# Ecoepidemics with two strains: diseased predators

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*Abstract:* - In this paper we present the first ecoepidemic model containing two disease strains in the same population, specifically in the predators. We present two models, in the first one of which the epidemics is transmitted only horizontally. The second one is more general, since it allows also vertical transmission of the disease, i.e. offsprings of infected parents also carry the disease. Answers to relevant biological questions are analysed. Surprisingly, however, this ecoepidemic system with two strains cannot be sustained at a stable coexistence equilibrium level.

*Key-Words:* - Epidemics, Population Models, Ecoepidemics, Two-Strain Models, Equilibria, Stability.

## 1 Introduction

This paper represents a novelty with respect to all the former investigations on ecoepidemic models. The novel feature lies in the fact that here for the first time two diseases are considered, to affect the same population, in this case the predators.

Epidemic models are named with acronims illustrating their main characteristics, so for instance SI stands for a simple model in which only susceptibles (S) and infected (I) are present, and the disease once contracted is carried for the whole lifespan of the individual; SIS denotes the model that allows disease recovery, a transition back from the class of infected into the class of susceptibles; here disease relapses are possible. In the SIR and SIRS models a class of removed individuals (R) is introduced, where by "removed" one has to understand individuals who are recognized to be disease-carriers and therefore quarantined, or individuals in which the infectious period, i.e. the ability of propagating the disease, is over; in the SIR system, after disease recovery, life immunization is obtained, in SIRS models a transition back into the class of susceptibles is possible, thereby allowing disease relapses. The SEI models and their SEIR and SEIRS variations, [12, 13] introduce instead also the incubation period, i.e. the exposed class (E) of individuals, i.e. those who have contracted the disease, but are not yet able to spread it. Here too the infectious (I) are the only individuals able to infect other susceptibles. More recent models account also for delays, [16], and pattern formation, [24]. For a specific application in real life situation, see [26].

Ecoepidemic models represent a step further in this picture. These models account first of all for more populations, among which a disease is propagating by contact, and also for underlying demographic interactions among them. They represent a natural extension of population theory, whose starting point dates back to two centuries ago, [23, 33], but which essentially was developed in the past century from the pioneering works of Volterra and Lotka, [21, 34]. The first investigations in this recent field of research are [17, 4, 27, 28]. More recent models are considering also stochastic environments, [15], time dependent parameters, [11], periodic structures, [3], age-dependencies, [10].

For a brief account of population theory including also ecoepidemics, the interested reader can consult Chapter 6 in the fairly recent book [22], or the Introduction of [18] or the short review [31].

A very general SI ecoepidemic model, with disease in the predators of interest here, see for instance [28, 30], can be written letting $P$ denote the prey population and $S$ and $I$ respectively the class of suscepti-

ble and infected predators, as follows

$$\frac{dP}{dt} = R(P) - p_S(S,P) - p_I(I,P), \quad (1)$$

$$\frac{dS}{dt} = ap_S(S,P) + bp_I(I,P) - M_S(I) - \beta(S,I), \quad (2)$$

$$\frac{dI}{dt} = \beta(S,I) - M_I(I), \quad (3)$$

where $R(P)$ is the reproduction function of the prey, $p_S(S,P)$ and $p_I(I,P)$ denote the hunting rates on prey by the sound and infected predators, which are obviously assumed to be different since infected predators are weaker and therefore less able to hunt, $\beta(S,P)$ represents the disease contact rate between susceptibles and infected and $M_S$ and $M_I$ denote natural and natural plus disease-related mortalities respectively.

Equation (1) models the prey dynamics, which reproduce and are hunted by the sound and infected predators, respectively. Instead in equation (2) we find the way the healthy predators' population changes. Newborns are all born healthy. They are recruited by converting captured prey into offsprings, from both healthy and diseased parents, this being expressed by the first two terms. Sound predators are also subject to natural mortality, and they migrate into the class of infected upon contracting the disease via contacts with infectious individuals. These statements are mathematically represented by the last two terms of (2). The class of disease-carriers is described in equation (3). The two terms describe the following transitions: new recruits into this class arrive only from the susceptibles that get infected, the only way out is represented by natural plus disease-induced mortality.

Here it is clearly assumed that the disease cannot be transmitted vertically, i.e. the offsprings are all born sound, and that it possibly affects the reproduction capacities of the predators, this being modeled by the different coefficients $a$ and $b$ multiplying the two functions $p_S(S,P)$ and $p_I(I,P)$ in the equation (2) for the susceptibles. We will make a profound modification in the above model (1-3), as we will assume that the predators are affected also by a second disease.

The paper is organized as follows. We present the basic model in the next Section. In Sections 3-8 we will investigate the answers to some relevant biological questions, namely:

- whether the system can be biologically viable, i.e. populations do not grow indefinitely thereby exhausting the resources;
- under what conditions the system can be wiped out;
- whether prey alone or prey and only susceptible predators survive;
- whether one disease can be eradicated, leaving only the other one endemic;
- whether both diseases together with the sound predators and the prey all survive.

In Section 9 we provide some numerical simulations supporting our previous analysis. In Section 10 we consider a more general model allowing vertical transmission of both diseases and investigate thoroughly by analytical means the boundedness of its trajectories. A final discussion concludes the paper.

## 2 Model setup

Some assumptions on this specific model are in order. First of all we assume that the two epidemics are of SIS type, i.e. both are recoverable but do not provide immunity. But the main assumption that we make relates the reciprocal relationship between the diseases and somehow restricts our scope. Specifically, we assume that the two epidemics affecting the predators do not interfere with each other, which means that at any given time one individual can carry at most one of the two diseases. In the first model we assume the diseased animals to be so weak that they cannot hunt. At a later stage, in a second model we will remove this last restrction. Let $P$ be the prey population, $S$ the susceptible predators, $V$ the predators infected by the first disease and $W$ those infected with the second one.

