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A European brown hare syndrome model within a foxes-cottontails-hares interaction system

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Abstract The introduction in Italy of the North American lagomorph *Sylvilagus floridanus*, simply named cottontail, has affected the predator-prey dynamics of native European hares and foxes, by increasing fox's predation rate on hares. This results in a sort of apparent competition, for which the presence of a new prey increases predation on another native prey, and could ultimately negatively impact hares. In addition, cottontails could carry several potentially harmful viruses and parasites, especially the European brown hare syndrome (EBHS) virus, which has devastating effects on hare populations. The cottontails' role in the disease spreading is still not known. The model introduced here for possible disease containment assumes that all foxes are healthy carriers and that they could infect other animals through the environment. The analysis allows the characterization of the system's equilibria. The rather exhaustive investigation of the possible system transitions among stable configurations would help the applied ecologist in the field work.

Keywords Predator-prey · competition · predation · invasion · equilibria · bifurcation

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1 Introduction

The introduction of species in new areas could change the interaction between species in recipient ecosystems. For example, the introduction in Italy of the Eastern cottontail (*Sylvilagus floridanus*, hereinafter cottontail), a lagomorph native to North America, affected the prey-predator dynamics of native European hares and foxes [1,4]. The presence of high-density populations of cottontail increases fox's predation rate on hares [4]. This negative indirect interaction is a sort of apparent competition – the presence of a new prey increases predation on another prey – and could have negative effects on hares populations. In [3] a mathematical model is formulated to simulate this three-species system. Introduced species could also interfere with host-parasites dynamics. Cottontails carry several viruses and parasites, which can potentially affect hares [2,11]. Recent field and laboratory

studies suggested that introduced populations of cottontails may be susceptible to infection with the European brown hare syndrome (EBHS) virus [7]. EBHS is transmitted by a lagovirus which causes a lethal form of hepatitis in hares [6]. Transmission presumably occurs directly through a faecal-oral route or through environmental contamination. Tizzani et al. [10] induced clinical disease and mortality in experimentally infected cottontails, showing possible transmissibility of EBHS in cottontails. However, the role of this introduced lagomorph in spreading the disease is yet not known. Viale and colleagues [13] extended the cottontail-hare-fox interaction system to include possible effects of EBHS. In this work, red foxes are considered as potential virus carriers, distinguishing among healthy and carrier individuals, and all cottontails are assumed to be infected, and therefore virus carriers. Carnivores are potential carriers of viruses although normally they are not susceptible to diseases. Chiari et al. [5] found genetic prints of the EBHS virus in the intestinal content of one fox in an area where EBHS was present in hares. This single evidence does not prove that foxes could carry the virus contaminating the environment; this eventuality however could not be excluded. Therefore, in [13] the hypothesis that foxes might at least theoretically, play a potential role in the indirect transmission of EBHS viruses is considered. In the present work we modify the model of [13], by allowing the possibility that all foxes are healthy carriers of the disease and that they could infect through the environment other animals. Infected cottontails may survive the disease, and they can infect healthy cottontails and hares. The hares die as soon as they contract the disease.

2 Model setup

The steps to model the situation concern the vital dynamics and the epidemiological situation. They consist in the discussion of the following four issues: reproduction and hunting and possible vertical transmission, infection through environment and by direct contact.

We consider the demographics first. For reproduction we consider the concept of emerging carrying capacities, [12,9], for all populations, to better emphasize the role of natural mortality, which still may drive the populations to extinction in spite of possible additional food sources. Thus

$$\begin{aligned} \frac{dV}{dt} &= rV - rc_{VV}V^2 - mV, \\ \frac{dS}{dt} &= sS - c_{SS}S^2 - c_{SI}SI - nS, \\ \frac{dI}{dt} &= -c_{II}I^2 - c_{IS}SI - nI - \nu I, \\ \frac{dL}{dt} &= uL - c_{LL}L^2 - pL. \end{aligned} \tag{2.1}$$

Hunting of foxes gives them an additional benefit

$$\frac{dV}{dt} = aeVS + beVI + ceVL, \tag{2.2}$$

while it causes a damage to all the prey

$$\frac{dS}{dt} = -aSV, \quad \frac{dI}{dt} = -bIV, \quad \frac{dL}{dt} = -cLV. \tag{2.3}$$

As for the epidemics, we need to distinguish between the intraspecific transmission and the one among different species, that occurs through the contamination of the environment. For infected cottontails, we account the possibility of vertical transmission σ and s_I possibly different from s, thus

$$\begin{aligned} \frac{dS}{dt} &= sS - c_{SS}S^2 - c_{SI}SI - nS + (1-\sigma)s_I I, \\ \frac{dI}{dt} &= \sigma s_I I - c_{II}I^2 - c_{IS}SI - nI - \nu I. \end{aligned} \tag{2.4}$$

The infection by direct contact among cottontails is modeled using the standard incidence:

$$\frac{dS}{dt} = -\lambda\frac{SI}{S+I}, \quad \frac{dI}{dt} = \lambda\frac{SI}{S+I}. \tag{2.5}$$

Infection through the environment for cottontails and hares instead is represented by a rational response function, in which the denominator accounts for all the agents polluting the environment, and the numerator the proper viral contamination:

$$\begin{aligned} \frac{dS}{dt} &= -S\frac{\gamma I + \alpha V}{V+S+I+L}, \\ \frac{dI}{dt} &= S\frac{\gamma I + \alpha V}{V+S+I+L}, \\ \frac{dL}{dt} &= -L\frac{\beta I + \delta V}{V+S+I+L}. \end{aligned} \tag{2.6}$$

Putting all equation (2.1), (2.2), (2.3), (2.4), (2.5) and (2.6) together we have the system:

$$\begin{aligned}
\frac{dV}{dt} &= rV - c_{VV}V^2 - mV + eaVS + ebVI + ecVL \qquad (2.7)\\
\frac{dS}{dt} &= sS - c_{SS}S^2 - c_{SI}SI - nS + (1-\sigma)s_I I\\
&\quad -aSV - \lambda\frac{SI}{S+I} - S\frac{\gamma I + \alpha V}{V+S+I+L},\\
\frac{dI}{dt} &= \sigma s_I I - c_{II}I^2 - c_{IS}SI - nI - \nu I\\
&\quad -bIV + \lambda\frac{SI}{S+I} + S\frac{\gamma I + \alpha V}{V+S+I+L},\\
\frac{dL}{dt} &= uL - c_{LL}L^2 - pL - cLV - L\frac{\beta I + \delta V}{V+S+I+L}.
\end{aligned}$$

In short, introducing the vector function $\mathbf{F} : R^4_+ \to R^4_+$ the system (2.7) can be written as

$$\frac{d\mathbf{x}}{dt} = \mathbf{F}(\mathbf{x}), \quad \mathbf{F} = (F^1, F^2, F^3, F^4)^T, \quad \mathbf{x} = (V, S, I, P)^T. \qquad (2.8)$$

All the model parameters are assumed to be nonnegative. They are listed together with their ecological meaning in Table 1.

3 Analysis

3.1 Boundedness

The system trajectories are bounded. To this end, we define the whole system population as

$$P = V + S + I + L \qquad (3.1)$$

and then we add the equations of (2.7). For an arbitrary $\eta > 0$, we obtain the estimate

$$\begin{aligned}
\frac{dP}{dt} + \eta P &\le V\left(r - m + \eta - c_{VV}V\right) + (e-1)(aS + bI + cL)V\\
&\quad + S\left(s - n + \eta - c_{SS}S\right) + I(s_I - c_{II}I - n - \nu + \eta)\\
&\quad + L\left(u - p + \eta - c_{LL}L\right) \le \chi_V + \chi_S + \chi_I + \chi_L
\end{aligned}$$

where the χ_As represent parabolae through the origin in terms of the generic population $A \in \{V, S, I, L\}$ and where we have used the fact that $e \le 1$ in

Table 1 The model parameters and their meaning

Parameter	interpretation
r	healthy foxes reproduction rate on other resources
c_{VV}	foxes intraspecific competition
m	foxes natural mortality rate
a	foxes predation rate on healthy cottontails
b	foxes predation rate on infected cottontails
c	foxes predation rate on hares
$e < 1$	foxes conversion coefficient of captured prey
s	healthy cottontails reproduction rate
s_I	infected cottontails reproduction rate
n	cottontails natural mortality rate
c_{SS}	competition among healthy cottontails
c_{SI}	infected cottontails intraspecific competition on healthy cottontails
c_{IS}	healthy cottontails intraspecific competition on infected cottontails
c_{II}	competition among infected cottontails
σ	fraction of cottontails' vertical virus transmission
λ	cottontails direct virus transmission
γ	cottontails infection by infected cottontails environment pollution
α	cottontails infection, by foxes environment pollution
u	hares reproduction rate
c_{LL}	hares intraspecific competition
p	hares natural mortality rate
β	hares infection, i.e. direct mortality rate, by infected cottontails environment pollution
δ	hares infection, i.e. direct mortality rate, by foxes environment pollution

the last estimate. Their maxima are χ_A^*, where

$$\chi_V^* = \frac{(r+\eta-m)^2}{4c_{VV}^2}, \quad \chi_S^* = \frac{(s+\eta-n)^2}{4c_{SS}^2},$$
$$\chi_I^* = \frac{(s_I+\eta-n-\nu)^2}{4c_{II}^2}, \quad \chi_L^* = \frac{(u+\eta-p)^2}{4c_{LL}^2}.$$

Thus, upon integration of the ordinary differential equation associated to the following differential inequality

$$\frac{dP}{dt} + \eta P \leq \chi^* = \chi_V^* + \chi_S^* + \chi_I^* + \chi_L^*$$

we obtain

$$P(t) \leq \max\left\{P(0), \frac{\chi^*}{\eta}\right\}$$

from which, in view of the nonnegativity of each population, also all system populations are bounded above.

3.2 System's steady states

The system has ten possible equilibria $E_i = (V_i, U_i, S_i, L_i)$, $i = 0, \ldots, 9$. The equilibria that can analytically be assessed are the origin, E_0, those where just one population thrives,

$$E_1 = \left(\frac{r-m}{c_{VV}}, 0, 0, 0\right), \quad E_2 = \left(0, \frac{s-n}{c_{SS}}, 0, 0\right), \quad E_5 = \left(0, 0, 0, \frac{u-p}{c_{LL}}\right).$$

They are feasible if the populations are nonnegative, i.e. the following conditions hold, for E_1

$$r \geq m, \tag{3.2}$$

for E_2

$$s \geq n, \tag{3.3}$$

for E_5

$$u \geq p. \tag{3.4}$$

For the particular case of perfect vertical transmission, $\sigma = 1$, also the point $E_* = (0, 0, I_*, 0)$ exists, $I_* = (s_I - n - \nu)c_{II}^{-1}$ and is feasible for

$$s_I \geq n + \nu. \tag{3.5}$$

There are three points with two nonvanishing populations,

$$E_3 = (0, S_3, I_3, 0), \quad E_6 = (V_6, 0, 0, L_6), \quad E_7 = \left(0, \frac{s-n}{c_{SS}}, 0, \frac{u-p}{c_{LL}}\right).$$

The former two will be investigated below. The latter is feasible when both (3.3) and (3.4) hold. Instead, the points

$$E_4 = (V_3, S_3, I_3, 0), \quad E_8 = (0, S_8, I_8, L_8)$$

and coexistence $E_9 = (V_9, S_9, I_9, L_9)$ must be investigated numerically.

In summary, we report the findings in Table 2.

3.2.1 E_3 feasibility

The equilibrium equations correspond to the second and third equations of (2.7). By adding them and considering the third one, we obtain the following two conic sections:

$$\begin{aligned}\Psi(S,I) = c_{SS}S^2 + (c_{SI} + c_{IS})SI + c_{II}I^2 + (n-s)S - (s_I - n - \nu)I = 0,\\ \Phi(S,I) = c_{IS}S^2 + (c_{II} + c_{IS} + n + \nu)SI + (c_{II} + n + \nu)I^2\\ -(\sigma s_I + \lambda + \gamma)S - \sigma s_I I = 0.\end{aligned}$$

Assuming nondegeneracy, the invariants characterizing the conic sections are respectively

$$\delta^{\Psi} = c_{SS}c_{II} - \frac{1}{4}(c_{SI} + c_{IS})^2,$$

$$\delta^{\Phi} = c_{IS}(c_{II} + n + \nu) - \frac{1}{4}(c_{II} + c_{IS} + n + \nu)^2 = -\frac{1}{4}(c_{II} + n + \nu - c_{IS})^2 < 0.$$

Therefore, the second one is a hyperbola. However, since the first one can be of any sign, it can be either an ellipse or a hyperbola. Both curves go through the origin, and further, we can determine their intersections with the axes:

$$P^{\Psi} = \left(0, S_0^{\Psi}\right), \quad Q^{\Psi} = \left(I_0^{\Psi}, 0\right), \quad P^{\Phi} = \left(0, S_0^{\Phi}\right), \quad Q^{\Phi} = \left(I_0^{\Phi}, 0\right),$$

$$S_0^{\Psi} = \frac{s - n}{c_{SS}}, \quad I_0^{\Psi} = \frac{s_I - n - \nu}{c_{II}}, \quad S_0^{\Phi} = \frac{\sigma s_I + \lambda + \gamma}{c_{IS}}, \quad I_0^{\Phi} = \frac{\sigma s_I}{c_{II} + n + \nu},$$

with $S_0^{\Phi} > 0$, $I_0^{\Phi} > 0$ The intersections of Ψ are positive in case

$$S_0^{\Psi} > 0, \text{ i.e. } s > n, \quad I_0^{\Psi} > 0, \text{ i.e. } s_I > n + \nu. \tag{3.6}$$

We now continue with the study of each conic section independently.

