A VIRAL TRANSMISSION MODEL FOR FOXES-COTTONTAILS-HARES INTERACTION: INFECTION THROUGH PREDATION

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Abstract. The Eastern cottontail Sylvilagus floridanus is a lagomorph native to North America, introduced in Italy since the 1960s. In Central and Northern Italy, the cottontail overlaps its range with the native European hare Lepus europaeus and affects the predator-prey dynamics of native hares and foxes. Field data indicate that the cottontail is susceptible to infection by the European brown hare syndrome (EBHS) virus. Although the real role of cottontails and native foxes in the spreading of EBHS viruses is yet uncertain, we present a cottontail-hare-fox model including possible effects of EBHS, imported by foxes, through environmental contamination. A rather complete map of the possible system equilibria and their mutual relationship and transition is established.

1. Introduction. Biological invasions are considered one of the major threats to native biodiversity and ecosystems [27, 33]. One of the mechanisms that can lead invasive species to have a negative impact on native species, is the transport of diseases. The role played by alien species in the onset of disease in wildlife has been increasingly recognized [28, 12]. The replacement in Europe of the native Eurasian red squirrel (Sciurus vulgaris) by the American Eastern Grey squirrel (Sciurus carolinensis) is a well know case. The replacement between the two species is mainly due to exploitation competition for food resources, with the American species being more efficient in their use [34]. In Great Britain, however, grey squirrels carry a squirrelpox virus which is lethal for the red squirrel and this diseases-mediated
competition increases the speed of the replacement [30, 31, 25] Models to explore two species interaction have been recently investigated, [31, 2, 21]. Alien species could also act as amplifiers of local pathogens. In New Zealand, the introduced Australian possums *Trichosurus vulpecula* became the main reservoir host for bovine tuberculosis [23].

The Eastern cottontail (*Sylvilagus floridanus*, hereafter cottontail) is a lagomorph native to North America, which has been introduced several times in Italy for hunting reasons since the 1960s [6]. The cottontail has colonized most of Central and Northern Italy due to a mix of natural spread and translocations [15, 22]. In this area, the cottontail overlaps its range with the native European hare. Where the two species are sympatric, they select different habitats during feeding activity and for resting [3, 4]. However, Cerri and colleagues [10] showed an interaction between the two lagomorphs and the red fox (*Vulpes vulpes*) as predator of both species. Introduced cottontails affect predator-prey dynamics of native hares and foxes: in areas where cottontails are present with high densities, increases in the abundance of foxes are negatively correlated with the abundance of European hares [10]. This pattern is suggestive of an indirect apparent competition between cottontails and hares mediated by foxes predation. In [8] a mathematical model to simulate this three-species system is proposed, where the apparent competition between introduced cottontails and native hares is mediated by an increased predation rate by foxes. The model results indicate an increase in foxes’ densities after the invasion of cottontail, which supports a hyperpredation on native hares.

Cottontails carry several viruses and parasites, which can potentially affect hares [5, 29], however competitive interactions mediated by parasites have not yet been highlighted. Field and experimental data indicate that the cottontail may be infected by the European brown hare syndrome (EBHS) [19]. EBHS is an acute and lethal form of hepatitis caused by a lagovirus, the European brown hare syndrome virus (EBHSV), which infects hares and entails high mortality rates [17]. Transmission presumably occurs directly, through a faecal-oral route, or indirectly through contaminated water and food sources. Tizzani and colleagues [29] induced clinical disease and mortality in a low number of experimentally infected cottontails. The results of these studies demonstrate the transmissibility of EBHS to cottontails and support the hypothesis that this species could play a role in the spreading of the disease; however, the relevance of this role is not yet known. For instance, [13] analysed biological samples from 267 cottontails hunted in Tuscany and found no evidence of EBHS circulation in this population. To consider this issue, we also introduced a disease in the three-species system to account for the EBHSV, [9]. In this model we assumed that red foxes are all potential virus carriers, and cottontails are assumed to be partly infected. We simulate a situation in which the virus is introduced in an area and spills over to the two prey populations, of which the hares are heavily affected in that they succumb to it almost immediately. This model has further ecological background. Indeed, carnivores are potential carriers of viruses and other pathogens that infect their prey, even if they may not be susceptible to diseases. In [11] genetic prints of the EBHSV in the intestinal content of one fox in an area where an EBHS outbreak was present in hares were found. The authors did not prove that lagovirus remained infective in the excreted faeces contaminating the environment; this possibility however could not be excluded suggesting that foxes might, at least theoretically, assume a potential role in the indirect transmission of EBHS viruses. Here, in contrast to [9], we are thus interested in simulating a
situation where infected cottontails are released in a place where hares are virus-free and foxes can become carriers through environmental contamination. This scenario might be less common, but could indeed occur and represents an interesting biological invasion example.

2. The model. We start by presenting the ecological background of this investigation. The mathematical model is formulated via some simplifying assumptions of the underlying very complex biological situation. In particular, in this paper we consider the red foxes as potential virus carriers, distinguished among healthy $V$ and carriers $U$. Sometimes, we might name them “infected” foxes instead, to distinguish them from the non-carrier ones. However, they should always be regarded as healthy virus carriers, but nevertheless able to spread the EBHS. The next point concerns the meaning of “carrying” the virus. It could be just in their guts, but also in some organs. Since not much is yet known in this situation, we assume both instances, and further assume that once the virus enters the body of the animal, the latter cannot get rid of it any longer. Thus recovery is not allowed here.

Vertical virus transmission by foxes is allowed in principle, for two reasons. First of all, the virus cannot be passed to offsprings by carrier parents, if it lies just in the guts. However, what we really want to model is the fact that the offsprings while reared by their parents in the den, may get the virus either from their parents or from the contamination within the den. Thus part of the new generation could be a carrier, at least theoretically. Since this issue is not clear from the available biological data so far, to add this type of transmission into the model does not harm it. In case it is proved that it cannot occur, it will be enough to set the parameter $\zeta$ to zero, to remove it. On the other hand, in case it is not contemplated in the model and in fact it is indeed found to occur, the model would not be usable any longer. Thus it is better to formulate a flexible model that can easily be adapted.

Note further that the viruses are not explicitly taken into consideration as a system variable, to keep the size of the dynamical system down, and because field data on them are essentially impossible to obtain. But they are considered implicitly, through the diseased animals and through the environmental contamination term described later that appears in the hares equation. All European hares $L$ are assumed to be healthy. If they become infected, they die very fast, before being able to be hunted or reproducing, and this is accounted for by assuming that a successful contact with the virus, independently of its source, leads immediately to their death. In this way an infected hares compartment is avoided. Also, all eastern cottontails $S$ are assumed to be infected, and therefore virus carriers.

EBHSV circulation in hares is directly linked to hare population densities [20]. The disease has not been observed in hares younger than approximately 40-50 days, while those of 2-3 months of age may contract the infection but usually do not develop clinical disease. At low-density values (less than 8 hares km$^{-2}$), the spread of the virus is reduced, and most juveniles become adults without entering in contact with the virus. When these animals are infected by EBHSV when adults, they could die. On the contrary, at higher densities (larger than 15 adults km$^{-2}$), the virus circulates within young hares, and they have the opportunity to be infected without developing clinical signs, acquiring a long-lasting protective immunity. However, we assume that hares have a low density, and therefore, in the model, we do not account for disease immunity.
The low density assumption also implies that the fox predation on hares can be modeled simply by a bilinear term, as in such case the Holling Type II (HTII) term, that is more appropriate to describe the feeding satiation phenomenon for low values of the prey, essentially coincides with the Holling Type I (HTI) term. We therefore assume the latter.

The infection of the hares occurs only through the environment where viruses are released in a continuous way by the animals. While the virus in the open decays, its continuous replenishment ensures that a viral charge is always present in the environment. To evaluate it, we use a fraction in which the numerator contains the contamination contribution of the virus-affected populations, i.e. carrier foxes and infected cottontails, and in the denominator appear all the dejections of the animals in the environment, that are proportional to the hares, cottontails and total foxes population sizes. Ultimately, the fraction representing contamination looks like the standard incidence disease transmission, but in fact it differs from it as discussed below. Note indeed that epidemic models account for transmission mainly by either a bilinear function, meaning mass action, or the standard, also called frequency-dependent, incidence. The latter indeed better explains the fact that in a large population of size $N$, for simplicity partitioned just among susceptibles and infected, an infected individual does not meet in the unit time the whole set of susceptibles, but only some of them. These represent a sizeable fraction of the susceptibles when $N$ is small, which reduces progressively with the increasing size of $N$. It is also more realistic, as the fraction in the term $\alpha N^{-1}$ represents the probability that a susceptible encounters an infected, from which the contact possibly results in a new infection and therefore the individual moves to the class of infected, the transition rate being expressed by the coefficient $\alpha$. As explained above, following this interpretation, in our case $N$ gets replaced by all the agents that possibly pollute the environment, i.e. a term that involves the whole system populations, $U + V + S + L$. The latter represents a simplification of the actual real situation, in which the dejections are proportional to the various animals body sizes, namely more precisely we would have a weighted sum of the various populations $w_U U + w_V V + w_S S + w_L L$. However, these animals are roughly of the same size, ranging from 4 up to 11 kilos for the red fox, [7], 1.5 to 6 kilos for the hares, while cottontails are smaller 0.9 to 1.8 kilos, [1]. Using Occam's razor then, we assume $w_U = w_V = w_S = w_L = w$ and incorporate this last constant within the virus contamination constants $\eta$ and $\xi$ discussed below. The infected $I$ instead are replaced by the pollution due to the virus-affected animals, given by $\eta U + \xi S$, with suitable scalings, which implicitly describe the possibly different virus contamination of the environment by the carrier foxes and the infected cottontails. The pollution in the environment is therefore represented by

$$\frac{\xi S + \eta U}{U + V + S + L}. \quad (1)$$

We assume that the fox becomes a healthy carrier, getting the virus only by feeding on infected prey. We allow for a possible additional mortality rate $\mu$, possibly $\mu = 0$ because it is very unlikely, for the carriers. Thus part of the predation goes into a direct benefit for the predator, and another one leads to new carriers. This is expressed by the fraction $\theta$. Biologically, it is not yet clear whether the foxes can contaminate the environment. We therefore allow it at rate $\eta$ as specified above in (1) and in case this cannot occur, it is enough to set this parameter to zero to account for the new ecological information. Also, they do not get infected...
through the environment. Finally, we assume foxes do not infect each other by direct contact. We also contemplate that offsprings may possibly contract the virus from their parents or while in the den, and therefore in part may contribute to the “infected” or carrier fox population, although as mentioned on this issue there is no evidence yet in either direction. This is expressed by the fraction $\zeta$. Note further that predation on the cottontails and hares may well occur at different rates.

As for the proper model formulation, we develop it step by step to better illustrate its various constitutive elements and adding different building blocks at each stage. We start by considering the reproduction of all populations involved. Foxes are assumed to have alternative feeding possibilities. Thus reproduction occurs first of all via resources that are not explicitly built in the model. Both healthy and infected foxes populations experience intraspecific competition. Essentially, rather than by a classical logistic formulation, these latter two features are expressed via the concept of an emerging carrying capacity, see [26] and the very earlier formulation of [32], for which the carrying capacity is replaced by suitable intraspecific competition terms with different weights for each different pair of populations involved. This is particularly important when one species is partitioned among healthy and infected individuals. The coefficients in the competition terms are then going to be different according to the types of interactions, because the intraspecific pressure exerted on healthy individuals by other healthy ones is generally different than the one due to infected; similarly for the pressure felt by the infected, healthy and infected individuals have different influences. Therefore, for the healthy foxes we have

$$\frac{dV}{dt} = rV - V \left( c_{VV}V + c_{VU}U \right) - mV, \quad (2)$$

$r$ being the reproduction rate and $m$ the natural mortality rate, while for the infected ones, omitting for the moment the reproduction we find

$$\frac{dU}{dt} = -U \left( c_{UU}U + c_{UV}V \right) - mU - \mu U, \quad (3)$$

where $\mu$ represents the infection-related mortality (which for foxes may be zero).

For cottontails $S$ and hares $L$ reproduction, we have a similar formulation with intraspecific competition terms $c_{SS}$ and $c_{LL}$:

$$\frac{dS}{dt} = sS - c_{SS}S^2 - nS, \quad \frac{dL}{dt} = uL - c_{LL}L^2 - pL. \quad (4)$$

We now discuss the interspecific interactions. They occur only by foxes predation on cottontails and hares. These two latter populations occupy different niches, and therefore do not interact among themselves, not even for resource competition, [6, 3, 4]. In the equations that follow, we model just the interspecific interaction terms, omitting for the moment the contribution of the reproduction equations (2), (3), (4) written so far.