The model reads

$$\begin{cases} \dfrac{dP}{dt} = r\left(1 - \dfrac{P}{k_P}\right)P - aPS \\ \dfrac{dS}{dt} = -mS + eaSP - \lambda SV + \gamma V - \beta SW + \varphi W \\ \dfrac{V}{dt} = \lambda SV - \gamma V - \mu V \\ \dfrac{W}{dt} = \beta SW - \varphi W - \nu W. \end{cases} \quad (4)$$

The parameter $r$ denotes the net prey reproduction rate, $k_P$ their carrying capacity, $a$ the predation rate on them; $m$ is the natural mortality rate of susceptible predators, $e$ the predators' conversion factor, $\lambda$ the first disease incidence, $\gamma$ the first disease recovery rate, $\beta$ the second disease contact rate, $\varphi$ the second disease recovery rate, $\mu$ the natural plus first disease mortality rate, $\nu$ the natural plus second disease mortality rate.

Compaing with (1-3), we see clearly that the first equation gives the prey dynamics, the second one the helthy predators dynamics, and the last two the infected predators' time evolution. From the first equation the prey exhibit logistic growth and are subject to predation only by the healthy predators. In the second equation we find the susceptible predators, subject to natural mortality; they survive by hunting the prey and turning them into newborns, via the conversion factor $e$. They are further subject to the two diseases, which are contracted by contacts with infected individuals of the suitable strain, modeled via a simple mass action law, represented by the third and fifth terms. From these diseases predators may recover, a transition modelled in the fourth and sixth terms. The third and fourth equations describe respectively the dynamics of each disease. Their first terms account always for new recruitments into the class of infected, at respective rates $\lambda$ and $\beta$, and the next terms allow disease recovery, at respective rates $\gamma$ and $\varphi$. The last terms denote natural plus disease-related mortalities.

For further analysis, it is useful to write down the system's Jacobian,

$$J(P,S,V,W) = J_{ik}, \quad i,k = 1,\dots,4, \qquad (5)$$

with components given by

$$\begin{aligned} J_{11} &= -\frac{2rP}{k_P} + r - aS, \quad J_{12} = -aP, \\ J_{21} &= eaS, \quad J_{22} = eaP - m - \lambda V - \beta W, \\ J_{23} &= -\lambda S + \gamma, \quad J_{24} = -\beta S + \varphi, \\ J_{32} &= \gamma V, \quad J_{33} = \lambda S - (\gamma + \mu), \\ J_{42} &= \beta W, \quad J_{44} = \beta S - (\varphi + \nu) \end{aligned}$$

and where the remaining entries vanish.

Note that there are two particular cases that need to be discussed, namely the system being disease-free, i.e. $V = W = 0$ and the system being affected only by one epidemic, i.e. $V = 0$ , or alternatively $W = 0$. In the former one obtains the system

$$\begin{cases} \dfrac{dP}{dt} = r\left(1 - \dfrac{P}{k_P}\right)P - aPS \\ \dfrac{dS}{dt} = -mS + eaSP \end{cases} \qquad (6)$$

i.e. a simple predator-prey model with no disease, which differs from the classical Lotka-Volterra model [34], since the prey here exhibit logistic growth. As a consequence, therefore, the system does not show the neutrally stable cycles which constitute the main objection against [34]. The coexistence equilibrium here is the only equilibrium of the system, which can be shown to be globally asymptotically stable, [14], using a suitable Lyapunov function. In the second case, we have instead

$$\begin{cases} \dfrac{dP}{dt} = r\left(1 - \dfrac{P}{k_P}\right)P - aPS \\ \dfrac{dS}{dt} = -mS + eaSP - \beta SW + \varphi W \\ \dfrac{dW}{dt} = \beta SW - \varphi W - \nu W \end{cases} \qquad (7)$$

which corresponds to a standard ecoepidemic model, [30]. Both these cases are now well-known in the literature, thus we do not discuss them further and rather concentrate on other more interesting biological issues.

## 3 Can trajectories grow unbounded?

In this Section we show that the system's trajectories cannot go to infinity. The technique is well know, see for instance [8, 18]. Let us define the total environmental population, $\Phi(t) = P + S + V + W$. Then, by summing the equations in (7), we get

$$\frac{d\Phi(t)}{dt} = r\left(1 - \frac{P}{k_P}\right)P - aPS - mS + eaSP - \mu V - \nu W.$$

From the first of (7) it easy to show that

$$\limsup_{t\to+\infty} P = k_P.$$

Thus for $t$ large, we have $P \le k_P$. Let us take $\epsilon > 0$. We have then

$$\begin{aligned} \frac{d\Phi}{dt} + \epsilon\Phi &= r\left(1 - \frac{P}{k_P}\right)P + \epsilon P - aPS - mS \\ &\quad + eaSP + \epsilon S - \mu V + \epsilon V - \nu W + \epsilon W \\ &\le r\left(1 - \frac{P}{k_P}\right)k_P + \epsilon k_P + aPS(e-1) - (m-\epsilon)S \\ &\quad -(\mu-\epsilon)V - (\nu-\epsilon)W \le rk_P + \epsilon k_P + aPS(e-1) \\ &\quad -(m-\epsilon)S - (\mu-\epsilon)V - (\nu-\epsilon)W \end{aligned}$$