For Ψ we assess the slope by implicit differentiation:

$$\frac{dS^{\Psi}}{dI} = -\frac{(c_{SI} + c_{SI})S + 2c_{II}I - (s_I - n - \nu)}{2c_{SS}S + (c_{SI} + c_{SI})I + n - s},$$

and evaluating at the origin we obtain

$$\left.\frac{dS^{\Psi}}{dI}\right|_O = \frac{s_I - n - \nu}{n - s}.$$

Thus, comparing with (3.6), this derivative is positive if and only if

$$I_0^{\Psi} S_0^{\Psi} < 0.$$

This result is compatible with Ψ being an ellipse, a situation which occurs for

$$\delta^{\Psi} > 0, \text{ i.e. } c_{SS}c_{II} > \frac{1}{4}(c_{SI} + c_{IS})^2. \tag{3.7}$$

Depending on the arrangements of the intersections with the coordinate axes we have the following situations:

(A) $I_0^{\Psi} > 0$, $S_0^{\Psi} > 0$: there is a feasible arc in the first quadrant, joining the points P^{Ψ} and Q^{Ψ};
(B) $I_0^{\Psi} > 0$, $S_0^{\Psi} < 0$: a feasible arc joins the origin and the point Q^{Ψ};
(C) $I_0^{\Psi} < 0$, $S_0^{\Psi} < 0$: no feasible arc exists in this case;
(D) $I_0^{\Psi} < 0$, $S_0^{\Psi} > 0$: a feasible arc joins the origin and the point P^{Ψ}.

When (3.7) does not hold Ψ is a hyperbola, namely for

$$\delta^{\Psi} < 0, \text{ i.e. } c_{SS}c_{II} < \frac{1}{4}(c_{SI} + c_{IS})^2, \tag{3.8}$$

the situation is more complex. There must be one or two arcs of the hyperbola crossing the two intersections with the coordinate axes other than the origin. In addition, the slope at the origin is negative if and only if these intersections occur both on the positive semiaxes. This gives rise to the following cases, the ones not listed are impossible as the slope at the origin is in conflict with the arcs arrangements. In particular, for $I_0^{\Psi} < 0$, $S_0^{\Psi} < 0$, no feasible arcs can be found in all arrangements. The possible situations are:

(X1) $I_0^{\Psi} > 0$, $S_0^{\Psi} > 0$: there are two arcs in the first quadrant, emanating from P^{Ψ} and Q^{Ψ};
(X2) $I_0^{\Psi} > 0$, $S_0^{\Psi} > 0$: there is a feasible arc in the first quadrant, joining the points P^{Ψ} and Q^{Ψ};
(Y1) $I_0^{\Psi} > 0$, $S_0^{\Psi} < 0$: a feasible arc joins the origin and the point Q^{Ψ};
(Y4) $I_0^{\Psi} > 0$, $S_0^{\Psi} < 0$: two feasible arcs, one emanating from the origin and one from the point Q^{Ψ} are found here;
(W1) $I_0^{\Psi} < 0$, $S_0^{\Psi} > 0$: a feasible arc joins the origin and the point P^{Ψ};
(W3) $I_0^{\Psi} < 0$, $S_0^{\Psi} > 0$: two feasible arcs, one emanating from the origin and one from the point P^{Ψ} are found here.

Note that the cases (A), (B) and (C) of the ellipse are topologically equivalent respectively to (X2), if we ignore the opposite curvatures, (Y1) and (W1). Thus we can ignore the cases of the ellipse in the following classification.

The slope of the hyperbola Φ is

$$\frac{dS^{\Phi}}{dI} = -\frac{(c_{II} + c_{IS} + n + \nu)S + 2(c_{II} + n + \nu)I - \sigma s_I}{2c_{SI}S + (c_{II} + c_{IS} + n + \nu)I - (\sigma s_I + \lambda + \gamma)}, \tag{3.9}$$

and evaluating at the origin we obtain

$$\left.\frac{dS^{\Phi}}{dI}\right|_O = \frac{-\sigma s_I}{\sigma s_I + \lambda + \gamma} < 0.$$

Because the intersections with the axes are positive, they could lie on the same branch of Φ, giving rise to two feasible arcs emanating each from one of these intersections, or the two points P^{Φ} and Q^{Φ} are joined by a convex arc in the first quadrant. The remaining two combinations are not allowed by the above result. Evaluating the derivative (3.9) further at the point P^{Φ} we find

$$\left.\frac{dS^{\Phi}}{dI}\right|_{P^{\Phi}} = -\frac{(c_{II} + c_{IS} + n + \nu)S_0^{\Phi} - \sigma s_I}{2c_{IS}S_0^{\Psi} - (\sigma s_I + \lambda + \gamma)} = -\frac{(c_{II} + n + \nu)S_0^{\Phi} + \lambda + \gamma}{\sigma s_I + \lambda + \gamma}.$$

Thus $S^{\Phi} > 0$ implies that the slope of Φ at the point P^{Φ} is negative,

$$\left.\frac{dS^{\Phi}}{dI}\right|_{P^{\Phi}} < 0.$$

This result is incompatible with the case of two feasible arcs emanating respectively from P^{Φ} and Q^{Φ}, leaving only the second option of the convex arc joining P^{Φ} and Q^{Φ}.

We can now combine the analyses of Ψ and Φ. Any intersection in the first quadrant gives rise to a possible equilibrium E_3. The existence of such intersections depends on the respective positions of I_0^{Ψ} and I_0^{Φ}, as well as S_0^{Ψ} and S_0^{Φ}.

(X1) : exactly one intersection exists for

$$(I_0^{\Psi} - I_0^{\Phi})(S_0^{\Psi} - S_0^{\Phi}) < 0; \tag{3.10}$$

two intersections arise instead in case

$$I_0^{\Psi} < I_0^{\Phi}, \quad S_0^{\Psi} < S_0^{\Phi}. \tag{3.11}$$

(X2) : exactly one intersection is guaranteed if again (3.10) holds.
(Y1) exactly one intersection is always guaranteed if

$$I_0^{\Psi} > I_0^{\Phi}; \tag{3.12}$$

none exists or two may arise through a saddle-node bifurcation if

$$I_0^{\Psi} < I_0^{\Phi}. \tag{3.13}$$

(Y4) exactly one intersection occurs for (3.12); two instead are guaranteed if (3.13) is satisfied.
(W1) one intersection is guaranteed if

$$S_0^{\Psi} > S_0^{\Phi}; \tag{3.14}$$

none exist or two occur through a saddle-node bifurcation if

$$S_0^{\Psi} < S_0^{\Phi}. \tag{3.15}$$

(W3) : two intersections are guaranteed again if (3.15) holds, while exactly one exists in the opposite case, (3.14).

3.2.2 E_6 feasibility

The existence of this equilibrium follows by the feasible intersection of the two functions, obtained from the first and last equilibrium equations of (2.7):

$$\begin{aligned} \Pi(S,I) &= r - m - c_{VV}V + ceL = 0, \\ \Gamma(S,I) &= c_{LL}L^2 + (c_{LL}+c)LV + cV^2 - (u-p)L - (u-p-\delta)V = 0. \end{aligned}$$

Π is a straight line, with intersections with the axes located at $Q^\Pi = (L_0^\Pi, 0)$, $P^\Pi = (0, V_0^\Pi)$ with

$$L_0^\Pi = \frac{m-r}{ce}, \quad V_0^\Pi = \frac{r-m}{c_{VV}},$$

so that only one of the two is positive at a time,

– (m) $r < m$, giving $L_0^\Pi > 0$,
– (n) $r > m$. giving $V_0^\Pi > 0$.

Assuming nondegeneracy for the conic Γ, the characterizing invariant shows that it is a hyperbola:

$$\delta^\Gamma = c_{LL}c - \frac{1}{4}(c_{LL}+c)^2 = -\frac{1}{4}(c_{LL}-c)^2 < 0.$$

Its intersections with the axes are the points $Q^\Gamma = (L_0^\Gamma, 0)$, $P^\Gamma = (0, V_0^\Gamma)$ with

$$L_0^\Gamma = \frac{u-p}{c_{LL}}, \quad V_0^\Gamma = \frac{u-p-\delta}{c},$$

so that $V_0^\Gamma > 0$ implies $L_0^\Gamma > 0$ and from $L_0^\Gamma < 0$, $V_0^\Gamma < 0$ follows. Differentiating the conic, we find

$$\frac{dV}{dL} = -\frac{2c_{LL}L + (c_{LL}+c)V - (u-p)}{(c_{LL}+c)L + 2cV - (u-p-\delta)} \tag{3.16}$$

and evaluation at the origing provides

$$\left.\frac{dV}{dL}\right|_O = \frac{p-u}{u-p-\delta}.$$

It follows that the slope at the origin is positive only for

$$p + \delta > u > p \tag{3.17}$$

and negative for either one of the alternative conditions

$$u > p + \delta; \quad u < p. \tag{3.18}$$

Evaluating the slope (3.16) at the point Q^Γ gives

$$\left.\frac{dV}{dL}\right|_{Q^\Gamma} = c_{LL}\frac{p-u}{u-p+c_{LL}\delta}.$$

The latter is negative for $u > p + \delta$, preventing that the origin and the two points Q^{Γ} and P^{Γ} lie all on the same branch of Γ.

Instead the slope (3.16) at the point P^{Γ} provides

$$\left.\frac{dV}{dL}\right|_{P^{\Gamma}} = \frac{\delta}{u - p - \delta} - \frac{c_{LL}}{c}.$$

Thus for $u < p + \delta$ we have

$$\left.\frac{dV}{dL}\right|_{P^{\Gamma}} < 0$$

and in such case only an arc joining the origin and Q^{Γ} lies in the first quadrant.

These results imply that the only possible configurations are given by

- (C) $u > p+\delta$: an arc in the first quadrant joins the points Q^{Γ} and P^{Γ}.
- (D) $p + \delta > u > p$: the arc in the first quadrant joins the origin and the point Q^{Γ}.

In the remaining case $u < p$, Γ does not have a feasible branch.

Feasible intersections between Γ and Π exist in the following situations:

- (Cm) $u > p + \delta$, $0 < V_0^{\Pi} < V_0^{\Gamma}$, $r > m$: a single intersection is guaranteed. Explicitly:

$$u > p + \delta, \quad 0 < \frac{r - m}{c_{VV}} < \frac{u - p - \delta}{c} \tag{3.19}$$

- (Cn) $u > p + \delta$, $0 < L_0^{\Pi} < L_0^{\Gamma}$, $r < m$: a single intersection is guaranteed. Explicitly:

$$u > p + \delta, \quad 0 < \frac{m - r}{ce} < \frac{u - p}{c_{LL}}. \tag{3.20}$$

- (Dm) $p+\delta > u > p$, $V_0^{\Pi} > 0$, $r > m$: through a saddle-node bifurcation two intersections may exist. Explicitly:

$$p + \delta > u > p, \quad r > m. \tag{3.21}$$

- (Dn) $p + \delta > u > p$, $0 < L_0^{\Pi} < L_0^{\Gamma}$, $r < m$: a single intersection is guaranteed. Explicitly:

$$p + \delta > u > p, \quad 0 < \frac{m - r}{ce} < \frac{u - p}{c_{LL}}. \tag{3.22}$$

Table 2 Equilibria feasibility

Equilibrium	Feasibility conditions
$E_0 = (0,0,0,0)$	–
$E_1 = (V_1,0,0,0)$	(3.2)
$E_2 = (0,S_2,0,0)$	(3.3)
$E_* = (0,0,I_*,0)$	$\sigma = 1$, (3.5)
$E_3 = (0,S_3,I_3,0)$	Ψ has one arc through P^Ψ and one through Q^Ψ: $\exists$! (3.10); $\exists$ 2 (3.11); Ψ has a feasible arc through P^Ψ and Q^Ψ: $\exists$! (3.10); Ψ has a feasible arc through O and Q^Ψ: $\exists$! (3.12); $\exists$ 2 or none (3.13); Ψ has one arc through O and one through Q^Ψ: $\exists$! (3.12); $\exists$ 2 (3.13); Ψ has an arc through O and P^Ψ: $\exists$! (3.14); $\exists$ 2 or none (3.15); Ψ has one arc through O and one through P^Ψ: $\exists$ 2 (3.15); $\exists$! (3.14);
$E_4 = (V_4,S_4,I_4,0)$	numerical
$E_5 = (0,0,0,L_5)$	(3.4)
$E_6 = (V_6,0,0,L_6)$	$\exists$! (3.19); $\exists$! (3.20); $\exists$ 2 or none (3.21); $\exists$! (3.22);
$E_7 = (0,S_7,0,L_7)$	(3.3), (3.4)
$E_8 = (0,S_8,I_8,L_8)$	numerical
$E_9 = (V_9,S_9,I_9,L_9)$	numerical

3.3 Equilibria stability

Let us introduce the functions

$$K = \lambda\frac{SI}{S+I}, \quad G = S\frac{\gamma I + \alpha V}{V+S+I+L}, \quad H = L\frac{\beta I + \delta V}{V+S+I+L}.$$

Denoting by subscripts the partial derivatives with respect to each population, the Jacobian J of (2.8) has the following entries, where some ancillary quantities are explicitly stated in the Appendix, namely (5.1),(5.5),(5.9):

$$F_V^1 = r - m - 2c_{VV}V + eaS + ebI + ecL, \quad F_S^1 = eaV, \quad F_I^1 = ebV,$$
$$F_L^1 = ecV, \quad F_V^2 = -aS - G_V, \quad F_S^2 = s - 2c_{SS}S - c_{SI}I - n - aV - K_S - G_S,$$
$$F_I^2 = -c_{SI}S + (1-\sigma)s_I - K_I - G_I, \quad F_L^2 = -G_L, \quad F_V^3 = -bI + G_V,$$
$$F_S^3 = -c_{IS}I + K_S + G_S, \quad F_I^3 = \sigma s_I - 2c_{II}I - c_{IS}S - n - \nu - bV + K_I + G_I,$$
$$F_L^3 = G_L, \quad F_V^4 = -cL - H_V, \quad F_S^4 = -H_S,$$
$$F_I^4 = -H_I, \quad F_L^4 = u - 2c_{LL}L - p - cV - H_L.$$

Because of the nonlinearities appearing in (2.7) some terms in the above Jacobian may show singularities when their denominator vanishes. This happens at the origin and at equilibria E_1 and E_5. In each such case care must be exerted in the Jacobian evaluation as well as in the bifurcation analysis of Section 4. Note that at the origin the nonlinear term in the last equation of (2.7) has the numerator vanishing faster than the denominator,

so that it can be disregarded in the linearization process. Similarly for E_1 and E_5 the function K vanishes for the same reason and consequently its contribution can be ignored in the Jacobian evaluation. Equivalently, we can state that K vanishes with its derivatives whenever $S = I = 0$,

$$\begin{aligned} K(0,0) = 0, \quad K_I(0,0) = 0, \quad K_S(0,0) = 0, \\ K_{SS}(0,0) = 0, \quad K_{SI}(0,0) = 0, \quad K_{II}(0,0) = 0. \end{aligned} \tag{3.23}$$

This consideration will be used both in this section as well as in the bifurcation analysis.

