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# A two-prey – diseased predator ecosystem ⋆

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**Abstract.** *In this paper we consider a disease-affected specialist predator that feeds on two resources. While the ecosystem is never wiped out, interestingly, just one prey cannot thrive in it. Transcritical bifurcations relate the simplest equilibria. Some sufficient conditions for the feasibility of the coexistence equilibrium are derived. In the particular case of the disease being unrecoverable, some additional healthy-predator-free equilibria are discovered, in which either one or both prey thrive, together with the infected predators.*

**Key words:** Ecoepidemiology, predator-prey, transmissible disease, two resources, stability.

## 1 Introduction

Ecoepidemic models investigate the relationships between populations in which diseases play a substantial role, one first paper in this domain being [18]. An account for the developments of this research field is contained in [29] and the more recent [34]. In ecoepidemiology, which joins demographic models with epidemic ones, [19, 20, 24, 14, 16, 26], disease can be considered a way of controlling one, or both, interacting populations, [2], especially if one of them is considered a pest, [4, 1, 30, 27], or when one population is not really affected by a disease, but may cause harm to the other one which is considered a resource, [10, 11]. Many models have been formulated in the course of the years. An attempt for a comparative study has been performed in [2]. However, not just predator-prey ecosystems have been investigated, see for instance [31] for a case involving competing populations. Further, recently, systems have been investigated leading to more complicated behaviors, [3]. To this end, we also cite some attempts at looking at food webs, [5, 6, 7, 13]. Note however that in the literature also a kind of symmetric case has been considered, in which two diseases affect the ecosystem, [12, 25].

We consider here a predator-prey ecoepidemic model in which the predator is affected by a disease and can feed on two different types of prey. In the absence of either one of them, the model reduces to well-known models in the literature, see e.g. [33, 9].

One example of such a situation in real life is described for instance as follows. Red foxes, (*Vulpus vulpus*), are omnivores primarily feeding on small rodents, e.g. voles such as (*Myodes glareolus*), squirrels e.g. (*Ratufa macroura, Glaucomys volans*), [23] p.

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513-524. but they feed also on birds, mainly passeriformes and waterfowl, as well as raccoons, opossums, reptiles, [15] p. 529, or even or small ungulates, [22]. Clearly these various prey populations have different habitats and do not interact directly for their search of food, so that our demographic assumptions are satisfied.

On the other hand, foxes are affected by a number of diseases, the most famous one being rabies, but they have been found to be affected by arthritis, [21] p. 421-422, leptospirosis and tularemia, and are also vectors for brucellosis and tick-born encephalitis. They are even infected by *Yersinia pestis*, [23] p. 547. Also parasites are found in the fox guts, e.g. nematodes such as *Toxocara canis* and *Uncinaria stenocephala, Capillaria aerophila* and *Crenosoma vulpis*, [28, 32].

Several other similar situations could be described in nature. For a panorama of various diseases affecting populations living on the ground or in the aquatic medium, or even avian species, see [17]. In this paper however our aim is not to discuss a specific ecosystem, but rather focus on the general properties of a system built on and containing these features.

The model is presented in the next Section, its equilibria are analyzed in Section 3 and some of their particular cases in the Subsection 3.2. Section 4 contains the local stability analysis, together with the one of the particular cases. Then a Section for the numerical simulations follows. A final discussion concludes the paper.

## 2 The model

Let $R$ and $U$ denote the two prey populations that live in the same environment of a predator population. Let $F$ be the healthy predators, while $V$ denote those that are disease-affected. All the parameters are assumed to be nonnegative.

$$R' = R\left[a\left(1-\frac{R}{K}\right) - cF - fV\right], \quad U' = U\left[b\left(1-\frac{U}{H}\right) - dF - gV\right], \tag{2.1}$$
$$F' = F\left[-m + ecR + edU - \lambda V\right] + \nu V, \quad V' = V\left[\lambda F + efR + egU - (\nu + m + \mu)\right].$$

The first two equations describe the dynamics of the prey. We assume that these two populations do not interfere with each other, having different habitats, although sharing the same physical location, as stated above. They reproduce logistically, with the environment providing respective carrying capacities at levels $K$ and $H$. These populations are subject to predators' hunting: both healthy and diseased predators hunt, at different rates, respectively $c$ and $f$ on the prey $R$ and at respective rates $d$ and $g$ on the population $U$. The third equation describes the healthy predators dynamics. We assume that the populations $R$ and $U$ are their sole source of food: in their absence, the predators experience natural mortality at rate $m$. They convert captured food, from either one of the prey populations, into newborns, with conversion factor $0 < e < 1$, which is assumed to be the same for both healthy and infected predators. The "successful" contact with an infectious individual moves them into the infected class, the disease contact rate being $\lambda$. They can also recover from the disease, so that at rate $\nu$ the infected reappear among the susceptibles. The infected predators have a similar dynamics as far as food intake is concerned, but they have a reversed behavior as far as entering their class: they do it at rate $\lambda$ upon "successful" contact among a susceptible and an infectious, and leave it at rate $\nu$. But in addition, they also experience a disease-related mortality at rate $\mu$. The fact that hunted prey is transformed into diseased newborns follows from the assumption that we make, namely that the disease is vertically transmitted.

## 3 The system's equilibria

### 3.1 Case of the recoverable disease

The model (2.1) admits the following equilibria $E_i^{(\nu)} = (R_i^{(\nu)}, U_i^{(\nu)}, F_i^{(\nu)}, V_i^{(\nu)})$, where the superscript emphasizes that these are obtained when the disease is recoverable, $\nu \neq 0$. These equilibria exist also in the particular case of no disease recovery $\nu = 0$, some of them will be explicitly obtained only in this situation and are discussed in the following Subsection 3.2, omitting in that case the superscript.

Easily, we find $E_0^{(\nu)} = (0,0,0,0)$, $E_1^{(\nu)} = (0,H,0,0)$, $E_2^{(\nu)} = (K,0,0,0)$, $E_3^{(\nu)} = (K,H,0,0)$. These are always feasible. We then have $E_4^{(\nu)} = \left(m(ec)^{-1}, 0, a(ecK-m)(Kec^2)^{-1}, 0\right)$ which is feasible for

$$ecK \geq m. \tag{3.1}$$

Then, the symmetric equilibrium $E_5^{(\nu)} = \left(0, m(ed)^{-1}, b(edH-m)(Hed^2)^{-1}, 0\right)$, feasible for

$$edH \geq m. \tag{3.2}$$

Next, $E_8^{(\nu)}$ is found by solving for $R$ and $U$ as functions of $F$ the first two equations of (2.1); substituting into the third one, we then find:

$$R_8^{(\nu)} = \frac{(a-cF_8)K}{a}, \quad U_8^{(\nu)} = \frac{(b-dF_8)H}{b}, \quad F_8^{(\nu)} = \frac{ab(Kec+Hed-m)}{e(ad^2H+bc^2K)}.$$

Replacing the value of $F_8^{(\nu)}$ thus found into the expressions for $R_8^{(\nu)}$ and $U_8^{(\nu)}$ we obtain the two explicit expressions, leading to

$$E_8^{(\nu)} = \left( \frac{K(mcb-edHcb+aed^2H)}{e(ad^2H+bc^2K)}, \frac{H(mda-ecKda+bec^2K)}{e(ad^2H+bc^2K)}, \frac{ab(Kec+Hed-m)}{e(ad^2H+bc^2K)}, 0 \right)$$

which is feasible for the following nonempty conditions, as will be seen in Section 6:

$$e(Kc+Hd) > m, \quad mda+bec^2K > ecKda, \quad mcb+aed^2H > edHcb. \tag{3.3}$$

The study of the equilibrium $E_{10}^{(\nu)}$ with $U_{10}^{(\nu)} = 0$ is performed as an intersection of suitable curves, as follows. In fact, this is the coexistence equilibrium of the one-prey-only subsystem. In that respect, this model has been introduced long ago, [33]. But there the analysis of coexistence is not decisive. Here instead we discuss the existence of the equilibrium in a different way, using a method based on graphical tools that ultimately gives some sufficient conditions for its existence.

From the fourth equilibrium equation of (2.1), we find $F$ as function of $R$,

$$F = \frac{A-efR}{\lambda}, \quad A = \nu+m+\mu \tag{3.4}$$

Using this result in the first equilibrium equation, we obtain $V$ as function of $R$:

$$V = jR+w \equiv \frac{cefK-a\lambda}{Kf\lambda}R + \frac{a\lambda-cA}{f\lambda}. \tag{3.5}$$

This is a straight line, intersecting the $R$ axis at the point with abscissa $Z = K(cA-a\lambda)(cefK-a\lambda)^{-1}$. From this consideration and (3.4) necessary conditions for the feasibility of the equilibrium are thus

$$R < \frac{A}{ef}; \text{ and} \qquad \text{either} \quad R > Z, \text{ for: } cefK > a\lambda, \quad \text{or} \quad R < Z, \text{ for: } cefK < a\lambda. \tag{3.6}$$

Substituting $F$ also into the third equilibrium equation we find the equation

$$-e^2fcR^2 + ef\lambda RV + (efm+ecA)R + \lambda(-m-\mu)V - mA = 0 \tag{3.7}$$

which represents a conic section.