As for the foxes, as mentioned above, they are infected only by eating infected prey, specifically just by the cottontails. In fact, if infected, the hares die very fast, before any reproduction of theirs can occur, and in addition we assume that they do so even before possibly being hunted by the foxes. Now, the hunting of the foxes leads mainly to their reproduction, but also infection, as mentioned above, may occur. We need to discuss this process in more detail. First of all, we stress this again here, field data show that the densities of all the populations in the model are low. This allows to use simple bilinear response functions, that represent linear approximations of the more realistic HT II form, that models feeding satiation. In
this case, in view of the low density of the prey, we can assume that feeding satiation does not occur.

Before turning to the hunting effects on the foxes, however, it is easier to discuss the negative effects on the prey. There is predation by healthy foxes on cottontails, at rate $a$, and at rate $b$ on hares, possibly different because the cottontails are a main prey for foxes, while hares are not. Thus

$$\frac{dS}{dt} = -aVS, \quad \frac{dL}{dt} = -bLV.$$  

Similarly, the same occurs for infected foxes predation, except that now the rates are different than those of healthy foxes, respectively $c$ and $h$, giving the following more complete picture

$$\frac{dS}{dt} = -aVS - cUS, \quad \frac{dL}{dt} = -bLV - hUL. \tag{5}$$

Coming now to foxes, we distinguish three phases following the hunting process, which occurs with the very same above terms, except clearly for a change of sign. They are feeding, followed by possible infection, and finally contribution to reproduction. We examine each one of them in detail.

After capturing the prey, the latter is eaten; the conversion coefficient $e$ expresses the fact that in general not the whole prey is devoured. Thus the first terms in the above equations would be accordingly modified for the healthy foxes

$$\frac{dV}{dt} = aeVS + beLV. \tag{6}$$

For the infected foxes similar modifications occur, but we recall that at this stage we ignore their reproduction, so that the expression that we write is just indicative of the process, and will need to be further discussed and modified below. In addition, this term will appear in more than one equation, and therefore it is best to describe it at first independently of the equations in which it will be accounted for. Thus, instead of assigning it to a differential equation, we consider it at this point as some kind of “benefit” $B_U$ for the infected foxes:

$$B_U = ceUS + heUL. \tag{7}$$

At this point, the second stage, the infection process for healthy foxes may occur, so that a fraction $\theta$ of healthy foxes becomes infected by feeding on cottontails and correspondingly a fraction $1 - \theta$ remains healthy. Again, the previous equations (6) is further modified and for the infected foxes the benefit (7) gets extended:

$$\frac{dV}{dt} = (1 - \theta)aeVS + beLV, \quad B_U = \theta aeVS + ceUS + heUL. \tag{8}$$

Finally, there is reproduction. We must account that the intake of food turns into newborns. For healthy foxes, the offsprings are healthy, generated at rate $r_H$, possibly different from the rate $r$ at which they are generated from other food sources.

$$\frac{dV}{dt} = r_H[(1 - \theta)aeVS + beLV]. \tag{9}$$

Infected instead reproduce at rate say $r_I$, and this will contribute to modify $B_U$, but we should consider that the individuals that entered this class through the feeding, remain in it. Thus the reproduction rate occurs in addition to this term. Overall, then the reproduction of this term of the new infected recruits must be of the form $(1 + r_I)\theta aeVS$. For the hunting of the infected over the cottontails and
hares instead there is only reproduction, as the infected predators were already in this class. The contribution of newborns in this way, vertical transmission apart, is thus \( r_I[ceUS + heUL] \). Thus the second equation in (8) gets modified:

\[
B_U = (1 + r_I)\theta aeVS + r_I[ceUS + heUL]. \tag{10}
\]

As mentioned, for the infected ones, vertical transmission may or may not occur, at respective rates \( \zeta \) and \( 1 - \zeta \). This further modifies the relevant equations, (9) and (10), leading now to the formulation of a system of differential equations:

\[
\frac{dV}{dt} = r_H[(1 - \theta)aeVS + beLV]
+ (1 - \zeta)r_I[\theta aeVS + ceUS + heUL],
\tag{11}
\]

\[
\frac{dU}{dt} = (1 + r_I\zeta)\theta aeVS + \zeta r_I[ceUS + heUL].
\tag{12}
\]

The vertical transmission process for infected foxes can occur also by reproduction due to other resources, at rate \( r_U \), again possibly different from \( r \), so that the equations (2) and (3) need to be modified accordingly

\[
\frac{dV}{dt} = rV - V(c_{VV}V + c_{VU}U) - mV + (1 - \zeta)r_UU,
\tag{13}
\]

\[
\frac{dU}{dt} = \zeta r_UU - U(c_{UU}U + c_{UV}V) - mU - \mu U,
\tag{14}
\]

we have the following dynamics accounting also for infected reproduction due to other resources,

\[
\frac{dV}{dt} = rV - V(c_{VV}V + c_{VU}U) - mV + (1 - \zeta)r_UU
+r_H[(1 - \theta)aeVS + beLV] + (1 - \zeta)r_I[\theta aeVS + ceUS + heUL],
\tag{15}
\]

\[
\frac{dU}{dt} = \zeta r_UU - U(c_{UU}U + c_{UV}V) - mU - \mu U
+ \zeta r_I[\theta aeVS + ceUS + heUL] + \theta aeVS.
\tag{16}
\]

Then for the prey, combining the reproduction and hunting features, namely (4) and (5), for the cottontails we have

\[
\frac{dS}{dt} = sS - c_{SS}S^2 - nS - aVS - cUS
\tag{17}
\]

while for the hares,

\[
\frac{dL}{dt} = uL - c_{LL}L^2 - pL - bVL - hUL.
\tag{18}
\]

The final step is to incorporate the hares infection process due to contaminated environment, recalling (1) given that infected foxes are assumed not to contribute to this effect:

\[
\frac{dL}{dt} = uL - c_{LL}L^2 - pL - bVL - hUL - L \frac{\xi S + \eta U}{U + V + S + L}.
\tag{19}
\]

Note that if all populations vanish, in the last fraction the numerator vanishes faster, so that the origin does not contain a singularity.
Table 1. The model parameters and their meaning

| Parameter | Interpretation |
|-----------|---------------|
| r         | healthy foxes reproduction rate on other resources |
| r_U       | infected foxes reproduction rate on other resources |
| r_H       | healthy foxes reproduction rate on cottontails and hares |
| r_I       | infected foxes reproduction rate on cottontails and hares |
| m         | foxes natural mortality rate |
| c_{UU}, c_{VV}, c_{UV}, c_{VU} | foxes intraspecific competition coefficients |
| ζ ≤ 1     | foxes vertical virus transmission |
| θ         | foxes transmission rate by feeding on infected cottontail |
| a         | healthy foxes predation rate on cottontails |
| b         | healthy foxes predation rate on hares |
| c         | infected foxes predation rate on cottontails |
| h         | infected foxes predation rate on hares |
| e         | foxes conversion coefficient of captured prey |
| µ         | foxes mortality rate due to virus, possibly µ = 0 |
| s         | cottontails reproduction rate |
| c_{SS}    | cottontails intraspecific competition |
| n         | cottontails natural mortality rate |
| u         | hares reproduction rate |
| c_{LL}    | hares intraspecific competition |
| p         | hares natural mortality rate |
| ξ         | hares infection, i.e. direct mortality rate, by cottontails environment pollution |
| η         | hares infection, i.e. direct mortality rate, by infected foxes environment pollution |

Overall, the first full formulation of the model is obtained by combining the equations (13), (14), (15), (16) above. To better emphasize the structure of this system, we rewrite it here below:

\[
\begin{align*}
\frac{dV}{dt} & = (r - m)V - c_{VV}V^2 - c_{VV}UV + (1 - \zeta)r_UU \\
& + [r_H(1 - \theta) + (1 - \zeta)r_I\theta]aeVS + r_HbeLV \\
& + (1 - \zeta)r_IceUS + (1 - \zeta)r_IheUL, \\
\frac{dU}{dt} & = \zeta r_UU - c_{UV}UV - c_{UU}U^2 - mU - \mu U \\
& + \theta(1 + \zeta r_I)aeVS + \zeta r_IceUS + \zeta r_IheUL, \\
\frac{dS}{dt} & = sS - c_{SS}S^2 - nS - aVS - cUS, \\
\frac{dL}{dt} & = uL - c_{LL}L^2 - pL - bVL - hUL - L \frac{\xi S + \eta U}{U + V + S + L}.
\end{align*}
\]

All the parameters are assumed to be nonnegative and their meaning is summarized in Table 1.

3. Analysis. In this section, we summarize the main results, whose proofs are discussed in the Appendix.

The system’s trajectories are bounded.
3.1. Equilibria feasibility. There are ten possible equilibria \( E_i = (V_i, U_i, S_i, L_i) \), \( i = 0, \ldots, 9 \), seven of which with population levels that can be analytically evaluated. The ones for which the values cannot be assessed are

\[
E_4 = (V_4, U_4, S_4, 0), \quad E_7 = (V_7, U_7, 0, L_7), \quad E_9 = (V_9, U_9, S_9, L_9).
\]

The simple equilibria are the origin, \( E_0 \), and those with just one nonvanishing population,

\[
E_1 = \left( \frac{r - m}{c_{VV}}, 0, 0, 0 \right), \quad E_3 = \left( 0, 0, \frac{s - n}{c_{SS}}, 0 \right), \quad E_5 = \left( 0, 0, 0, \frac{u - p}{c_{LL}} \right),
\]

with respective feasibility conditions, for \( E_1 \)

\[
r \geq m, \quad \text{(18)}
\]

for \( E_3 \)

\[
s \geq n, \quad \text{(19)}
\]

for \( E_5 \)

\[
u \geq p, \quad \text{(20)}
\]

In addition, the equilibria with two populations are

\[
E_2 = \left( V_2, \frac{\zeta r_U - m - \mu - c_{UV}V_2}{c_{UU}} \right), \quad E_8 = \left( 0, 0, \frac{s - n}{c_{SS}}, L_8^\pm \right),
\]

\[
E_6 = \left( \frac{(r - m)c_{LL} + (u - p)r_H b c}{c_{VV}c_{LL}u + b^2 r_H e}, 0, 0, \frac{(u - p)c_{VV}b - b(r - m)}{c_{VV}c_{LL}u + b^2 r_H e} \right).
\]

Here

\[
L_8^\pm = \frac{1}{2c_{LL}} \left\{ u - p - c_{ll} S_8 \pm \left[ (u - p - c_{ll} S_8)^2 + 4c_{ll} S_8 (u - p - \xi) \right]^{1/2} \right\}
\]

so that one positive value \( E_8^+ \) exists if

\[
u \geq p + \xi \quad \text{(21)}
\]

and two are feasible, \( E_8^\pm \), if instead

\[
u < \xi, \quad (u - p - c_{ll} S_8)^2 \geq 4c_{ll} S_8 (p + \xi - u). \quad \text{(22)}
\]

For the feasibility of \( E_8 \) in addition to either (21) and (22) we will need the condition (19).

The first set of feasibility conditions for \( E_2 \) can at least in principle be stated as

\[
0 \leq V_2 \leq \frac{c_{UU}(\zeta r_U - m - \mu)}{c_{UV}}.
\]

Furthermore, solving the equilibrium equations for \( E_2 \), we find the functions

\[
U = \Theta(V) = \frac{r - m - c_{VV}V}{c_{VV}V + (1 - \zeta)r_U}, \quad U = \Gamma(V) = \frac{1}{c_{UU}}[\zeta r_U - c_{VV}V - m - \mu].
\]

Now, \( \Theta \) has a positive branch in \([0, r - m]\) only if (19) holds. Indeed it goes to \(-\infty\) as \( V \to -\infty \), crosses the origin and vanishes at \( V_0 = r - m \). \( \Gamma \) instead is a straight line with negative slope, with its zero and height at the origin respectively given by

\[
V_0 = \frac{\zeta r_U - m - \mu}{c_{UV}}, \quad U_0 = \frac{\zeta r_U - m - \mu}{c_{UU}}.
\]

Thus it lies partly in the first quadrant only in case

\[
\zeta r_U \geq m + \mu. \quad \text{(24)}
\]
Table 2. Equilibria feasibility

| Equilibrium | Feasibility conditions |
|-------------|------------------------|
| $E_0$       | $r \geq m$             |
| $E_1$       |                        |
| $E_2^{+}$   | (23), (24), (25)      |
| $E_2^{-}$   | sufficient (26)       |
| $E_3$       | $s \geq n$            |
| $E_4$       | numerical              |
| $E_5$       | $u \geq p$            |
| $E_6$       | (27)                   |
| $E_7$       | numerical              |
| $E_8^{+}$   | sufficient: $u \geq p + \xi$ |
| $E_8^{-}$   | $u < \xi$, $(u - p)^2 \geq 4c_{LL}S_8(p + \xi - u)$ |
| $E_9$       | numerical              |

Thus a unique intersection $E_2^{-}$ between $\Theta$ and $\Gamma$ exists in the first quadrant if, in addition to (24), also $V_0 \in [0, r - m]$ holds, i.e. if

$$\zeta r_U \geq m + \mu + c_{UV}(r - m)$$

is satisfied. Through a saddle-node bifurcation, two such intersections $E_2^{\pm}$ could occur if the following sufficient conditions are verified:

$$U_0 \leq U_m, \quad V_0 \geq r - m,$$

where $U_m = \Theta(V_m)$, $V_m \in [0, V_0]$ denotes the positive relative maximum of the function $\Theta$.