since $0 \le \left(1 - \frac{P}{k_P}\right) \le 1$ in view of the previous result. Next, taking $\epsilon_0 = \min\{m, \mu, \nu\}$, from the previous inequalities for a suitable constant $C$ we get

$$\frac{d\Phi}{dt} + \epsilon\Phi \le C + aPS(e-1). \qquad (8)$$

Here we need to analyse two distinc cases. First of all, let us assume $e \le 1$. Thus, the right hand side of (8) is bounded above by $C$ and integration leads to

$$\Phi(t) \le \exp(-\epsilon t) + \frac{C}{\epsilon}[1 - \exp(-\epsilon t)] \le M$$

for some suitable constant $M$, so that the total population and therefore each subpopulation is bounded. Alternatively, if $e > 1$, we need to preceed in a slightly different way. From (8) we backstep and regain a term that was lost in the previous estimates, to get

$$\begin{aligned}\frac{d\Phi}{dt} + \epsilon\Phi &\leq C + aPS(e-1) - (m-\epsilon)S \\ &\leq C + ak_P S(e-1) - (m-\epsilon)S \\ &\leq C - (m - ak_P e + ak_P - \epsilon)S.\end{aligned}$$

Let us now set $\theta = m - ak_P e + ak_P$. If $\theta > 0$, we can take $\epsilon_1 = \min\{\epsilon_0, \theta\}$ and assuming $0 < \epsilon \leq \epsilon_1$, the coefficient of $S$ becomes negative. The right hand side can then again be bounded by the constant $C$ and the proof ends as in the previous case. The values of the parameter $e$ for which $\theta > 0$ are given below. Since we need $m - ak_P e + ak_P > 0$, we find that it is equivalent to

$$e < 1 + \frac{m}{ak_P}. \tag{9}$$

Thus boundedness in this second case can be achieved for a positive $e$ bounded above as in (9). Now this is only slightly better than the former restriction $e < 1$ in view of the fact that in general $k_P$ is a few orders of magnitude larger than $m$ and $a$. Thus this constitutes only a little improvement with respect to the previous case.

The results just shown indicate anyway that the total system population boundedness is thus achieved. As an alternative formulation in summary we can state that under suitable assumptions trajectories cannot grow unboundedly.

# 4 Can the ecoepidemic system be wiped out?

Clearly the origin is a trivial solution of the system (4), since the latter is homogeneous. The eigenvalues of the Jacobian (5), which now becomes a diagonal matrix, are analytically evaluated to give $\lambda_1 = r > 0$, $\lambda_2 = -m < 0$, $\lambda_3 = -(\gamma+\mu) < 0$, $\lambda_4 = -(\varphi+\nu) < 0$. Therefore this equilibrium is a saddle, i.e. it is unstable. As a consequence the ecosystem under our assumptions will never be wiped out. This is a positive conclusion from the biological and environmentalist point of view.

# 5 Can prey alone survive?

This equilibrium corresponds to the coordinates $P > 0$, $S = V = W = 0$ and explicitly, we find $\widehat{P} = k_P$. The prey settle at the environment's carrying capacity.

The eigenvalues are once again easily calculated from an upper triangular Jacobian (5), to get $\lambda_1 = -r < 0$, $\lambda_2 = -m + eak_P$, $\lambda_3 = -(\gamma+\mu) < 0$, $\lambda_4 = -(\varphi+\nu) < 0$. Thus stability is regulated by the only eigenvalue with uncertain sign, $\lambda_2$. The prey survive alone in the ecosystem and settle to their carrying capacity if and only if, introducing a new quantity $A$,

$$A < 1, \quad A \equiv \frac{eak_P}{m}. \tag{10}$$

Thus $A$ can be thought of as the invasion threshold of the predators. In fact, when

$$A > 1, \tag{11}$$

the predators, whether healhty or diseased, will always be present in the ecosystem.

# 6 Can prey and only healthy predators survive?

In this case we have the predator-prey subsystem (6), for which it is well known that the coexistence equilibrium is

$$P = \frac{m}{ea}, \quad S = \frac{r}{a}\left(1 - \frac{m}{eak_P}\right).$$

Feasibility holds if the opposite of (10), i.e. (11) is verified, which is biologically plausible. The eigenvalues of (5) are explicitly computable. With $\Delta = r^2m^2 - 4rme^2a^2k_P^2 + 4rm^2eak_P$, we obtain

$$\begin{aligned}\lambda_1 &= -\left(\frac{\lambda r}{a}\left(\frac{m}{eak_P} - 1\right) + (\gamma+\mu)\right) \\ \lambda_2 &= -\left(\frac{\beta r}{a}\left(\frac{m}{eak_P} - 1\right) + (\varphi+\nu)\right) \\ \lambda_3 &= \frac{1}{2eak_P}\left(-rm + \sqrt{\Delta}\right) \\ \lambda_4 &= \frac{1}{2eak_P}\left(-rm - \sqrt{\Delta}\right).\end{aligned}$$

For stability we need all of them to have negative real parts.

