m}{b_1}. \tag{40}$$

For (34) and (37) there could be a saddle-node bifurcation leading to two intersections or none at all. But this case is rather complicated and will not be further investigated.

The analysis for the case $E_6 = (0,0,S_6,I_6)$ parallels the one above, the details are omitted, but the results leading to sure feasible intersections are summarized here below.

We need the auxiliary conditions

$$\theta > \gamma_2 + n + \nu; \tag{41}$$

$$s > n, \quad n+\nu > s; \tag{42}$$

$$s > n, \quad n+\nu < s; \tag{43}$$

For (42) and (41), the intersection depends on the combination of heights and slopes at the origin, namely it is necessary that either one of the following pairs is satisfied:

$$\frac{\theta-n-\gamma_2-\nu}{g_3} > \frac{s-n}{g_1}, \quad \frac{n+\gamma_2+\nu}{\theta-n-\gamma_2-\nu} > \frac{n+\nu-s}{s-n}; \tag{44}$$
$$\frac{\theta-n-\gamma_2-\nu}{g_3} < \frac{s-n}{g_1}, \quad \frac{n+\gamma_2+\nu}{\theta-n-\gamma_2-\nu} < \frac{n+\nu-s}{s-n}.$$

For (43) and (41), the intersection exists if

$$\frac{\theta-n-\gamma_2-\nu}{g_3} > \frac{s-n}{g_1}. \tag{45}$$

TABLE 6: POSSIBLE GUARANTEED FEASIBILITY CONDITIONS FOR THE EQUILIBRIA OF (2)

Equilibrium	Feasibility
$E_0 = (0,0,0,0)$	-
$E_1 = \left(\frac{r-m}{b_1},0,0,0\right)$	(4)
$E_2 = \left(0,0,\frac{s-n}{g_1},0\right)$	(5)
$E_3 = (F_3,0,S_3,0)$	(6)
$E_5 = (F_5,C_5,0,0)$	(32), (37), (39); (33), (37), (40);
$E_6 = (0,0,S_6,I_6)$	(42), (41), (44); (43), (41), (45);
$E_4 = (F_4,C_4,S_4,I_4)$	numerical

Stability of the equilibrium points

The Jacobian $\widehat{J} = \widehat{J}_{i,k}$, $i,k = 1,\dots,4$ of the system (2) has the following entries:

$$\widehat{J}_{1,1} = ek_1S - \alpha\left(\frac{C}{F+C} - \frac{FC}{(F+C)^2}\right) - b_2C$$
$$-2b_1F - \lambda\frac{I}{S+I} - m + r, \quad \widehat{J}_{1,4} = ek_3C - \lambda F\frac{S}{(S+I)^2},$$
$$\widehat{J}_{1,2} = r + e(k_2S + k_3I) - b_2F - \alpha F\frac{F}{(F+C)^2} + \gamma_1,$$
$$\widehat{J}_{1,3} = ek_2C + ek_1F + \lambda F\frac{I}{(S+I)^2},$$
$$\widehat{J}_{2,1} = \alpha\left(\frac{C}{F+C} - \frac{FC}{(F+C)^2}\right) - c_1C + \lambda\frac{I}{S+I},$$
$$\widehat{J}_{2,2} = -2c_2C + \alpha F\frac{F}{(F+C)^2} - c_1F - m - \mu - \gamma_1,$$
$$\widehat{J}_{2,3} = -\lambda F\frac{I}{(S+I)^2}, \quad \widehat{J}_{3,1} = -k_1S + \beta S\frac{C}{(F+C)^2},$$
$$\widehat{J}_{2,4} = \lambda F\frac{S}{(S+I)^2}, \quad \widehat{J}_{3,2} = -\beta S\frac{F}{(F+C)^2} - k_2S,$$
$$\widehat{J}_{3,3} = -\beta\frac{C}{F+C} - k_2C - k_1F - 2g_1S - g_2I$$
$$-\theta\left(\frac{I}{S+I} - \frac{SI}{(S+I)^2}\right) - n + s,$$
$$\widehat{J}_{3,4} = -g_2S - \theta S\frac{S}{(S+I)^2} + s + \gamma_2,$$
$$\widehat{J}_{4,1} = -\lambda I - \beta S\frac{C}{(F+C)^2}, \quad \widehat{J}_{4,2} = \beta S\frac{F}{(F+C)^2} - k_3I,$$
$$\widehat{J}_{4,3} = \beta\frac{C}{F+C} - g_3I + \theta\left(\frac{I}{S+I} - \frac{SI}{(S+I)^2}\right),$$
$$\widehat{J}_{4,4} = -k_3C - \lambda F - g_3S + \theta S\frac{S}{(S+I)^2}$$
$$-2g_4I - n - \nu - \gamma_2.$$

Recall that when each pairs F, C and S, I vanish, the corresponding fractional terms do not appear in the model, and therefore will also be omitted in the Jacobian.