Finally for $E_6$ feasibility follows from

$$rc_{LL} + r_Hb_{eu} \geq mc_{LL} + r_Hb_{cp}, \quad uc_{VV} + bm \geq pc_{VV} + br.$$  (27)

3.2. Equilibria stability. As for stability, all equilibria are conditionally stable. We provide a summarizing table for this feature as well, deferring the details to the Appendix. Further, in view of the fact that some of the stability issues cannot be fully investigated analytically, we provide the pictures of the equilibria $E_4$, $E_7$ and $E_9$, see Figures 1, 2, 3, while listing possible sets of the parameter values for which the remaining equilibria are also attained, but are not reported in pictures.

A reference set of parameter values is given by:

$$r = \log(3), \quad s = \log(4.5), \quad u = \log(5), \quad r_H = 0.3, \quad r_U = 0.9, \quad r_I = 0.4, \quad m = 5, \quad \mu = 0.3, \quad n = 5, \quad p = 5, \quad a = 2, \quad b = 3, \quad c = 0.2, \quad h = 0.4,$$

$$e = 0.91, \quad c_{UV} = \log(3) - \frac{2}{7}, \quad c_{VV} = c_{UV} - 0.1, \quad c_{UU} = \log(3) - \frac{2}{7},$$

$$c_{UV} = c_{UU} + 0.1, \quad c_{SS} = \frac{\log(4.5)}{100} - \frac{4}{500}, \quad c_{LL} = \frac{\log(5)}{30} - \frac{2}{330},$$

with initial conditions

$$V(0) = 1, \quad U(0) = 0, \quad S(0) = 8, \quad L(0) = 3.$$  (29)

The parameters to attain $E_0$ are (28), with initial conditions (29).
Table 3. Equilibria stability

| Equilibria | Stability conditions |
|------------|----------------------|
| $E_0$      | $m > r$, $s > n$, $u > p$ |
| $E_1$      | $\max \left\{ \frac{\zeta r_U - m - \mu}{c_U V}, \frac{s - n}{a}, \frac{u - p}{b} \right\} < V_1$ |
| $E_2$      | $s < n + aV_2 + cU_2$, $u < p + bV_2 + hU_2 + \eta \frac{L_2}{L_2 + L_3}$, (39) |
| $E_3$      | $n < s$, $u < p + \xi$, (41) |
| $E_4$      | $u < p + bV_4 + hU_4 + \frac{cS_4 + nU_4}{V_4 + U_4 + S_4}$, (43) |
| $E_5$      | $r + r_H e b L_5 < m$, $\zeta r_U + \zeta r_I h e L_5 < m + \mu$, $s < n$ |
| $E_6$      | $\zeta r_U - cUV_6 + \zeta r_I h e L_6 < m + \mu$, $s < n + aV_6$ |
| $E_7$      | $s < n + aV_7 + cU_7$, (47) |
| $E_8$      | $\frac{cS_8}{(S_8 + L_8)} < c_{LL}$, $n < s$, (49) |
| $E_9$      | numerical |

Figure 1. Equilibrium $E_4$, attained for the parameter values $r = \log(3)$, $s = \log(5)$, $U = 0.3$, $r_U = 0.9$, $r_I = 0.4$, $m = \frac{2}{7}$, $\mu = 0.1$, $n = 4/5$, $p = 2/11$, $a = 0.2$, $b = 0.1$, $c = 0.2$, $h = 0.4$, $e = 0.91$, $c_{VV} = \log(3) - \frac{2}{7}$, $c_{UU} = c_{VV} - 0.1$, $c_{UU} = \log(3) - \frac{2}{7}$, $c_{UV} = c_{UU} + 0.1$, $c_{SS} = \log(4.5)/100 - 4/500$, $c_{LL} = \log(5)/30 - 2/330$, $\zeta = 0.4$, $\theta = 0.7$, $\xi = 3$, $\eta = 2$ and initial conditions (29).

For the same initial conditions (29), those for $E_1$ are given by (28) in which however we take

$$m = \frac{2}{7}, \quad n = \frac{4}{5}, \quad p = \frac{2}{11}.$$
Equilibrium $E_7$, attained for the parameter values $r = \log(3)$, $s = \log(4.5)$, $u = \log(5)$, $r_H = 0.3$, $r_U = 0.9$, $r_I = 0.4$, $m = 3$, $\mu = 0.1$, $n = 4/5$, $p = 2/11$, $a = 5$, $b = 3$, $c = 4$, $h = 4$, $e = 0.91$, $c_{VV} = \log(3) - \frac{27}{7}$, $c_{UU} = c_{UV} - 0.1$, $c_{UV} = \log(3) - \frac{27}{7}$, $c_{UV} = c_{UU} + 0.1$, $c_{SS} = \log(4.5)/100 - 4/500$, $c_{LL} = \log(5)/30 - 2/330$, $\zeta = 0.8$, $\theta = 0.7$, $\xi = 0.3$, $\eta = 0.2$ and initial conditions (29). Interestingly, this equilibrium shows damped oscillations.

For $E_2$, again with the same initial conditions (29) we use (28) with the change:

$$m = \frac{2}{7}, \quad \mu = 0.1, \quad c = 2, \quad h = 4, \quad \zeta = 0.9.$$  

$E_3$ is attained by the choice (29) and (28) in which we substitute these values:

$$m = 20, \quad \mu = 1, \quad n = \frac{4}{5}, \quad a = 0.5, \quad b = 0.3, \quad c = 0.4, \quad h = 0.4,$$

as well as

$$c_{UV} = c_{UU} + 1, \quad \zeta = 0.1, \quad \theta = 0.1, \quad \xi = 0.1, \quad \eta = 0.3. \quad (30)$$

Again using (29) and (30), the parameters giving $E_5$ are given by (28) with the changes:

$$m = 20, \quad \mu = 1, \quad p = \frac{2}{11}, \quad a = 0.5, \quad b = 0.3, \quad c = 0.4.$$

$E_6$ is attained using (29) and changing the following parameter values in (28)

$$m = \frac{2}{7}, \quad n = \frac{4}{5}, \quad p = \frac{2}{11}, \quad b = 0.1.$$
Finally, from the same initial conditions (29) as well as (30), to obtain $E_8$ we have the following further substitutions in (28)

$$m = 20, \quad \mu = 1, \quad n = 4/5, \quad p = 2/11, \quad a = 0.2, \quad b = 0.1, \quad c = 0.2, \quad h = 0.4,$$

$$c = 0.91, \quad c_{UV} = \log(3) - \frac{2}{5}, \quad c_{UU} = c_{VV} - 0.1, \quad c_{UU} = \log(3) - \frac{2}{5},$$

$$c_{UV} = c_{UU} + 0.1, \quad c_{SS} = \log(4.5)/100 - 4/500, \quad c_{LL} = \log(5)/30 - 2/330,$$

$$\zeta = 0.4, \quad \theta = 0.7, \quad \xi = 0.3, \quad \eta = 0.2\text{ and initial conditions (29).}$$

4. **Bifurcations analysis.** Using the notation of Perko, [24], the system (17), $F(x, \alpha)$ being its right hand side, is written in compact form as

$$\frac{dx}{dt} = F(x, \alpha),$$

where $x = (V, U, S, L)^T$ represents its state and $\alpha$ the bifurcation parameter, with critical value $\tilde{\alpha}$ and the equilibrium is $x_0$.

The aim of this section is to analyze all the possible bifurcations at every equilibrium. In each case, we will confine the investigation to the analytically known eigenvalues of the Jacobian, and provide the relevant calculations in the Appendix.

It turns out that in each and every case transcritical bifurcations occur. We list here the pairs of equilibria that are connected in this way and their threshold parameter values:

1. $E_1$ and $E_0$ indicated by $r_{1,0} := \tilde{r} = m$;
2. $E_1$ and $E_2$ denoted by $\mu_{1,2} := \tilde{\mu} = \zeta r_U - c_{UV} V_1 - m$, if (53) differs from zero;
3. $E_1$ and $E_4$ indicated by $s_{1,4} := \tilde{s} = n + aV_1$;
4. $E_1$ and $E_6$ for $u = \tilde{u}$ denoted by $u_{1,6} := \tilde{u} = p + bV_1$;
5. $E_2$ and $E_4$ denoted by $s_{2,4} := \tilde{s} = n + aV_2 + cU_2$, if (58) hold;
6. $E_1$ and $E_7$ for $u = \tilde{u}$, denoted by $u_{2,7} := \tilde{u} = p + bV_2 + hU_2 + \eta U_2(V_2 + U_2)^{-1}$;
7. $E_3$ and $E_0$ denoted by $s_{3,0} := \tilde{s} = n$;
8. $E_3$ and $E_6$ denoted by $u_{3,6} := \tilde{u} = p + \xi$;
9. $E_4$ and $E_9$ denoted by $u_{4,9} := \tilde{u} = p + bV_4 + hU_4 + (\xi S_4 + \eta U_4)(V_4 + U_4 + S_4)^{-1}$
   if (63) does not vanish;
10. $E_5$ and $E_6$ denoted by $r_{5,6} := r = r_H b L_5$;
11. $E_5$ and $E_7$ denoted by $\mu_{5,7} := \tilde{\mu} = \zeta r_U - m + \zeta r_L E_0$ if (65) does not vanish;
12. $E_5$ and $E_8$ denoted by $s_{5,8} := \tilde{s} = n$;
13. $E_5$ and $E_6$ denoted by $u_{5,6} := \tilde{u} = p$;
14. $E_6$ and $E_7$ denoted by $\mu_{6,7} := \tilde{\mu} = \zeta r_U - c_{UV} V_6 - m + \zeta r_L E_0$ if (67) holds;
15. $E_7$ and $E_9$ denoted by $s_{7,9} := \tilde{s} = n + a V_7 + c U_7$.

In three more cases, additionally, transcritical bifurcation have been discovered numerically. To better elucidate this listing, we will provide a picture for the equilibria mutual relationships, Figure 7.

4.0.1. **Transcritical bifurcation** $E_2 - E_0$. In this case we also show a bifurcation that has been found via simulations, for which the corresponding eigenvalue is not known analytically. It relates equilibrium $E_2$ with $E_0$, for increasing values of the foxes virus-related mortality $\mu$, see Fig. 4.

Together with the initial conditions (29), the parameters have been chosen as in (28) but for

\[ r = 1.1, \quad r_U = 4, \quad m = 1.2, \quad c = 2, \quad h = 4, \quad \zeta = 0.9 \]

4.0.2. **Transcritical bifurcation** $E_3 - E_4$. For $E_4$ we also provide a bifurcation that has been obtained numerically, joining it with $E_3$, for increasing values of the healthy foxes reproduction rate $r$, see Fig. 5. With initial conditions (29), the parameters are (28) with the following exceptions:

\[ r_H = 0.1, \quad m = 7, \quad \mu = 1, \quad n = \frac{4}{5}, \quad p = \frac{2}{11}, \quad a = 0.1, \quad b = 0.1, \quad c = 0.1, \quad h = 0.1, \quad \xi = 3, \quad \eta = 2. \]

4.0.3. **Transcritical bifurcation** $E_8 - E_9$. In this case too an additional transcritical bifurcation is obtained numerically, connecting $E_8$ and $E_9$, again in terms of increasing values of the healthy foxes reproduction rate $r$, see Fig. 6. The parameters in this case are those of (28) with the changes indicated below:

\[ r_H = 0.1, \quad r_U = 0.1, \quad r_L = 0.1, \quad \mu = 3, \quad n = \frac{4}{5}, \quad p = \frac{2}{11}, \quad a = 0.1, \quad b = 0.1, \quad c = 0.1, \quad h = 0.1, \quad \zeta = 0.8, \quad \theta = 0.9, \quad \xi = 0.1. \]

and the initial conditions (29).

5. **Bifurcations’ interpretation.** Figure 7 shows the structure of the bifurcations for model (17) based on the analysis of the previous section.