All eigenvalues are real if

$$r^2m^2 - 4rme^2a^2k_P^2 + 4rm^2eak_P \geq 0.$$

Recalling the definition (10) of $A$, then the above requirement becomes

$$\frac{r}{m} - 4A^2 + 4A \geq 0. \tag{12}$$

We then find

$$\lambda_1 < 0 \quad \Leftrightarrow \quad \frac{1}{A} > -(\gamma+\mu)\cdot\frac{a}{\lambda r}+1, \quad (13)$$

$$\lambda_2 < 0 \quad \Leftrightarrow \quad \frac{1}{A} > -(\varphi+\nu)\cdot\frac{a}{\beta r}+1, \quad (14)$$

$$\lambda_3 < 0 \quad \Leftrightarrow \quad \frac{1}{A} < 1, \quad (15)$$

while $\lambda_4 < 0$ is always verified. Now by suitably coupling (15) and (13) at first, and then (15) and (14), we get

$$\begin{aligned} -(\gamma+\mu)\frac{a}{\lambda r} &< \frac{1}{A}-1<0 \quad (16)\\ -(\varphi+\nu)\frac{a}{\beta r} &< \frac{1}{A}-1<0 \end{aligned}$$

which are the necessary and sufficient conditons for this equilibrium to be a stable node.

There are instead two complex conjugate eigenvalues if

$$\frac{r}{m}-4A^2+4A<0. \quad (17)$$

In such situation we have, in addition to (13) and (14),

$$\begin{aligned} \Re(\lambda_3)<0 \quad &\Leftrightarrow \quad -\frac{r}{A}<0, \quad (18)\\ \Re(\lambda_4)<0 \quad &\Leftrightarrow \quad -\frac{r}{A}<0 \end{aligned}$$

and both conditions are clearly always satisfied. Thus we can conclude that whenever (17) holds true, we always get a stable focus. These results are in line with the classical predator-prey model with logistic growth in the prey, except for the fact that the presence of the disease acts as a destabilizing factor. In fact the epidemiological parameters appear in all the stability conditions (13)-(16). Hence the introduction of an epidemic can bring the system away from the natural predator-prey equilibrium of the disease-free model, if any of the above stability conditions is violated.

# 7 Can only one disease be eradicated?

In view of the symmetry of the problem, it does not make any difference whether we consider the first or the second disease. Therefore let us consider specifically the case $P>0$, $S>0$, $V=0$, $W>0$, while for $P>0$, $S>0$, $V>0$, $W=0$ entirely symmetrical results hold. Only obvious changes in the parameter names occur and will be apparent from the final expressions reported below.

Solving for $S$ the last equilibrium equation, we find

$$S=\frac{\varphi+\nu}{\beta}.$$

From the first one we then find, upon substitution

$$P=\left[1-a\left(\frac{\varphi+\nu}{\beta r}\right)\right]k_P$$

which is nonnegative if

$$a(\varphi+\nu)<\beta r. \quad (19)$$

Finally, from the second equilibrium equation we get

$$W=\frac{\varphi+\nu}{\beta\nu}\left\{ea\left[1-a\left(\frac{\varphi+\nu}{\beta r}\right)\right]k_P-m\right\}$$

which must be nonnegative, $W\geq 0$. This condition becomes

$$S_0<\frac{eak_P\cdot r\nu}{mr+ea^2k_P\nu}. \quad (20)$$

In summary, this equilibrium reads

$$\begin{aligned} P_0 &= k_P\left[1-a\left(\frac{\varphi+\nu}{\beta r}\right)\right] \quad (21)\\ S_0 &= \frac{\varphi+\nu}{\beta}\\ V_0 &= 0\\ W_0 &= \frac{\varphi+\nu}{\beta\nu}\left\{eak_P\left[1-a\left(\frac{\varphi+\nu}{\beta r}\right)\right]-m\right\}. \end{aligned}$$

The structure of the Jacobian gives immediately the eigenvalue $\lambda\left(\frac{\varphi+\nu}{\beta}\right)-(\gamma+\mu)$, while the other three are the roots of a cubic. The latter however proves to be mathematically intractable, in view of the very long expressions of its coefficients in terms of the original model parameters. We will then analyse this situation only numerically. However, stability of this equilibrium requires the following condition to hold

$$\lambda(\varphi+\nu)<(\gamma+\mu)\beta. \quad (22)$$

For the dual case $P>0, S>0, V>0, W=0$, instead the equilibrium is

$$\begin{aligned} P_1 &= k_P\left[1-a\left(\frac{\mu+\gamma}{\lambda r}\right)\right] \quad (23)\\ S_1 &= \frac{\mu+\gamma}{\lambda}\\ V_1 &= \frac{\gamma+\mu}{\lambda\mu}\left\{eak_P\left[1-a\left(\frac{\gamma+\mu}{\lambda r}\right)\right]-m\right\}\\ W_1 &= 0 \end{aligned}$$

and again one eigenvalue is immediate, $\beta\left(\frac{\mu+\gamma}{\lambda}\right)-(\varphi+\nu)$. The other ones once more solve a very complicated cubic. For stability of this equilibrium, the opposite condition of (22) is in any case necessary

$$\beta(\mu+\gamma)<(\varphi+\nu)\lambda. \quad (24)$$

# 8 Can the whole ecosystem survive?

In this situation it is immediately evident that from the last two equilibrium equations, two different values of $S$ are obtained, namely

$$S = \frac{\gamma+\mu}{\lambda}, \quad S = \frac{\varphi+\nu}{\beta}$$

respectively from the third and fourth equations. Thus, the equilibrium exists only if the following restriction on the parameters holds,

$$\frac{\gamma+\mu}{\lambda} = \frac{\varphi+\nu}{\beta}, \tag{25}$$

which in fact is unlikely to be verified. In addition should this condition be fulfilled, the resulting equilibrium will be a whole set and not a point, i.e. uniqueness would be lost, since the value of one variable would not be defined. In fact we find