At E_0 the Jacobian eigenvalues are

$$r-m, \quad -m-\mu-\gamma_1, \quad s-n, \quad -n-\nu-\gamma_2$$

and in view of the parameters' assumptions the stability conditions become just

$$r < m, \quad s < n. \tag{46}$$

At $E_1 = (F_1, 0, 0, 0)$ again the eigenvalues are explicit,

$$m - r, \quad -m - \mu + \alpha - \gamma_1 - \frac{c_1(r-m)}{b_1},$$
$$s - n + \frac{k_1(m-r)}{b_1} \quad -n - \nu - \gamma_2 + \frac{\lambda(m-r)}{b_1},$$

and stability is achieved for

$$\alpha < m + \mu + \gamma_1 + \frac{c_1(r-m)}{b_1}, \quad s + \frac{k_1(m-r)}{b_1} < n. \tag{47}$$

For $E_2 = (0, 0, S_2, 0)$ we again explicitly find the eigenvalues

$$n - s, \quad -n - \gamma_2 + \theta - \nu - \frac{g_3(s-n)}{g_1},$$
$$r - m + \frac{ek_1(s-n)}{g_1}, \quad -m - \mu - \gamma_1$$

and stability follows if just

$$\theta < n + \gamma_2 + \nu + \frac{g_3(s-n)}{g_1}, \quad r + \frac{ek_1(s-n)}{g_1} < m \tag{48}$$

hold.

At $E_3 = (F_3, 0, S_3, 0)$ the characteristic equation factorizes into the product of two quadratic equations. Using the feasibility of E_3 the Routh-Hurwitz conditions in one case are satisfied,

$$-b_1F_3 - g_1S_3 < 0, \quad (-b_1F_3)(-g_1S_3) + ek_1^2F_3S_3 > 0$$

while the remaining ones ensure stability if satisfied:

$$\alpha + \theta < m + \mu + F_3(c_1 + \lambda) + \gamma_1 + \gamma_2 + n + \nu + g_3S_3, \tag{49}$$
$$(\alpha - m - \mu - c_1F_3 - \gamma_1)(\theta - n - \nu - \lambda F_3 - g_3S_3 - \gamma_2) > \beta\lambda.$$

For the stability of the rodent-free and foxes-free points, we leave in the stability conditions the contributions of the fractions coming from the standard incidence terms, namely S and I for E_5 and F and C for E_6, remarking thus that the Routh-Hurwitz conditions being satisfied depend on the relative speeds of the vanishing populations to zero, and will not be investigated any further.

At $E_5 = (F_5, C_5, 0, 0)$ the characteristic equation factorizes into the product of two quadratic equations, for which the Routh-Hurwitz conditions give

$$r + \frac{\alpha F_5^2}{(F_5+C_5)^2} < 2m + 2b_1F_5 + b_2C_5 \tag{50}$$
$$+ \frac{\alpha C_5^2}{(F_5+C_5)^2} + \mu + \gamma_1 + c_1F_5 + 2c_2C_5 + \frac{\lambda I}{S+I};$$
$$\left[r - m - \frac{\alpha C_5^2}{(F_5+C_5)^2} - 2b_1F_5 - b_2C_5 - \frac{\lambda I}{S+I}\right]$$
$$\times \left[\frac{\alpha F_5^2}{(F_5+C_5)^2} - m - \mu - c_1F_5 - 2c_2C_5 - \gamma_1\right]$$
$$> \left[\frac{\alpha C_5^2}{(F_5+C_5)^2} - c_1 - \frac{\lambda I}{S+I}\right]$$
$$\times \left[r - b_2F_5 - \frac{\alpha F_5^2}{(F_5+C_5)^2} + \gamma_1\right],$$

as well as

$$s < \frac{\beta C_5}{F_5+C_5} + 2n + k_1F_5 + k_2C_5 + \nu \tag{51}$$
$$+ \lambda F_5 + k_3C_5 + \gamma_2 + \theta\frac{S^2+I^2}{(S+I)^2};$$
$$\left[s - n - k_1F_5 - k_2C_5 - \frac{\beta C_5}{F_5+C_5} - \frac{\theta I^2}{(S+I)^2}\right]$$
$$\times \left[n + \nu + \lambda F_5 + k_3C_5 + \gamma_2 + \frac{\theta S^2}{(S+I)^2}\right]$$
$$+ \frac{\beta C_5}{F_5+C_5}(s + \gamma_2) < 0.$$

Now this equilibrium can indeed be feasible and stable, as it is shown empirically in Figure 3, for the parameter values given in its caption.

The characteristic equation of $E_6 = (0, 0, S_6, I_6)$ also factorizes into the product of two quadratic equations, and the Routh-Hurwitz conditions yield

$$r + ek_1S_6 < 2m + \mu + \gamma_1 + \frac{\lambda I_6}{S_6+I_6} + \frac{\alpha(C^2-F^2)}{(F+C)^2}, \tag{52}$$
$$\left[r - m + ek_1S_6 - \frac{\lambda I_6}{S_6+I_6} - \frac{\alpha C^2}{(F+C)^2}\right]$$
$$\times \left[m + \mu + \gamma_1 + \frac{\alpha F^2}{(F+C)^2}\right] + \left[\frac{\lambda I_6}{S_6+I_6} + \frac{\alpha C^2}{(F+C)^2}\right]$$
$$\times \left[r + e(k_2S_6 + k_3I_6) + \gamma_1 - \frac{\alpha F^2}{(F+C)^2}\right] < 0,$$