For a generic conic section of the form $pR^2+2qRV+rV^2+2sR+2tV+u=0$, the invariants are defined as $C = pr-q^2$, $D = pru+2tsq-pt^2-rs^2-uq^2$. In our case they give

$$D = \frac{1}{4}\left[e^2f\lambda^2(\nu-A)(fm+cA)+e^2fc\lambda^2(\nu-A)^2+mAe^2f^2\lambda^2\right] = \frac{1}{4}\nu e^2f\lambda^2(fm-cm-c\mu), \quad C = -\frac{1}{4}e^2f^2\lambda^2 < 0.$$

Since $C < 0$, excluding the degenerate case $D = 0$, the conic is a hyperbola. It intersects the $R$ axis at the positive abscissae $R_1 = m(ec)^{-1}$, $R_2 = A(ef)^{-1}$. For simplicity, since we are looking only for sufficient conditions, and do not aim at a complete study of all the possible cases that can arise, we will assume that $R_2 > R_1$, i.e.

$$c(m+\mu+\nu) > fm. \tag{3.8}$$

The intersection with the $V$ axis occurs at the negative abscissa $V_1 = -mA[\lambda(m+\mu)]^{-1}$. Its center is located at

$$(x_0, y_0) = \left( \frac{tq-rs}{pr-q^2}, \frac{sq-pt}{pr-q^2} \right) = \left( \frac{m+\mu}{ef}, \frac{c(m+\mu-\nu)-fm}{f\lambda} \right).$$

There are several possible cases that can arise, for the various positions of the hyperbola and of the straight line (3.5). However, note that $x_0 > 0$. Three cases are possible, reported in Figures 1-3. In each picture, note that we show the three possible positions of the straight line (3.5). We consider in particular Figure 1. In this case observe that we are assuming $D \neq 0$, $y_0 > 0$, $R_2 > R_1$, respectively corresponding to

$$fm \neq c(m+\mu), \quad c(m+\mu-\nu) > mf, \quad c(m+\mu+\nu) > fm.$$

There are four possible positions for the straight line (3.5), which may lead however to further subcases.

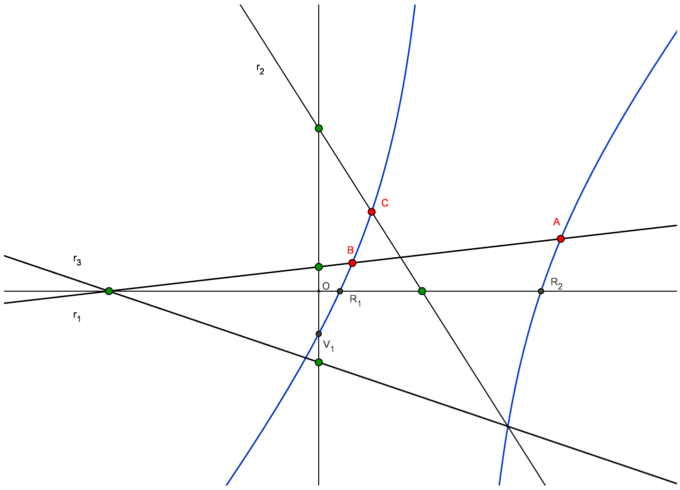


**Fig. 1** An example: the hyperbola with $y_0 > 0$. For the discussion of the possible intersections with the straight line, see the main body of the paper.

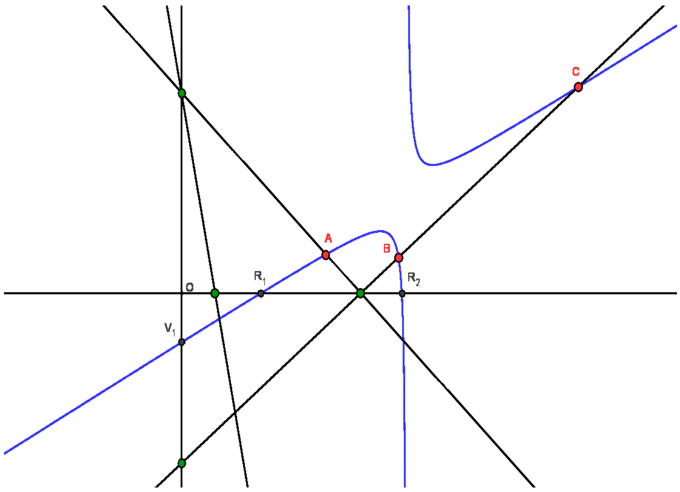


**Fig. 2** A second example: another hyperbola with $y_0 > 0$. Here for the straight line indicated by $\mathbf{r_2}$ in the body of the paper, either no intersection in the first quadrant exists or exactly one is shown in the picture, but there could be two or none if $Z > R_2$. The straight line $\mathbf{r_4}$ instead is shown to have two feasible intersections if $R_1 < Z < R_2$.

1. $\mathbf{r_1}$: in this case there is least one feasible intersection with the hyperbola, for $j > 0$, $w > 0$, i.e.

$$cefK > a\lambda, \quad a\lambda > cA. \tag{3.9}$$

2. $\mathbf{r_2}$: there is exactly one intersection in the first quadrant for $j < 0$, $w > 0$ and $R_1 < Z < R_2$, i.e.

$$cefK < a\lambda, \quad \frac{m}{ec} < K\frac{cA - a\lambda}{cefK - a\lambda} < \frac{A}{ef}. \tag{3.10}$$

But further, for $Z < R_1$ there is no intersection in the first quadrant, while there are two, not shown in Figure 1, for $Z > R_2$

$$cefK < a\lambda, \quad K\frac{cA - a\lambda}{cefK - a\lambda} > \frac{A}{ef}. \tag{3.11}$$

3. $\mathbf{r_3}$: for $j < 0$, $w < 0$, i.e. $cefK < a\lambda$, $a\lambda < cA$, there are no feasible intersections.

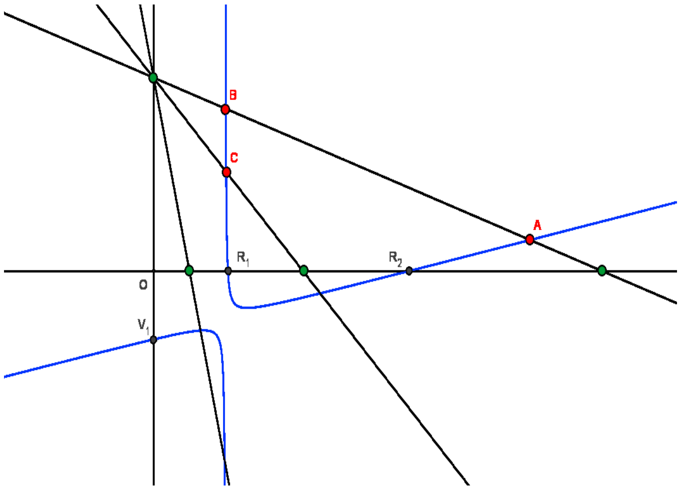


**Fig. 3** Another example: the hyperbola with $y_0 < 0$. In this case we show only $\mathbf{r_1}$. There is no feasible intersection for $Z < R_1$, exactly one for $R_1 < Z < R_2$, two instead if $Z > R_2$.

4. $\mathbf{r_4}$: this case is not shown in Figure 1, as it leads to several subcases, depending mainly on the slope of the straight line. In general there could be two, one or no intersection in the first quadrant. We do not examine it further.

In order that the intersection be feasible, one must further require that $F_{10}^{(\nu)} \geq 0$.

Similar considerations can be made on Figures 2 and 3.