$$\begin{aligned} S &= \frac{\gamma+\mu}{\lambda} \\ P &= k_P\left[1-a\left(\frac{\gamma+\mu}{\lambda r}\right)\right] \\ V &= \frac{1}{\mu}\left\{eak_P\left(\frac{\gamma+\mu}{\lambda}\right)\left[1-a\left(\frac{\gamma+\mu}{\lambda r}\right)\right]\right. \\ &\quad \left.-\nu W - m\left(\frac{\gamma+\mu}{\lambda}\right)\right\} \end{aligned}$$

with $W$ assuming any possible arbitrary value. To ensure nonnegativity of $P$ we need

$$S_0 < \frac{r}{a}. \tag{26}$$

To determine the values for which $V(w) > 0$, we need to solve the inequality

$$S_0^2 + \frac{S_0 r}{ea^2k_P}(m-eak_P) + \frac{r\nu w}{ea^2k_P} < 0.$$

Letting $\Theta = r^2(m-eak_P)^2 - 4r\nu wea^2k_P$, the roots of the associated equation are

$$S_{0\pm} = -\frac{1}{2ea^2k_P}\left[r(m-eak_P) \pm \sqrt{\Theta}\right]$$

and to ensure them to be real, we impose

$$\Theta = r^2(m-eak_P)^2 - 4r\nu wea^2k_P > 0.$$

Combining with $W > 0$, we find

$$0 < W < \frac{r(m-eak_P)^2}{4\nu ea^2k_P} \equiv H.$$

Assuming $m-eak_P > 0$ without loss of generality, since $m-eak_P = 0$ would imply $S_0 = 0$, which is a contradiction, and the opposite case $m-eak_P < 0$, would exchange the lower and upper bounds, we find that

$$\sup S_{0-} = -\frac{(1-r)(m-eak_P)}{2ea^2k_P}$$

is obtained for $W \to 0^+$, while

$$\inf S_{0-} = -\frac{m-eak_P}{2ea^2k_P}$$

is obtained for $W \to H^-$. The same results hold for $\inf S_{0+}$, while instead

$$\sup S_{0+} = -\frac{(1+r)(m-eak_P)}{2ea^2k_P}.$$

Summarizing, letting

$$B = m-eak_P, \quad L = \frac{m-eak_P}{2ea^2k_P} = \frac{B}{2ea^2k_P},$$

we have

$$\begin{aligned} &-L < S_{0-} < -L(1-r) && \text{if } B > 0 \\ &-L(1-r) < S_{0-} < -L && \text{if } B < 0 \\ &-L(1+r) < S_{0+} < -L && \text{if } B > 0 \\ &-L < S_{0+} < -L(1+r) && \text{if } B < 0 \end{aligned}$$

which can be restated as

$$0 < S_0 < \frac{r}{a}, \quad S_{0-} < S_0 < S_{0+}.$$

The stability analysis hinges on the Jacobian,

$$\begin{pmatrix} -r+\frac{a(\varphi+\nu)}{\beta} & -ak_P\left[1-a\frac{\varphi+\nu}{\beta r}\right] & 0 & 0 \\ ea\frac{\varphi+\nu}{\beta} & J_{22} & -\mu & -\nu \\ 0 & J_{32} & 0 & 0 \\ 0 & \beta w & 0 & 0 \end{pmatrix}$$

where

$$\begin{aligned} J_{22} &= \frac{\gamma}{\mu}\left[m-eak_P+ea^2k_P\frac{\gamma+\mu}{\lambda r}+\frac{\lambda\nu}{\gamma}w\right] \\ J_{32} &= \frac{\lambda}{\mu}\left\{eak_P\frac{\gamma+\mu}{\lambda}\left[1-a\frac{\gamma+\mu}{\lambda r}\right]\right. \\ &\quad \left.-\nu w - m\frac{\gamma+\mu}{\lambda}\right\}. \end{aligned}$$

# 9 Some numerical results

In this Section at first we show that the feasibility and stability conditions of the last equilibria are indeed found. We have run computer experiments using our own Matlab routines.

### 9.1 Stability example of the equilibrium $P > 0, S > 0, V = 0, W > 0$

For the parameter values $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.2$, $\varphi = 0.3$, $\beta = 0.6$, $\lambda = 0.4$, $\mu = 0.25$, $\nu = 0.40$ we find the eigenvalues $-98.5838$, $-1.7292$, $-0.0237$, $0.0167$, showing instability. Instead, for the values $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.2$, $\varphi = 0.3$, $\beta = 0.6$, $\lambda = 0.4$, $\mu = 0.25$, $\nu = 0.35$ we find instead $-129.9788$, $-1.5896$, $-0.0700$, $-0.0167$, showing stability. The stable behavior is shown in Figure 1 for a different choice of the parameters. For another different set of values with similar behavior, and more specifically slowly decaying oscillations in the $P - S$ phase subplane, see Figure 2.

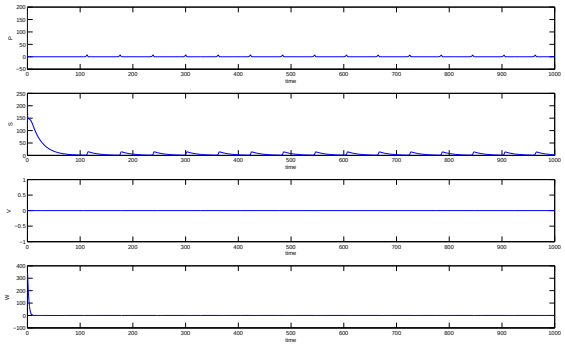

Figure 1: Top to bottom, $P$, $S$, $V$, $W$; parameter values $a = 0.2, \beta = 0.02, e = 0.7, \varphi = 3, \gamma = 0.9, k = 5000, \lambda = 0.4, m = 0.05, r = 1, \nu = 0.4, \mu = 0.25, P_0 = 200, S_0 = 100, V_0 = 0, W_0 = 300$