and

$$s + \frac{\theta S_6^2}{(S_6+I_6)^2} < 2n + (2g_1 + g_3)S_6 + g_2I_6 \tag{53}$$
$$+ \frac{\theta I_6^2}{(S_6+I_6)^2} + \nu + \gamma_2 + 2g_4I_6 + \frac{\beta C}{F+C},$$
$$\left[s - n - 2g_1S_6 - g_2I_6 - \frac{\theta I_6^2}{(S_6+I_6)^2} - \frac{\beta C}{F+C}\right]$$
$$\times \left[\frac{\theta S_6^2}{(S_6+I_6)^2} - n - \nu - g_3S_6 - 2g_4I_6 - \gamma_2\right]$$
$$> \left[\frac{\theta I_6^2}{(S_6+I_6)^2} - g_3I_6 + \frac{\beta C}{F+C}\right]$$
$$\times \left[s - g_2S_6 - \frac{\theta S_6^2}{(S_6+I_6)^2} + \gamma_2\right].$$

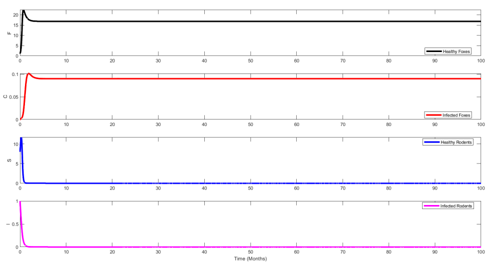

Figure 3: Equilibrium E_5 of model (2) obtained for the parameter values (30), but for $b_1 = 0{,}1$, $r = 2$, $s = 4$, and $b_2 = 0{,}1$, $c_1 = 0{,}1$, $c_2 = 0{,}11$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 0{,}1$, $\beta = 0{,}2$, $\gamma_1 = 0{,}5$, $\gamma_2 = 0{,}1$, $\theta = 0{,}2$, $\lambda = 0{,}1$, $\mu = 5$, $\nu = 0{,}1$.

This equilibrium can also be achieved, see the simulation reported in Figure 4. The parameter values are liste in the caption.

At $E_4 = (F_4, C_4, S_4, I_4)$ one must impose the Routh-Hurwitz conditions on the full matrix:

$$\mathrm{tr}(\widehat{J}(E_4)) < 0, \quad M_2 > 0, \quad M_3 < 0, \quad \det(\widehat{J}(E_4)) > 0, \quad \mathrm{tr}(\widehat{J}(E_4)) \cdot M_2 < M_3, \quad \mathrm{tr}(\widehat{J}(E_4)) \cdot M_2 \cdot M_3 > \mathrm{tr}(\widehat{J}(E_4))^2 \cdot \det(\widehat{J}(E_4)) + M_3^2. \tag{54}$$

They are complicated and do not lead to analytical expressions easy to interpret, thus they are not further explored.

Table 7 summarizes our findings.

TABLE 7: STABILITY CONDITIONS FOR THE EQUILIBRIA OF (2)

Equilibrium point	Stability conditions
$E_0 = (0,0,0,0)$	(46)
$E_1 = \left(\frac{r-m}{b_1}, 0, 0, 0\right)$	(47)
$E_2 = \left(0, 0, \frac{s-n}{g_1}, 0\right)$	(48)
$E_3 = (F_3, 0, S_3, 0)$	(49)
$E_5 = (F_5, C_5, 0, 0)$	(50), (51)
$E_6 = (0, 0, S_6, I_6)$	(52), (53)
$E_4 = (F_4, C_4, S_4, I_4)$	numerical

BIFURCATIONS OF MODEL (2)

Bifurcations at E_0

For E_0 the Jacobian has four explicit eigenvalues, $\Lambda_1 = r - m$, $\Lambda_2 = -m - \mu - \gamma_1$, $\Lambda_3 = s - n$, $\Lambda_4 = -n - \nu - \gamma_2$.

Eigenvalue Λ_1

Take as bifurcation parameter m and let $\tilde{m} := r$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} + \mu + \gamma_1, \tilde{m} + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_0, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T F}_m(E_0, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_0, \tilde{m})\mathbf{v} = (-1,0,0,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_0, \tilde{m})\mathbf{v}] = -(\tilde{m} + \mu + \gamma_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2b_1(\tilde{m} + \mu + \gamma_1) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_0 and E_1.