Thus for E_0, keeping only the linear terms in the system equations, we easily obtain the following stability conditions, that are the opposite ones respectively of (3.2), (3.3), (3.4):

$$m > r, \quad s > n, \quad u > p. \tag{3.24}$$

Let us introduce the following notation. By $J^P_{[i,j;h,k]}$ or $J^P_{[i,j,g;h,k,\ell]}$ we denote the minor of the Jacobian evaluated at the equilibrium point P, where only the rows i, j and g, as well as the columns h, k and ℓ are retained.

Recalling (3.23), two eigenvalues of the Jacobian J^{E_1} evaluated at E_1 are explicitly known, $\lambda_{1,1} = m - r$ and $\lambda_{1,4} = u - p - \delta - cV_1$. They give the first set of stability conditions, (3.2) and:

$$u < p + \delta + cV_1. \tag{3.25}$$

Imposing the Routh-Hurwitz conditions to the remaining minor $J^{E_1}_{[2,3;2,3]}$,

$$\mathrm{tr}(J^{E_1}_{[2,3;2,3]}) < 0, \quad \det(J^{E_1}_{[2,3;2,3]}) > 0,$$

we find the additional stability conditions

$$2n+(a+b)V_1+\nu+\alpha > \sigma s_I + s, \quad (s-n-aV_1-\alpha)(\sigma s_I - n - \nu - bV_1) > \alpha(1-\sigma)s_I. \tag{3.26}$$

At E_2 all eigenvalues are explicit, $-c_{SS}S_2 < 0$, $r - m + eaS_2$, $\sigma s_I - c_{IS}S_2 - n - \nu + \lambda + \gamma$ and $u - p$, and provide the stability conditions

$$r + eaS_2 < m, \quad \sigma s_I S_2 + \lambda + \gamma < n + \nu - c_{IS}S_2, \quad u < p. \tag{3.27}$$

For the particular case $\sigma = 1$, the equilibrium I_* is found. In such case the Jacobian is lower triangular, and the eigenvalues are $r - m + beI_*$, $s - c_{II}I_* - n - \lambda - \gamma$, $s_I - 2c_{II}I_* - n - \nu$, $u - p - \beta$. Thus the stability conditions for I_* can be explicitly written as

$$\begin{aligned} c_{II}r+n+\nu < ebs_I+c_{II}m, \quad \sigma s c_{II}+n+\nu < (n+\lambda+\gamma)c_{II}+s_I, \\ n+\nu < s_I, \quad u < p+\beta. \end{aligned} \tag{3.28}$$

At E_3 we find the two eigenvalues

$$r - m + eaS_3 + abI_3, \quad u - p - \beta\frac{I}{S+I}.$$

The remaining minor $J^{E_3}_{[2,3;2,3]}$ has a negative trace. We need to require further just that $\det(J^{E_1}_{[2,3;2,3]}) > 0$ to ensure stability. To sum up, stability is achieved under the conditions:

$$r+eaS_3+abI_3<m \quad u<p+\beta\frac{I_3}{S_3+I_3}, \tag{3.29}$$
$$\left(s - 2c_{SS}S_3 - c_{SI}I_3 - n - \lambda\frac{I_3^2}{(S_3+I_3)^2} - \frac{\gamma I_3}{S_3+I_3} + S_3\frac{\gamma I_3}{(S_3+I_3)^2}\right)$$
$$\times\left(\sigma s_I - 2c_{II}I_3 - c_{SI}S_3 + \lambda\frac{I_3^2}{(S_3+I_3)^2} - n - \nu + \frac{\gamma S_3^2}{(S_3+I_3)^2}\right)$$
$$> \left(\sigma s_I - 2c_{II}I_3 + \lambda\frac{I_3^2}{(S_3+I_3)^2} - n - \nu + \frac{\gamma S_3}{(S_3+I_3)^2}\right)$$
$$\times\left(-c_{SI}S_3 - \lambda\frac{S_3^2}{(S_3+I_3)^2} + (1-\sigma)s_I - \frac{\gamma S_3^2}{(S_3+I_3)^2}\right)$$

At E_4 only one eigenvalue is explicit, giving the stability condition

$$u < p + cV_4 + \frac{\beta I_4 + \delta V_4}{V_4 + S_4 + I_4}. \tag{3.30}$$

For the remaining minor $J^{E_4}_{[1,2,3;1,2,3]}$ we need to calculate the sum of the minors of order 2, $M^{E_4}_{[1,2,3;1,2,3]}$. We find

$$M^{E_4}_{[1,2,3;1,2,3]} = J^{E_4}_{11}J^{E_4}_{22} - J^{E_4}_{21}J^{E_4}_{12} + J^{E_4}_{11}J^{E_4}_{33} - J^{E_4}_{31}J^{E_4}_{13} + J^{E_4}_{22}J^{E_4}_{33} - J^{E_4}_{23}J^{E_4}_{32},$$
$$\mathrm{tr}(J^{E_4}_{[1,2,3;1,2,3]}) = J^{E_4}_{11} + J^{E_4}_{22} + J^{E_4}_{33}, \quad \det(J^{E_4}_{[1,2,3;1,2,3]}) = J^{E_4}_{11}J^{E_4}_{22}J^{E_4}_{33}$$
$$+J^{E_4}_{12}J^{E_4}_{23}J^{E_4}_{31} + J^{E_4}_{21}J^{E_4}_{13}J^{E_4}_{32} - J^{E_4}_{31}J^{E_4}_{22}J^{E_4}_{13} - J^{E_4}_{11}J^{E_4}_{23}J^{E_4}_{32} - J^{E_4}_{12}J^{E_4}_{21}J^{E_4}_{33}.$$

Stability is provided then by applying the Routh-Hurwitz conditions

$$\mathrm{tr}(J^{E_4}_{[1,2,3;1,2,3]}) < 0, \quad \det(J^{E_4}_{[1,2,3;1,2,3]}) < 0, \tag{3.31}$$
$$\mathrm{tr}(J^{E_4}_{[1,2,3;1,2,3]})M^{E_4}_{[1,2,3;1,2,3]} < \det(J^{E_4}_{[1,2,3;1,2,3]}).$$

Using again (3.23), for E_5 we have all the eigenvalues. Since $-2c_{LL}L_5 < 0$, the stability conditions are

$$r + ecL_5 < m, \quad s < n, \quad \sigma s_I < n + \nu. \tag{3.32}$$

For E_6 the Jacobian splits into the product of two minors of order 2, $J^{E_6}_{[1,4;1,4]}$ and $J^{E_6}_{[2,3;2,3]}$ for which the Routh-Hurwitz conditions provide

$$\mathrm{tr}(J^{E_6}_{[1,4;1,4]}) = J^{E_6}_{44} - c_{VV}V_6 < 0,$$
$$\det(J^{E_6}_{[1,4;1,4]}) = V_6\left(ceJ^{E_6}_{41} - c_{VV}J^{E_6}_{44}\right) > 0 \tag{3.33}$$

Table 3 Equilibria stability

Equilibrium	Stability conditions
$E_0 = (0, 0, 0, 0)$	numerical
$E_1 = (V_1, 0, 0, 0)$	(3.2), (3.25), (3.26)
$E_2 = (0, S_2, 0, 0)$	(3.27),
$E_* = (0, 0, I_*, 0)$	$\sigma = 1$, (3.28)
$E_3 = (0, S_3, I_3, 0)$	(3.29)
$E_4 = (V_4, S_4, I_4, 0)$	(3.30), (3.31)
$E_5 = (0, 0, 0, L_5)$	(3.32)
$E_6 = (V_6, 0, 0, L_6)$	(3.33), (3.34)
$E_7 = (0, S_7, 0, L_7)$	(3.35), (3.4)
$E_8 = (0, S_8, I_8, L_8)$	(3.36), (3.37)
$E_9 = (V_9, S_9, I_9, L_9)$	numerical

as well as

$$\begin{aligned} \mathrm{tr}(J^{E_6}_{[2,3;2,3]}) &= J^{E_6}_{22} + J^{E_6}_{33} < 0, \\ \det(J^{E_6}_{[2,3;2,3]}) &= J^{E_6}_{22} J^{E_6}_{33} - J^{E_6}_{32} + J^{E_6}_{23} > 0. \end{aligned} \tag{3.34}$$

At E_7 all eigenvalues are known. But $-2c_{SS}S_7 < 0$ and $-2c_{LL}L_7 < 0$, hence stability is given by

$$r + eaS_7 + ecL_7 < m, \quad \sigma s_I + \lambda + \gamma \frac{S_7}{S_7 + I_7} < c_{IS}S_7 + n + \nu. \tag{3.35}$$

The Jacobian at E_8 gives one eigenvalue, from which the first stability condition

$$r + eaS_8 + ebI_8 + ecL_8 < m. \tag{3.36}$$

The remaining conditions arise from the Routh-Hurwitz criterion applied to the minor $J^{E_8}_{[2,3,4;2,3,4]}$. We have

$$\begin{aligned} M^{E_8}_{[2,3,4;2,3,4]} &= J^{E_8}_{22} J^{E_8}_{33} - J^{E_8}_{32} J^{E_8}_{23} + J^{E_8}_{22} J^{E_8}_{44} - J^{E_8}_{42} J^{E_8}_{24} + J^{E_8}_{33} J^{E_8}_{44} - J^{E_8}_{34} J^{E_8}_{43}, \\ \mathrm{tr}(J^{E_8}_{[2,3,4;2,3,4]}) &= J^{E_8}_{22} + J^{E_8}_{33} + J^{E_8}_{44}, \quad \det(J^{E_8}_{[2,3,4;2,3,4]}) = J^{E_8}_{22} J^{E_8}_{33} J^{E_8}_{44} \\ &+ J^{E_8}_{23} J^{E_8}_{34} J^{E_8}_{42} + J^{E_8}_{32} J^{E_8}_{24} J^{E_8}_{43} - J^{E_8}_{42} J^{E_8}_{33} J^{E_8}_{24} - J^{E_8}_{22} J^{E_8}_{34} J^{E_8}_{43} - J^{E_8}_{23} J^{E_8}_{32} J^{E_8}_{44}. \end{aligned}$$

Stability is provided then by applying the Routh-Hurwitz conditions

$$\begin{aligned} \mathrm{tr}(J^{E_8}_{[2,3,4;2,3,4]}) < 0, \quad \det(J^{E_8}_{[2,3,4;2,3,4]}) < 0, \\ \mathrm{tr}(J^{E_8}_{[2,3,4;2,3,4]}) M^{E_8}_{[2,3,4;2,3,4]} < \det(J^{E_8}_{[2,3,4;2,3,4]}). \end{aligned} \tag{3.37}$$

The equilibria E_0, E_4, E_8 and E_9 can be attained, as shown in Figures 2, 3, 4. Initial conditions are always taken as follows:

$$V(0) = 1, \quad S(0) = 8, \quad I(0) = 0, \quad L(0) = 3. \tag{3.38}$$

The ecologically available information used in [13], is here reproduced. In fact we take the very same parameters when they are biologically motivated. For the remaining ones, the values are hypothetical. In any case, the reference parameter values are as follows:

$$r = \log(3), s = \log(4.5), u = \log(5), s_I = 0.1, m = \frac{2}{7}, n = \frac{4}{5}, \tag{3.39}$$

$$\nu = 0.1, p = \frac{2}{11}, \quad a = 0.5, \quad b = 0.5, \quad c = 4, \quad e = 0.91,$$

$$c_{VV} = \log(3) - \frac{2}{7}, \quad c_{SS} = \frac{1}{100}\log(4.5) - \frac{4}{500}, \quad c_{LL} = \frac{1}{30}\log(5) - \frac{2}{330},$$

$$c_{II} = \frac{1}{100}\log(4.5) - \frac{4}{500}, \quad c_{SI} = c_{SS} - 0.1, \quad c_{IS} = c_{II} + 1, \quad \sigma = 0.8,$$

$$\lambda = 0.9, \quad \gamma = 0.9, \quad \alpha = 0.9, \quad \beta = 0.1, \quad \delta = 0.1.$$

which provide equilibrium E_1, the remaining equilibria are attained for the choice (3.39) except the parameter values that are listed below in each case.