Note that this equilibrium in the particular case $\nu = 0$ can be explicitly evaluated, solving for $V$ and $F$ as functions of $R$ from the last two equations; substituting into the first one we find $R$, which finally leads to

$$E_{10} = \left( \frac{K(\lambda a + fm - c(m+\mu))}{\lambda a}, 0, \frac{\lambda a(m+\mu) - efK(\lambda a + fm - c(m+\mu))}{\lambda^2 a}, \frac{ecK(\lambda a + fm - c(m+\mu)) - m\lambda a}{\lambda^2 a} \right)$$

which is feasible for the following nonempty set of parameter values, as it will be seen in Section 6:

$$\lambda a + fm > c(m+\mu), \quad \lambda a(m+\mu) > efK(\lambda a + fm - c(m+\mu)), \quad m\lambda a < ecK(\lambda a + fm - c(m+\mu)). \tag{3.12}$$

The symmetric equilibrium $E_{11}^{(\nu)}$ can again be obtained with a similar procedure, solving for $F$ as a function of $U$ in the fourth equilibrium equation,

$$F = \frac{A - egU}{\lambda}, \tag{3.13}$$

then substituting into the second one we obtain once again a straight line,

$$V = \frac{degH - b\lambda}{Hg\lambda} U + \frac{b\lambda - dA}{g\lambda}.$$

From this and (3.13) we find the following necessary conditions for the feasibility of the equilibrium:

$$U < \frac{A}{eg}; \text{ and } \quad \text{either} \quad U > H\frac{dA - b\lambda}{degH - b\lambda}, \text{ for: } degH > b\lambda, \quad \text{or} \quad U < H\frac{dA - b\lambda}{degH - b\lambda}, \text{ for: } degH < b\lambda. \tag{3.14}$$

From the third equilibrium equation we then obtain the hyperbola

$$-e^2 gdU^2 + eg\lambda UV + (egm + edA)U + \lambda(-m - \mu)V - mA = 0,$$

and the analysis follows the previous pattern and is therefore omitted. Once again, for $\nu = 0$ it can be explicitly evaluated, solving for $V$ and $F$ as functions of $U$ from the last two equilibrium equations, and substituting into the second one to find $U$ so that, finally,

$$E_{11} = \left( 0, \frac{H(\lambda b + gm - d(m+\mu))}{\lambda b}, \frac{\lambda b(m+\mu) - egH(\lambda b + gm - d(m+\mu))}{\lambda^2 b}, \frac{edH(\lambda b + gm - d(m+\mu)) - m\lambda b}{\lambda^2 b} \right)$$

and it is feasible for the following conditions which are nonempty as shown in Section 6:

$$\lambda b + gm > d(m+\mu), \quad \lambda b(m+\mu) > egH(\lambda b + gm - d(m+\mu)), \quad m\lambda b < edH(\lambda b + gm - d(m+\mu)). \tag{3.15}$$

Finally, the coexistence equilibrium is investigated numerically.

## 3.2 The particular cases

Three new equilibria arise when $\nu = 0$. Easily, we find

$$E_6 = \left(\frac{m+\mu}{ef}, 0, 0, \frac{a(efK-(m+\mu))}{Kef^2}\right), \quad E_7 = \left(0, \frac{m+\mu}{eg}, 0, \frac{b(egH-(m+\mu))}{Heg^2}\right),$$

with respective feasibility conditions given by

$$efK > m+\mu, \quad egH > m+\mu. \tag{3.16}$$

Further, solving for $R$ and $U$ as functions of $F$ from the first two equations and substituting into the third one, we find $V$, which leads to the new equilibrium

$$E_9 = \left(\frac{K(mfb-efgHb+aeg^2H+\mu fb)}{e(ag^2H+bf^2K)}, \frac{H(mga-efgKa+bef^2K+\mu ga)}{e(ag^2H+bf^2K)}, 0, \frac{ab(efK+egH-m-\mu)}{e(ag^2H+bf^2K)}\right),$$

which is feasible for

$$e(Kf+Hg) > m+\mu, \quad mga+bef^2K+\mu ga > efgKa, \quad mfb+aeg^2H+\mu fb > efgHb. \tag{3.17}$$

# 4 Stability

The Jacobian $J(R,U,F,V)$ of (2.1) is

$$J = \begin{bmatrix} a\left(1-2\frac{R}{K}\right)-cF-fV & 0 & -cR & -fR \\ 0 & b\left(1-2\frac{U}{H}\right)-dF-gV & -dU & -gU \\ ecF & edF & -m+ecR+edU-\lambda V & -\lambda F+\nu \\ efV & egV & \lambda V & \lambda F+efR+egU-\nu-(m+\mu) \end{bmatrix} \tag{4.1}$$

It is easily established that the equilibria $E_0^{(\nu)}$, $E_1^{(\nu)}$, $E_2^{(\nu)}$, are always unstable; indeed they have respectively the following sets of eigenvalues: $\gamma_1 = a$, $\gamma_2 = b$, $\gamma_3 = -m$, $\gamma_4 = -(\nu+m+\mu)$; $\gamma_1 = a$, $\gamma_2 = -b$, $\gamma_3 = edH-m$, $\gamma_4 = egH-(\nu+m+\mu)$; $\gamma_1 = -a$, $\gamma_2 = b$, $\gamma_3 = ecK-m$, $\gamma_4 = efK-(\nu+m+\mu)$.

For $E_3^{(\nu)}$ we have instead $\gamma_1 = -a$, $\gamma_2 = -b$, $\gamma_3 = ecK+edH-m$, $\gamma_4 = efK+egH-(\nu+m+\mu)$, giving the stability conditions

$$e < \min\left\{\frac{m}{cK+dH}, \frac{\mu+m+\nu}{fK+gH}\right\} \tag{4.2}$$

For all the former equilibria, no Hopf bifurcations can arise, as the eigenvalues are all real.

For $E_4^{(\nu)}$, two eigenvalues are explicit,

$$\gamma_1 = b - \frac{ad(ecK-m)}{Kec^2}, \quad \gamma_2 = \frac{\lambda a(ecK-m)}{Kec^2} + \frac{fm}{c} - \nu - (m+\mu)$$

while the Routh-Hurwitz conditions for the remaining minor $\widehat{J}$ are easily seen to be satisfied, in view of the feasibility condition (3.1):

$$-\mathrm{tr}(\widehat{J}) = \frac{am}{ecK} > 0, \quad \det(\widehat{J}) = \frac{am(ecK-m)}{ecK} > 0.$$

Stability depends only on the sign of the first two eigenvalues, giving the conditions:

$$b < \frac{ad(ecK-m)}{Kec^2}, \quad \frac{ecK(\lambda a+fm)-\lambda am}{Kec^2} < \nu+m+\mu. \tag{4.3}$$

At $E_5^{(\nu)}$ we find again two explicit eigenvalues,

$$\gamma_1 = a - \frac{bc(edH-m)}{Hed^2}, \quad \gamma_2 = \frac{\lambda b(edH-m)}{Hed^2} + \frac{gm}{d} - \nu - (m+\mu)$$

while the Routh-Hurwitz conditions for the remaining minor once again hold, $bH^{-1}U_5^{(\nu)} > 0$, $ed^2U_5^{(\nu)}F_5^{(\nu)} > 0$. In summary, the stability conditions are thus:

$$a < \frac{bc(edH-m)}{Hed^2}, \quad \frac{edH(\lambda b+gm)-\lambda bm}{Hed^2} < \nu+m+\mu. \tag{4.4}$$

Also for the equilibria $E_i^{(\nu)}$, $i = 4,5$ there cannot be Hopf bifurcations, as the traces of the 2 by 2 minors are always stricly positive.

At $E_8^{(\nu)}$ one eigenvalue is assessed immediately, $\gamma_1 = \lambda F_8^{(\nu)} + efR_8^{(\nu)} + egU_8^{(\nu)} - (\nu+m+\mu)$. The Routh-Hurwitz criterion on the remaining minor $\widetilde{J}$ of order 3 gives

$$-\mathrm{tr}(\widetilde{J}) = \frac{aR_8^{(\nu)}}{K} + \frac{bU_8^{(\nu)}}{H} > 0, \quad -\det(\widetilde{J}) = \left[\frac{ad^2e}{K} + \frac{bc^2e}{H}\right] R_8^{(\nu)}U_8^{(\nu)}F_8^{(\nu)} > 0, \quad M_2(\widetilde{J}) = \frac{abR_8^{(\nu)}U_8^{(\nu)}}{HK} + \left[ed^2U_8^{(\nu)} + ec^2R_8^{(\nu)}\right] F_8^{(\nu)},$$

where $M_2$ represents the sum of the principal minors of order 2 of $\widetilde{J}$. It follows also

$$-tr(\widetilde{J})M_2(\widetilde{J}) + det(\widetilde{J}) = \frac{a^2b(R_8^{(\nu)})^2U_8^{(\nu)}}{HK^2} + \frac{ab^2R_8^{(\nu)}(U_8^{(\nu)})^2}{H^2K} + \frac{bd^2e(U_8^{(\nu)})^2F_8^{(\nu)}}{H} + \frac{ac^2e(R_8^{(\nu)})^2F_8^{(\nu)}}{K} > 0$$

so that stability depends only on the first eigenvalue, giving the condition:

$$\lambda F_8^{(\nu)} + efR_8^{(\nu)} + egU_8^{(\nu)} < \nu+m+\mu. \tag{4.5}$$

$E_{10}^{(\nu)}$ has also an explicit eigenvalue $\gamma_1 = b - dF_{10}^{(\nu)} - gV_{10}^{(\nu)}$, the Routh-Hurwitz conditions on the remaining minor $\bar{J}$ are rather complicated, but some information can be gathered, for instance,

$$-\mathrm{tr}(\bar{J}) = \frac{aR_{10}^{(\nu)}}{K} + \nu\frac{V_{10}^{(\nu)}}{F_{10}^{(\nu)}} > 0, \quad -\det(\bar{J}) = R_{10}^{(\nu)}V_{10}^{(\nu)}\left[\lambda^2\frac{aF_{10}^{(\nu)}}{K} - \lambda\frac{a\nu}{K} + ef\nu\left(c + f\frac{V_{10}^{(\nu)}}{F_{10}^{(\nu)}}\right)\right],$$
$$M_2(\bar{J}) = c^2eR_{10}^{(\nu)}F_{10}^{(\nu)} + \lambda^2F_{10}^{(\nu)}V_{10}^{(\nu)} + ef^2R_{10}^{(\nu)}V_{10}^{(\nu)} - \lambda\nu V_{10}^{(\nu)} + \frac{a\nu}{KF_{10}^{(\nu)}}R_{10}^{(\nu)}V_{10}^{(\nu)},$$

but for the last Routh-Hurwitz condition the expression is somewhat more involved and therefore omitted. Note that the sign of $\det(\bar{J})$ must be negative, which gives an additional necessary stability condition on top of the one provided by the first eigenvalue,

$$\lambda^2\frac{aF_{10}^{(\nu)}}{K} + ef\nu\left(c + f\frac{V_{10}^{(\nu)}}{F_{10}^{(\nu)}}\right) < \lambda\frac{a\nu}{K}, \quad b < dF_{10}^{(\nu)} + gV_{10}^{(\nu)}. \tag{4.6}$$

For the specular equilibrium $E_{11}^{(\nu)}$ similar considerations hold, which are omitted.