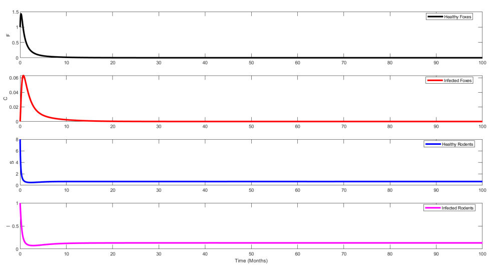

Figure 4: Equilibrium E_6 of model (2) obtained for the parameters (30), in which however some changes occur, $b_1 = 1$, $g_1 = 1$, $g_2 = 1$, $g_4 = 0{,}1$, $k_1 = 1$, $k_3 = 1$, $m = 1$, $n = 1$, $r = 0{,}2$, $s = 2$, and the other values: $b_2 = 1$, $c_2 = 0{,}4$, $g_3 = 0{,}1$, $c_1 = 2$, $k_2 = 1$, $\theta = 3$, $\lambda = 1$, $\gamma_2 = 0{,}1$, $\gamma_1 = 1$, $\alpha = 1$, $\beta = 1$, $\nu = 2$, $\mu = 0{,}1$

Eigenvalue Λ_3

Take as bifurcation parameter n and let $\tilde{n} := s$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0,0,1,0)^T$, $\mathbf{w} = (0,0,\tilde{n} + \nu + \gamma_2, \tilde{n} + \gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_0, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_0, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_0, \tilde{n})\mathbf{v} = (0,0,-1,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_0, \tilde{n})\mathbf{v}] = -(\tilde{n} + \nu + \gamma_2) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_0, \tilde{n})(\mathbf{v}, \mathbf{v})] = -2g_1(\tilde{n} + \nu + \gamma_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_0 and E_2.

Bifurcations at E_1

For E_1 the Jacobian has four explicit eigenvalues,

$$\Lambda_1 = m - r, \quad \Lambda_2 = -m + \alpha - \gamma_1 - \mu - c_1 F_1,$$

$$\Lambda_3 = s - n - k_1 F_1, \quad \Lambda_4 = -n - \gamma_2 - \nu - \lambda F_1.$$

Eigenvalue Λ_1

Take as bifurcation parameter m and let $\tilde{m} := r$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (1,0,0,0)^T$, $\mathbf{w} = (\tilde{m} - \alpha + \gamma_1 + \mu, \tilde{m} - \alpha + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T F}_m(E_1, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_1, \tilde{n})\mathbf{v} = (-1,0,0,0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v}] = -(\tilde{m} - \alpha + \gamma_1 + \mu)$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2b_1(\tilde{m} - \alpha + \gamma_1 + \mu)$. Hence if $\alpha \neq \tilde{m} + \gamma_1 + \mu$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_0.

Eigenvalue Λ_2

Take as bifurcation parameter m and let $\tilde{m} := \dfrac{b_1(\mu + \gamma_1 - \alpha) + c_1 r}{c_1 - b_1}$, feasible for $b_1(\mu + \gamma_1 - \alpha) + c_1 r > 0$ and $c_1 > b_1$ or $b_1(\mu + \gamma_1 - \alpha) + c_1 r < 0$ and $c_1 < b_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (r - b_2 F_1 - \alpha + \gamma_1, b_1 F_1, 0, 0)^T$, $\mathbf{w} = (0,1,0,0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_1, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T F}_m(E_1, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v} = (-v_1, -v_2, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_1, \tilde{m})\mathbf{v}] = -b_1 F_1 \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2b_1(c_1(r - b_2 F_1 - \alpha + \gamma_1) + b_1 c_2 F_1)$. Hence if $c_1(r - b_2 F_1 - \alpha + \gamma_1) + b_1 c_2 F_1 \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_1 and E_5.

Eigenvalue Λ_2

Take as bifurcation parameter μ and let $\tilde{\mu} := -m - c_1 \dfrac{r-m}{b_1} + \alpha - \gamma_1$, feasible for $\alpha > m + c_1 \dfrac{r-m}{b_1} + \gamma_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (r - b_2 F_1 - \alpha + \gamma_1, b_1 F_1, 0, 0)^T$, $\mathbf{w} = (0,1,0,0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_1, \tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\mu(E_1, \tilde{\mu}) = 0$, implying $D\mathbf{F}_\mu(E_1, \tilde{\mu})\mathbf{v} = (0, -b_1 F_1, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\mu(E_1, \tilde{\mu})\mathbf{v}] = -b_1 F_1 \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{\mu})(\mathbf{v}, \mathbf{v})] = -2b_1(c_1(r - b_2 F_1 - \alpha + \gamma_1) + b_1 c_2 F_1)$. Hence if $c_1(r - b_2 F_1 - \alpha + \gamma_1) + b_1 c_2 F_1 \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_1 and E_5.

Eigenvalue Λ_3

Take as bifurcation parameter n and let $\tilde{n} := s - k_1F_1$, feasible for $s > k_1F_1$ with $s > n$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_1, 0, b_1F_1, 0)^T$, $\mathbf{w} = (0, 0, n+\gamma_2+\nu+\lambda F_1, s+\gamma_2)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_1, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_1, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v} = (0, 0, -b_1F_1, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_1, \tilde{n})\mathbf{v}] = -b_1F_1(n+\gamma_2+\nu+\lambda F_1) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_1, \tilde{n})(\mathbf{v}, \mathbf{v})] = -b_1F_1(n+\gamma_2+\nu+\lambda F_1)(2ek_1^2F_1 + b_1k_2F_1 + b_1\beta) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_1 and E_3.