We provide now an interpretation of this diagram, which may be useful for the theoretical ecologists, in that the possible changes that may arise in the environment are outlined, based on changes in the system parameter values. The latter could perhaps be deliberately influenced by humans, but sometimes their implications
may not result in the desired ones. It is therefore important to keep in mind the picture of all the possible whole system outcomes, depending on critical thresholds, that have been identified in Section 4.

The empty environment, $E_0$, can be occupied by either one of the healthy foxes, cottontails or hares populations, if their respective reproduction rates fall above their respective mortalities, events that occur at the critical values $r_{0,1}$, $u_{0,3}$, $u_{0,5}$. From the equilibrium with only healthy foxes, a disease outbreak can become endemic, if the disease-related mortality is low enough, below the threshold $\mu_{1,2}$. The endemically disease-affected fox equilibrium, $E_2$, can disappear, giving a pristine environment, if the combined natural and disease-related fox mortalities exceed the threshold $\mu_{0,2}$ that has been determined numerically. However, this scenario is theoretical since there are no indications that EBHS could induce fox mortality. Both the cottontail and hare populations can share the environment with the fox carrier population, at equilibria $E_4$ or $E_7$. This occurs when their respective reproductive rates are high enough, above the critical values $s_{2,4}$ and $u_{2,7}$. The hares-free equilibrium $E_4$ can be reached also directly from the fox-only environment, with disease and cottontails both appearing, if the cottontail reproduction rate lies above $s_{1,4}$. The cottontail-only configuration can move to equilibrium $E_4$, with a disease carrier foxes invasion, for a high enough fox reproduction rate, past the numerically found value $r_{3,4}$. On the other hand, hares can thrive together with cottontails, if their birth rate exceeds the combined effects of their mortality and the additional virus-related mortality due to the environmental contamination by the cottontails, $u_{3,8}$. From this configuration at which the two lagomorphs thrive together, either the foxes can invade together with the disease, at the numerically found threshold.
Figure 5. Transcritical bifurcation relating equilibria $E_3$ and $E_4$ of the system (17) in terms of the healthy foxes reproduction rate $r \in [1, 3.5]$ as bifurcation parameter. The parameters are given by (28) with the exception of those in (31).

$r_{8,9}$, or cottontails can disappear if their reproduction rate falls below $s_{5,8}$. For a suitably high fox reproduction rate, above $r_{5,6}$, foxes can invade the hare-only environment at point $E_6$. From this equilibrium, with the opposite changes discussed above, the fox-only point can be attained through a suitable reduction of the hares reproduction rate, but it is also possible that carrier foxes appear, equilibrium $E_7$, if the disease-related mortality rate lies below $\mu_{6,7}$. From this equilibrium $E_7$, as well as from the hares-free point $E_4$, the coexistence point can be obtained, if respectively the cottontails and hares birth rates exceed the values $s_{7,9}$ and $u_{4,9}$. From the coexistence equilibrium, if the former reproduction rate falls below $s_{6,9}$, both cottontails and disease are removed from the environment.

6. **Comparisons.** The current model is based on several simplifying assumptions of a still poorly understood ecological situation. To try to understand it, we formulated two models that complement each other, of which this is one. In [9] instead, red foxes are all taken as healthy virus carriers, but able to propagate the virus to other animals, while the cottontail population is composed of susceptible and infected individuals. In this paper, as seen, we assume the cottontails all infected, while the foxes can possibly spread the virus and are thus partitioned among healthy and carrier individuals.

Now, comparing the summarizing bifurcation diagram of [9] and Figure 7, there is a good agreement, provided that the disease-free equilibria and those with both healthy and infected individuals of a single population are merged together. The
Figure 6. Transcritical bifurcation connecting equilibria $E_8$ and $E_9$ of the system (17) for the bifurcation parameter given by the healthy foxes reproduction rate $r \in [3, 6]$. The parameters are given by (28) with the exception of those in (32). The transcritical bifurcations relating these various equilibria to each other would provide a “transition map” for the applied ecologist to achieve a desired outcome from possibly any current situation.

Let us examine this model first. In case the particularly desirable virus-free configuration is wanted, only three points are allowed: the original invader-free equilibrium $E_6$ where hares and susceptible foxes coexist, the healthy-foxes-only point $E_1$ and the hares-only equilibrium $E_5$. All other equilibria would contain the virus and even if, initially, say, it is present only among cottontails and these thrive just with hares at equilibrium $E_8$, the virus through environmental spilling could propagate to foxes, via the $r_{8,9}$ numerically discovered transcritical bifurcation, and the system would settle at coexistence, $E_9$. To return to the pristine conditions, we would need to eradicate simultaneously invader cottontails as well as carrier foxes, to achieve $E_6$, via the bifurcation $s_{6,9}$. The other possible alternatives from coexistence would lead to hares removal, through $u_{4,9}$ to reach $E_4$ or cottontails removal, via $s_{7,9}$ attaining $E_7$ but leaving the virus endemic among foxes. From this latter point, the pristine condition can be attained by acting on the virus-related foxes mortality $\mu_{6,7}$. As mentioned earlier, most of these parameters are intrinsic of the species under consideration and would perhaps prove to be resilient to human intervention. Thus the alternatives illustrated above may in the end not be feasible in practice. These remarks are essentially from a mathematical point of view. In the real world, while the control and even the eradication of invasive alien species is one of the primary management options to reduce their impact on biodiversity, eradicating native species to remove a disease is contrary to any
Figure 7. Picture of the whole bifurcation structure of the model (17) arising from the analysis of Section 4. In each node, the equilibrium name is reported, together with its nonvanishing populations. The red lines indicate the bifurcations that have been found only numerically.

Bifurcation thresholds:

\[ r_0, m, \mu_1, \mu_2 = \zeta r U - m, \]
\[ s_{1,4} = n + a V, \]
\[ u_{1,6} = p + b V_1, \]
\[ s_{2,4} = n + u V + c U, \]
\[ u_{2,7} = p + b V_2 + h U_2 + \eta U_2, \]
\[ \mu_{0,2} = \zeta U - m, \]
\[ s_{0,3} = n, \]
\[ u_{0,5} = p, \]
\[ r_{5,0} = m - r H be L_5, \]
\[ s_{5,8} = n, \]
\[ \mu_{5,7} = \zeta r U - m + r_1 he L_5, \]
\[ \mu_{6,7} = \zeta r U - c U V_6 - m + \zeta r_1 he L_4, \]
\[ s_{6,9} = n + a V_6, \]
\[ u_{4,9} = p + b V_4 + h U_4 + \frac{\zeta S_4 + a U_4}{S_4}, \]
\[ s_{7,9} = n + a V_7 + c U_7. \]

The asymmetry in the graph could be interpreted biologically as follows. Consider for instance the absence of the arc \( E_8 \rightarrow E_4 \) while arc \( E_2 \rightarrow E_7 \) is present. Both apparently connect points with 2 and 3 populations, but in reality \( E_2 \) contains only foxes, susceptible \( V \) and infected \( U \), while \( E_8 \) has two different system populations, cottontails \( S \) and hares \( L \). A similar claim can be made for the pairs \( E_0 \rightarrow E_8 \) and \( E_0 \rightarrow E_2 \).

principle of biodiversity conservation, besides being prohibited by law. Therefore, the only practical application is to limit cottontail populations.

The assumptions of [9] however, are different from the start. Indeed even the pristine situation is not virus-free, as virus is imbedded in the foxes. From this equilibrium, the virus is eliminated from the environment if also foxes are. Now this occurs by acting on the parameter \( m_{5,6} \), the foxes mortality rate. From the hare-only point, then the healthy invader can appear through the transcritical bifurcation \( n_{5,7} \), i.e. if the cottontails mortality rate is not too high. A similar situation can be obtained in this current model: a direct transition between \( E_6 \) and \( E_8 \) is not possible, but it is through the hares-only point \( E_5 \), from which \( E_8 \) is achieved for a high enough cottontails reproduction rate, \( s_{5,8} \).

In summary, this model and the one of [9] are more complementary of each other, because even in the case of the invader-free situation, they express different assumptions. They represent theoretical tools that can become useful for the field ecologist. But before their usage in field conditions can be recommended it is imperative that their assumptions are empirically verified, to assess if they indeed hold.
7. Conclusions. The model presented here is based on some assumptions not yet fully supported by field data. Presently, we do not know the role of cottontails and foxes in carrying the virus and infect other animals, of both the same or different species, directly or through the environment. Furthermore, a simplification in the assumptions has been necessary to render the modeling of a very complex biological situation possible. However, the scheme reported above should facilitate the work of applied ecologists, in the sense that it could be a map for understanding management scenarios, such as predator control or the eradication or control of invasive cottontails. An example of this claim in a slight different situation is represented by [8], where a model similar to the one considere here, but without disease, has successfully been proposed to try to elucidate the field findings for which a “hyperpredation” phenomenon on hares by foxes occurs, when cottontails invade the territory formerly occupied only by the other two species. In spite of the presence of the new prey, in the new situation the hares turn out to suffer more from increased hunting by foxes, and this becomes more accentuated with higher cottontails densities.

In this context the paper fits in the general framework of mathematical ecological models, whose role consists first in revealing potential fallacies of the possibly alternative policies available and secondly constitutes a help in avoiding the adoption of strategies that lead to unwanted outcomes.

8. Appendix.

8.1. Boundedness. First of all, we show that the system trajectories are bounded. Defining the whole system population, \( A = V + U + S + L \), adding together the equations (17) and reordering, we find at first for an arbitrary \( \pi > 0 \),

\[
\frac{dA}{dt} + \pi A = V (r - m + \pi - c_{VV} V) + U (r_U - m - \mu + \pi - c_{UU} U) + S (s - n + \pi - c_{SS} S) + L (u - p + \pi - c_{LL} L) + VU (c_{VV} + c_{UV}) + VSa [r_H e(1 - \theta) + r_I e \theta + e \theta - 1] + VLb (r_H e - 1) + USc (r_I e - 1) + ULh (r_I e - 1) - L \xi S + \eta U \frac{V}{V + U} + \frac{S}{S + L}.
\]

Dropping the two negative terms, the one in \( VU \) and the last one, the rational function multiplying \( L \), and assuming

\[
e < \min \left\{ \frac{1}{r_H (1 - \theta) + r_I \theta + \theta}, \frac{1}{r_H}, \frac{1}{r_I} \right\}
\]

we can also remove the terms in \( VU, VS, VL \), as they will all be negative as well. Now we can bound from above the rate of change of the total population as follows, by replacing the first four remaining terms on the right hand side, each being a convex parabola, with the height of its vertex, namely:

\[
\frac{dA}{dt} + \pi A \leq V (r - m + \pi - c_{VV} V) + U (r_U - m - \mu + \pi - c_{UU} U) + S (s - n + \pi - c_{SS} S) + L (u - p + \pi - c_{LL} L) \leq V_m + U_m + S_m + L_m = A_m,
\]

where

\[
V_m := \frac{1}{4c_{VV}} (r - m + \pi)^2, \quad U_m := \frac{1}{4c_{UU}} (r_U - m - \mu + \pi)^2,
\]

\[
S_m := \frac{1}{4c_{SS}} (s - n + \pi)^2, \quad L_m := \frac{1}{4c_{LL}} (u - p + \pi)^2.
\]
Solving the above differential inequality, we have

\[ A(t) \leq \frac{A_m}{\pi} (1 - \exp(\pi t)) + A(0). \]

We thus find for an arbitrary \( \epsilon > 0 \),

\[ 0 \leq A(t) \leq \max \left\{ \frac{A_m}{\pi} \epsilon, A(0) \right\}. \]

Since all the populations are nonnegative, the boundedness of each one of them follows from this estimate.