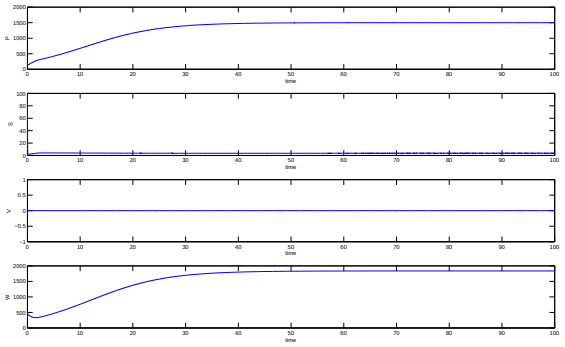

Figure 2: Top to bottom, $P$, $S$, $V$, $W$; parameter values $a = 0.2, \beta = 0.2, e = 0.7, \varphi = 0.3, \gamma = 0.9, k = 5000, \lambda = 0.4, m = 0.05, r = 1, \nu = 0.4, \mu = 0.25, P_0 = 200, S_0 = 100, V_0 = 0, W_0 = 300$

### 9.2 Stability example of the equilibrium $P > 0, S > 0, V > 0, W = 0$

The parameter values $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.2$, $\varphi = 0.3$, $\beta = 0.6$, $\lambda = 0.4$, $\mu = 0.25$, $\nu = 0.35$ give instability, since the eigenvalues are $-195.2501$, $-1.4176$, $-0.1556$, $0.0250$, while we have stability for $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.2$, $\varphi = 0.3$, $\beta = 0.6$, $\lambda = 0.4$, $\mu = 0.25$, $\nu = 0.40$ in view of the eigenvalues $-154.7794$, $-1.7077$, $-0.1629$, $-0.0250$.

### 9.3 Stability example of the equilibrium $P > 0, S > 0, V > 0, W > 0$

Here we always have one eigenvalue zero, since in this case the last two rows of the Jacobian at the equilibrium are linearly dependent. As a verification, we have observed this behavior for the values $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.25$, $\varphi = 0.47$, $\beta = 0.6$, $\lambda = 0.48$, $\mu = 0.39$, $\nu = 0.33$, $w = 100$ which provide the following eigenvalues $-62.6414$, $-3.7241$, $-0.1580$, $0$. This point behaves like a saddle, the trajectories are attracted by it along three different coordinate directions, but not along the fourth one since it is unstable.

In the next example, for the choice $r = 1$, $m = 0.05$, $e = 1$, $a = 0.5$, $k = 1000$, $\gamma = 0.25$, $\varphi = 0.47$, $\beta = 0.6$, $\lambda = 0.48$, $\mu = 0.39$, $\nu = 0.33$, $w = 300$ we find instead an unstable focus, as two of the eigenvalues are complex conjugate: $-0.1739$, $7.4406 \pm 13.1087i$, $0$.

## 10 A more general case

In contrast to (4), we assume here that also infected predators do reproduce and the disease is vertically transmitted, i.e. the offsprings of diseased parents also carry the disease. The model thus becomes

$$\begin{cases} \dot{P} = r\left(1 - \dfrac{P}{k_P}\right)P - aPS - bVP - gWP \\ \dot{S} = -mS + eaSP - \lambda SV + \gamma V - \beta SW + \varphi W \\ \dot{V} = \lambda SV - \gamma V - \mu V + cbVP \\ \dot{W} = \beta SW - \varphi W - \nu W + fgWP \end{cases} . \tag{27}$$

The parameters in this model retain their meaning as in (4), but here we have four additional parameters, namely: $b$ represents the hunting rate of the diseased predators $V$; $g$ denotes the predation rate of the diseased predators $W$; $c$ is the conversion factor of the

diseased predators $V$; $f$ stands for the conversion factor of the diseased predators $W$.

By repeating the equilibrium analysis, we find that all cases in which $P = 0$ are identical to the former model (4), since in all the changes in (27) the variable $P$ is always present. In a similar way we can deal with the cases in which both diseases are absent, $(V, W) = (0, 0)$, since all the new terms in (27) depend also on $V$ and $W$. The cases $(P, S, V, W) = (+, 0, 0, +)$ and $(P, S, V, W) = (+, 0, +, +)$ are impossible. Instead, $(P, S, V, W) = (+, +, 0, +)$ is a possible nonunique equilibrium for

$$P = p, \quad S = \frac{\varphi + \nu - fgp}{\beta} = S_0,$$

$$W = \frac{-p^2(eafg) + p(mfg + ea(\varphi + \nu)) - m(\varphi + \nu)}{S_0},$$

where $p$ is an arbitrary value for which $P$, $S$, $W$ are positive, conditions which give

$$p \leq \frac{\varphi + \nu}{fg},$$

and the quadratic inequality

$$eafgp^2 - p[mfg + ea(\varphi + \nu)] + m(\varphi + \nu) \geq 0.$$

Letting $\Gamma = [mfg + ea(\varphi + \nu)]^2 - 4eafgm(\varphi + \nu)$ the latter gives either no restrictions for $\Gamma < 0$, or the conditions

$$\Gamma \geq 0, \quad 0 \leq p_- \leq p \leq p_+,$$

where

$$p_\pm = \frac{1}{2}\{mfg + ea(\varphi + \nu) \pm \sqrt{\Gamma}\}(eafg)^{-1}.$$

There is obviously a symmetric result in case of the other disease.