Bifurcations at E_2

For E_2 the Jacobian has four explicit eigenvalues,

$$\Lambda_1 = n - s, \quad \Lambda_2 = -n - \gamma_2 + \theta - \nu - g_3S_2,$$

$$\Lambda_3 = r - m + ek_1S_2, \quad \Lambda_4 = -m - \mu - \gamma_1.$$

Eigenvalue Λ_1

Take as bifurcation parameter n and let $\tilde{n} := s$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, 1, 0)^T$, $\mathbf{w} = (0, 0, \tilde{n} + \gamma_2 - \theta + \nu, s + \gamma_2 - \theta)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_2, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v} = (0, 0, -1, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v}] = -(\tilde{n} + \gamma_2 - \theta + \nu)$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{n})(\mathbf{v}, \mathbf{v})] = -2g_1(\tilde{n} + \gamma_2 - \theta + \nu)$. Hence if $\theta \neq \tilde{n} + \gamma_2 + \nu$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_0.

Eigenvalue Λ_2

Take as bifurcation parameter n and let $\tilde{n} := \dfrac{g_1(\nu + \gamma_2 - \theta) + g_3s}{g_3 - g_1}$, feasible for $g_1(\nu + \gamma_2 - \theta) + g_3s > 0$ and $g_3 > g_1$ or $g_1(\nu + \gamma_2 - \theta) + g_3s < 0$ and $g_3 < g_1$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - g_2S_2 - \theta + \gamma_2, g_1S_2)^T$, $\mathbf{w} = (0, 0, 0, 1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_2, \tilde{n}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_2, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v} = (0, 0, -v_3, -v_4)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_2, \tilde{n})\mathbf{v}] = -g_1S_2 \neq 0$. Hence if $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_2 and E_6.

Eigenvalue Λ_2

Take as bifurcation parameter ν and let $\tilde{\nu} := -n - g_3\dfrac{s-n}{g_1} + \theta - \gamma_2$, feasible for $\theta > n + g_3\dfrac{s-n}{g_1} + \gamma_2$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (0, 0, s - g_2S_2 - \theta + \gamma_2, g_1S_2)^T$, $\mathbf{w} = (0, 0, 0, 1)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_2, \tilde{\nu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\nu(E_2, \tilde{\nu}) = 0$, implying $D\mathbf{F}_\nu(E_2, \tilde{\nu})\mathbf{v} = (0, 0, -g_1S_2, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\nu(E_2, \tilde{\nu})\mathbf{v}] = -g_1S_2 \neq 0$. Hence if $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{\nu})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$, between E_2 and E_6.

Eigenvalue Λ_3

Take as bifurcation parameter m and let $\tilde{m} := r + ek_1S_2$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (g_1S_2, 0, -k_1S_2, 0)^T$, $\mathbf{w} = (\tilde{m} + \gamma_1 + \mu, r + ek_2S_2 + \gamma_1, 0, 0)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_2, \tilde{m}) = \mathbf{0}$, for which $\mathbf{w^T F}_n(E_2, \tilde{m}) = 0$, implying $D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v} = (-g_1S_2, 0, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_2, \tilde{m})\mathbf{v}] = -g_1S_2(m + \gamma_1 + \mu) \neq 0$. Also, $\mathbf{w}^T[D^2\mathbf{F}(E_2, \tilde{m})(\mathbf{v}, \mathbf{v})] = -2g_1S_2(\tilde{m} + \gamma_1 + \mu)(b_1g_1S_2 + ek_1^2S_2) \neq 0$. Hence a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_2 and E_3.

Bifurcations at E_3

For E_3 the Jacobian has four explicit eigenvalues,

$$\Lambda_{A_{1,2}} = \frac{1}{2}[-b_1F_3 - g_1S_3 \pm \sqrt{\Sigma}],$$

$$\Lambda_{B_{1,2}} = \frac{1}{2}(K \pm \sqrt{\Delta}),$$

where

$$\begin{aligned}\Sigma &= b_1^2F_3^2 + g_1^2S_3^2 - 2b_1g_1F_3S_3 - 4ek_1^2F_3S_3,\\ K &= -m - n + \alpha - \gamma_1 - \gamma_2 + \theta - \mu - \nu - F_3(c_1 + \lambda) - g_3S_3,\\ \Delta &= [m + n - \alpha + \gamma_1 + \gamma_2 - \theta + \mu + \nu + F_3(c_1 + \lambda) + g_3S_3]^2\\ &\quad -4[(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3\\ &\quad -\gamma_2 + \theta - \nu) - \beta\lambda].\end{aligned}$$