8.2. **Equilibria stability.** The Jacobian of the system (17) is a full matrix \( J \) with entries as follows:

\[
\begin{align*}
J_{1,1} &= r - m - 2c_{UV}V - c_{UU}U + [r_H(1 - \theta) + (1 - \zeta)r_f\epsilon]\sigma S + r_HebL, \\
J_{1,2} &= -c_{UV}V + (1 - \zeta)r_U + (1 - \zeta)r_f\epsilon(cS + hL), \\
J_{1,3} &= [r_H(1 - \theta) + (1 - \zeta)r_f\epsilon]\sigma V + (1 - \zeta)r_fceU, \\
J_{2,1} &= -c_{UU}U + \theta(1 + \zeta r_f)\sigma S, \\
J_{2,2} &= \zeta r_U - c_{UV}V - 2c_{UU}U - m - \mu + \zeta r_fceS + \zeta r_fheL, \\
J_{2,3} &= \zeta r_fheU, \\
J_{3,1} &= r_HebV + (1 - \zeta)r_fheL, \\
J_{3,2} &= -aS, \\
J_{3,3} &= s - 2c_{SS}S - n - aV - cU, \\
J_{4,1} &= -bL + L \frac{\xi S + \eta U}{(V + U + S + L)^2}, \\
J_{4,2} &= -hL - L \frac{\eta V + \eta S + \eta L - \xi S}{(V + U + S + L)^2}, \\
J_{4,3} &= -L \frac{\xi V + \xi U + \xi L - \eta U}{(V + U + S + L)^2}, \\
J_{4,4} &= u - 2c_{LL}L - p - bV - hU - \frac{\xi S + \eta U}{V + U + S + L} + L \frac{\xi S + \eta U}{(V + U + S + L)^2}.
\]

Note that at the origin the nonlinear term in the last equation of (17) has the numerator vanishing faster than the denominator, so that it can be disregarded. Keeping only the linear terms in the system equations, we easily obtain the following stability conditions:

\[ m > r, \quad s > n, \quad u > p. \]  

(33)

Stability of \( E_1 \) is easily assessed from the four explicit eigenvalues

\[ m - r, \quad \zeta r_U - c_{UV}V_1 - m - \mu, \quad s - n - aV_1, \quad u - p - bV_1 \]

giving, in view of (18),

\[ \max \left\{ \frac{\zeta r_U - m - \mu}{c_{UV}}, \frac{s - n}{a}, \frac{u - p}{b} \right\} < V_1. \]  

(34)

Two eigenvalues for the Jacobian evaluated at \( E_2 \) are known, giving the first two stability conditions:

\[ s < n + aV_2 + cU_2, \quad u < p + bV_2 + hU_2 + \eta \frac{U_2}{U_2 + V_2}. \]  

(35)

These can be investigated further, observing that the corresponding equations in the \( V_2 - U_2 \) parameter plane they define respectively a straight line \( L \) with negative slope joining the points

\[
\left( \frac{s - n}{a}, 0 \right), \quad \left( 0, \frac{s - n}{c} \right)
\]
and a conic section through the origin, 
\[ \Lambda(V_2, U_2) = -bV_2^2 - hU_2^2 - (b + h)V_2U_2 + (u - p)V_2 + (u - p - \eta)U_2 = v^T A v = 0, \]
where \( v = (V_2, U_2)^T \). The first condition (35) is satisfied above the line \( L \), i.e. in the half plane containing the origin if \( s < n \) and in the one not containing the origin for \( s > n \). Let \( A \) denote the quadratic form associated to \( \Lambda \),
\[
A = \begin{pmatrix}
-b & -\frac{b + h}{2} & -\frac{u - p}{2}
\end{pmatrix}
\begin{pmatrix}
-b & -\frac{b + h}{2} & -\frac{u - p}{2}
\end{pmatrix}
\begin{pmatrix}
\end{pmatrix}.
\]
Now the determinant of the quadratic form \( A \) associated to \( \Lambda \),
\[
\det A = \frac{1}{4}(u - p)^2h + \frac{1}{4}(u - p - \eta)^2b - \frac{1}{4}(b + h)(u - p)(u - p - \eta)
\]
and the calculation of the remaining invariants, namely trace and determinant of the submatrix \( A_{1,2;1,2} \), where the subscripts indicate respectively the surviving rows and columns of the original matrix, allow the conic classification:
\[
\text{tr}A_{1,2;1,2} = -(b + h) < 0, \quad \text{det} A_{1,2;1,2} = bh - \frac{1}{4}(b + h)^2 = -\frac{1}{4}(b - h)^2 < 0.
\]
If the trace has the same sign of \( \det A \), \( \Lambda \) represents no locus, while if they are opposite, i.e. \( \det A > 0 \), or, explicitly
\[
\frac{1}{4}(u - p)^2h + \frac{1}{4}(u - p - \eta)^2b > \frac{1}{4}(b + h)(u - p)(u - p - \eta)
\]
\( \Lambda \) is an ellipse, through the origin and the axes intercepts
\[
\left( \frac{u - p}{b}, 0 \right), \quad \left( 0, \frac{u - p - \eta}{h} \right).
\]
A sufficient condition for a nonempty intersection between the solutions of the two inequalities (35) is guaranteed by requiring an interlacing property between their intercepts on the axes, namely one of the following two alternative sets of conditions
\[
\begin{align*}
\frac{s - n}{a} & > \frac{u - p}{b}, \quad \frac{s - n}{c} < \frac{u - p - \eta}{h}; \\
\frac{s - n}{a} & < \frac{u - p}{b}, \quad \frac{s - n}{c} > \frac{u - p - \eta}{h}.
\end{align*}
\]
(37) (38)

The remaining minor of order two has a negative trace, namely \(-(1 - \xi)r_U U_2 V_2^{-1} - c_{UV} V_2 - c_{UU} U_2\) and from the second Routh-Hurwitz condition imposing that the determinant is positive we obtain the additional stability condition:
\[
c_{UV} U_2 \left[ (1 - \xi)r_U U_2 V_2^{1} + c_{VV} V_2 \right] + c_{UV} V_2 [(1 - \xi)r_U - c_{UV} V_2] > 0. \quad (39)
\]
At \( E_3 \) again two eigenvalues are known, \((n - s)c_{SS}^{-1}\) and \(u - p - \xi\), giving
\[
n < s, \quad u < p + \xi.
\]
(40)

Again the Routh-Hurwitz conditions on the remaining minor provide the other stability conditions
\[
\begin{align*}
r + \xi r_U + \{[r_H (1 - \theta) + (1 - \xi)r_I \theta]a + \xi r_I c\} e S_3 & < 2m + \mu, \\
g \{r - m + [r_H (1 - \theta) + (1 - \xi)r_I \theta] c S_3 \} [\xi r_U - m - \mu + \xi r_I c S_3] & > (1 - \xi)[r_U + r_I c e S_3] \theta (1 + \xi r_I) a e S_3.
\end{align*}
\]
(41)
At $E_4$ only one eigenvalue is known, implying the stability condition
\[ u < p + bV + hU + \frac{\xi S_4 + \eta U_4}{V_4 + U_4 + S_4} \]  \hspace{1cm} (42)

The remaining minor of order three $J^{E_4}_{1,2,3,1,2,3}$ has a negative trace, namely
\[ \text{tr}(J^{E_4}_{1,2,3,1,2,3}) = -c_{VV}V_4 - (1 - \zeta)r_U \frac{U_4}{V_4} - \theta(1 + \xi r_I)ae \frac{S_4V_4}{U_4} - c_{UU}U_4 - c_{SS}S_4. \]

Evaluating the sum of its minors of order two, we find
\[ M^{(2)}_4 = \left[ c_{VV}V_4 + (1 - \zeta)r_U \frac{U_4}{V_4} \right] \left[ \theta(1 + \xi r_I)ae \frac{S_4V_4}{U_4} + c_{UU}U_4 \right] \]
\[ - [\theta(1 + \xi r_I)ae S_4 - c_{UU}U_4]\left[(1 - \zeta)r_U - c_{VV}V_4 + (1 + \zeta)r_Ice \right] \]
\[ + \left[c_{VV}V_4 + (1 - \zeta)r_U \frac{U_4}{V_4} \right] c_{SS}S_4 \]
\[ + aS_4 \{r_H(1 - \theta) + (1 - \zeta)r_I \theta \} eaV_4 + (1 + \zeta)r_IceU_4 \} \]
\[ + \left[\theta(1 + \xi r_I)ae \frac{S_4V_4}{U_4} + c_{UU}U_4 \right] c_{SS}S_4 + cS_4 \left[\theta(1 + \xi r_I)ae V_4 + \xi r_IceU_4 \right]. \]

The remaining Routh-Hurwitz conditions are
\[ \det (J^{E_4}_{1,2,3,1,2,3}) > 0, \hspace{1cm} \text{tr}(J^{E_4}_{1,2,3,1,2,3}) M^{(2)}_4 > \det (J^{E_4}_{1,2,3,1,2,3}). \]  \hspace{1cm} (43)

The stability of $E_5$ is easily assessed, as all the eigenvalues are known, of which one is $-c_{LL}L_5 < 0$. The conditions resulting from the other ones are just
\[ r + r_{Heb}L_5 < m, \hspace{1cm} \zeta r_U + \zeta r_I heL_5 < m + \mu, \hspace{1cm} s < n. \]  \hspace{1cm} (44)

For $E_6$ stability reduces to
\[ \zeta r_U - c_{VV}V_6 + \zeta r_I heL_6 < m + \mu, \hspace{1cm} s < n + aV_6, \]  \hspace{1cm} (45)

because the remaining minor of order two, $J^{E_6}_{1,4,1,4}$ has negative trace and positive determinant,
\[ \text{tr}(J^{E_6}_{1,4,1,4}) = -c_{VV}V_6 - c_{LL}L_6, \hspace{1cm} \det (J^{E_6}_{1,4,1,4}) = c_{VV}V_6c_{LL}L_6 + b^2c_{LL}r_HV_6. \]

One eigenvalue is known at $E_7$, providing the stability condition
\[ s < n + aV_7 + cU_7. \]  \hspace{1cm} (46)

The Routh-Hurwitz conditions on the minor $J^{E_7}_{1,2,4,1,2,4}$ are obtained from
\[ \text{tr}(J^{E_7}_{1,2,4,1,2,4}) = -c_{VV}aV_7 - (1 - \zeta)r_U \frac{U_7}{V_7} - c_{UU}U_7 - c_{LL}L_7 + \eta \frac{L_7U_7}{(V_7 + U_7 + L_7)^2}, \]
\[ M^{(2)}_7 = \left[ c_{VV}aV_7 + (1 - \zeta)r_U \frac{U_7}{V_7} \right] c_{UU}U_7 \]
\[ + c_{VV}U_7[(1 - \zeta)r_U - c_{VV}V_7 + (1 - \zeta)r_IheL_7]\]
\[ + \left[c_{VV}V_7 + (1 - \zeta)r_U \frac{U_7}{V_7} \right] \left[\eta \frac{L_7U_7}{(V_7 + U_7 + L_7)^2} - c_{LL}L_7 \right] \]
\[ - [r_{Heb}V_7 + (1 - \zeta)r_IheU_7 \left\{\frac{\eta U_7}{(V_7 + U_7 + L_7)^2 - b} \right\} L_7 \]
\[ + c_{UU}U_7 \left[\frac{\eta U_7}{(V_7 + U_7 + L_7)^2 - c_{LL}L_7} \right] + \zeta r_IheU_7 \left[ h + \frac{\eta V_7 + \eta L_7}{(V_7 + U_7 + L_7)^2} \right] L_7, \]
\[\det J_{1,2,4,1,2,4}^{E_5} = [r_H ebV_7 + (1 - \zeta) r_I he U_7] c_{U V} U_7 \left[ \frac{\eta U_7}{(V_7 + U_7 + L_7)^2} - b \right] L_7 \]

\[-c_{U V} U_7 [r_H beV_7 + (1 - \zeta) r_I he U_7] c_{U V} U_7 L_7 \left[ \frac{U_7}{(V_7 + U_7 + L_7)^2} - c_{L L} \right] \left[ (1 - \zeta) r_U - c_{U V} V_7 + (1 - \zeta) r_I he L_7 \right] \]

\[+ c_{U V} U_7 L_7 \left[ \frac{U_7}{(V_7 + U_7 + L_7)^2} - c_{L L} \right] \left[ (1 - \zeta) r_U - c_{U V} V_7 + (1 - \zeta) r_I he L_7 \right] c_{L L} U_7 L_7 \left[ \frac{U_7}{(V_7 + U_7 + L_7)^2} - h \right] \]

and give

\[c_{U V} a V_7 + (1 - \zeta) r_U \frac{U_7}{V_7} + c_{U U} U_7 + c_{L L} L_7 > \eta \frac{L_7 U_7}{(V_7 + U_7 + L_7)^2}, \quad (47)\]

\[\det J_{1,2,4,1,2,4}^{E_5} > 0, \quad \text{tr}(J_{1,2,4,1,2,4}^{E_5}) M_1^{(2)} > \det J_{1,2,4,1,2,4}^{E_5}. \]