**Remark**. Note that equilibria $E_4^{(\nu)}$ and $E_5^{(\nu)}$ are mutually exclusive, as their first stability conditions can be rewritten as

$$ecK(bc-ad) + adm < 0, \quad edH(ad-bc) + bcm < 0,$$

so that no matter what the sign of the term $ad-bc$ is, either one of the two must be positive, making the corresponding stability condition impossible. For similar reasons, also $E_3^{(\nu)}$ is incompatible with both $E_4^{(\nu)}$ and $E_5^{(\nu)}$; if $E_3^{(\nu)}$ is stable, neither $E_4^{(\nu)}$ nor $E_5^{(\nu)}$ can be feasible, compare the first of (4.2) with (3.1) and (3.2).

## 4.1 The particular cases

For the additional equilibria arising for $\nu = 0$ examined in Subsection 3.2, the stability can be assessed as follows.

$E_6$ has the two explicit eigenvalues, $\gamma_1 = -m + ecR_6 - \lambda V_6$, $\gamma_2 = b - gV_6$, while the remaining minor $\widehat{J}$ of order 2 shows that the Routh-Hurwitz conditions hold, $-\mathrm{tr}(\widehat{J}) = \dfrac{aR_6}{K} > 0$ and $\det(\widehat{J}) = ef^2R_6V_6 > 0$. The stability conditions are

$$ec\frac{m+\mu}{ef} < m + \lambda\frac{a(efK-(m+\mu))}{Kef^2}, \quad b < g\frac{a(efK-(m+\mu))}{Kef^2}. \tag{4.7}$$

For the symmetric case $E_7$ we obtain similarly two eigenvalues $\gamma_1 = -m + edU_7 - \lambda V_7$, $\gamma_2 = a - fV_7$ and again the Routh-Hurwitz conditions hold, giving the stability conditions

$$\frac{b(egH-(m+\mu))}{Heg^2} > \max\left\{d\frac{m+\mu}{\lambda g}-\frac{m}{\lambda}, \frac{a}{f}\right\}. \tag{4.8}$$

Again for these equilibria Hopf bifurcations cannot arise, since the traces of the submatrices never vanish.

For the equilibrium $E_9$ one eigenvalue is $\gamma_1 = -m + ecR_9 + edU_9 - \lambda V_9$; the Routh-Hurwitz criterion on the remaining minor $J^*$ of order 3 gives:

$$-\text{tr}(J^*) = \frac{aR_9}{K} + \frac{bU_9}{H} > 0, \quad -\det(J^*) = fR_9\frac{befU_9V_9}{H} + gU_9\frac{aegR_9V_9}{K} > 0, \quad M_2(J^*) = \frac{abR_9U_9}{HK} + eg^2U_9V_9 + ef^2R_9V_9$$

from which it follows

$$-\text{tr}(J^*)M_2(J^*) + \det(J^*) = \frac{a^2bR_9^2U_9}{HK^2} + \frac{ab^2R_9U_9^2}{H^2K} + \frac{beg^2U_9^2V_9}{H} + \frac{aef^2R_9^2V_9}{K} > 0,$$

thereby satisfying the conditions for negative real part eigenvalues. Stability is ensured by

$$ec\frac{K(mfb-efgHb+aeg^2H+\mu fb)}{e(ag^2H+bf^2K)} + ed\frac{H(mga-efgKa+bef^2K+\mu ga)}{e(ag^2H+bf^2K)} < m + \lambda\frac{ab(efK+egH-m-\mu)}{e(ag^2H+bf^2K)}. \tag{4.9}$$

$E_{10}$ has also an explicit eigenvalue $\gamma_1 = b - dF_{10} - gV_{10}$, the Routh-Hurwitz conditions on the remaining minor $J^0$ are once again seen to be satisfied,

$$-\text{tr}(J^0) = \frac{aR_{10}}{K} > 0, \quad -\det(J^0) = \frac{\lambda^2 aR_{10}F_{10}V_{10}}{K} > 0, \quad M_2(J^0) = c^2eR_{10}F_{10} + \lambda^2F_{10}V_{10} + ef^2R_{10}V_{10},$$

and thus

$$-\text{tr}(J^0)M_2(J^0) + \det(J^0) = \frac{ac^2eR_{10}^2F_{10}}{K} + \frac{aef^2R_{10}^2V_{10}}{K} > 0.$$

The stability condition is

$$b < d\frac{\lambda a(m+\mu) - efK(\lambda a + fm - c(m+\mu))}{\lambda^2 a} + g\frac{ecK(\lambda a + fm - c(m+\mu)) - m\lambda a}{\lambda^2 a}. \tag{4.10}$$

At $E_{11}$ similarly we find the stability condition

$$a < c\frac{\lambda b(m+\mu) - egH(\lambda b + gm - d(m+\mu))}{\lambda^2 b} + f\frac{edH(\lambda b + gm - d(m+\mu)) - m\lambda b}{\lambda^2 b}. \tag{4.11}$$

Also for the equilibria $E_i$, $i = 9, 10, 11$, no Hopf bifurcations can arise.

## 5 Global stability

We establish at first that the system's trajectories are bounded, by defining the total ecosystem population $W = R + U + F + V$. On summing the equations in (2.1) we find, for an arbitrary $0 < \eta < m$,

$$W' + \eta W = (a+\eta)R - \frac{a}{K}R^2 + (b+\eta)U - \frac{b}{H}U^2 + (e-1)[cFR + fVR + dFU + gVU] + (F+V)(\eta - m) - \mu V \leq L$$

where $L = \frac{1}{4}[(a+\eta)^2Ka^{-1} + (b+\eta)^2Hb^{-1}]$ is obtained as the sum of the maxima of the two parabolae in $R$ and $U$, since in view of the restriction $e < 1$ all the remaining terms on the right hand side can be eliminated. From the differential inequality it follows

$$W \leq W(0)\exp(-\eta t) + L\eta^{-1}[1 - \exp(-\eta t)] \leq \max\{W(0), L\eta^{-1}\}.$$

We examine now each equilibrium of the system. Consider at first $E_3^{(\nu)}$ and the following associated function:

$$L_3(R,U,F,V) = \alpha K\left[\frac{R-K}{K} - \ln\left(1 + \frac{R-K}{K}\right)\right] + \beta H\left[\frac{U-H}{H} - \ln\left(1 + \frac{U-H}{H}\right)\right] + \gamma F + \delta V,$$

where here and in what follows $\alpha$, $\beta$, $\gamma$ and $\delta$ are arbitrary nonnegative constants. Evidently, $L_3(E_3^{(\nu)}) = 0$ and in the whole positive cone in $\mathbf{R}^4$, $L_3 \geq 0$. We now establish that this function is a Lyapunov function, by showing that its time derivative is nonpositive. Using (2.1), we find

$$\frac{dL_3}{dt} = \alpha\frac{R'}{R}(R-K) + \beta\frac{U'}{U}(U-H) + \gamma F' + \delta V' = \alpha\left[\frac{a}{K}(K-R) - cF - fV\right](R-K) + \beta\left[\frac{b}{H}(H-U) - dF - gV\right](U-H)$$
$$+\gamma F\left[-m + ecK + edH - \lambda V + ec(R-K) + ed(U-H)\right] + \gamma\nu V + \delta V\left[\lambda F + efK + egH - \nu - m - \mu + ef(R-K) + eg(U-H)\right].$$

Reshuffling and collecting similar terms, we find

$$\frac{dL_3}{dt} = -\alpha\frac{a}{K}(R-K)^2 - \beta\frac{b}{H}(U-H)^2 + F(R-K)c(e\gamma - \alpha) + V(R-K)f(e\delta - \alpha) + F(U-H)d(e\gamma - \beta)$$
$$+V(U-H)g(e\delta - \beta) + FV\lambda(\delta - \gamma) + \gamma F(ecK + edH - m) + V[\delta(efK + egH - m - \mu - \nu) + \gamma\nu].$$

If we impose $\alpha = \beta = e\gamma = e\delta$, all the terms but the first two and the last two vanish. Imposing further

$$e < \min\left\{\frac{m}{cK+dH}, \frac{m+\mu}{fK+gH}\right\} \tag{5.1}$$

guarantees that $L_3' < 0$, so that it is a Lyapunov function and this shows that $E_3^{(\nu)}$ is globally asymptotically stable if (5.1) is satisfied.