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter m and getting $\tilde{m}$ from $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) - \beta\lambda = 0$, feasible for $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) > 0$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda\frac{F_3}{S_3}, b_1F_3, \tilde{m} - \alpha + \gamma_1 + \mu + c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta\frac{F_3}{S_3}, ek_1F_3, \tilde{m} - \alpha + \gamma_1 + \mu + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_m(E_3, \tilde{m}) = (-F_3, 0, 0, 0)$, for which $\mathbf{w^T F}_m(E_3, \tilde{m}) = 0$, implying $D\mathbf{F_m}(E_3, \tilde{m})\mathbf{v} = (-ek_1F_3, -\lambda\frac{F_3}{S_3}, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_m(E_3, \tilde{m})\mathbf{v}] = -ek_1g_1F_3S_3 - \beta\lambda \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{m})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $m = \tilde{m}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter n and getting $\tilde{n}$ from $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) - \beta\lambda = 0$, feasible for $(-m + \alpha - \mu - \gamma_1 - c_1F_3)(-n - \lambda F_3 - g_3S_3 - \gamma_2 + \theta - \nu) > 0$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda\frac{F_3}{S_3}, b_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta\frac{F_3}{S_3}, ek_1F_3, m - \alpha + \gamma_1 + \mu + c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_n(E_3, \tilde{n}) = (0, 0, -S_3, 0)$, for which $\mathbf{w^T F}_n(E_3, \tilde{n}) = 0$, implying $D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v} = (0, 0, -b_1F_3, -(m - \alpha + \gamma_1 + \mu + c_1F_3))^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_n(E_3, \tilde{n})\mathbf{v}] = -eb_1k_1F_3^2 - (m - \alpha + \gamma_1 + \mu + c_1F_3)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3, \tilde{n})(\mathbf{v}, \mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $n = \tilde{n}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter μ and let $\tilde{\mu} = -m + \alpha - \gamma_1 - c_1F_3 + \dfrac{\beta\lambda}{n+\lambda F_3+g_3S_3+\gamma_2-\theta+\nu}$, feasible for $(-m+\alpha-\gamma_1-c_1F_3)(n+\lambda F_3+g_3S_3+\gamma_2-\theta+\nu)+\beta\lambda > 0$. The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda\frac{F_3}{S_3}, b_1F_3, m-\alpha+\gamma_1+\tilde{\mu}+c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta\frac{F_3}{S_3}, ek_1F_3, m-\alpha+\gamma_1+\tilde{\mu}+c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\mu(E_3,\tilde{\mu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\mu(E_3,\tilde{\mu}) = 0$, implying $D\mathbf{F}_\mu(E_3,\tilde{\mu})\mathbf{v} = (0, -\lambda\frac{F_3}{S_3}, 0, 0)^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\mu(E_3,\tilde{\mu})\mathbf{v}] = -\beta\lambda \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3,\tilde{\mu})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\mu = \tilde{\mu}$, between E_3 and E_4.

Eigenvalue $\Lambda_{B_{1,2}}$

Take as bifurcation parameter ν and let

$$\tilde{\nu} = -n-\lambda F_3-g_3S_3-\gamma_2+\theta-\frac{\beta\lambda}{-m+\alpha-\mu-\gamma_1-c_1F_3},$$

feasible for

$$\theta > n+\lambda F_3+g_3S_3+\gamma_2+\frac{\beta\lambda}{-m+\alpha-\mu-\gamma_1-c_1F_3}.$$

The right $\mathbf{v}$ and left $\mathbf{w}$ eigenvectors of the Jacobian are $\mathbf{v} = (ek_1F_3, \lambda\frac{F_3}{S_3}, b_1F_3, m-\alpha+\gamma_1+\mu+c_1F_3)^T$, $\mathbf{w} = (g_1S_3, \beta\frac{F_3}{S_3}, ek_1F_3, m-\alpha+\gamma_1+\mu+c_1F_3)^T$. Upon suitable differentiation, in this case we find $\mathbf{F}_\nu(E_3,\tilde{\nu}) = \mathbf{0}$, for which $\mathbf{w^T F}_\nu(E_3,\tilde{\nu}) = 0$, implying $D\mathbf{F}_\nu(E_3,\tilde{\nu})\mathbf{v} = (0,0,0,-(m-\alpha+\gamma_1+\mu+c_1F_3))^T$ and therefore $\mathbf{w^T}[D\mathbf{F}_\nu(E_3,\tilde{\nu})\mathbf{v}] = -(m-\alpha+\gamma_1+\mu+c_1F_3)^2 \neq 0$. Now if $\mathbf{w}^T[D^2\mathbf{F}(E_3,\tilde{\nu})(\mathbf{v},\mathbf{v})] \neq 0$ a transcritical bifurcation arises for the critical parameter value $\nu = \tilde{\nu}$, between E_3 and E_4.

Numerically, we have also determined other transcritical bifurcations, reported in Figures 5-6 as well as a sequence of transitions, Figure 7. Finally, Figure 8 summarizes the mutual relationships among the equilibria of (2) via transcritical bifurcations.

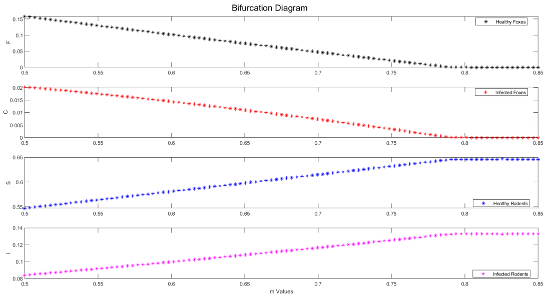

Figure 5: Transcritical bifurcation $E_4 - E_6$ in terms of the bifurcation parameter m. Note that in the bottom two frames the vertical axis starts from a positive value.