For the coexistence of all populations, we find

$$\begin{aligned}
P_0 &= \frac{\lambda(\varphi + \nu) - \beta(\gamma + \mu)}{\lambda fg - \beta cb}, \\
S_0 &= \frac{(\varphi + \nu) - fgP_0}{\beta}, \\
W_0 &= \frac{(\gamma - \lambda S_0)\left[aS_0 - r\left(1 - \frac{P_0}{k_P}\right)\right]}{b(\varphi - \beta S_0) - g(\gamma - \lambda S_0)} \\
&\quad - \frac{b(eaS_0P_0 - mS_0)}{b(\varphi - \beta S_0) - g(\gamma - \lambda S_0)}, \\
V &= -\frac{r\left(1 - \frac{P_0}{k_P}\right) + aS_0 + gW_0}{b}.
\end{aligned}$$

In this more general model, in contrast to the situation of (4), the coexistence is possible, since no specific relationship among the parameters is here necessary. We need of course to ensure feasibility.

If $P_0 < k_P$ the last equation gives clearly a negative value for $V_0$, so that the resulting equilibrium is unfeasible. If $P_0 > k_P$, nonnegativity of $V$ becomes

$$1 + \frac{aS_0 + gW_0}{r} < \frac{P_0}{k_P}.$$

Since $P_0$ in the case $P_0 > k_P$ tends to decrease toward its carrying capacity $k_P$, it decreases even more when predators are present. Indeed they contribute a negative quantity to the differential equation for $P$. Thus for every

$$\varepsilon := \frac{aS_0 + gW_0}{r}$$

there is a time $t_0$ for which for all $t > t_0$ we have $P(t)k_P^{-1} < 1 + \varepsilon$, which implies $V < 0$, i.e. the above inequality cannot hold, which means that a feasible equilibrium cannot be found. Alternatively, we could also argue that from the equation for $P$ in (27), the time derivative of $P$ is the sum of four terms, which are all negative for $P > k_P$, implying that

$$\frac{dP}{dt} = 0$$

is impossible.

For the stability of the feasible equilibria, the Jacobian in this case proves too hard to be analysed analytically.

### 10.1 Boundedness

We instead analyse in more detail the boundedness issue. There are several subcases to study. As done for (4) we assume $P \leq k_P$ and define again the total population of the environment, $\Phi(t) = P + S + V + W$. Thus

$$\begin{aligned}
&\frac{d\Phi(t)}{dt} = r\left(1 - \frac{P}{k_P}\right)P - ms - \mu V - \nu W \\
&+aPS(e-1) + bPV(c-1) + gPW(f-1).
\end{aligned}$$

Let $K \equiv aPS(e-1) + bPV(c-1) + gPW(f-1)$. We have the estimates

$$\begin{aligned}
\frac{d\Phi(t)}{dt} + \epsilon\Phi &= r\left(1 - \frac{P}{k_P}\right)P + \epsilon P - (m - \epsilon)S \\
-(\mu - \epsilon)V - (\nu - \epsilon)W + K &\leq r\left(1 - \frac{P}{k_P}\right)k_P + \epsilon k_P \\
-(m - \epsilon)S - (\mu - \epsilon)V - (\nu - \epsilon)W + K &\leq rk_P \\
+\epsilon k_P - (m - \epsilon)S - (\mu - \epsilon)V - (\nu - \epsilon)W + K & \\
\leq C - (m - \epsilon)S - (\mu - \epsilon)V - (\nu - \epsilon)W & \\
+aPS(e-1) + bPV(c-1) + gPW(f-1). &
\end{aligned}$$

At this point, we consider several different cases.

**10.1.1** $e \leq 1$, $c \leq 1$, $f \leq 1$

Here $K < 0$ so that we can ignore it and obtain the following upper bound

$$\frac{d\Phi(t)}{dt} + \epsilon\Phi \leq C - (m-\epsilon)S - (\mu-\epsilon)V - (\nu-\epsilon)W$$

and with $\epsilon_0 = \min\{m, \mu, \nu\}$, we find that for all $0 \leq \epsilon \leq \epsilon_0$, we have

$$\frac{d\Phi(t)}{dt} + \epsilon\Phi \leq C,$$

so that we can proceed as in Section 3 and obtain the boundedness of the system's trajectories.

**10.1.2** $e > 1$, $c \leq 1$, $f \leq 1$

In this case, we keep the value of $\epsilon_0$ as above, although $\epsilon^* = \min\{\mu, \nu\}$ would suffice. For smaller values of $\epsilon$ we have

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (m-\epsilon)S + aPS(e-1)\\ &\leq C - (m-\epsilon)S + ak_PS(e-1)\\ &\leq C - (m - ak_Pe + ak_P - \epsilon)S.\end{aligned}$$

Let us once again set $\theta_s = m - ak_Pe + ak_P$. If $\theta_s > 0$, we take $\epsilon_1 = \min\{\epsilon_0, \theta_s\}$; then with $0 < \epsilon \leq \epsilon_1$, we have again

$$\frac{d\Phi(t)}{dt} + \epsilon\Phi \leq C.$$

If $e < 1 + \frac{m}{ak_P}$ we find $\theta_s > 0$.