At $E_4^{(\nu)}$ we consider instead

$$L_4(R,U,F,V) = \alpha R_4^{(\nu)}\left[\frac{R-R_4^{(\nu)}}{R_4^{(\nu)}} - \ln\left(1 + \frac{R-R_4^{(\nu)}}{R_4^{(\nu)}}\right)\right] + \beta U + \gamma F_4^{(\nu)}\left[\frac{F-F_4^{(\nu)}}{F_4^{(\nu)}} - \ln\left(1 + \frac{F-F_4^{(\nu)}}{F_4^{(\nu)}}\right)\right] + \delta V.$$

Proceeding as above, we find

$$\frac{dL_4}{dt} = -\alpha\frac{a}{K}\left(R - R_4^{(\nu)}\right)^2 - \beta\frac{b}{H}\left(U - U_4^{(\nu)}\right)^2 + \left(b - dF_4^{(\nu)}\right)\beta U - \delta V\left(m + \mu - \lambda F_4^{(\nu)} - efR_4^{(\nu)}\right) - \gamma\nu V\frac{F_4^{(\nu)}}{F},$$

so that $L_4' \leq 0$ choosing again $\alpha = \beta = e\gamma = e\delta$ and imposing

$$m + \mu > \lambda F_4^{(\nu)} + efR_4^{(\nu)}, \quad b < dF_4^{(\nu)}. \tag{5.2}$$

Next, at $E_5^{(\nu)}$ we use

$$L_5(R,U,F,V) = \alpha R + \beta U_5^{(\nu)}\left[\frac{U-U_5^{(\nu)}}{U_5^{(\nu)}} - \ln\left(1 + \frac{U-U_5^{(\nu)}}{U_5^{(\nu)}}\right)\right] + \gamma F_5^{(\nu)}\left[\frac{F-F_5^{(\nu)}}{F_5^{(\nu)}} - \ln\left(1 + \frac{F-F_5^{(\nu)}}{F_5^{(\nu)}}\right)\right] + \delta V,$$

to obtain finally, if we set the arbitrary constants again as above,

$$\frac{dL_5}{dt} = -\alpha\frac{a}{K}R^2 - \beta\frac{b}{H}\left(U - U_5^{(\nu)}\right)^2 + \alpha R\left(a - cF_5^{(\nu)}\right) - \gamma\nu V\frac{F_5^{(\nu)}}{F} + \delta V\left(-m - \mu + \lambda F_5^{(\nu)}\right),$$

which is negative definite by imposing additionally:

$$\frac{a}{c} \leq F_5^{(\nu)} \leq \frac{m+\mu}{\lambda}. \tag{5.3}$$

At $E_6$ we start with

$$L_6(R,U,F,V) = \alpha R_6\left[\frac{R-R_6}{R_6} - \ln\left(1 + \frac{R-R_6}{R_6}\right)\right] + \beta U + \gamma F + \delta V_6\left[\frac{V-V_6}{V_6} - \ln\left(1 + \frac{V-V_6}{V_6}\right)\right],$$

which, again with the above choice of the constants, leads to

$$\frac{dL_6}{dt} = -\alpha\frac{a}{K}(R-R_6)^2 - \beta\frac{b}{H}U^2 + \beta U(b - gV_6) + \gamma F(ecR_6 - \lambda V_6 - m),$$

that turns out to be negative definite by requiring:

$$b < gV_6, \quad ecR_6 < \lambda V_6 + m. \tag{5.4}$$

$E_7$ is a kind of "symmetric point" of $E_6$, so that the function $L_7$ can be easily established and leads to the "dual" conditions

$$a < fV_7, \quad edU_7 < \lambda V_7 + m. \tag{5.5}$$

The Lyapunov function candidate for $E_8^{(\nu)}$ is

$$L_8(R,U,F,V) = \alpha R_8^{(\nu)}\left[\frac{R-R_8^{(\nu)}}{R_8^{(\nu)}} - \ln\left(1+\frac{R-R_8^{(\nu)}}{R_8^{(\nu)}}\right)\right] + \beta U_8^{(\nu)}\left[\frac{U-U_8^{(\nu)}}{U_8^{(\nu)}} - \ln\left(1+\frac{U-U_8^{(\nu)}}{U_8^{(\nu)}}\right)\right] + \gamma F_8^{(\nu)}\left[\frac{F-F_8^{(\nu)}}{F_8^{(\nu)}} - \ln\left(1+\frac{F-F_8^{(\nu)}}{F_8^{(\nu)}}\right)\right] + \delta V.$$

Once more the choice of the constants as previously done, leads to

$$\frac{dL_8}{dt} = -\alpha\frac{a}{K}\left(R-R_8^{(\nu)}\right)^2 - \beta\frac{b}{H}\left(U-U_8^{(\nu)}\right)^2 + \nu\gamma V\frac{F-F_8^{(\nu)}}{F} + \delta V\left[\lambda F_8^{(\nu)} + efR_8^{(\nu)} + egU_8^{(\nu)} - m - \mu\right] - \nu\delta V,$$

for which $L_8' \le 0$ if we impose

$$\lambda F_8^{(\nu)} + efR_8^{(\nu)} + egU_8^{(\nu)} < m + \mu. \tag{5.6}$$

At $E_9$ set

$$L_9(R,U,F,V) = \alpha R_9\left[\frac{R-R_9}{R_9} - \ln\left(1+\frac{R-R_9}{R_9}\right)\right] + \beta U_9\left[\frac{U-U_9}{U_9} - \ln\left(1+\frac{U-U_9}{U_9}\right)\right] + \gamma F + \delta V_9\left[\frac{V-V_9}{V_9} - \ln\left(1+\frac{V-V_9}{V_9}\right)\right].$$

so that, again with the same choice for the arbitrary parameters,

$$\frac{dL_9}{dt} = -\alpha\frac{a}{K}(R-R_9)^2 - \beta\frac{b}{H}(U-U_9)^2 + \gamma F(ecR_9 + edU_9 - m - \lambda V_9),$$

negative whenever the following condition holds:

$$ecR_9 + edU_9 < m + \lambda V_9. \tag{5.7}$$

Again, equilibria $E_{10}^{(\nu)}$ and $E_{11}^{(\nu)}$ are kind of "symmetric", for which we examine only the latter. Choose

$$L_{11} = \alpha R + \beta U_{11}^{(\nu)}\left[\frac{U-U_{11}^{(\nu)}}{U_{11}^{(\nu)}} - \ln\left(1+\frac{U-U_{11}^{(\nu)}}{U_{11}^{(\nu)}}\right)\right] + \gamma F_{11}^{(\nu)}\left[\frac{F-F_{11}^{(\nu)}}{F_{11}^{(\nu)}} - \ln\left(1+\frac{F-F_{11}^{(\nu)}}{F_{11}^{(\nu)}}\right)\right] + \delta V_{11}^{(\nu)}\left[\frac{V-V_{11}^{(\nu)}}{V_{11}^{(\nu)}} - \ln\left(1+\frac{V-V_{11}^{(\nu)}}{V_{11}^{(\nu)}}\right)\right].$$

to obtain

$$\begin{aligned}\frac{dL_{11}}{dt} &= -\mathbf{y}^T M\mathbf{y} + \alpha R\left(a - cF_{11}^{(\nu)} - fV_{11}^{(\nu)}\right) + \gamma\left(F-F_{11}^{(\nu)}\right)\left[edU_{11}^{(\nu)} - \lambda V_{11}^{(\nu)} - m\right] + \gamma\nu V\left(1-\frac{F_{11}^{(\nu)}}{F}\right)\\ &= -\mathbf{y}^T M\mathbf{y} + \alpha R\left(a - cF_{11}^{(\nu)} - fV_{11}^{(\nu)}\right) + \gamma\nu\frac{1}{F_{11}^{(\nu)}}\left(F-F_{11}^{(\nu)}\right)\left(V-V_{11}^{(\nu)}\right) - \gamma\nu\frac{V}{F_{11}^{(\nu)}F}\left(F-F_{11}^{(\nu)}\right)^2\\ &= -\mathbf{y}^T\widetilde{M}\mathbf{y} + \alpha R\left(a - cF_{11}^{(\nu)} - fV_{11}^{(\nu)}\right) - \gamma\nu\frac{V}{F_{11}^{(\nu)}F}\left(F-F_{11}^{(\nu)}\right)^2,\end{aligned}$$

where $\mathbf{y}^T = \left(R, U-U_{11}^{(\nu)}, F-F_{11}^{(\nu)}, V-V_{11}^{(\nu)}\right)$, $\widetilde{M}$ coincides with $M$ but for the elements

$$\widetilde{M}_{34} = \widetilde{M}_{43} = M_{43} - \frac{\nu\gamma}{2F_{11}^{(\nu)}}$$

and

$$-M = \begin{pmatrix} \alpha\frac{a}{K} & 0 & -\frac{1}{2}c(e\gamma-\alpha) & -\frac{1}{2}f(e\delta-\alpha)\\ 0 & \beta\frac{b}{H} & -\frac{1}{2}d(e\gamma-\beta) & -\frac{1}{2}g(e\delta-\beta)\\ -\frac{1}{2}c(e\gamma-\alpha) & -\frac{1}{2}d(e\gamma-\beta) & 0 & -\frac{1}{2}\lambda(\delta-\gamma)\\ -\frac{1}{2}f(e\delta-\alpha) & -\frac{1}{2}g(e\delta-\beta) & -\frac{1}{2}\lambda(\delta-\gamma) & 0\end{pmatrix}.$$