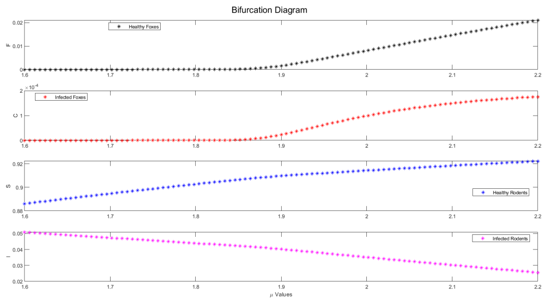

Figure 6: Transcritical bifurcation $E_6 - E_4$ in terms of the bifurcation parameter μ. Note that in the bottom two frames the vertical axis starts from a positive value.

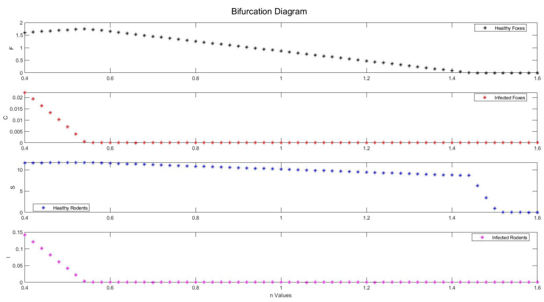

Figure 7: The sequence of transcritical bifurcations $E_4 - E_3 - E_2 - E_0$ in terms of the bifurcation parameter n.

Non-existence of Hopf bifurcations

We consider here only E_3. Again the Jacobian factorizes into the product of two quadratic equations, the first one of which has the strictly positive trace $b_1F_3 + g_1S_3$, so that the Hopf bifurcation cannot arise. Annihilating the trace of the other one, i.e. making the first inequality of (49) an equality, we obtain

$$-m+\alpha-\mu-c_1F_3-\gamma_1 = n+\nu+\lambda F_3+g_3S_3+\gamma_2-\theta$$

and substiting it into the determinant inequality, the second one in (49), we find

$$-(-m+\alpha-\mu-c_1F_3-\gamma_1)^2-\beta\lambda > 0$$

which of course cannot be satisfied.

For E_5 again there are two minors of order two to be considered. From the Routh-Hurwitz conditions for the first one, annihilating the trace gives

$$-\beta\frac{C}{F+C}-k_2C-k_1F-n+s = k_3C+\lambda F+n+\nu+\gamma_2$$

and substitution into the determinant condition leads to the inconsistency

$$-(k_3C+\lambda F+n+\nu+\gamma_2)^2-(s+\gamma_2)\beta\frac{C}{F+C} > 0.$$

At E_6 a similar situation occurs, from the trace we get

$$ek_1S-\lambda\frac{I}{S+I}-m+r = m+\mu+\gamma_1$$

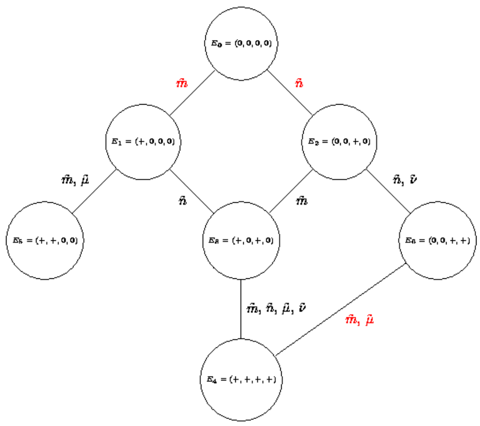

Figure 8: Transcritical bifurcations representation of model (2); in red those numerically found.

so that from substitution into the determinant, once again a contradiction arises,

$$-(m+\mu+\gamma_1)^2 - \lambda \frac{I}{S+I}(r+e(k_2S+k_3I)+\gamma_1) > 0.$$

We have not analysed any further the two remaining minors.

DISCUSSION

The two proposed models differ only in the way the parasite is transmitted. In view of this remark, the disease-free equilibria of the two models, namely E_0, E_1, E_2, E_3, are identical both in feasibility as well as stability conditions, at least for the first three points, as for the latter the conditions are more involved and even substituting explicitly the population equilibrium values does not allow a comparison.

There are however differences in the remaining equilibria that do not contain all the populations.

The feasibility of rodents-free point E_5 in both models has been investigated through the intersection of suitable lines in the $C-F$ plane. There are several sets of possible conditions leading to feasible points in both models, therefore a direct comparison it not possible. They have been shown in both cases not to be empty, through numerical simulations, that of course show also these equilibria to be stable. The analytical stability conditions in case of model (1) are explicit, since one of the Routh-Hurwitz conditions is satisfied, for (2) all of them must be taken into account. In addition, in case of (2) the satisfaction of the inequalities is more complicated, as it depends on the speed at which both rodents subpopulations vanish. This element may make the stability more difficult to be achieved.

For the foxes-free point E_6 similar considerations hold. Coexistence in both cases has been obtained through simulations.