The first stability conditions at \(E_8\) are obtained by explicit eigenvalues:

\[\frac{\xi S_8}{(S_8 + L_8)^2} < c_{L L}, \quad n < s, \quad (48)\]

and the remaining ones from the minor of order two, \(J_{1,2,4,1,2,4}^{E_5}\) using the Routh-Hurwitz criterion, from the trace and determinant we have

\[\text{tr}(J_{1,2,4,1,2,4}^{E_5}) = 2m - r - [r_H (1 - \theta) + (1 - \zeta) r_I \theta] e a S_8 - r_H e b L_8 \]

\[-c_{U V} + \mu - \zeta r_I c e S_8 - \zeta r_I h e L_8, \]

det \(J_{1,2,4,1,2,4}^{E_5} = \{r - m + [r_H (1 - \theta) + (1 - \zeta) r_I \theta] e a S_8 + r_H e b L_8 \} \{\zeta r_U - m + \mu + \zeta r_I c e S_8 + \zeta r_I h e L_8\} - \theta (1 + \zeta r_I) a e S_8 [(1 - \zeta) r_U + (1 - \zeta) r_I e (c S_8 + h L_8)],\]

from which

\[2m + \mu < r + [r_H (1 - \theta) + (1 - \zeta) r_I \theta] e a S_8 + \zeta r_U + \zeta r_I c e S_8 + (r_h b + \zeta r_I h) e L_8, \]

\[\{r - m + [r_H (1 - \theta) + (1 - \zeta) r_I \theta] e a S_8 + r_H e b L_8 \} \{\zeta r_U - m + \mu + \zeta r_I c e S_8 + \zeta r_I h e L_8 - \mu\} > \theta (1 + \zeta r_I) a e S_8 [(1 - \zeta) r_U + (1 - \zeta) r_I e (c S_8 + h L_8)]. \quad (49)\]

### 8.3. Bifurcations at \(E_1\)

The known eigenvalues of the Jacobian at \(E_1\) are:

\[\lambda_{1,1} = m - r, \quad \lambda_{1,2} = \zeta r_U - c_{U V} V_1 - m - \mu, \quad \lambda_{1,3} = s - n - a V_1, \quad \lambda_{1,4} = u - p - b V_1. \]

#### 8.3.1. Eigenvalue: \(\lambda_{1,1}\)

The vanishing of the eigenvalue \(\lambda_{1,1} = m - r\) is obtained by the choice of \(r\) giving the critical value \(r =: \tilde{r} = m\). Letting

\[J(E_1)_{1,3} = [r_H (1 - \theta) + (1 - \zeta) r_I \theta] e a V_1 \quad (50)\]

the Jacobian at this point becomes

\[J(E_1, \tilde{r}) = \begin{bmatrix} 0 & (1 - \zeta) r_U - c_{U V} V_1 & J(E_1)_{1,3} & r_H e b V_1 \\ \zeta r_U - m - \mu - c_{U V} V_1 & \theta (1 + \zeta r_I) a e V_1 & 0 & 0 \\ 0 & 0 & s - n & 0 \\ 0 & 0 & 0 & u - p \end{bmatrix}\]
with right eigenvector \( \mathbf{v} = (1, 0, 0, 0)^T \) and right eigenvector of \([J(E_1, \hat{r})]^T \) given by \( \mathbf{w} = (1, w_2, w_3, w_4)^T \). Differentiation with respect to the chosen bifurcation parameter yields the vector function \( \mathbf{F}_r \) and its Jacobian \( D\mathbf{F}_r \):

\[
\mathbf{F}_r = \begin{pmatrix}
\dot{V} = V \\
\dot{U} = 0 \\
\dot{S} = 0 \\
\dot{L} = 0
\end{pmatrix}, \quad D\mathbf{F}_r = \begin{bmatrix}
1 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}.
\]

(51)

We now check whether the conditions appearing in Sotomayor’s Theorem hold:

\[
\mathbf{w}^T \mathbf{F}_r(E_1, \hat{r}) = \frac{r - m}{c_{VV}} = 0
\]

because \( r = \hat{r} = m \). Further, \( \mathbf{w}^T [D\mathbf{F}_r(E_1, \hat{r}) \mathbf{v}] = 1 \neq 0 \), as well as

\[
\mathbf{w}^T [D^2\mathbf{F}(E_1, \hat{\mu}) \mathbf{v}, \mathbf{v}] = -2c_{VV}(m + \mu - \zeta r_U) \neq 0
\]

because \( \lambda_{1,2} \neq 0 \). Thus by Sotomayor’s Theorem the system experiences a transcritical bifurcation between \( E_1 \) and \( E_0 \) for \( \hat{r} = m \), which we indicate by \( r_{1,0} := \hat{r} = m \).

8.3.2. **Eigenvalue:** \( \lambda_{1,2} \). By the choice \( \mu =: \hat{\mu} = \zeta r_U - c_{UV}V_1 - m \), the eigenvalue \( \lambda_{1,2} = \zeta r_U - c_{UV}V_1 - m - \mu \) vanishes. The Jacobian becomes then

\[
J(E_1, \hat{\mu}) = \begin{bmatrix}
m - r & -c_{UV}V_1 + (1 - \zeta)r_U & J(E_1)_{1,3} & r_{Heb}V_1 \\
n & 0 & \theta(1 + \zeta r_I)aeV_1 & 0 \\
0 & 0 & s - n - aV_1 & 0 \\
0 & 0 & 0 & u - p - bV_1
\end{bmatrix},
\]

and right and left eigenvectors given by

\[
\mathbf{v} = (c_{VV}V_1 - (1 - \zeta)r_U, m - r, 0, 0)^T, \quad \mathbf{w} = (0, aV_1 - s + n, \theta(1 + \zeta r_I)aeV_1, 0)^T.
\]

In this case differentiation of the right hand side of (17) provides

\[
\mathbf{F}_\mu = \begin{pmatrix}
\dot{V} = 0 \\
\dot{U} = -U \\
\dot{S} = 0 \\
\dot{L} = 0
\end{pmatrix}, \quad D\mathbf{F}_\mu = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & -1 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}.
\]

(52)

from which we find \( \mathbf{F}_\mu(E_1, \hat{\mu}) = (0, 0, 0, 0)^T \) so that \( \mathbf{w}^T \mathbf{F}_\mu(E_1, \hat{\mu}) = 0 \). In addition, \( \mathbf{w}^T [D\mathbf{F}_\mu(E_1, \hat{\mu}) \mathbf{v}] = -(aV_1 - s + n)(m - r) \neq 0 \), because \( \lambda_{1,1} \neq 0 \) and \( \lambda_{1,3} \neq 0 \), as well as

\[
\mathbf{w}^T [D^2\mathbf{F}(E_1, \hat{\mu}) \mathbf{v}, \mathbf{v}] = 2(aV_1 - s + n)(m - r)[c_{UV}r_U(1 - \zeta) - c_{UV}c_{VV}V_1 - c_{UV}(m - r)].
\]

(53)

Note that the last term does not have a definite sign. Now, if (53) is not equal to zero the system experiences a transcritical bifurcation between \( E_1 \) and \( E_2 \) for \( \mu = \hat{\mu} \), which we denote by \( \mu_{1,2} := \hat{\mu} = \zeta r_U - c_{UV}V_1 - m \).

Note also that all the third derivatives of the second and third equations in (17) vanish identically. Thus \( \mathbf{w}^T [D^3\mathbf{F}(E_1, \hat{\mu}) \mathbf{v}, \mathbf{v}, \mathbf{v}] = 0 \) and no pitchfork bifurcation can occur if the transcritical bifurcation does not arise.
8.3.3. Eigenvalue: $\lambda_{1,3}$. Setting the eigenvalue $\lambda_{1,3} = s - n - aV_1$ to zero gives the critical value $s = \hat{s} = n + aV_1$, and the Jacobian is
\[
J(E_1, \hat{s}) = \begin{bmatrix}
m - r & -c_{UV}V_1 + (1 - \zeta)r_U & J(E_1)_{1,3} & r_H beV_1 \\
0 & \zeta r_U - c_{UV}V_1 - m - \mu & \theta(1 + \zeta r_f)aeV_1 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & u - p - bV_1
\end{bmatrix}
\]
again with $J(E_1)_{1,3}$ given by (50). The right eigenvector of $J(E_1, \hat{s})$ and the right eigenvector of $[J(E_1, \hat{s})]^T$ respectively are:
\[
v = (v_1, v_2, 1, 0)^T \quad w = (0, 0, 1, 0)^T.
\]
Differentiation in this case gives
\[
F_s = \begin{cases}
\dot{V} = 0 \\
\dot{U} = 0 \\
\dot{S} = S \\
\dot{L} = 0
\end{cases} \quad DF_s = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix}
\]
so that $F_s(E_1, \hat{s}) = (0, 0, 0, 0)^T$, which entails $w^T F_s(E_1, \hat{s}) = 0$. The remaining needed quantities do not vanish,
\[
w^T [DF_s(E_1, \hat{s})v] = 1 \neq 0, \quad w^T [D^2 F_s(E_1, \hat{s})(v, v)] = -2(c_{SS} + av_1 + cv_2) \neq 0
\]
and show that a transcritical bifurcation between $E_1$ and $E_4$ arises for $s = \hat{s}$, indicated by $s_{1,4} := \hat{s} = n + aV_1$.

8.3.4. Eigenvalue: $\lambda_{1,4}$. The eigenvalue $\lambda_{1,4} = u - p - bV_1$ set to zero provides the threshold $u =: \tilde{u} = p + bV_1$, with the Jacobian, using (50),
\[
J(E_1, \tilde{u}) = \begin{bmatrix}
m - r & -c_{UV}V_1 + (1 - \zeta)r_U & J(E_1)_{1,3} & r_H beV_1 \\
0 & \zeta r_U - c_{UV}V_1 - m - \mu & \theta(1 + \zeta r_f)aeV_1 & 0 \\
0 & 0 & 0 & s - n - aV_1 \\
0 & 0 & 0 & 0
\end{bmatrix}
\]
where its right and left eigenvectors respectively are
\[
v = (r_H beV_1, 0, 0, r - m)^T, \quad w = (0, 0, 1, 0)^T.
\]
Differentiating,
\[
F_u = \begin{cases}
\dot{V} = 0 \\
\dot{U} = 0 \\
\dot{S} = 0 \\
\dot{L} = L
\end{cases} \quad DF_u = \begin{bmatrix}
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1
\end{bmatrix}
\]
which entail $F_u(E_1, \tilde{u}) = (0, 0, 0, 0)^T$, $w^T F_u(E_1, \tilde{u}) = 0$ and
\[
w^T [DF_u(E_1, \tilde{u})v] = r - m \neq 0, \quad w^T [D^2 F_u(E_1, \tilde{u})(v, v)] = -2b^2 c_{UU}V_1(r - m)^2 - 2c_{LL}(r - m)^2 \neq 0,
\]
both because $\lambda_{1,1} \neq 0$. Thus the system experiences a transcritical bifurcation between $E_1$ and $E_5$ for $u = \tilde{u}$ which we denote by $u_{1,5} := \tilde{u} = p + bV_1$.

8.4. Bifurcations at $E_2$. We now consider the possible bifurcations arising at $E_2$. The known eigenvalues of the Jacobian matrix are:
\[
\lambda_{2,3} = s - (n + aV_2 + cU_2), \quad \lambda_{2,4} = u - \left(p + bV_2 + hU_2 + \eta \frac{U_2}{V_2 + U_2}\right).
\]
8.4.1. Eigenvalue: $\lambda_{2,3}$. If the eigenvalue $\lambda_{2,3} = s - (n + aV_2 + cU_2)$ vanishes we find the threshold $s =: \tilde{s} \equiv n + aV_2 + cU_2$. Letting now
\[
J(E_2)_{1,3} = [r_H(1 - \theta) + (1 - \zeta)r_I\theta]eV_2 + (1 - \zeta)r_I ceU_2, \quad J(E_2)_{1,4} = r_HebV_2 + (1 - \zeta)r_I heU_2,
\]
the right and left eigenvectors of the Jacobian
\[
J(E_2, \tilde{s}) = \begin{bmatrix}
m - r & -c_{VU}V_2 + (1 - \zeta)r_U & J(E_2)_{1,3} & J(E_2)_{1,4} \\
0 & \zeta r_U - c_{UU}V_2 - m - \mu & 0 & 0 \\
0 & 0 & 0 & u - p - bV_2
\end{bmatrix},
\]
are $v = (v_1, v_2, v_3, 0)^T$ and $w = (0, 0, 1, 0)^T$, where, using the shorthand $J_{i,j} = J(E_2)_{i,j}$,
\[
v_1 = J_{2,1}E_2 - J_{2,1}E_{2,2}, \quad v_2 = (m - r)J_{2,2}, \quad v_3 = -(m - r)J_{2,1}.
\]
Calculating the derivative of the right hand side of (17), we obtain (54), giving $F_s(E_2, \tilde{s}) = (0, 0, 0, 0)^T$ from which also $w^T F_s(E_2, \tilde{s}) = 0$ follows. We also find
\[
w^T [DF_s(E_2, \tilde{s})]w = v_3, \quad w^T [D^2F(E_2, \tilde{s})]\{v, v, v\} = -2v_3(av_1 + cv_2 + c_{SS}v_3).
\]
The expressions of the components of $w^T$ show that the signs are not determined. It follows that we must require these expressions to be different from zero to have a transcritical bifurcation between $E_2$ and $E_4$ for $s = \tilde{s}$:
\[
v_3 \neq 0, \quad av_1 + cv_2 + c_{SS}v_3 \neq 0.
\]
The resulting bifurcation is denoted by $s_{2,4} := \tilde{s} = n + aV_2 + cU_2$
Now, all the third derivatives in the equation for $S$ in (17) are identically zero. Thus $w^T [D^3F(E_2, \tilde{s})]\{v, v, v\} = 0$ so that should the second condition in (58) be violated, nevertheless no pitchfork bifurcation can occur.