Now the choices $e\gamma = \alpha = \beta$ allow the matrix $\widetilde{M}$ to be positive semidefinite, since its principal minors are then $\Delta_1 = \alpha aK^{-1} > 0$, $\Delta_2 = \alpha\beta ab(KH)^{-1} > 0$, $\Delta_3 = 0$ and we can make $\Delta_4$ vanish by setting $\widetilde{M}_{34} = 0$, i.e. by choosing the constants $\gamma$, $\nu$ and $\lambda$ and $\delta$ to satisfy the condition given below. In addition, to have the time derivative of $L_{11}$ nonpositive, we must further require an additional condition:

$$\lambda\delta = \gamma\left(\lambda - \frac{\nu}{F_{11}^{(\nu)}}\right), \quad a < cF_{11}^{(\nu)} + fV_{11}^{(\nu)}. \tag{5.8}$$

For $E_{10}^{(\nu)}$ the same choice for the arbitrary constants are required together with the following further requirements

$$\lambda\delta = \gamma\left(\lambda - \frac{\nu}{F_{10}^{(\nu)}}\right), \quad b < dF_{10}^{(\nu)} + gV_{10}^{(\nu)}. \tag{5.9}$$

For the coexistence equilibrium, the chosen form is

$$\begin{aligned} L_{12} = {} & \alpha R_{12}^{(\nu)}\left[\frac{R-R_{12}^{(\nu)}}{R_{12}^{(\nu)}} - \ln\left(1+\frac{R-R_{12}^{(\nu)}}{R_{12}^{(\nu)}}\right)\right] + \beta U_{12}^{(\nu)}\left[\frac{U-U_{12}^{(\nu)}}{U_{12}^{(\nu)}} - \ln\left(1+\frac{U-U_{12}^{(\nu)}}{U_{12}^{(\nu)}}\right)\right] \\ & + \gamma F_{12}^{(\nu)}\left[\frac{F-F_{12}^{(\nu)}}{F_{12}^{(\nu)}} - \ln\left(1+\frac{F-F_{12}^{(\nu)}}{F_{12}^{(\nu)}}\right)\right] + \delta V_{12}^{(\nu)}\left[\frac{V-V_{12}^{(\nu)}}{V_{12}^{(\nu)}} - \ln\left(1+\frac{V-V_{12}^{(\nu)}}{V_{12}^{(\nu)}}\right)\right] \end{aligned}$$

and setting $\mathbf{x}^T = \left(R-R_{12}^{(\nu)}, U-U_{12}^{(\nu)}, F-F_{12}^{(\nu)}, V-V_{12}^{(\nu)}\right)$, we obtain

$$\frac{dL_{12}}{dt} = -\mathbf{x}^T M\mathbf{x} + \gamma\left(F-F_{12}^{(\nu)}\right)\left[ecR_{12}^{(\nu)} + edU_{12}^{(\nu)} - \lambda V_{12}^{(\nu)} - m\right] + \gamma\nu\frac{V}{F}\left(F-F_{12}^{(\nu)}\right) = -\mathbf{x}^T M\mathbf{x} - \gamma\nu\left(F-F_{12}^{(\nu)}\right)\left(\frac{V_{12}^{(\nu)}}{F_{12}^{(\nu)}} - \frac{V}{F}\right).$$

But

$$\frac{V_{12}^{(\nu)}}{F_{12}^{(\nu)}} - \frac{V}{F} = \frac{V}{F_{12}^{(\nu)}F}\left(F_{12}^{(\nu)} - F\right) - \frac{1}{F_{12}^{(\nu)}}\left(V - V_{12}^{(\nu)}\right),$$

so that finally

$$\frac{dL_{12}^{(\nu)}}{dt} = -\mathbf{x}^T N\mathbf{x} - \gamma\nu\frac{V_{12}}{F_{12}^{(\nu)}F}\left(F-F_{12}^{(\nu)}\right)^2,$$

where

$$-N = \begin{pmatrix} \alpha\dfrac{a}{K} & 0 & -\frac{1}{2}c(e\gamma-\alpha) & -\frac{1}{2}f(e\delta-\alpha) \\ 0 & \beta\dfrac{b}{H} & -\frac{1}{2}d(e\gamma-\beta) & -\frac{1}{2}g(e\delta-\beta) \\ -\frac{1}{2}c(e\gamma-\alpha) & -\frac{1}{2}d(e\gamma-\beta) & 0 & -\frac{1}{2}\left[\lambda(\delta-\gamma)+\frac{\nu\gamma}{F_{12}^{(\nu)}}\right] \\ -\frac{1}{2}f(e\delta-\alpha) & -\frac{1}{2}g(e\delta-\beta) & -\frac{1}{2}\left[\lambda(\delta-\gamma)+\frac{\nu\gamma}{F_{12}^{(\nu)}}\right] & 0 \end{pmatrix}.$$

Now the choices $e\gamma = \alpha = \beta$ allow the matrix $N$ to be positive semidefinite, since its principal minors are then $\Delta_1 = \alpha a K^{-1} > 0$, $\Delta_2 = \alpha\beta ab(KH)^{-1} > 0$, $\Delta_3 = 0$ and $\Delta_4 = -\alpha a(4K)^{-1}\left[\lambda(\delta-\gamma) + \nu\gamma(F_{12}^{(\nu)})^{-1}\right]^2 = 0$ if we impose the condition

$$\lambda\delta = \gamma\left(\lambda - \frac{\nu}{F_{12}^{(\nu)}}\right). \tag{5.10}$$

It follows therefore that $L_{12}$ is a Lyapunov function, since its derivative along the solution trajectories is nonpositive.

# 6 Simulations

The equilibria that have not been found analytically are here shown that can be stably achieved, by means of numerical simulations.

$E_8^{(\nu)}$ is shown to be stable by the following choice of parameters: $m = 0.8$, $e = 0.9$, $b = 28$, $c = 0.16$, $K = 2$, $H = 3$, $d = 1$, $a = 10$, $f = 9$, $g = 16$, $\lambda = 2$, $\nu = 30$, $\mu = 50$, see Figure 4 left frame, showing that (3.3) is nonempty as claimed earlier. Note however that it is also stable in the case $\nu = 0$ for the same choice of parameters, but $\nu = 0$, $\mu = 75$, Figure 4 right frame.

For $E_{10}^{(\nu)}$ we use the following set of parameters: $a = 11$, $K = 12$, $c = 6$, $f = 2$, $b = 3$, $H = 8$, $d = 8$, $g = 4$, $m = 1$, $e = 0.841915$, $\lambda = 10$, $\nu = 6$, $\mu = 8$. In this case we obtain a conic section with characteristic properties as shown in Figure 1. The simulations are shown in Figure 5 left frame. For the particular case $\nu = 0$ we have instead the equilibrium shown in Figure 5, right frame, with