We have also provided two graphs that link together the various equilibria, via transcritical bifurcations. The structure is the same for both models. The two transitions from the origin to either the healthy foxes-only point E_1 or the healthy rodents-only equilibrium E_2 are obtained if the respectives mortality rates of the species that disappears is low enough. From these points, the disease can appear in the thriving population if its mortality is low, this being either the natural or the disease-related one. Thus, to be specific, from E_1 we can obtain E_5 by acting either on m or μ, and a similar situation involving n and ν exists between E_2 and E_6. Another possibility exists here as well, namely the disease-free point E_3 can be reached from either E_1 or E_2. It is necessary in both cases to act on the mortality of the species that is absent in the original equilibrium, suitably reducing it.

In model (2), coexistence has been shown that it can be achieved from the disease-free point E_3 by acting on the combined mortalities of both species, either natural or disease-related, or also from the foxes-free point, if their mortalities are lowered enough. For system (1), coexistence can similarly be attained also from E_6, where foxes are absent, if their mortalities are low enough. In the same way from E_5 the mortalities of the rodents should be low to achieve coexistence. Numerically however, this has been seen to occur also if both foxes mortalities increase, see Figures 9, 10.

In addition, at least for model (1), saddle-node bifurcations could occur generating pairs of equilibria. This has been seen in the feasibility analysis, in the cases when the intersection of the curves leading to the equilibrium could be double, and vanish if the curves are slightly shifted. We gave a hint to this phenomenon, without deepening its analysis. On the other hand, the investigation of the bifurcations through Sotomayor's theorem indicates that they are indeed possible, for the points E_5 and E_6 where only one species survives, with the parasite endemic in it.

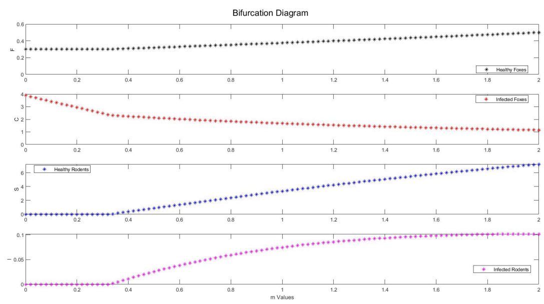

Figure 9: Transcritical bifurcations $E_5 - E_4$ for model (1) in terms of the foxes natural mortality m. Parameter values in addition to those listed in (30): $b_2 = 0{,}2$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 4$, $\beta = 0{,}2$, $\gamma_1 = 0{,}1$, $\gamma_2 = 3$, $\theta = 0{,}2$, $\lambda = 15$, $\mu = 0{,}22$, $\nu = 5$

We have also addressed the question whether persistent oscillations can be found in these models. Their onset through a Hopf bifurcation is immediately seen to be impossible at the origin and at the healthy species-only points E_1 and E_2, because in such cases the eigenvalues are all real. For the equilibria that involve more populations, a nonexistence proof has also been provided in some cases.

From the ecological and conservationist point of view, the aim of the biologist would be the achievement of the disease-free environment, which is attained at equilibrium E_3 where *Echinococcus* is eradicated. Of course also E_1 and E_2, apart from the ecosystem collapse at E_0, do not harbor the parasite,

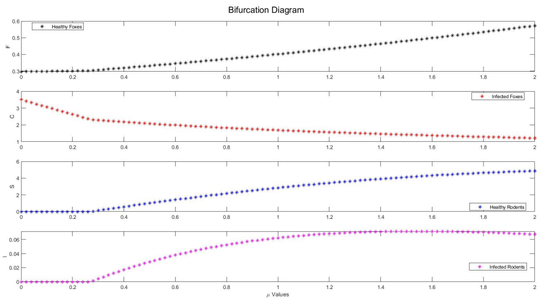

Figure 10: Transcritical bifurcations $E_5 - E_4$ for model (1) in terms of the foxes natural mortality μ. Parameter values other than the reference ones (30): $b_2 = 0{,}2$, $c_1 = 0{,}22$, $c_2 = 0{,}21$, $g_3 = 0{,}11$, $k_2 = 0{,}1$, $\alpha = 4$, $\beta = 0{,}2$, $\gamma_1 = 0{,}1$, $\gamma_2 = 3$, $\theta = 0{,}2$, $\lambda = 15$, $\nu = 5$

but at the expense of having one species eradicated, which in general is not a good situation. This except for the case in which they are the rodents, and in particular if they are considered pests, e.g. mouses. Note that even removing their main prey, the foxes can survive. Indeed they are generalist predators. Other food sources are present in the environment, and suitably accounted for in both models via the inclusion of the logistic-like terms, or, with a different terminology, by using the concept of emerging carrying capacities Sieber et al. (2014).

For the ecosystem to attain stably the desired situations, the bifurcation maps of Figures 2 and 8 turn out to be rather useful. Figure 7 shows for instance one possible such path, for which as n increases, the system moves away from coexistence of all the populations to the disease-free point, and eventually, if the rodents mortality keeps on increasing, to the healthy rodents-only state and eventually to extinction of all species. This appears counterintuitive, but a high rodents mortality may indeed deplete their predators, and if the latter cannot find suitably sizeable alternative food source, they may suffer more than their prey. Given any state in which the system is found, these maps indicate to the ecologist the possible ways to achieve the parasite-free equilibrium E_3. But above all they also provide the parameters on which it is necessary to operate in order to reach the desired outcome.

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