8.4.2. Eigenvalue: $\lambda_{2,4}$. The eigenvalue
\[
\lambda_{2,4} = u - \left(p + bV_2 + hU_2 + \eta \frac{U_2}{V_2 + U_2}\right)
\]
is set to zero to give the threshold
\[
u =: \bar{u} = p + bV_2 + hU_2 + \eta \frac{U_2}{V_2 + U_2}
\]
Using (56) and keeping the same shorthand notation of the previous eigenvalue $\lambda_{2,3}$, the Jacobian is
\[
J(E_2, \bar{u}) = \begin{bmatrix}
m - r & -c_{VU}V_2 + (1 - \zeta)r_U & J(E_2)_{1,3} & J(E_2)_{1,4} \\
0 & \zeta r_U - c_{UU}V_2 - m - \mu & 0 & 0 \\
0 & 0 & s - n - aV_2 & 0 \\
0 & 0 & 0 & 0
\end{bmatrix},
\]
with right and left eigenvectors given by
\[
v = (v_1, 0, 0, v_3)^T = (r_HebV_2 + (1 - \zeta)r_I heU_2, 0, 0, r - m)^T, \quad w = (0, 0, 0, 1)^T.
\]
Differentiation gives (55) and then we find $F_u(E_2, \bar{u}) = (0, 0, 0, 0)^T$ which entails $w^T F_u(E_2, \bar{u}) = 0$. Also $w^T [D^2F_u(E_2, \bar{u})]w = r - m \neq 0$ and
\[
w^T [D^2F(E_2, \bar{u})]\{v, v\} = -2v_3 \left\{av_1 + c_{LL}v_4 - \frac{\eta U_2(v_4 + v_1)}{(V_2 + U_2)^2}\right\}.
\]
Thus, if
\[ \eta \frac{U_2}{(V_2 + U_2)^2}(v_4 + v_1) \neq bv_1 + c_{LL}v_4 \] (59)
the system experiences a transcritical bifurcation between \( E_1 \) and \( E_7 \) for \( u = \bar{u} \), denoted by
\[ u_{2.7} := \bar{u} = p + bV_2 + hU_2 + \eta \frac{U_2}{V_2 + U_2}. \]
If (59) does not hold, i.e. for
\[ \eta \frac{U_2}{(V_2 + U_2)^2}(v_4 + v_1) = bv_1 + c_{LL}v_4 \] (60)
the third derivatives of the last equation in (17) can be evaluated in terms of the variables \( V \) and \( L \), for which the corresponding components of the eigenvalue \( v \) do not vanish, and then evaluated at \( E_2 \). The result is
\[ \mathbf{w}^T [D^3 \mathbf{F}(E_2, \bar{u})(\mathbf{v}, \mathbf{v}, \mathbf{v})] = -6\eta U_2 \frac{1}{(V_2 + U_2)^3} v_4[v_4 + 4v_1v_4 + 2v_1^2] \neq 0 \]
In such case a pitchfork bifurcation arises.

8.5. Bifurcations at \( E_3 \). We now analyze the possible bifurcations at \( E_3 \) for all known eigenvalues.

8.5.1. Eigenvalue: \( \lambda_{3.3} \). The eigenvalue \( \lambda_{3.3} = n - s \) is set to zero for \( s =: \bar{s} = n \).
The right and left eigenvectors of \( J(E_3, \bar{s}) \) respectively are
\[ \mathbf{v} = (0, 0, 1, 0)^T, \quad \mathbf{w} = (w_1, w_2, 1, 0)^T. \]
Evaluating the derivative of the right hand side of (17) with respect to the bifurcation parameter, we obtain (54). The conditions appearing in Sotomayor’s theorem are then as follows
\[ \mathbf{w}^T \mathbf{F}(E_3, \bar{s}) = \frac{\bar{s} - n}{c_{SS}} = 0 \]
and \( \mathbf{w}^T [D\mathbf{F}(E_3, \bar{s})\mathbf{v}] = 1 \neq 0, \mathbf{w}^T [D^2 \mathbf{F}(E_3, \bar{s})(\mathbf{v}, \mathbf{v})] = -2c_{SS} \neq 0 \). Thus the system experiences a transcritical bifurcation between \( E_3 \) and \( E_0 \) for \( \bar{s} = n \) denoted by \( s_{3,0} := \bar{s} = n \).

8.5.2. Eigenvalue: \( \lambda_{3.4} \). The eigenvalue \( \lambda_{3.4} = u-(p+\xi) \) vanishes for \( u =: \ddot{u} = p+\xi \).
The right and left eigenvectors of \( J(E_3, \ddot{u}) \) are:
\[ \mathbf{v} = (0, 0, 0, 1)^T, \quad \mathbf{w} = (0, 0, 0, 1)^T \]
and differentiation provides we obtain (55), so that \( \mathbf{F}_u(E_3, \ddot{u}) = (0, 0, 0, 0)^T \) and consequently \( \mathbf{w}^T \mathbf{F}_u(E_3, \ddot{u}) = 0 \). We also have \( \mathbf{w}^T [D\mathbf{F}_u(E_3, \ddot{u})\mathbf{v}] = 1 \neq 0 \) as well as
\[ \mathbf{w}^T [D^2 \mathbf{F}(E_3, \ddot{u})(\mathbf{v}, \mathbf{v})] = -2c_{LL} + 2\frac{\xi}{S_3} \]
If this expression is not equal to zero, thus for
\[ c_{LL}S_3^2 \neq \xi, \] (61)
the system experiences a transcritical bifurcation between \( E_3 \) and \( E_8 \) for \( u = \ddot{u} \), denoted by \( u_{3,8} := \ddot{u} = p+\xi \).
Observe that to determine the value of \( \mathbf{w}^T \left[ D^3 \mathbf{F}(E_3, \hat{u})(\mathbf{v}, \mathbf{v}, \mathbf{v}) \right] \), focusing on the fourth equation of (17), we just need to evaluate
\[
\frac{\partial^3 F_4}{\partial L^3} = (\xi S + \eta U) \frac{\partial^3}{\partial L^3} \left[ \frac{L}{U + V + S + L} \right]_{E_3} = -\frac{6}{S_3^4} \neq 0.
\]
because the only nonzero component of \( \mathbf{v} \) is the last one. Thus a pitchfork bifurcation arises whenever
\[
c_{LL} S_3^2 = \xi. \quad (62)
\]

8.6. **Bifurcations at** \( E_4 \). We now consider the possible bifurcations at the only known eigenvalue of \( E_4 \).

8.6.1. **Eigenvalue:** \( \lambda_{4,1} \). The vanishing of the eigenvalue
\[
\lambda_{4,1} = u - \left( p + bV + hU + \frac{\xi S_4 + \eta U_4}{V_4 + U_4 + S_4} \right)
\]
gives the threshold
\[
u =: \hat{u} = p + bV + hU + \frac{\xi S_4 + \eta U_4}{V_4 + U_4 + S_4}.
\]
The right and left eigenvectors of \( J(E_4, \hat{u}) \) are
\[
\mathbf{v} = (v_V, v_U, v_S, 1)^T, \quad \mathbf{w} = (0, 0, 0, 1)^T
\]
and differentiation yields (55) from which it follows
\[
\mathbf{w}^T \left[ D^2 \mathbf{F}(E_4, \hat{u})(\mathbf{v}, \mathbf{v}) \right] = 2 \frac{\xi S_4 + \eta U_4}{(V_4 + U_4 + S_4)^2} (v_V + v_U + v_S + 1)
\]
\[+ 2 [b v_V + h v_U + c_{LL}] - 2 \frac{\xi v_S + \eta v_U}{V_4 + U_4 + S_4},
\]
If this expression does not vanish, i.e.
\[
\frac{\xi S_4 + \eta U_4}{(V_4 + U_4 + S_4)^2} (v_V + v_U + v_S + 1) \neq [b v_V + h v_U + c_{LL}] + \frac{\xi v_S + \eta v_U}{V_4 + U_4 + S_4}, \quad (63)
\]
the system experiences a transcritical bifurcation
\[
u_{4,9} := \hat{u} = p + bV + hU + \frac{\xi S_4 + \eta U_4}{V_4 + U_4 + S_4}
\]
between \( E_4 \) and \( E_9 \) for \( u = \hat{u} \).

On the contrary, if (63) is violated, we need the partial third derivatives with respect to all possible populations of
\[
\frac{L(\xi S + \eta U)}{U + V + S + L}
\]
evaluated at \( E_4 \), i.e. with \( L_4 = 0 \). Thus, partial differentiation with respect to any variable, but \( L \), will leave \( L \) in the numerator, and this will annihilate the
contribution of the corresponding term upon evaluation of the result at $E_4$.

$$D^3\mathbf{F}(E_4, \bar{u})(\mathbf{v}, \mathbf{v}, \mathbf{v})|_{E_4} = \left. \left[ \sum_{H,K \in \{U,V,S\}} v_H v_K \frac{\partial}{\partial H} \frac{\partial^2}{\partial H \partial K} \right] + \sum_{H \in \{U,V,S\}} v_H \frac{\partial}{\partial L} \frac{\partial}{\partial H} + \frac{\partial^3}{\partial^3 L} \right] \left. \left[ \frac{L(\xi S + \eta U)}{U + V + S + L} \right] \right|_{E_4}$$

In other words, we need at least one partial derivative with respect to $L$ in order to have expressions that do not vanish. Thus, after such differentiation, we can evaluate

$$D^3\mathbf{F}(E_4, \bar{u})(\mathbf{v}, \mathbf{v}, \mathbf{v})|_{E_4} = \left. \left[ \sum_{H,K \in \{U,V,S\}} v_H v_K \frac{\partial^2}{\partial H \partial K} \right] \right|_{E_4}$$

$$= 36 \frac{\xi S_4 + \eta U_4}{(U_4 + V_4 + S_4)^2} - 6 \frac{\xi + \eta}{(U_4 + V_4 + S_4)^2} - 2 \frac{\xi S_4 + \eta U_4}{(U_4 + V_4 + S_4)^2} \neq 0$$

so that a pitchfork bifurcation occurs if

$$18(\xi S_4 + \eta U_4) \neq [3(\xi + \eta) + \xi S_4 + \eta U_4](U_4 + V_4 + S_4). \quad (64)$$

8.7. **Bifurcations at $E_5$.** The aim of what follows is the analysis of the possible bifurcations at $E_5$ for all the eigenvalues.

8.7.1. **Eigenvalue: $\lambda_{5,1}$.** The vanishing of the eigenvalue $\lambda_{5,1} = r - m + r_h b L_5$ occurs for the threshold value $r = \tilde{r} = m - r_h b L_5$. The right and left eigenvectors of $J(E_5, \tilde{\mu})$ are $\mathbf{v} = (-c_{LL} L_5, 0, 0, b)^T$ and

$$\mathbf{w} = (\zeta (r_U + r_l h e L_5) - m - \mu, (\zeta - 1)(r_U + r_l h e L_5), 0, 0)^T$$

and differentiation with respect to the bifurcation parameter gives (51) from which we easily obtain $\mathbf{F}_r(E_5, \tilde{\mu}) = (0, 0, 0, 0)^T$ and $\mathbf{w}^T \mathbf{F}_r(E_5, \tilde{\mu}) = 0$. Next we find

$$\mathbf{w}^T [D\mathbf{F}_r(E_5, \tilde{\mu})] \mathbf{v} = -[\zeta (r_U + r_l h e L_5) - m - \mu] c_{LL} L_5 \neq 0$$

and differentiation with respect to the bifurcation parameter gives (51) from which we easily obtain $\mathbf{F}_r(E_5, \tilde{\mu}) = (0, 0, 0, 0)^T$ and $\mathbf{w}^T \mathbf{F}_r(E_5, \tilde{\mu}) = 0$. Next we find

$$\mathbf{w}^T [D^2\mathbf{F}(E_5, \tilde{\mu})(\mathbf{v}, \mathbf{v})] = 2w \nu \nu (r_h b e L_5 - c_{UV} \nu \nu)$$

$$= -2[\zeta (r_U + r_l h e L_5) - m - \mu] c_{LL} L_5 (c_{UV} c_{LL} + r_h b^2 e) \neq 0,$$

both inequalities holding because $\lambda_{5,2} \neq 0$. Thus the conditions for the system to experience a transcritical bifurcation between $E_5$ and $E_6$ for $r = \tilde{r}$ are satisfied. The bifurcation is denoted by $r_{5,6} := \tilde{r} = m - r_h b L_5$.