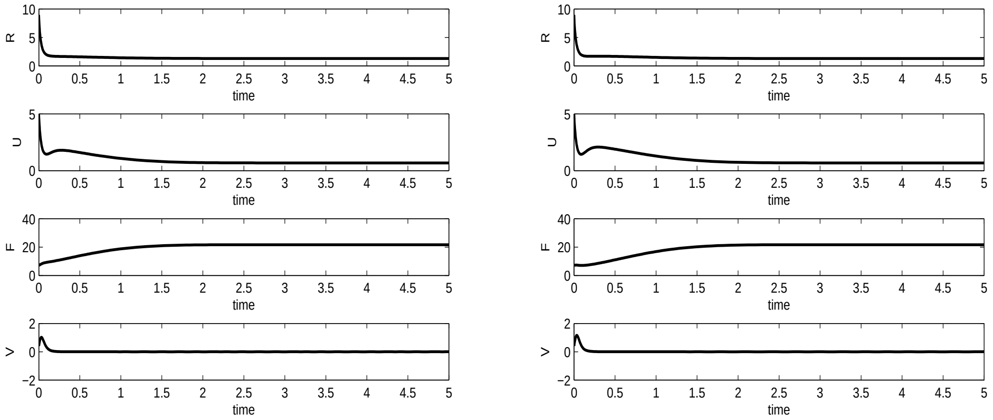


**Fig. 4** Left: Equilibrium $E_8^{(\nu)}$. Right: Equilibrium $E_8$ with $\nu = 0$.

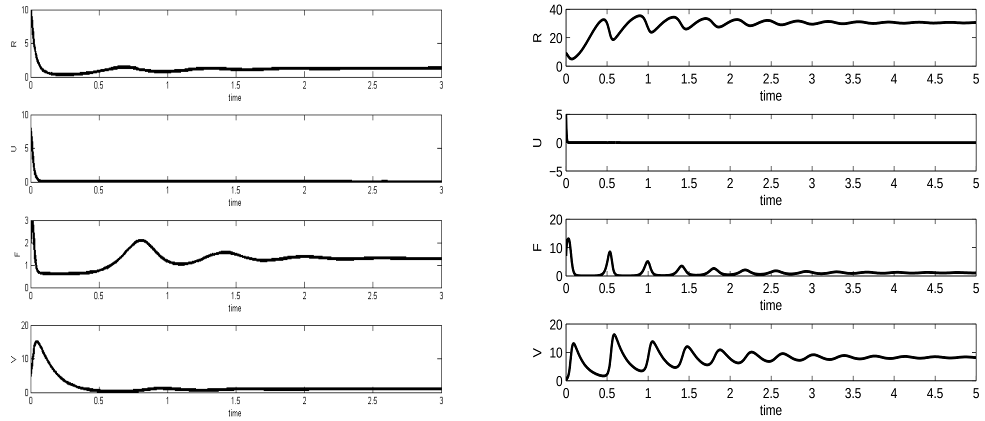


**Fig. 5** Left: Equilibrium $E_{10}^{(\nu)}$. Right: Equilibrium $E_{10}$ for $\nu = 0$.

parameter values $m = 0.1$, $e = 0.841915$, $b = 3$, $c = 1.6$, $K = 40$, $H = 400$, $d = 18$, $a = 11$, $f = 0.1$, $g = 4$, $\lambda = 5$, $\nu = 0$, $\mu = 8$, showing that (3.12) is nonempty.

For $E_{11}^{(\nu)}$ we use $a = 15$, $K = 20$, $c = 16$, $f = 19$, $b = 28$, $H = 30$, $d = 11$, $g = 16$, $m = 8$, $e = 0.12699$, $\lambda = 22$, $\nu = 10$, $\mu = 13$, giving the result of Figure 6 left frame. For the case $\nu = 0$, the equilibrium is achieved for the parameter values $m = 4$, $e = 0.12699$, $b = 28$, $c = 16$, $K = 20$, $H = 4$, $d = 15$, $a = 0.15$, $f = 19$, $g = 36$, $\lambda = 22$, $\nu = 0$, $\mu = 13$, as shown in Figure 6 right frame.

For the coexistence equilibrium $E_{12}^{(\nu)}$ we consider $a = 20$, $K = 9$, $c = 5$, $f = 2$, $b = 30$, $H = 10$, $d = 6$, $g = 3$, $m = 11$, $e = 0.5$, $\lambda = 14$, $\nu = 6$, $\mu = 12$. The result is contained in Figure 7 left frame. In the particular case when $\nu = 0$, we have for the coexistence also the following choice, $a = 11$, $K = 10$, $c = 6$, $f = 2$, $b = 15$, $H = 8$, $d = 8$, $g = 3$, $m = 9$, $e = 0.85$, $\lambda = 12$, $\nu = 0$, $\mu = 10$ giving the graph of Figure 7 right frame.

The Tables 1, for the recoverable disease, and 2 in case the disease cannot be overcome, summarize our findings. In Table 1 comparison of the feasibility conditions for $E_8^{(\nu)}$ with the stability conditions of $E_3^{(\nu)}$, $E_4^{(\nu)}$ and $E_5^{(\nu)}$ indicates that there are transcritical bifurcations from these equilibria, for which while the diseased predators are always absent, each missing population in each one of the points $E_3^{(\nu)}$, $E_4^{(\nu)}$ and $E_5^{(\nu)}$ invades the environment whenever this point becomes unstable, giving rise to the disease-free coexistence equilibrium $E_8^{(\nu)}$.

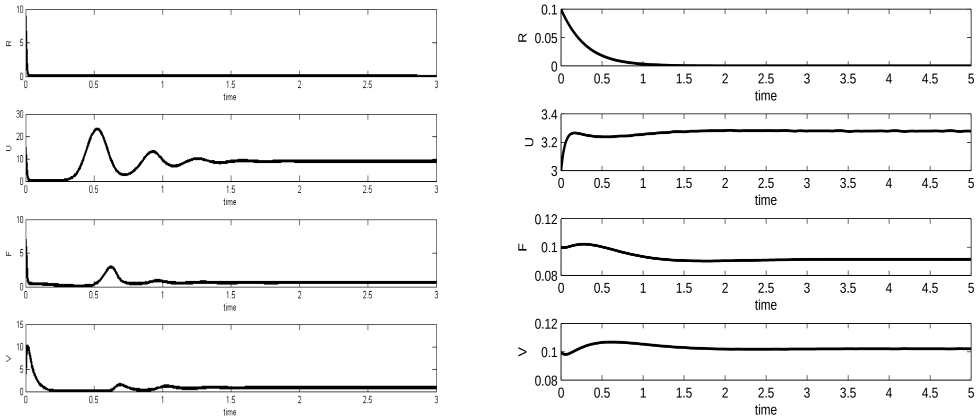


**Fig. 6** Left: Equilibrium $E_{11}^{(\nu)}$. Right: Equilibrium $E_{11}$ for $\nu = 0$.

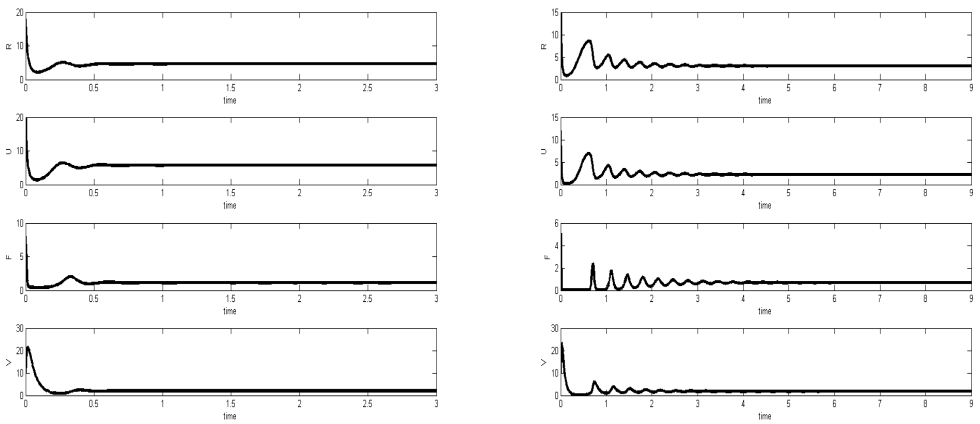


**Fig. 7** Left: Coexistence equilibrium $E_{12}^{(\nu)}$. Right: Coexistence equilibrium $E_{12}$ when $\nu = 0$.

A similar conclusion can be obtained from the very same equilibria $E_3$, $E_4$ and $E_5$ and $E_9$ for $\nu = 0$, i.e. whenever the disease is unrecoverable, compare the conditions given in Table 2. In this case the equilibrium obtained is the endemic, healthy-prey-free one, in which the disease affects the whole prey population.

## 7 Discussion

The ecosystem introduced here comprises an environment in which two non interfering prey thrive, together with a specialist predator that feeds on both of them. The latter is also affected by a disease, that cannot be passed to the prey, but it can be transmitted by contact to the other predator individuals.

One positive result that follows from the assumptions made is that the ecosystem cannot be wiped away. It is also interesting to remark that no single prey system can thrive, in spite of what one could think a priori. Indeed the equilibria $E_0^{(\nu)}$, $E_1^{(\nu)}$ and $E_2^{(\nu)}$ are all unstable.

It is interesting to note that the fact that prey do not experience interspecific competition makes the survival of each one of them alone in the environment impossible. This is quite counterintuitive, but there are reasons for this to occur. In fact, the impossibility of having $E_1^{(\nu)}$, say, stable, is due to the presence of the positive eigenvalue $a$, which stems from the the very first equilibrium equation.