For E_2

$$s_I = 2, \quad m = 20, \quad n = \frac{4}{5}, \quad p = 11, \quad a = 0.2, \quad b = 0.1, \quad c = 0.4.$$

For E_3

$$s_I = 20, \quad m = 20, \quad p = 11, \quad a = 0.2, \quad b = 0.1, \quad c = 0.4, \quad \lambda = 5, \quad \gamma = 7.$$

For E_5

$$s_I = 2, \quad m = 4, \quad n = 5, \quad a = 0.2, \quad b = 0.1, \quad c = 0.1.$$

For E_6

$$s_I = 2, \quad a = 1, \quad b = 1, \quad c = 0.4.$$

For E_7

$$s_I = 2, \quad m = 13, \quad a = 0.1, \quad b = 0.1, \quad c = 0.1, \quad c_{VV} = 5.$$

4 Bifurcation analysis

Numerically we find the bifurcations reported in Figures 5, 6, 7 and 8.

We now analytically assess the system bifurcations at various equilibria, for most of the explicitly known eigenvalues. Note that in what follows some quantities stemming from the environment contamination terms, namely the functions G and H, as well as the disease incidence K will be needed and are summarized in the Appendix for the ease of the reader, because their evaluation at some of the equilibria may vanish, compare (5.1), (5.2), (5.3), (5.4), (5.5), (5.6), (5.7), (5.8), (5.9), (5.10).

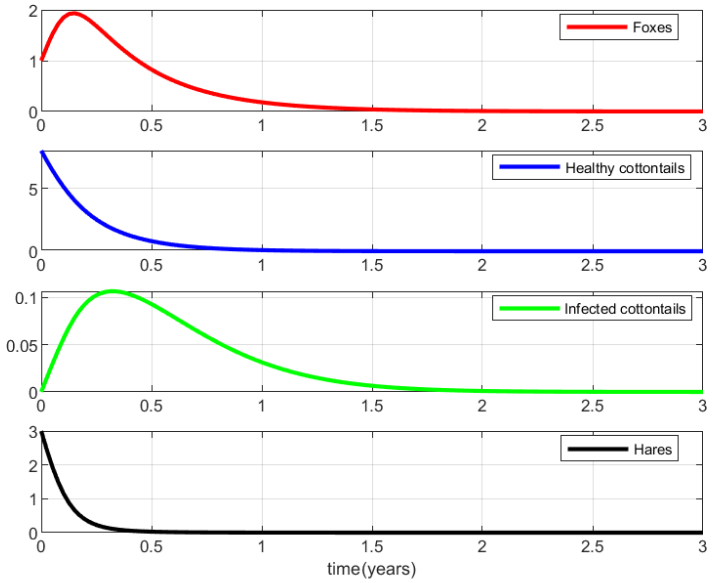

Fig. 1 Equilibrium E_0 is obtained for the parameter values (3.39) with the exception of $m = 4$, $n = 5$, $p = 5$, and the initial conditions (3.38).

4.1 Equilibrium E_1

At E_1 we know two of the Jacobian's eigenvalues,

$$\lambda_{1,1} = r - m, \quad \lambda_{1,2} = u - p - \delta - cV_1.$$

4.1.1 Eigenvalue: $\lambda_{1,1}$

The critical value that annihilates $\lambda_{1,1}$ is $r =: \tilde{r} = m$. Thus for this value, $V_1 = 0$. The Jacobian at this point and for this threshold value becomes

$$J(E_1, \tilde{r}) = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & s - n - \alpha & (1-\sigma)s_I - (\gamma + \alpha) & 0 \\ 0 & \alpha & \sigma s_I - n - \nu & 0 \\ 0 & 0 & 0 & u - p - \delta \end{bmatrix}$$

with right eigenvector $\mathbf{v} = (1, 0, 0, 0)^T$ and right eigenvector of $[J(E_1, \tilde{r})]^T$ given by $\mathbf{w} = (1, 0, 0, 0)^T$. Differentiating the right hand side of (2.7) with

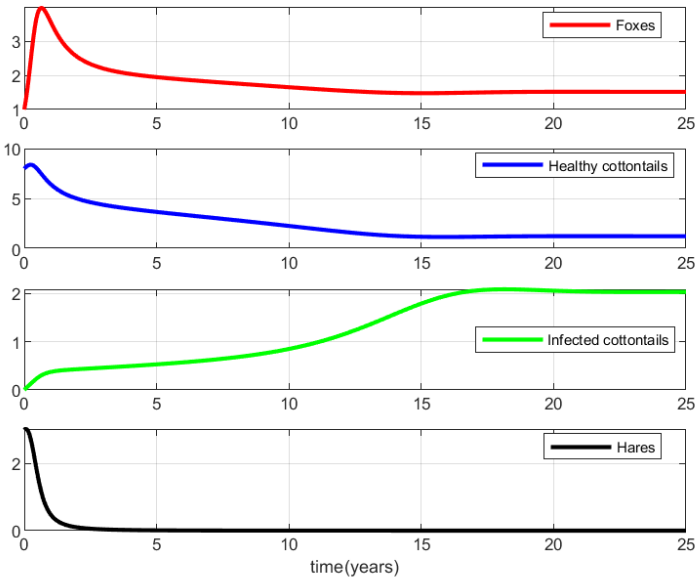

Fig. 2 Equilibrium E_4 is obtained for the parameter values (3.39) with the exception of $s_I = 2$, $a = 0.2$, $b = 0.1$, $c = 1$, and the initial conditions (3.38).

respect to the bifurcation parameter gives

$$\mathbf{F}_r = \begin{pmatrix} V \\ 0 \\ 0 \\ 0 \end{pmatrix} \quad D\mathbf{F}_r = \begin{bmatrix} 1\,0\,0\,0 \\ 0\,0\,0\,0 \\ 0\,0\,0\,0 \\ 0\,0\,0\,0 \end{bmatrix}. \tag{4.1}$$

Evaluation at the equilibrium and at the threshold gives $\mathbf{F}_r(E_1, \tilde{r}) = \mathbf{0}^T$, from which also $\mathbf{w}^T\mathbf{F}_r(E_1, \tilde{r}) = 0$ follows. On the other hand, $D\mathbf{F}_r(E_1, \tilde{r})\mathbf{v} = \mathbf{v}$ and consequently $\mathbf{w}^T D\mathbf{F}_r(E_1, \tilde{r})\mathbf{v} = 1$. Since this quantity does not vanish, the first condition in Sotomayor's theorem [8] holds. Further differentiation leads to

$$\mathbf{w}^T \left[D^2\mathbf{F}(E_1, \tilde{\mu})(\mathbf{v}, \mathbf{v})\right] = D^2F^1_{VV}(E_1, \tilde{\mu}) = -2c_{VV} \neq 0.$$

Thus the system shows the transcritical bifurcation $r_{1,0} := \tilde{r} = m$ between E_1 and E_0. Note indeed that below the critical value, all conditions (3.24) for the stability of the origin are satisfied.

4.1.2 Eigenvalue: $\lambda_{1,4}$

Here the threshold value is $\tilde{u} = p + \delta + cV_1$. The left and right eigenvectors of the Jacobian evaluated at this point and threshold are $\mathbf{v} =$

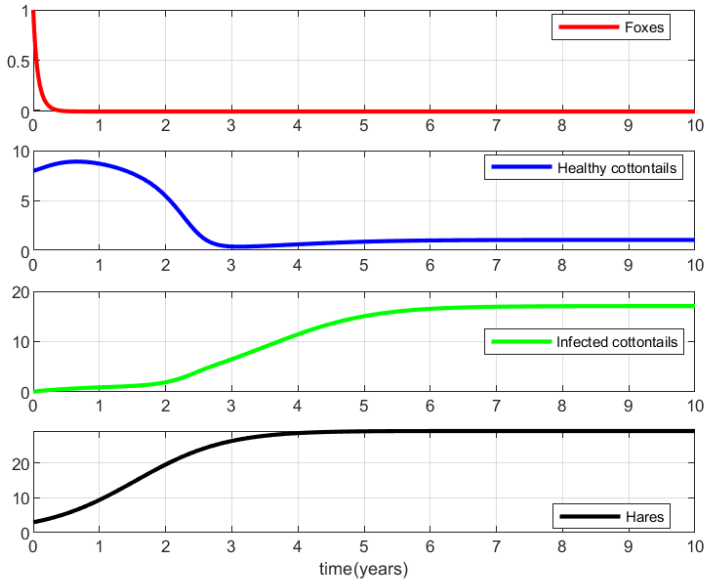

Fig. 3 Equilibrium E_8 is obtained for the parameter values (3.39) with the exception of $s_I = 2$, $m = 13$, $a = 0.1$, $b = 0.1$, $c = 0.1$, $c_{VV} = 5$, $\lambda = 7$, $\gamma = 5$, $\alpha = 5$ and the initial conditions (3.38).

$(ecV_1, 0, 0, r-m)^T$ and $\mathbf{w} = (0,0,0,1)^T$. Further,

$$\mathbf{F}_u = \begin{pmatrix} 0 \\ 0 \\ 0 \\ L \end{pmatrix} \quad D\mathbf{F}_u = \begin{bmatrix} 0\,0\,0\,0 \\ 0\,0\,0\,0 \\ 0\,0\,0\,0 \\ 0\,0\,0\,1 \end{bmatrix}, \tag{4.2}$$

so that $\mathbf{F}_u(E_1, \tilde{u}) = 0$ and thus $\mathbf{w}^T \mathbf{F}_u(E_1, \tilde{u}) = 0$. Also,

$$\mathbf{w}^T D\mathbf{F}_u(E_1, \tilde{u})\mathbf{v} = r - m \neq 0,$$

in view of the fact that in this situation $\lambda_{1,1} \neq 0$. The second derivatives give

$$\begin{aligned} \mathbf{w}^T D^2\mathbf{F}(E_1, \tilde{u})(\mathbf{v}, \mathbf{v}) &= D^2 F^4(E_1, \tilde{u})(\mathbf{v}, \mathbf{v}) \\ &= F^4_{VV}(E_1, \tilde{u})v_1^2 + 2F^4_{VL}(E_1, \tilde{u})v_1 v_4 + F^4_{LL}(E_1, \tilde{u})v_4^2 \\ = -H_{VV}(E_1, \tilde{u})v_1^2 - 2H_{VL}(E_1, \tilde{u})v_1 v_4 - H_{LL}(E_1, \tilde{u})v_4^2 - 2cv_1 v_4 - 2c_{LL}v_4^2. \end{aligned}$$

Use of (5.6) and evaluation at the equilibrium gives finally

$$\begin{aligned} \mathbf{w}^T D^2\mathbf{F}(E_1, \tilde{u})(\mathbf{v}, \mathbf{v}) &= 2v_4[(\delta - c_{LL})v_4 - cv_1] \\ &= 2\frac{r-m}{c_{VV}}[(\delta - c_{LL})c_{VV} - ec^2] \neq 0. \end{aligned} \tag{4.3}$$

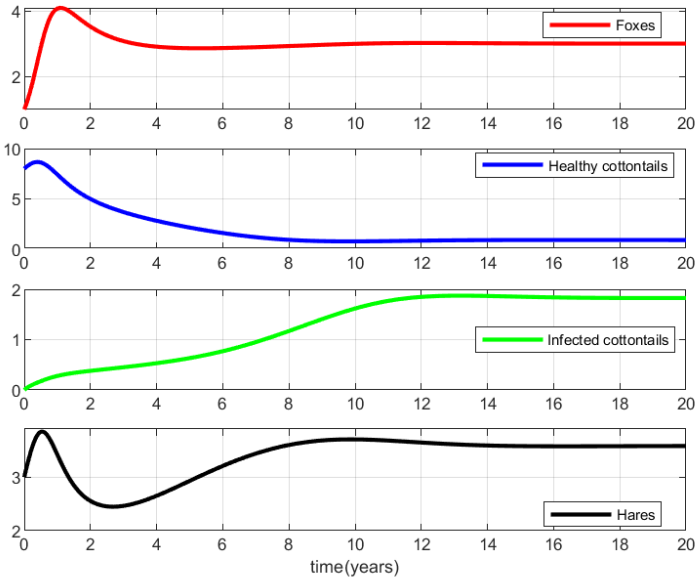

Fig. 4 The coexistence equilibrium is obtained for the parameter values (3.39) with the exception of $s_I = 2$, $a = 0.2$, $b = 0.1$, $c = 0.4$, and the initial conditions (3.38).

Thus the transcritical bifurcation arises $u_{1,6} := \tilde{u} = p + \delta + cV_1$ between E_1 and E_6 if (4.3) is satisfied. Indeed, in such case the L population is destabilized from its zero value, thus it invades the system and the latter must settle to the equilibrium where both V and L do not vanish, i.e. E_6. In the opposite case, we evaluate the third derivatives:

$$\begin{aligned}\mathbf{w}^T D^3\mathbf{F}(E_1,\tilde{u})(\mathbf{v},\mathbf{v},\mathbf{v}) = D^3F^4(E_1,\tilde{u})(\mathbf{v},\mathbf{v},\mathbf{v})\\ = -H_{VVV}(E_1,\tilde{u})v_1^3 - 3H_{VVL}(E_1,\tilde{u})v_1^2v_4 - 3H_{VLL}(E_1,\tilde{u})v_1v_4^2 - H_{LLL}(E_1,\tilde{u})v_4^3\\ = -3\delta\frac{v_4}{V_1^2}[(v_1+v_4)^2 + 2v_4] = -3\delta\left[(r-m)\,(ec+c_{VV})^2 + 2c_{VV}^2\right] \neq 0.\end{aligned}$$

Thus a pitchfork bifurcation arises.