8.7.2. **Eigenvalue: $\lambda_{5,2}$.** We set the eigenvalue $\lambda_{5,2} = \zeta r_l h e L_5 + \zeta r_U - m - \mu$ to zero and find the critical value $\mu =: \tilde{\mu} = \zeta r_U - m + \zeta r_l h e L_5$. Now, the right and left eigenvectors of $J(E_5, \tilde{\mu})$ are $\mathbf{v} = (v_1, v_2, 0, v_4)^T$ with

$$v_1 = (1 - \zeta)(r_U + r_l h e L_5), \quad v_2 = m - r - r_h b L_5, \quad v_4 = -\frac{b L_5 v_1 + (h L_5 + \eta) v_2}{c_{LL} L_5}$$
and \( \mathbf{w} = (0, 1, 0, 0)^T \). Differentiating with respect to \( \mu \) provides (52) so that 
\[
\mathbf{F}_\mu(E_5, \bar{\mu}) = (0, 0, 0, 0)^T, \quad \mathbf{w}^T \mathbf{F}_\mu(E_5, \bar{\mu}) = 0 \quad \text{and} \quad \mathbf{w}^T [D\mathbf{F}_\mu(E_5, \bar{\mu})] \mathbf{v} = -v_2 \neq 0, \because \lambda_{5,2} \neq 0.
\]
Moreover, \( \mathbf{w}^T [D^2\mathbf{F}(E_5, \bar{\mu})(\mathbf{v}, \mathbf{v})] = -2v_2[c_{UUV}v_1 + c_{UUU}v_2 - \zeta r_I h e L_5] \). Now if
\[
c_{UUV}v_1 + c_{UUU}v_2 - \zeta r_I h e L_5 \neq 0 \tag{65}
\]
the system experiences a transcritical bifurcation \( \mu_{5,7} := \bar{\mu} = \zeta r_U + m + \zeta r_I h e L_5 \) relating \( E_5 \) and \( E_7 \) for \( \mu = \bar{\mu} \).

Note that the second equation in (17) has at most quadratic nonlinearities, so that its third derivative with respect to any variables combination vanishes identically. Thus \( \mathbf{w}^T [D^3\mathbf{F}(E_5, \bar{\mu})(\mathbf{v}, \mathbf{v}, \mathbf{v})] = 0 \) and no pitchfork bifurcation can be found in this case.

8.7.3. **Eigenvalue:** \( \lambda_{5,3} \). The eigenvalue \( \lambda_{5,3} = s - n \) vanishes for \( s =: \tilde{s} = n \), the eigenvectors of \( J(E_5, \tilde{s}) \) and its transpose are
\[
\mathbf{v} = (0, 0, -c_{LLL}L_5, \xi)^T, \quad \mathbf{w} = (0, 0, 1, 0)^T
\]
and differentiation with respect to the chosen bifurcation parameter gives (54) so that 
\( \mathbf{F}_\xi(E_5, \tilde{s}) = (0, 0, 0, 0)^T \) and \( \mathbf{w}^T \mathbf{F}_\xi(E_5, \tilde{s}) = 0 \) follow. Evaluating the other needed quantities, we find \( \mathbf{w}^T[D\mathbf{F}_\xi(E_5, \tilde{s})] \mathbf{v} = -c_{LLL}L_5 \neq 0 \) and \( \mathbf{w}^T[D^2\mathbf{F}(E_5, \tilde{s})(\mathbf{v}, \mathbf{v})] = -2c_{SSV}^2L_5^2 \neq 0 \). Thus the system experiences a transcritical bifurcation \( s_{5,8} := \tilde{s} = n \) between \( E_5 \) and \( E_8 \) for \( s = \tilde{s} \).

8.7.4. **Eigenvalue:** \( \lambda_{5,4} \). The eigenvalue \( \lambda_{5,4} = -c_{LLL}L_5 \) gives the threshold \( u =: \bar{u} = p + 2c_{LLL}L_5 \) when set to zero. The right eigenvector of the Jacobian is \( \mathbf{v} = (0, 0, 0, 1)^T \). The left one is instead \( \mathbf{w} = (w_1, w_2, w_3, 1)^T \) where \( w_i, i = 1, 2, 3, \) are nonzero quantities, the explicit values of which are not needed in what follows. Differentiation gives once again (55). Now, \( \mathbf{F}_u(E_5, \bar{u}) = (0, 0, 0, L_5)^T = (0, 0, 0, 0)^T \), because \( \bar{u} = p \). Then we also find \( \mathbf{w}^T \mathbf{F}_u(E_5, \bar{u}) = 0 \) as well as \( \mathbf{w}^T[D\mathbf{F}_u(E_5, \bar{u})] \mathbf{v} = 1 \neq 0 \) and \( \mathbf{w}^T[D^2\mathbf{F}(E_5, \bar{u})(\mathbf{v}, \mathbf{v})] = -2c_{LLL} \neq 0 \). In conclusion, the system shows a transcritical bifurcation \( u_{5,0} := \bar{u} = p \) between \( E_5 \) and \( E_0 \) for \( u = \bar{u} \).

8.8. **Bifurcations at** \( E_6 \). We now examine the the possible bifurcations at \( E_6 \).

8.8.1. **Eigenvalue:** \( \lambda_{6,2} \). The eigenvalue \( \lambda_{6,2} = \mu - (\zeta r_U - c_{UUV}V_6 - m + \zeta r_I h e L_6) \) vanishes for the choice \( \mu =: \bar{\mu} = \zeta r_U - c_{UUV}V_6 - m + \zeta r_I h e L_6 \). The right and left eigenvectors of the Jacobian are
\[
\mathbf{v} = (v_1, 1, 0, v_4)^T, \quad \mathbf{w} = (0, n - s + aV_6, \theta(1 + \zeta r_I)aeV_6, 0)^T
\]
with
\[
v_1 = -\frac{1}{\Delta} \left[ (c_{UUV}V_6 - (1 - \zeta)(r_U + r_I h e L_6)c_{LLL} + \left( hL_6 + \frac{\eta}{V_6 + L_6} \right) r_H beV_6 \right],
\]
\[
v_4 = \frac{1}{\Delta} \left[ (c_{UUV}V_6 + (1 - \zeta)(r_U + r_I h e L_6)) - c_{VVV}V_6 \left( hL_6 + \frac{\eta}{V_6 + L_6} \right) \right],
\]
where
\[
\Delta = (c_{LLL}c_{UUV} + b^2 \epsilon r_H) \geq 0, \tag{66}
\]
and subsequent differentiation provides (52), from which we easily find \( \mathbf{F}_\mu(E_6, \bar{\mu}) = (0, 0, 0, 0)^T \) and \( \mathbf{w}^T \mathbf{F}_\mu(E_6, \bar{\mu}) = 0 \). It follows also \( \mathbf{w}^T[D\mathbf{F}_\mu(E_6, \bar{\mu})] \mathbf{v} = s - n - aV_6 \neq 0 \) because \( \lambda_{6,3} \neq 0 \) and
\[
\mathbf{w}^T[D^2\mathbf{F}(E_6, \bar{\mu})(\mathbf{v}, \mathbf{v})] = 2(s - n - aV_6)(c_{UUV}v_1 + c_{UUU} - \zeta r_I h e L_5).
Thus if
\[ \zeta r_1 h e v_4 - c_{UU} v_1 \neq c_{UU} \] (67)
is satisfied, the system experiences a transcritical bifurcation \( \mu_{6,7} := \tilde{\mu} = \zeta r_1 - c_{UU} V_6 - m + \zeta r_1 h e L_6 \) between \( E_6 \) and \( E_7 \) for \( \mu = \tilde{\mu} \).

Further, because the only term that could give rise to a nonvanishing third derivative appears in the last equation of (17), and that should be multiplied by \( w_4 = 0 \), it follows that the expression \( w^T \left[ D^3 \mathbf{F}(E_6, \tilde{\mu})(\mathbf{v}, \mathbf{v}, \mathbf{v}) \right] \) annihilates, so that no pitchfork bifurcation can arise.

8.8.2. Eigenvalue: \( \lambda_{6,3} \). We now annihilate the eigenvalue \( \lambda_{6,3} = s - (n + a V_6) \) to get the critical value \( s =: \bar{s} = n + a V_6 \). The right and left eigenvectors of the Jacobian are
\[ \mathbf{v} = (v_1, v_2, v_3, v_4)^T, \quad \mathbf{w} = (0, 0, 1, 0)^T, \quad v_2 = -J_{2,3}^{E_6} < 0, \quad v_3 = J_{2,2}^{E_6}, \]
where \( J_{1,2}^{E_6} = -c_{UU} V_6 + (1 - \zeta) (r_U + r_1 h e L_6), \quad J_{1,3}^{E_6} = [r_H (1 - \theta) + (1 - \zeta) r_1 \theta] a V_6, \quad J_{2,2}^{E_6} = \zeta r_U - c_{UU} V_6 - m - \mu + \zeta r_1 h e L_6, \quad J_{2,3}^{E_6} = \theta (1 + \zeta r_1) a V_6. \)

We set
\[ \delta_1 = J_{1,2}^{E_6} J_{2,3}^{E_6} - J_{2,2}^{E_6} J_{1,3}^{E_6}, \quad \delta_2 = J_{3,3}^{E_6} J_{2,2}^{E_6} - J_{2,3}^{E_6} J_{2,3}^{E_6} \]
and recalling (66) we find
\[ v_1 = \frac{1}{\Delta} [\delta_1 c_{LL} + \delta_2 r_H b e V_6] > 0, \quad v_4 = \frac{1}{\Delta} [c_{UU} \delta_2 - b \delta_1]. \]
Then we obtain again (54) so that \( \mathbf{F}_s(E_6, \bar{s}) = (0, 0, 0, 0)^T \) and \( \mathbf{w}^T \mathbf{F}_s(E_6, \bar{s}) = 0. \)
Also, \( \mathbf{w}^T \left[ D \mathbf{F}_s(E_6, \bar{s})(\mathbf{v}, \mathbf{v}) \right] = v_3 \neq 0 \) and
\[ \mathbf{w}^T \left[ D^2 \mathbf{F}(E_6, \bar{s})(\mathbf{v}, \mathbf{v}) \right] = -2 (a v_1 + c v_2 + c_{SS} v_3) v_3 \]
If the latter is not zero, i.e.
\[ a v_1 + c v_2 + c_{SS} v_3 \neq 0, \] (68)
the system experiences a transcritical bifurcation \( \tilde{s}_6,9 := \bar{s} = n + a V_6 \) between \( E_6 \) and \( E_9 \) for \( s = \bar{s} \).

In the opposite case, note that the third equation of (17) has all the third derivatives vanishing. Therefore \( \mathbf{w}^T \left[ D^3 \mathbf{F}(E_6, \tilde{\mu})(\mathbf{v}, \mathbf{v}, \mathbf{v}) \right] = 0 \) and no pitchfork bifurcation can occur.

8.9. Bifurcations at \( E_7 \). In this case we have only one known eigenvalue.

8.9.1. Eigenvalue: \( \lambda_{7,3} \). The vanishing of the eigenvalue \( \lambda_{7,3} = s - (n + a V_7 + c U_7) \) gives the threshold \( s =: \bar{s} = n + a V_7 + c U_7 \). The needed eigenvectors of \( J(E_7, \bar{s}) \) are found as
\[ \mathbf{v} = (v_1, v_2, v_3, v_4)^T, \quad \mathbf{w} = (0, 0, 1, 0)^T \]
and differentiation provides once more (54). Easily, \( \mathbf{F}_s(E_1, \bar{s}) = (0, 0, 0, 0)^T, \quad \mathbf{w}^T \mathbf{F}_s(E_1, \bar{s}) = 0. \)
\( \mathbf{w}^T [D \mathbf{F}_s(E_1, \bar{s})] = v_3 \neq 0 \) and \( \mathbf{w}^T \left[ D^2 \mathbf{F}(E_1, \bar{s})(\mathbf{v}, \mathbf{v}) \right] = -2 v_3 (a v_1 + c v_2 + c_{SS} v_3). \)
If this expression does not vanish, namely if (68) holds, where now the components \( v_k, k = 1, 2, 3 \), refer to the eigenvector \( \mathbf{v} \) found above, the system experiences a transcritical bifurcation \( s_{7,9} := \bar{s} = n + a V_7 + c U_7 \) between \( E_7 \) and \( E_9 \) for \( s = \bar{s} \).
For the same reasons stated in case of the eigenvalue \( \lambda_{6,3} \), no pitchfork bifurcation can arise in this situation as well.
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