**Table 1** Summary of equilibria for the model with disease recovery, $\nu \neq 0$.

| Equilibria | **Feasibility conditions** | **Stability conditions** |
|---|---|---|
| $E_0^{(\nu)} = (0,0,0,0)$ | — | unstable |
| $E_1^{(\nu)} = (0,H,0,0)$ | — | unstable |
| $E_2^{(\nu)} = (K,0,0,0)$ | — | unstable |
| $E_3^{(\nu)} = (K,H,0,0)$ | — | $\begin{cases} cK+dH < \frac{m}{e} \\ fK+gH < \frac{m+\mu+\nu}{e} \end{cases}$ |
| $E_4^{(\nu)} = \left(\frac{m}{ec}, 0, a\frac{ecK-m}{Kec^2}, 0\right)$ | $ecK > m$ | $\begin{cases} b < \frac{ad(ecK-m)}{Kec^2} \equiv L \\ Q \equiv \frac{\lambda a(ecK-m)}{Kec^2} + \frac{fm}{c} < \mu+m+\nu \end{cases}$ |
| $E_5^{(\nu)} = \left(0, \frac{m}{ed}, b\frac{edH-m}{Hed^2}, 0\right)$ | $edH > m$ | $\begin{cases} a < \frac{bc(edH-m)}{Hed^2} \\ \frac{\lambda b(edH-m)}{Hed^2} + \frac{gm}{d} < \mu+m+\nu \end{cases}$ |
| $E_8^{(\nu)} = \left(R_8^{(\nu)}, U_8^{(\nu)}, F_8^{(\nu)}, 0\right)$ <br> $R_8^{(\nu)} = \dfrac{K(mcb-edHcb+aed^2H)}{e(ad^2H+bc^2K)}$ <br> $U_8^{(\nu)} = \dfrac{H(mda-ecKda+bec^2K)}{e(ad^2H+bc^2K)}$ <br> $F_8^{(\nu)} = \dfrac{ab(Kec+Hed-m)}{e(ad^2H+bc^2K)}$ | $e(Kc+Hd) > m$ <br> $mda+bec^2K > ecKda$ <br> $mcb+aed^2H > edHcb$ | $\lambda F_8^{(\nu)} + efR_8^{(\nu)} + egU_8^{(\nu)} < m+\mu+\nu$ |
| $E_{10}^{(\nu)} = \left(R_{10}^{(\nu)}, 0, F_{10}^{(\nu)}, V_{10}^{(\nu)}\right)$ | $F_{10}^{(\nu)} = \frac{A-efR_{10}^{(\nu)}}{\lambda}$, $R_{10}^{(\nu)} < \frac{A}{ef}$ and either <br> $R_{10}^{(\nu)} > K\frac{cA-a\lambda}{cefK-a\lambda}$, for $cefK > a\lambda$ <br> or $R_{10}^{(\nu)} < K\frac{cA-a\lambda}{cefK-a\lambda}$, for $cefK < a\lambda$. | $b < dF_{10}^{(\nu)} + gV_{10}^{(\nu)}$ |
| $E_{11}^{(\nu)} = \left(0, U_{11}^{(\nu)}, F_{11}^{(\nu)}, V_{11}^{(\nu)}\right)$ | $F_{11}^{(\nu)} = \frac{A-egU_{11}^{(\nu)}}{\lambda}$, $U_{11}^{(\nu)} < \frac{A}{eg}$ and either <br> $U_{11}^{(\nu)} > H\frac{dA-b\lambda}{degH-b\lambda}$, for $degH > b\lambda$ <br> or $U_{11}^{(\nu)} < H\frac{dA-b\lambda}{degH-b\lambda}$, for $degH < b\lambda$. | $a < cF_{11}^{(\nu)} + fV_{11}^{(\nu)}$ |

If competition were introduced among the two prey instead, e.g. looking at $E_1^{(\nu)}$, a bilinear term of the type $-wRU$ should be accounted for in the first equation and a similar one in the second one. Correspondingly e.g. the very first entry in the Jacobian would contain also the term $-wU$. This modification would change the first eigenvalue in $a - wH$ and therefore make the stabilization of the equilibrium possible.

The two prey instead can coexist together, but for this to occur the healthy predators' "mortality rate" $m$ and the "total mortality rate" of the infected predators $m+\mu$ must exceed a combination of the two prey carrying capacities, respectively $e(cK+dH)$ and $e(fK+gH)$. These quantities represent the total gain that healthy predators and infected predators obtain from the two prey with their hunting. In other words, these are essentially reproduction rates, and if they fall below the mortality rates, the predators cannot survive.

We then find disease-free equilibria with one prey only, feasible if the mortality rate of predators falls below the gain they get from hunting the thriving prey. Looking e.g. at $E_4^{(\nu)}$, we need $m < ecK$. Stability instead depends on having a rather small reproduction rate of the alternate prey, namely $b < L$, where $L$ is a suitable upper bound. The second stability condition instead imposes a high exit rate from the infected predator class, namely $Q < m+\mu+\nu$, either by natural plus disease-related mortality or by recovery, compare Table 1.

The equilibria with three populations are those in which the healthy predators are always present. This is intuitively not so clear, as if this subpopulation disappears, there is still a way of feeding new individuals into the class of infected, since the disease is assumed to be vertically transmissible, and therefore the latter are not necessarily bound to disappear. But the stability conditions, Table 1, essentially state that the new recruits into the infected class are less than the individuals that die in it, compare the stability condition of $E_8^{(\nu)}$. For $E_{10}^{(\nu)}$ and $E_{11}^{(\nu)}$ the stability conditions would instead imply that the vanishing prey population has a smaller birth rate than the mortality rate due to predators' hunting.

In case the disease is not recoverable, infected predators can thrive with just one prey population, equilibria $E_6$ and $E_7$. But for feasibility the whole mortality rate of the infected predators must be lower than the food intake from the thriving prey at carrying

**Table 2** Summary of equilibria for the particular case of unrecoverable disease, $\nu = 0$.

| Equilibria | **Feasibility conditions** | **Stability conditions** |
| --- | --- | --- |
| $E_6 = \left( \frac{m+\mu}{ef}, 0, 0, \frac{a(efK-(m+\mu))}{Kef^2} \right)$ | $efK > m+\mu$ | $\begin{cases} ecR_6 < m+\lambda V_6 \\ b < gV_6 \end{cases}$ |
| $E_7 = \left( 0, \frac{m+\mu}{eg}, 0, \frac{b(egH-(m+\mu))}{Heg^2} \right)$ | $egH > m+\mu$ | $\begin{cases} edU_7 < m+\lambda V_7 \\ a < fV_7 \end{cases}$ |
| $E_9 = (R_9, U_9, 0, V_9)$<br>$R_9 = \frac{K(mfb - efgHb + aeg^2H + \mu fb)}{e(ag^2H + bf^2K)}$<br>$U_9 = \frac{H(mga - efgKa + bef^2K + \mu ga)}{e(ag^2H + bf^2K)}$<br>$V_9 = \frac{ab(efK + egH - m - \mu)}{e(ag^2H + bf^2K)}$ | $e(Kf + Hg) > m+\mu$<br>$mga + bef^2K + \mu ga > efgKa$<br>$mfb + aeg^2H + \mu fb > efgHb$ | $ecR_9 + edU_9 < m + \lambda V_9$ |
| $E_{10} = (R_{10}, 0, F_{10}, V_{10})$<br>$R_{10} = \frac{K(\lambda a + fm - c(m+\mu))}{\lambda a}$<br>$F_{10} = \frac{\lambda a(m+\mu) - efK(\lambda a + fm - c(m+\mu))}{\lambda^2 a}$<br>$V_{10} = \frac{ecK(\lambda a + fm - c(m+\mu)) - m\lambda a}{\lambda^2 a}$ | $\lambda a + fm > c(m+\mu)$<br>$\lambda a(m+\mu) > efK(\lambda a + fm - c(m+\mu))$<br>$m\lambda a < ecK(\lambda a + fm - c(m+\mu))$ | $b < dF_{10} + gV_{10}$ |
| $E_{11} = (0, U_{11}, F_{11}, V_{11})$<br>$U_{11} = \frac{H(\lambda b + gm - d(m+\mu))}{\lambda b}$<br>$F_{11} = \frac{\lambda b(m+\mu) - egH(\lambda b + gm - d(m+\mu))}{\lambda^2 b}$<br>$V_{11} = \frac{edH(\lambda b + gm - d(m+\mu)) - m\lambda b}{\lambda^2 b}$ | $\lambda b + gm > d(m+\mu)$<br>$\lambda b(m+\mu) > egH(\lambda b + gm - d(m+\mu))$<br>$m\lambda b < edH(\lambda b + gm - d(m+\mu))$ | $a < cF_{11} + fV_{11}$ |

capacity. For stability, the reproduction rate of the healthy predators, feeding on the surviving prey, must be lower than their total losses, obtained combining mortality and new infected recruits. In addition, the prey that disappears from the ecosystem must have a birth rate lower than the damage they experience through hunting by the infected predators.

Finally, at $E_9$ we find the two prey thriving with just the infected predators. Here the disease affects then the whole predator population. The infected newborns must be larger than the total losses due to natural plus disease-related mortality, see Table 2, in addition to two more involved feasibility conditions. Stability holds if the healthy predators do not reproduce fast enough, namely at a lower rate than the one for which individuals leave this class, obtained combining the mortality with the disease contact rate.

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