4.2 Equilibrium E_2

At E_2 we know all Jacobian's eigenvalues,

$$\lambda_{2,1} = r - m + eaS_2, \quad \lambda_{2,2} = s - n - 2c_{SS}S_2 = n - s,$$
$$\lambda_{2,3} = \sigma s_I S_2 - n - \nu + \lambda + \gamma, \quad \lambda_{2,4} = u - p.$$

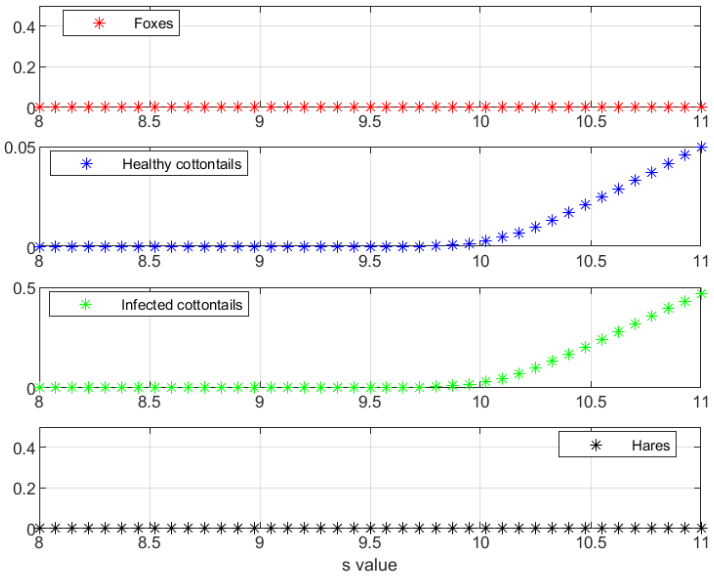

Fig. 5 The bifurcation between E_0 and E_3 is obtained for the parameter values (3.39) with the exception of the following changes $s_I = 20$, $m = 20$, $n = 19$, $p = 11$, $a = 0.2$, $b = 0.1$, $c = 0.4$, $\sigma = 0.9$, $\lambda = 5$, $\gamma = 7$ and the initial conditions (3.38).

4.2.1 Eigenvalue: $\lambda_{2,1}$

Take

$$r^+ = m - ae\frac{s-n}{c_{SS}}$$

Then $\mathbf{v} = (v_1, v_2, v_3, 0)^T$ and $\mathbf{w} = (1, 0, 0, 0)^T$. Differentiating using (4.1), we find $\mathbf{F}_r(E_2, r^+) = (V_2, 0, 0, 0)^T = \mathbf{0}$ so that $\mathbf{w}^T\mathbf{F}_r(E_2, r^+) = 0$ while $D\mathbf{F}_r(E_2, r^+)\mathbf{v} = (v_1, 0, 0, 0)^T$ from which $\mathbf{w}^T D\mathbf{F}_r(E_2, r^+)\mathbf{v} = v_1 \neq 0$. Further,

$$\mathbf{w}^T D^2\mathbf{F}(E_2, n^+)(\mathbf{v}, \mathbf{v}) = D^2F^1(E_2, n^+)(\mathbf{v}, \mathbf{v}) = F^1_{VV}(E_2, n^+)v_1^2$$
$$+2F^1_{VS}(E_2, n^+)v_1v_2 + 2F^1_{VI}(E_2, n^+)v_1v_3 + F^1_{SS}(E_2, n^+)v_2^2 + 2F^1_{SI}(E_2, n^+)v_2v_3$$
$$+F^1_{II}(E_2, n^+)v_3^2 = 2v_1(aev_2 + bev_3 - c_{VV}v_1).$$

Thus if

$$aev_2 + bev_3 \neq c_{VV}v_1 \tag{4.4}$$

the transcritical bifurcation $r_{2,4} := r^+ = m - ae\frac{s-n}{c_{SS}}$ between E_2 and E_4 occurs. In such case the foxes must enter into the system carrying the virus, which implies that also the cottontails will be infected. Thus both V and

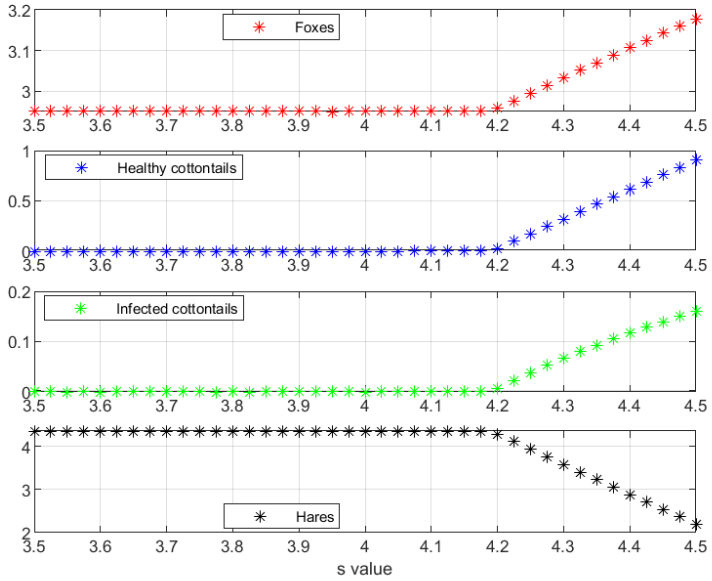

Fig. 6 The bifurcation between E_6 and E_9 is obtained for the parameter values (3.39) with the exception of the following changes $s_I = 2$, $a = 1$, $b = 1$, $c = 0.4$, and the initial conditions (3.38).

I are destabilized, and invade the system, which settles to the equilibrium where also V and I do not vanish, namely E_4. If (4.4) does not hold, because

$$\mathbf{w}^T D^3\mathbf{F}(E_2, n^+)(\mathbf{v},\mathbf{v},\mathbf{v}) = D^3F^1(E_2, n^+)(\mathbf{v},\mathbf{v},\mathbf{v}) = 0$$

no pitchfork bifurcation can arise.

4.2.2 Eigenvalue: $\lambda_{2,2}$

Here we find the simplification $\lambda_{2,2} = n - s$. Taking the bifurcation parameter s and relative critical value $\tilde{s} = n$, the left and right eigenvectors of the Jacobian are $\mathbf{v} = (0, 1, 0, 0)^T$ and $\mathbf{w} = (w_1, 1, w_3, 0)^T$. Appropriate differentiation gives

$$\mathbf{F}_s = \begin{pmatrix} 0 \\ S \\ 0 \\ 0 \end{pmatrix} \quad D\mathbf{F}_s = \begin{bmatrix} 0\,0\,0\,0 \\ 0\,1\,0\,0 \\ 0\,0\,0\,0 \\ 0\,0\,0\,0 \end{bmatrix}, \tag{4.5}$$

where now $\mathbf{F}_s(E_2, \tilde{s}) = \mathbf{0}$, from which

$$\mathbf{w}^T\mathbf{F}_s(E_2, \tilde{s}) = 0 \tag{4.6}$$

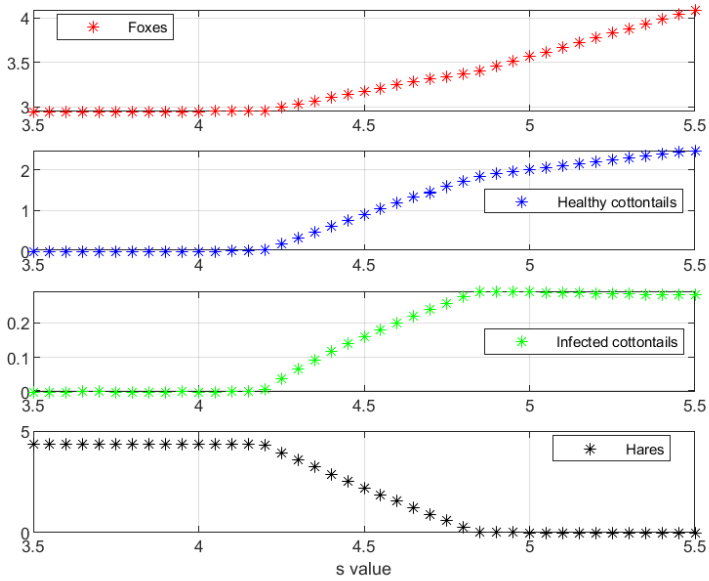

Fig. 7 The bifurcation between E_6 and E_9 then E_4 is obtained for the parameter values (3.39) with the exception of the following changes $s_I = 2$, $a = 1$, $b = 1$, $c = 0.4$, and the initial conditions (3.38).

and

$$\mathbf{w}^T D\mathbf{F}_u(E_2, \tilde{s})\mathbf{v} = 1 \neq 0. \tag{4.7}$$

Furthermore,

$$D^2\mathbf{F}_u(E_1, \tilde{u})(\mathbf{v}, \mathbf{v}) = \begin{bmatrix} 0 \\ F^2_{SS}(E_2, \tilde{s}) \\ F^3_{SS}(E_2, \tilde{s}) \\ F^4_{SS}(E_2, \tilde{s}) \end{bmatrix} \tag{4.8}$$

$$= \begin{bmatrix} 0 \\ -2c_{SS} - K_{SS}(E_2, \tilde{s}) - G_{SS}(E_2, \tilde{s}) \\ K_{SS}(E_2, \tilde{s}) + G_{SS}(E_2, \tilde{s}) \\ -H_{SS}(E_2, \tilde{s}) \end{bmatrix} = \begin{bmatrix} 0 \\ -2c_{SS} \\ 0 \\ 0 \end{bmatrix}$$

so that $\mathbf{w}^T D^2\mathbf{F}_u(E_1, \tilde{u})(\mathbf{v}, \mathbf{v}) = -2c_{SS} \neq 0$. Combining this result with (4.6) and (4.7), the transcritical bifurcation $s_{2,0} := \tilde{s} = n$ is seen to exist between E_2 and E_0. For $s < s_{2,0}$ conditions (3.24) ensuring stability of the origin are satisfied.

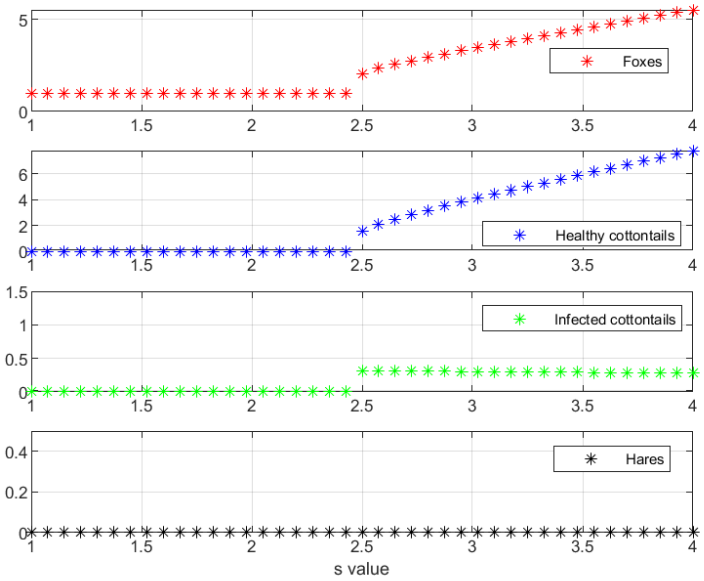

Fig. 8 The bifurcation between E_1 and E_4 is obtained for the parameter values (3.39) and the initial conditions (3.38).

4.2.3 Eigenvalue: $\lambda_{2,3}$

In this case take

$$n^{\dagger} = \frac{c_{SS}}{c_{IS} + c_{SS}} \left[\sigma s_I - \nu + \lambda + \gamma - \frac{c_{IS}}{c_{SS}} s \right].$$

In this case $\mathbf{v} = (0, v_2, v_3, 0)^T$ and $\mathbf{w} = (w_1, 0, w_3, 0)^T$. We find

$$\mathbf{F}_n = \begin{pmatrix} 0 \\ -S \\ -I \\ 0 \end{pmatrix} \quad D\mathbf{F}_n = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 \\ 0 & 0 & -1 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}. \tag{4.9}$$

Hence $\mathbf{F}_n(E_2, n^\dagger) = (0, S_2, 0, 0)^T$ from which $\mathbf{w}^T\mathbf{F}_n(E_2, n^\dagger) = 0$ as well as $\mathbf{w}^T D\mathbf{F}(E_2, n^\dagger)\mathbf{v} = -v_3 w_3 \neq 0$. We then calculate

$$\begin{aligned}\mathbf{w}^T D^2\mathbf{F}(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}) &= w_1 D^2F^1(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}) + w_3 D^2F^3(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}) \\ &= w_1[F^1_{SS}(E_2, n^\dagger)v_2^2 + 2F^1_{SI}(E_2, n^\dagger)v_2v_3 + F^1_{II}(E_2, n^\dagger)v_3^2] \\ &\quad + w_3[F^3_{SS}(E_2, n^\dagger)v_2^2 + 2F^3_{SI}(E_2, n^\dagger)v_2v_3 + F^3_{II}(E_2, n^\dagger)v_3^2] \\ &= w_3[(G_{SS}(E_2, n^\dagger) + K_{SS}(E_2, n^\dagger))v_2^2 + 2(G_{SI}(E_2, n^\dagger) + K_{SI}(E_2, n^\dagger))v_2v_3 \\ &\quad - 2c_{SI}v_2v_3 - 2c_{II}v_3^2 + (G_{II}(E_2, n^\dagger) + K_{II}(E_2, n^\dagger))v_3^2] \\ &= -2w_3\left[c_{SI}v_2v_3 + \frac{\gamma+\lambda}{S_2}v_3^2 + 2c_{II}v_3^2\right] \neq 0.\end{aligned} \tag{4.10}$$

Thus the transcritical bifurcation $n_{2,3} := n^\dagger$ arises between E_2 and E_3 if (4.10) holds, because the infected cottontails are destabilzed from their zero value, and appear in the system. Otherwise, differentiating further, and keeping only the nonvanishing derivatives appearing in (5.3), (5.4) and (5.10),

$$\begin{aligned}\mathbf{w}^T D^3\mathbf{F}(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}, \mathbf{v}) &= w_1 D^3F^1(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}, \mathbf{v}) + w_3 D^3F^3(E_2, n^\dagger)(\mathbf{v}, \mathbf{v}, \mathbf{v}) \\ &= w_3[3(G_{SSI}+K_{SSI})v_2^2v_3 + 3(G_{SII}+K_{SII})v_2v_3^2 + K_{III})v_3^3]\big|_{(E_2, n^\dagger)} \\ &= -3w_3\left[\frac{2\lambda}{S_2^3}v_2^2v_3 + \lambda\left(\frac{2}{S_2^2} - \frac{4}{S_2^3} + \frac{6}{S_2^4}\right)v_2v_3^2 + 4\frac{\lambda}{S_2^2}v_3^3\right] \neq 0.\end{aligned} \tag{4.11}$$

Then if (4.11) holds, a pitchfork bifurcation arises.

4.2.4 Eigenvalue: $\lambda_{2,4}$

Take $u^+ = p$. Then $\mathbf{v} = (0, 0, 0, 1)^T$ and $\mathbf{w} = (0, 0, 0, 1)^T$. Then using again (4.2), we have $\mathbf{F}_u(E_2, u^+) = \mathbf{0}$ implying $\mathbf{w}^T\mathbf{F}_u(E_2, u^+) = 0$. Further, $\mathbf{w}^T D\mathbf{F}_u(E_2, u^+)\mathbf{v} = 1 \neq 0$. Finally

$$\mathbf{w}^T D^2\mathbf{F}(E_2, u^+)(\mathbf{v}, \mathbf{v}) = D^2F^4(E_2, u^+)(\mathbf{v}, \mathbf{v}) = F^4_{LL}(E_2, u^+) = -2c_{LL} \neq 0,$$

because $H_{LL}(E_2, u^+) = 0$. Thus the transcritical bifurcation $u_{2,7} := u^+ = p$ arises between E_2 and E_7, in view of the fact that the eigenvalue $\lambda_{2,4}$ becoming positive implies that the corresponding hares population invades the system.

4.3 Equilibrium E_3

At E_3 we know the following Jacobian's eigenvalues,

$$\lambda_{3,1} = r - m + eaS_3 + abI_3, \quad \lambda_{3,4} = u - p - \beta\frac{I}{S+I}.$$

4.3.1 Eigenvalue: $\lambda_{3,1}$

Take $m^+ = r + eaS_3 + abI_3$. Then $\mathbf{v} = (v_1, v_2, v_3, 0)^T$ and $\mathbf{w} = (1, 0, 0, 0)^T$. Then

$$\mathbf{F}_m = \begin{pmatrix} -V \\ 0 \\ 0 \\ 0 \end{pmatrix} \quad D\mathbf{F}_m = \begin{bmatrix} -1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}, \tag{4.12}$$

but $\mathbf{F}_m(E_3, m^+) = \mathbf{0}$, so that $\mathbf{w}^T\mathbf{F}_m(E_3, m^+) = 0$. Also, $D\mathbf{F}_m(E_3, m^+)\mathbf{v} = (v_1, 0, 0, 0)^T$ so that $\mathbf{w}^T D\mathbf{F}_m(E_3, m^+)\mathbf{v} = v_1 \neq 0$. Further,

$$\begin{aligned} \mathbf{w}^T D^2\mathbf{F}(E_3, m^+)(\mathbf{v}, \mathbf{v}) &= D^2F^1(E_3, m^+)(\mathbf{v}, \mathbf{v}) \\ &= F^1_{VV}v_1^2 = -2v_1[c_{VV}v_1 - e(av_2 + bv_3)] \neq 0. \end{aligned} \tag{4.13}$$

Thus if (4.13) holds, we find the transcritical bifurcation $m_{3,4} := m^+ = r + eaS_3 + abI_3$ between E_3 and E_4, because the foxes are destabilized from vanishing, and therefore invade the system. Otherwise, observe that $\mathbf{w}^T D^3\mathbf{F}(E_3, m^+)(\mathbf{v}, \mathbf{v}, \mathbf{v}) = D^3F^1(E_3, m^+)(\mathbf{v}, \mathbf{v}, \mathbf{v}) = 0$, so that no pitchfork bifurcation can occur.

4.3.2 Eigenvalue: $\lambda_{3,4}$

Take

$$u^\ddagger = p + \frac{\beta I_3}{S_3 + I_3}$$

to have $\mathbf{v} = (0, v_2, v_3, v_4)^T$ and $\mathbf{w} = (0, 0, 0, 1)^T$. We have again (4.2), with $\mathbf{F}_u(E_3, u^\ddagger) = \mathbf{0}$, so that $\mathbf{w}^T\mathbf{F}_u(E_3, u^\ddagger) = 0$. Now, $D\mathbf{F}_u(E_3, u^\ddagger)\mathbf{v} = (0, 0, 0, v_4)^T$ so that $\mathbf{w}^T D\mathbf{F}_u(E_3, u^\ddagger)\mathbf{v} = v_4 \neq 0$. Moreover,

$$\begin{aligned} \mathbf{w}^T D^2\mathbf{F}(E_3, u^\ddagger)(\mathbf{v}, \mathbf{v}) &= D^2F^4(E_3, u^\ddagger)(\mathbf{v}, \mathbf{v}) \\ = F^4_{SS}v_2^2 + 2F^4_{SI}v_2v_3 + 2F^4_{SL}v_2v_4 + F^4_{II}v_3^2 + 2F^4_{IL}v_3v_4 + F^4_{LL}v_4^2. \end{aligned}$$

Now, observe that at E_3 the only nonvanishing derivatives of H, apart from those with respect to V which would disappear anyway, are H_{SL}, H_{IL}, H_{LL}. Thus we get

$$\begin{aligned} \mathbf{w}^T D^2\mathbf{F}(E_3, u^\ddagger)(\mathbf{v}, \mathbf{v}) = -2c_{LL}v_4^2 + 2\frac{\beta I_3}{(S_3 + I_3)^2}v_2v_4 \\ -2\frac{\beta S_3}{(S_3 + I_3)^2}v_3v_4 + \frac{\beta I_3}{(S_3 + I_3)^2}v_4^2. \end{aligned}$$

If the latter vanishes we get the transcritical bifurcation $u_{3,8} := u^{\ddagger} = p + \frac{\beta I_3}{S_3+I_3}$ between E_3 and E_8. In such case indeed, the hares population is destabilized from zero and enters in the system. If not, differentiating further, the only derivatives of H that do not disappear at E_3, apart from those with respect to V, which do not count because $v_1 = 0$, are H_{SSL}, H_{SIL}, H_{SLL}, H_{IIL}, H_{ILL}, H_{LLL}. It follows

$$\mathbf{w}^T D^3\mathbf{F}(E_3, u^{\ddagger})(\mathbf{v},\mathbf{v},\mathbf{v}) = -6\frac{\beta I_3}{(S_3+I_3)^3}v_2^2 v_4 - 3\beta\frac{I_3-S_3}{(S_3+I_3)^3}v_2 v_3 v_4$$
$$-12\frac{\beta I_3}{(S_3+I_3)^3}v_2 v_4^2 + 6\beta\frac{S_3}{(S_3+I_3)^3}v_3^2 v_4 - 6\beta\frac{I_3-S_3}{(S_3+I_3)^3}v_3 v_4^2 - 6\frac{\beta I_3}{(S_3+I_3)^3}v_4^3.$$

If the above expression is different from zero, we get a pitchfork bifurcation.

4.4 Equilibrium E_4

At E_4 we know only the following Jacobian's eigenvalue

$$\lambda_{4,4} = u - p - cV_4 - \frac{\beta I + \delta V}{V+S+I}.$$

4.4.1 Eigenvalue: $\lambda_{4,4}$

Take

$$u^* = p + cV_4 + \frac{\beta I + \delta V}{V+S+I}.$$

Here $\mathbf{v} = (v_1, v_2, v_3, 1)^T$ and $\mathbf{w} = (0,0,0,1)^T$. We find anew (4.2), with $\mathbf{F}_u(E_4, u^*) = \mathbf{0}$, so that $\mathbf{w}^T\mathbf{F}_u(E_4, u^*) = 0$.

Now, $D\mathbf{F}_u(E_4, u^*)\mathbf{v} = (0,0,0,1)^T$ so that $\mathbf{w}^T D\mathbf{F}_u(E_4, u^*)\mathbf{v} = 1 \neq 0$. Moreover,

$$\mathbf{w}^T D^2\mathbf{F}(E_4, u^*)(\mathbf{v},\mathbf{v}) = D^2F^4(E_4, u^*)(\mathbf{v},\mathbf{v}).$$

Now of all the possible partial derivatives of F^4, those that contain H and do not vanish at E_4 are H_{VL}, H_{SL}, H_{IL}, H_{LL}. Evaluation and substitution gives

$$\mathbf{w}^T D^2\mathbf{F}(E_4, u^*)(\mathbf{v},\mathbf{v}) = -2c_{LL} - 2cv_1 - 2\frac{\beta I_4 - \delta(S_4+I_4)}{(V_4+S_4+I_4)^2}v_1$$
$$+2\frac{\beta I_4 + \delta V_4}{(V_4+S_4+I_4)^2}v_2 + 2\frac{\beta(V_4+S_4) - \delta V_4}{(V_4+S_4+I_4)^2}v_3 + 2\frac{\beta I_4 + \delta V_4}{(V_4+S_4+I_4)^2}.$$

We thus get a transcritical bifurcation if the above quantity does not vanish, for the critical value $u_{4,9} := u^* = p + cV_4 + \frac{\beta I + \delta V_4}{V_4+S_4+I_4}$ in view of the fact that the zero value for the hares is now unstable. It connects the points

E_4 and E_9. Otherwise, keeping on differentiating, we find that the only nonvanishing derivatives of H are H_{VVL}, H_{VSL}, H_{VIL}, H_{VLL}, H_{SSL}, H_{SIL}, H_{SLL}, H_{ILL}, H_{LLL}. Their evaluation at the equilibrium point and at the critical bifurcation parameter threshold then gives

$$\begin{aligned}
-\mathbf{w}^T D^3\mathbf{F}(E_4,u^*)(\mathbf{v},\mathbf{v},\mathbf{v}) &= 3\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}v_1^2\\
&+6\left(\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\delta}{(V_4+S_4+I_4)^2}\right)v_1^2\\
&+3\left(2\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\delta}{(V_4+S_4+I_4)^2}\right)v_1v_2\\
&+3\left(2\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\beta+\delta}{(V_4+S_4+I_4)^2}\right)v_1v_3\\
&+6\left(2\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\delta}{(V_4+S_4+I_4)^2}\right)v_1\\
+3\left(2\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\beta}{(V_4+S_4+I_4)^2}\right)v_2v_3 &+12\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}v_2\\
&+6\left(\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\beta}{(V_4+S_4+I_4)^2}\right)v_3^2\\
+6\left(2\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}-\frac{\beta}{(V_4+S_4+I_4)^2}\right)v_3 &+6\frac{\beta I_4+\delta V_4}{(V_4+S_4+I_4)^3}.
\end{aligned}$$

Thus if $\mathbf{w}^T D^3\mathbf{F}(E_4,u^*)(\mathbf{v},\mathbf{v},\mathbf{v})\neq 0$ there is a pitchfork bifurcation.

4.5 Equilibrium E_5

At E_5 we know all the Jacobian's eigenvalues,

$$\lambda_{5,1}=r+ecL_5-m,\quad \lambda_{5,2}=s-n,\quad \lambda_{5,3}=\sigma s_I-n-\nu,\quad \lambda_{5,4}=-2c_{LL}L_5.$$

4.5.1 Eigenvalue: $\lambda_{5,1}$

Take $m^*=r+ecL_5$. Differentiating we have again (4.12) together with $\mathbf{v}=(v_1,0,0,v_4)^T$ and $\mathbf{w}=(1,0,0,0)^T$. In view of the fact that $\mathbf{F}_m(E_5,m^*)=\mathbf{0}$, it follows $\mathbf{w}^T\mathbf{F}_m(E_5,m^*)=0$. Moreover $\mathbf{w}^T D\mathbf{F}_m(E_5,m^*)\mathbf{v}=-v_1\neq 0$. In addition,

$$\begin{aligned}
\mathbf{w}^T D^2\mathbf{F}(E_5,m^*)(\mathbf{v},\mathbf{v}) &= F^1_{VV}v_1^2+2F^1_{VL}v_1v_4+F^1_{LL}v_4^2\\
&=-2c_{VV}v_1^2+2ecv_1v_4.
\end{aligned}$$

If

$$c_{VV}v_1\neq ecv_4 \tag{4.14}$$

then because now the fox population must appear in the system, the transcritical bifurcation $m_{5,6} := m^* = r + ecL_5$ takes place between the points E_5 and E_6. Conversely, we find

$$\mathbf{w}^T D^3\mathbf{F}(E_5, m^*)(\mathbf{v},\mathbf{v},\mathbf{v}) = D^3F^1(E_5, m^*)(\mathbf{v},\mathbf{v},\mathbf{v}) = 0,$$

so that no pitchfork bifurcation can arise.

4.5.2 Eigenvalue: $\lambda_{5,2}$

Take $\tilde{s} = n$. Then $\mathbf{v} = (0,1,0,0)^T$ and $\mathbf{w} = (0, w_2, w_3, 0)^T$. Differentiating we have again (4.5). In view of the fact that $\mathbf{F}_s(E_5, \tilde{s}) = \mathbf{0}$, it follows $\mathbf{w}^T\mathbf{F}_s(E_5, \tilde{s}) = 0$. Moreover $\mathbf{w}^T D\mathbf{F}_s(E_5, \tilde{s})\mathbf{v} = w_2 \neq 0$. In addition,

$$\begin{aligned}\mathbf{w}^T D^2\mathbf{F}(E_5, \tilde{s})(\mathbf{v},\mathbf{v}) &= w_2 D^2F^2(E_5, \tilde{s})(\mathbf{v},\mathbf{v}) + w_3 D^2F^3(E_5, \tilde{s})(\mathbf{v},\mathbf{v}) \\ &= w_2 F^2_{SS} + w_3 F^3_{SS} = -2c_{SS}w_2 \neq 0,\end{aligned}$$

because $G_{SS}(E_5, \tilde{s}) = 0$ and $K_{SS}(E_5, \tilde{s}) = 0$. Thus there is the transcritical bifurcation $n_{5,7} := \tilde{s} = n$ connecting E_5 with E_7, as the susceptible cottontails must enter in the system.

4.5.3 Eigenvalue: $\lambda_{5,3}$

Take $\tilde{s}_I = (n+\nu)\sigma^{-1}$. Then $\mathbf{v} = (0, v_2, v_3, v_4)^T$ and $\mathbf{w} = (0,0,1,0)^T$. Differentiating

$$\mathbf{F}_{s_I} = \begin{pmatrix} 0 \\ (1-\sigma)I \\ \sigma I \\ 0 \end{pmatrix} \quad D\mathbf{F}_{s_I} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & (1-\sigma) & 0 \\ 0 & 0 & \sigma & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}, \tag{4.15}$$

In view of the fact that $\mathbf{F}_{s_I}(E_5, \tilde{s}_I) = \mathbf{0}$, it follows $\mathbf{w}^T\mathbf{F}_{s_I}(E_5, \tilde{s}_I) = 0$. Moreover $\mathbf{w}^T D\mathbf{F}_{s_I}(E_5, \tilde{s}_I)\mathbf{v} = \sigma(n-s) \neq 0$ because $\lambda_{5,2} \neq 0$. In addition,

$$\begin{aligned}&\mathbf{w}^T D^2\mathbf{F}(E_5, \tilde{s}_I)(\mathbf{v},\mathbf{v}) = D^2F^3(E_5, \tilde{s}_I)(\mathbf{v},\mathbf{v}) = \\ &F^3_{SS}(E_5, \tilde{s}_I)v_2^2 + 2D^2F^3_{SI}(E_5, \tilde{s}_I)v_2v_3F^3_{II}(E_5, \tilde{s}_I)v_3^2\end{aligned}$$

Here we need to recall (3.23) and the discussion after writing the Jacobian in Section 3.3.

Observe that for the second derivatives of G we have

$$G_{SS}(E_5, \tilde{s}_I) = 0, \quad G_{SI} = \frac{\gamma}{L_5}, \quad G_{II}(E_5, \tilde{s}_I) = 0.$$

All those of K instead vanish in view of the assumption (3.23). Thus

$$\mathbf{w}^T D^2\mathbf{F}(E_5, \tilde{s}_I)(\mathbf{v},\mathbf{v}) = \left(\frac{\gamma}{L_5} - 2c_{SI}\right) v_2v_3 \tag{4.16}$$

If the above quantity does not vanish, we have the transcritical bifurcation $s_{I5,8} := \tilde{s}_I = (n+\nu)\sigma^{-1}$ joining E_5 and E_8, because the infected cottontails must enter in the environment, their zero value is destabilized, and with them the healthy ones as well. Instead, if the quantity in (4.16) vanishes, we evaluate further, still recalling (3.23).

$$\mathbf{w}^T D^2\mathbf{F}(E_5,\tilde{s}_I)(\mathbf{v},\mathbf{v},\mathbf{v}) = D^2F^3(E_5,\tilde{s}_I)(\mathbf{v},\mathbf{v}) = G_{SSS}(E_5,\tilde{s}_I)v_2^3$$
$$+3G_{SSI}(E_5,\tilde{s}_I)v_2^2v_3 + 3G_{SII}(E_5,\tilde{s}_I)v_2v_3^2 + G_{III}(E_5,\tilde{s}_I)v_3^3 = 6\frac{\gamma}{L_5}(v_2L_5+v_3)$$

If this quantity does not vanish, a pitchfork bifurcation exists instead.

4.5.4 Eigenvalue: $\lambda_{5,4}$

Take $u^+ = p$. Then $\mathbf{v} = (0,0,0,1)^T$ and $\mathbf{w} = (w_1,0,w_3,w_4)^T$. Using (4.2), $\mathbf{F}_u(E_5,u^+) = \mathbf{0}$, because $L_5 = 0$ for $u = u^+$. Hence $\mathbf{w}^T\mathbf{F}_u(E_5,u^+) = 0$, as well as $\mathbf{w}^T D\mathbf{F}_u(E_5,u^+)\mathbf{v} = w_4 \neq 0$. Also, because the only nonvanishing component of $\mathbf{v}$ is the fourth one,

$$D^2\mathbf{F}(E_5,u^+)(\mathbf{v},\mathbf{v}) = \mathbf{F}_{LL}(E_5,u^+) = (0,-G_{LL}-K_{LL},G_{LL}+K_{LL},-2c_{LL}-H_{LL})^T.$$

On the other hand, $G_{LL}(E_5,u^+) = 0$, $H_{LL}(E_5,u^+) = 0$, so that we obtain $\mathbf{w}^T D^2\mathbf{F}(E_5,u^+)(\mathbf{v},\mathbf{v}) = -2c_{LL}w_4 \neq 0$ and there is the transcritical bifurcation $u_{5,0} := u^+ = p$ joining the origin with E_5. Indeed whenever $u < u_{5,0}$, conditions (3.24) hold.

4.6 Equilibrium E_7

At E_7 we know all the Jacobian's eigenvalues,

$$\lambda_{7,1} = r + eaS_7 + ecL_7 - m, \quad \lambda_{7,2} = -2c_{SS}S_7,$$
$$\lambda_{7,3} = s_I + \lambda + \gamma S_7S_7 + I_7 - c_{IS}S_7n - \nu, \quad \lambda_{7,4} = -2c_{LL}L_7.$$

In this situation, we observe that the eigenvalues $\lambda_{7,2}$ and $\lambda_{7,4}$ give rise to the same bifurcations $n_{5,7}$ and $u_{2,7}$ already found before and thus will not be analysed again.

4.6.1 Eigenvalue: $\lambda_{7,1}$

Take $\tilde{m} = r + aeS_7 + ecL_7$. Hence $\mathbf{v} = (v_1,v_2,v_3,v_4)^T$ and $\mathbf{w} = (1,0,0,0)^T$. From (4.12), $\mathbf{F}_m(E_7,\tilde{m}) = (-V_7,0,0,0)^T = \mathbf{0}$, because $V_7 = 0$, and from this $\mathbf{w}^T\mathbf{F}_m(E_7,\tilde{m}) = 0$. Further $\mathbf{w}^T D\mathbf{F}_m(E_7,\tilde{m})\mathbf{v} = -v_1 \neq 0$.

Moreover,

$$\mathbf{w}^T D^2\mathbf{F}(E_7,\tilde{m})(\mathbf{v},\mathbf{v}) = D^2F^1(E_7,\tilde{m})(\mathbf{v},\mathbf{v}) = 2v_1[e(av_2+bv_3+cv_4)-c_{VV}v_1]$$

If it is different from zero, there is the transcritical bifurcation $m_{7,9} = \tilde{m} = r + aeS_7 + ecL_7$ between E_7 and E_9 because the foxes are destabilized from their vanishing; if not, since

$$\mathbf{w}^T D^3\mathbf{F}(E_7, \tilde{m})(\mathbf{v}, \mathbf{v}, \mathbf{v}) = D^3F^1(E_7, \tilde{m})(\mathbf{v}, \mathbf{v}, \mathbf{v}) = 0,$$

no pitchfork bifurcation can occur.

4.6.2 Eigenvalue: $\lambda_{7,3}$

Take

$$s_I^+ = \frac{1}{\sigma}\left[c_{IS}S_7 + n + \nu - \lambda - \frac{\gamma S_7}{S_7 + L_7}\right].$$

Here $\mathbf{v} = (0, v_2, v_3, v_4)^T$ and $\mathbf{w} = (w_1, 0, w_3, 0)^T$. From (4.15) we thus have $\mathbf{w}^T\mathbf{F}_{s_I}(E_7, s_I^+) = \mathbf{0}$ and $\mathbf{w}^T D\mathbf{F}_{s_I}(E_7, s_I^+)\mathbf{v} = \sigma v_3 \neq 0$. Also, because $v_1 = 0$, it is easily seen that $D^2F^1(\mathbf{v}, \mathbf{v}) = \mathbf{0}$. Hence

$$\begin{aligned}\mathbf{w}^T D^2\mathbf{F}(E_7, s_I^+)(\mathbf{v}, \mathbf{v}) &= w_3 D^2F^3(E_7, s_I^+)(\mathbf{v}, \mathbf{v}) \\ &= w_3[F^3_{SS}v_2^2 + 2F^3_{SI}v_2v_3 + 2F^3_{SL}v_2v_4 + F^3_{II}v_3^2 + 2F^3_{IL}v_3v_4^2 + F^3_{LL}v_4^2] \\ = -2v_3w_3\left[c_{IS}v_2 + c_{II}v_3 - \frac{\gamma L_7}{S_7 + L_7}v_2 + \frac{\gamma S_7}{(S_7 + L_7)^2}(v_3 + v_4) - \frac{\lambda}{S_7^2}v_4 + \frac{\lambda}{S_7}v_3\right].\end{aligned}$$

If the latter does not vanish, the infected cottontail population is destabilized and must appear in the system. We thus have the transcritical bifurcation $s_{I7,8} = s_I^+$ between E_7 and E_8. If not, again observe that $D^3F^1(\mathbf{v}, \mathbf{v}, \mathbf{v}) = \mathbf{0}$. It follows

$$\begin{aligned}\mathbf{w}^T D^3\mathbf{F}(E_7, s_I^+)(\mathbf{v}, \mathbf{v}, \mathbf{v}) &= w_3 D^3F^3(E_7, s_I^+)(\mathbf{v}, \mathbf{v}) \\ = \Bigg[-6\frac{\lambda}{S_7^3}v_2^2v_3 - 12\frac{\lambda}{S_7^3}v_2v_3^2 + 6\frac{\lambda}{S_7^2}v_3^3 + 6\frac{\gamma(S_7 - L_7)}{(S_7 + L_7)^3}v_2v_3^2 + 3\frac{\gamma(S_7 - L_7)}{(S_7 + L_7)^3}v_2v_3v_4 \\ +6\frac{\gamma S_7}{(S_7 + L_7)^3}v_3^3 - 12\frac{\gamma S_7}{(S_7 + L_7)^3}v_3^2v_4 + 6\frac{\gamma S_7}{(S_7 + L_7)^3}v_3v_4^2\Bigg] w_3\end{aligned}$$

so that if the quantity in the bracket does not vanish, a pitchfork bifurcation occurs.

4.7 Equilibrium E_8

At E_8 we know only

$$\lambda_{8,1} = r + eaS_8 + ebI_8 + ceL_8 - m.$$

4.7.1 Eigenvalue: $\lambda_{8,1}$

Take $r^* = m - eaS_8 - ebI_8 - ceL_8$. Then $\mathbf{v} = (v_1, v_2, v_3, v_4)^T$ and $\mathbf{w} = (1, 0, 0, 0)^T$. Using (4.1), $\mathbf{F}_r(E_8, r^*) = \mathbf{0}$ and then $\mathbf{w}^T\mathbf{F}_r(E_8, r^*) = 0$. Also, $\mathbf{w}^T D\mathbf{F}_r(E_8, r^*)\mathbf{v} = v_1 \neq 0$ and

$$\mathbf{w}^T D^2\mathbf{F}(E_8, r^*)(\mathbf{v}, \mathbf{v}) = F^1_{VV}v_1^2 + 2F^1_{VS}v_1v_2 + 2F^1_{VI}v_1v_3 + 2F^1_{VL}v_1v_4$$

because $F^1_{JM} = 0$ for all other indices $J, M \in \{V, S, I, L\}$. Finally,

$$\mathbf{w}^T D^2\mathbf{F}(E_8, r^*)(\mathbf{v}, \mathbf{v}) = -2c_{VV}v_1^2 + 2ev_1(av_2 + bv_3 + cv_4).$$

If it does not vanish, i.e. for

$$e(av_2 + bv_3 + cv_4) \neq c_{VV}v_1$$

the foxes must appear in the system and we get the transcritical bifurcation $r_{8,9} = r^* = m - eaS_8 - ebI_8 - ceL_8$ joining E_8 and E_9. Else, since $F^1_{JMN} = 0$ for all indices $J, M, N \in \{V, S, I, L\}$, $\mathbf{w}^T D^3\mathbf{F}(E_8, r^*)(\mathbf{v}, \mathbf{v}, \mathbf{v}) = 0$ follows, hence no pitchfork bifurcation can arise.

5 Conclusions

Figure 9 summarizes the bifurcations found, both analytically and numerically. It constitutes the main tool for the applied ecologist that wants to act on the disease spread, trying to contain the virus propagation. In applying possible containment programs, one important issue is to be kept in mind, that possible interference with the system may not always lead to the desired outcomes. Indeed, the destabilization of a configuration that is stable in some actual conditions not always corresponds to attaining another one that is wanted. For instance, in the presence of the virus and all populations in the system, at the coexistence equilibrium E_9, a control program for the foxes for instance could be envisaged, to remove the virus carriers. However, as it is clearly seen in Figure 9, acting on the foxes reproduction rate r, the outcome leads to the equilibrium E_8 where the infected cottontails thrive, and the problem is not solved. Instead, acting on the foxes mortality rate m would allow also the removal of the infected cottontails. However, note also that each bifurcation parameter contains the other one: rewriting for instance the transition between E_8 and E_9 in terms of m, we would get $m_{8,9} = m^\dagger = r + eaS_8 + ebI_8 + ceL_8$. In this situation, we can easily check that $\mathbf{F}_m(E_8, m^\dagger) = \mathbf{0}$ and then $\mathbf{w}^T\mathbf{F}_m(E_8, m^\dagger) = 0$, while $\mathbf{w}^T D\mathbf{F}_m(E_8, m^\dagger)\mathbf{v} = v_1 \neq 0$ is also satisfied. There would be no relevant change in what concerns the second derivative $\mathbf{w}^T D^2\mathbf{F}(E_8, m^\dagger)(\mathbf{v}, \mathbf{v})$, so that if it does not vanish, the same transcritical bifurcation connecting E_8 and E_9 occurs in terms of $m_{8,9} = m^\dagger$, a threshold value that depends on the populations at E_8. Then, comparing this value with $m_{7,9}$, that depends

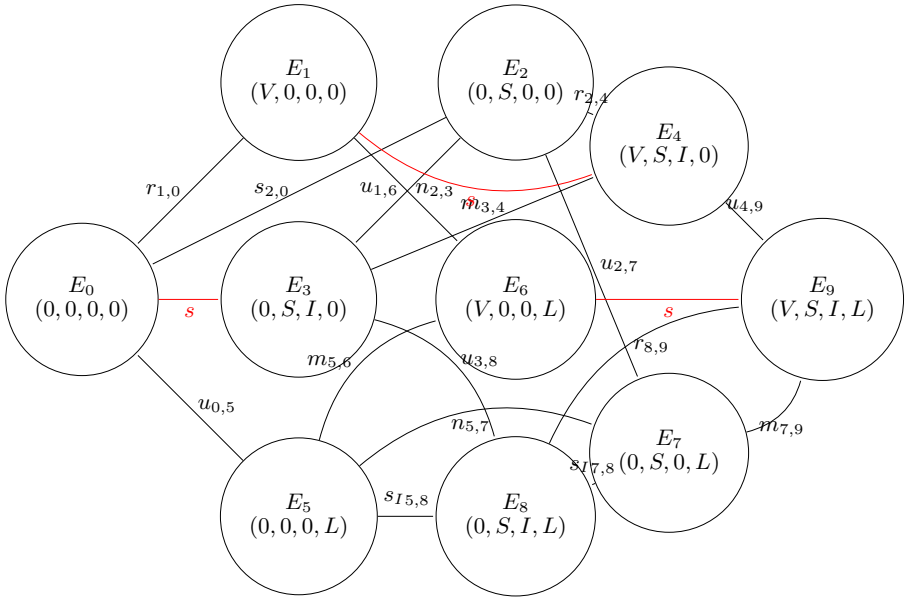

Fig. 9 Picture of the whole bifurcation structure of the model (2.7) arising from the analysis of Section 4. In each node, the name of equilibrium is reported, together with its nonvanishing populations. Bifurcation thresholds: $r_{1,0} = m$, $u_{1,6} = p + \delta + cV_1$, $r_{2,4} = m - ae\frac{s-n}{c_{SS}}$, $s_{2,0} = n$, $n_{2,3} = n^{\dagger}$, $u_{2,7} = p$, $m_{3,4} = r + eaS_3 + abI_3$, $u_{3,8} = p + \frac{\beta I_3}{S_3+I_3}$, $u_{4,9} = p + cV_4 + \frac{\beta I + \delta V_4}{V_4+S_4+I_4}$, $m_{5,6} = r + ecL_5$, $n_{5,7} = n$, $s_{I5,8} := \tilde{s}_I = (n+\nu)\sigma^{-1}$, $u_{5,0} = p$, $m_{7,9} = r + aeS_7 + ecL_7$, $s_{I7,8} = s_I^+$, $r_{8,9} = m - eaS_8 - ebI_8 - ceL_8$. The bifurcations obtained only numerically are shown in red.

on the populations at equilibrium E_7, allows to determine which transition actually occurs first in decreasing the fox mortality, and thus where would the system settle from coexistence. As this action could also be carried out by external human-related control measures, the information is important from the ecological point of view. The analysis therefore could clarify these situations and avoid pitfalls in the epidemics management.

Appendix

Recalling (3.1), we find:

$$G_V = S\frac{\alpha(S+I+L)-\gamma I}{P^2}, G_S = \frac{\gamma I(V+I+L)+\alpha V(V+I+L)}{P^2}, \quad (5.1)$$
$$G_I = S\frac{\gamma(V+S+L)-\alpha V}{P^2}, G_L = -S\frac{\alpha V+\gamma I}{P^2};$$

$$G_{VV}=-2S\frac{\alpha(S+I+L)-\gamma I}{P^3}, G_{VI}=S\frac{\alpha-\gamma}{P^2}-2S\frac{\alpha(S+I+L)-\gamma I}{P^3},$$
$$G_{VS}=\frac{\alpha(2S+I+L)-\gamma I}{P^2}-2S\frac{\alpha(S+I+L)-\gamma I}{P^3},$$
$$G_{VL}=\frac{\alpha S}{P^2}-2S\frac{\alpha(S+I+L)-\gamma I}{P^3}, G_{SS}=-2\frac{(\gamma I+\alpha V)(V+I+L)}{P^3},$$
$$G_{SI}=\frac{\gamma(V+2I+L)+\alpha V}{P^2}-2\frac{(\gamma I+\alpha V)(V+I+L)}{P^3},$$
$$G_{SL}=\frac{\gamma I+\alpha V}{P^2}-2\frac{(\gamma I+\alpha V)(V+I+L)}{P^3}, G_{LL}=2S\frac{\alpha V+\gamma I}{P^3},$$
$$G_{IL}=\frac{\gamma S}{P^2}-2S\frac{\gamma(V+S+L)-\alpha V}{P^3}, G_{II}=-2S\frac{\gamma(V+S+L)-\alpha V}{P^3};$$

(5.2)

$$G_{VVV}=6S\frac{\alpha(S+I+L)-\gamma I}{P^4}, G_{SSS}=6\frac{(\gamma I+\alpha V)(V+I+L)}{P^4},$$
$$G_{VVS}=-2\frac{\alpha(2S+I+L)-\gamma I}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VVI}=-2S\frac{\alpha-\gamma}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VVL}=-2S\frac{\alpha}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VSS}=2\frac{\alpha}{P^2}-4\frac{\alpha(2S+I+L)-\gamma I}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VSI}=\frac{\alpha-\gamma}{P^2}-2\frac{\alpha(2S+I+L)-\gamma I}{P^3}-2S\frac{\alpha-\gamma}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VSL}=\frac{\alpha}{P^2}-2\frac{\alpha(2S+I+L)-\gamma I}{P^3}-2S\frac{\alpha}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{VIL}=-2S\frac{\alpha-\gamma}{P^3}-2\frac{\alpha S}{P^3}+6S\frac{\alpha(S+I+L)-\gamma I}{P^4},$$
$$G_{SSI}=-2\frac{(\gamma I+\alpha V)+\gamma(V+I+L)}{P^3}+6\frac{(\gamma I+\alpha V)+\gamma(V+I+L)}{P^4},$$
$$G_{SSL}=-2\frac{\gamma I+\alpha V}{P^3}+6\frac{(\gamma I+\alpha V)(V+I+L)}{P^4},$$

(5.3)

$$G_{SII} = \frac{2\gamma}{P^2} - 2\frac{\gamma(V+I+L)+\alpha V}{P^3} \tag{5.4}$$
$$-2\frac{\gamma I+\alpha V+\gamma(V+I+L)}{P^3} + 6\frac{(\gamma I+\alpha V)(V+I+L)}{P^4},$$
$$G_{SIL} = \frac{\gamma}{P^2} - \frac{2\gamma(V+L)+4(\gamma I+\alpha V)}{P^3} + 6\frac{(\gamma I+\alpha V)(V+I+L)}{P^4},$$
$$G_{SLL} = 6\frac{(\gamma I+\alpha V)(V+I+L)}{P^4} - 4\frac{\gamma I+\alpha V}{P^3}, \quad G_{LLL} = -6S\frac{\gamma I+\alpha V}{P^4},$$
$$G_{VII} = -2\frac{(\gamma-\alpha)S}{P^3} + 6S\frac{\gamma(V+S+L)-\alpha V}{P^4},$$
$$G_{III} = 6S\frac{\gamma(V+S+L)-\alpha V}{P^4}, \quad G_{IIL} = 6S\frac{\gamma(V+S+L)-\alpha V}{P^4} - 2\frac{\gamma S}{P^3},$$
$$G_{VLL} = \frac{2\alpha S}{P^3} - 6S\frac{\alpha V+\gamma I}{P^4}, \quad G_{ILL} = -4\frac{\gamma S}{P^3} + 6S\frac{\gamma(V+S+L)-\alpha V}{P^4}.$$

$$H_V = -L\frac{\beta I+\delta V}{P^2} + \frac{\delta L}{P}, \quad H_S = -L\frac{\beta I+\delta V}{P^2}, \tag{5.5}$$
$$H_I = L\frac{\beta(V+S+L)-\delta V}{P^2}, \quad H_L = \frac{\beta I+\delta V}{P} - L\frac{\beta I+\delta V}{P^2};$$

$$H_{VV} = -\frac{2\delta L}{P^2} + 2L\frac{\beta I+\delta V}{P^3}, \quad H_{VS} = 2L\frac{\beta I+\delta V}{P^3} - \frac{\delta L}{P^2}, \tag{5.6}$$
$$H_{VI} = -L\frac{\beta+\delta}{P^2} + 2L\frac{\beta I+\delta V}{P^3}, \quad H_{SI} = 2L\frac{\beta I+\delta V}{P^3} - \frac{\beta L}{P^2},$$
$$H_{VL} = -\frac{\beta I+\delta(V+L)}{P^2} + 2L\frac{\beta I+\delta V}{P^3} + \frac{\delta}{P}, \quad H_{SS} = 2L\frac{\beta I+\delta V}{P^3},$$
$$H_{SL} = 2L\frac{\beta I+\delta V}{P^3} - \frac{\beta I+\delta V}{P^2}, \quad H_{II} = -\frac{2\beta L}{P^2} + 2L\frac{\beta I+\delta V}{P^3},$$
$$H_{IL} = \frac{\beta}{P} - \frac{\beta(I+L)+\delta V}{P^2} + 2L\frac{\beta I+\delta V}{P^3},$$
$$H_{LL} = -\frac{\beta I+\delta V}{P^2} + 2L\frac{\beta I+\delta V}{P^3};$$

$$H_{VVV} = -\frac{6\delta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{VVS} = 4\frac{\delta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \tag{5.7}$$
$$H_{VVI} = 4\frac{\delta L}{P^3} + 2\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{VSI} = 2L\frac{\beta + \delta}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{VVL} = 4\frac{\delta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4} - 2\frac{\delta L}{P^2} + \frac{\beta I + \delta V}{P^3},$$
$$H_{VSL} = 2\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4} + \frac{\delta(2L - P)}{P^3} \quad H_{SSS} = -6L\frac{\beta I + \delta V}{P^4},$$
$$H_{VIL} = -\frac{\beta + \delta}{P^2} + 2\frac{\beta I + \delta V}{P^3} + 2L\frac{\beta + \delta}{P^3} - 6L\frac{\beta I + \delta V}{P^4};$$

$$H_{VLL} = 4\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4} - 2\frac{\delta}{P^2} + 2L\frac{\delta}{P^3}, \tag{5.8}$$
$$H_{VSS} = 2\frac{\delta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{VII} = 6\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{SSI} = 2\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{SSL} = 2\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{SIL} = -\frac{\beta}{P^3} + 2\frac{\beta L}{P^3} + 2\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{SII} = 4\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{SLL} = 4\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{III} = 6\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}, \quad H_{LLL} = 6\frac{\beta I + \delta V}{P^3} - 6L\frac{\beta I + \delta V}{P^4},$$
$$H_{IIL} = -2\frac{\beta}{P^2} + 4L\frac{\beta}{P^3} + 2\frac{\beta L + \delta V}{P^3} - 6L\frac{\beta L + \delta V}{P^4},$$
$$H_{ILL} = -2\frac{\beta}{P^2} + 4L\frac{\beta I + \delta V}{P^3} + 2\frac{\beta L}{P^3} - 6L\frac{\beta I + \delta V}{P^4}.$$

$$K_S = \lambda\frac{I^2}{(S+I)^2}, \quad K_I = \lambda\frac{S^2}{(S+I)^2}; \quad K_{SS} = -2\lambda\frac{I^2}{(S+I)^3}, \tag{5.9}$$
$$K_{SI} = 2\lambda\frac{I}{(S+I)^2} - 2\lambda\frac{I^2}{(S+I)^3}, \quad K_{II} = -2\lambda\frac{S^2}{(S+I)^3};$$

$$K_{SSS} = 6\lambda\frac{I}{(S+I)^4}, \quad K_{SSI} = -\frac{2\lambda}{(S+I)^3} + 6\lambda\frac{I}{(S+I)^4}, \tag{5.10}$$
$$K_{SII} = -\frac{4\lambda}{(S+I)^3} + 6\lambda\frac{I}{(S+I)^4}, \quad K_{III} = 6\lambda\frac{S^2}{(S+I)^4}.$$

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