**10.1.3** $e \leq 1$, $c > 1$, $f \leq 1$

In this situation we proceed similarly. Let us consider the usual value of $\epsilon_0$, observing that again we could just take $\epsilon^* = \min\{m, \nu\}$. If $\epsilon \leq \epsilon_0$:

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (\mu-\epsilon)V + bPV(c-1)\\ &\leq C - (\mu-\epsilon)V + bk_PV(c-1)\\ &\leq C - (\mu - bk_Pc + bk_P - \epsilon)V.\end{aligned}$$

Let us set now $\theta_v = \mu - bk_Pc + bk_P$. If $\theta_v > 0$, we take $\epsilon_1 = \min\{\epsilon_0, \theta_v\}$; with $0 < \epsilon \leq \epsilon_1$, we have again

$$\frac{d\Phi(t)}{dt} + \epsilon\Phi \leq C.$$

If $c < 1 + \frac{\mu}{bk_P}$ then $\theta_v > 0$.

**10.1.4** $e \leq 1$, $c \leq 1$, $f > 1$

We could take the value $\epsilon^* = \min\{m, \mu\}$ as an upper bound for $\epsilon$; using the same assumption on $\epsilon$ as before, we have

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (\nu-\epsilon)W + gPW(f-1)\\ &\leq C - (\nu-\epsilon)W + gk_PW(f-1)\\ &\leq C - (\nu - gk_Pf + gk_P - \epsilon)W.\end{aligned}$$

Let us define $\theta_w = \nu - gk_Pf + gk_P$. If $\theta_w > 0$, we take $\epsilon_1 = \min\{\epsilon_0, \theta_w\}$; with $0 < \epsilon \leq \epsilon_1$, we find

$$\frac{d\Phi(t)}{dt} + \epsilon\Phi \leq C$$

and $\theta_w > 0$ holds if $f < 1 + \frac{\nu}{gk_P}$.

**10.1.5** $e > 1$, $c > 1$, $f \leq 1$

In this case, it suffices to impose the bound $\epsilon < \nu$, but also the usual bound $\epsilon < \epsilon_0$ could be used. We then get

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (m-\epsilon)S - (\mu-\epsilon)V\\ &\quad + aPS(e-1) + bPV(c-1)\\ &\leq C - (m-\epsilon)S - (\mu-\epsilon)V\\ &\quad + ak_PS(e-1) + bk_PV(c-1)\\ &\leq C - (m - ak_Pe + ak_P - \epsilon)S\\ &\quad - (\mu - bk_Pc + bk_P - \epsilon)V.\end{aligned}$$

Let us now define $\theta_s$, $\theta_v$ as before. Both need to be positive, thus both conditions on $e$ and $c$ found in the two previous cases must hold, provided we take $\epsilon_1 = \min\{\nu, \theta_s, \theta_v\}$.

**10.1.6** $e > 1$, $c \leq 1$, $f > 1$

Here the first step is ensured by imposing the bound $\epsilon < \mu$. In fact we find

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (m-\epsilon)S - (\nu-\epsilon)W\\ &\quad + aPS(e-1) + gPW(f-1)\\ &\leq C - (m-\epsilon)S - (\nu-\epsilon)W\\ &\quad + ak_PS(e-1) + gk_PW(f-1)\\ &\leq C - (m - ak_Pe + ak_P - \epsilon)S\\ &\quad - (\nu - gk_Pf + gk_P - \epsilon)W.\end{aligned}$$

Take then $\theta_s$, $\theta_w$ as before. They both need to be positive and this follows from the conditions on $e$ and $f$ found in the previous cases, taking $\epsilon_1 = \min\{\mu, \theta_s, \theta_w\}$.

**10.1.7** $e \leq 1, c > 1, f > 1$

As first step, take $\epsilon < m$.

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (\mu - \epsilon)V - (\nu - \epsilon)W \\ &+bPV(c-1) + gPW(f-1) \\ &\leq C - (\mu - \epsilon)V - (\nu - \epsilon)W \\ &+bk_PV(c-1) + gk_PW(f-1) \\ &\leq C - (\mu - bk_Pc + bk_P - \epsilon)V \\ &-(\nu - gk_Pf + gk_P - \epsilon)W.\end{aligned}$$

Now, let us consider $\theta_v$, $\theta_w$ as before. They once more must both be positive, so that once again the previous conditions on $c$ and $f$ must hold, by taking $\epsilon_1 = \min\{m, \theta_v, \theta_w\}$.

**10.1.8** $e > 1, c > 1, f > 1$

The first step here is just $P \leq k_P$, no term disappears in this case. We have

$$\begin{aligned}\frac{d\Phi(t)}{dt} + \epsilon\Phi &\leq C - (m - \epsilon)S \\ &-(\mu - \epsilon)V - (\nu - \epsilon)W \\ &+aPS(e-1) + bPV(c-1) + gPW(f-1) \\ &\leq C - (m - \epsilon)S - (\mu - \epsilon)V - (\nu - \epsilon)W \\ &+ak_PS(e-1) + bk_PV(c-1) + gk_PW(f-1) \\ &\leq C - (m - ak_Pe + ak_P - \epsilon)S \\ &-(\mu - bk_Pc + bk_P - \epsilon)V \\ &-(\nu - gk_Pf + gk_P - \epsilon)W.\end{aligned}$$

Again take $\theta_s$, $\theta_v$, $\theta_w$ as before. All these quantities need to be positive, and thus the conditions on $e$, $c$, $f$ formerly found must all hold, taking $\epsilon_1 = \min\{\theta_s, \theta_v, \theta_w\}$.

Thus the boundedness of the populations has been shown in a box in the $e-c-f$ parameter space, given by the cartesian product in $\mathbf{R}^3$ of the intervals $(0, 1 + \frac{m}{ak_P}) \times (0, 1 + \frac{\mu}{bk_P}) \times (0, 1 + \frac{\nu}{gk_P})$.

# 11 A simulation

In this case, we have been able to obtain convergence to a point in the $P - V$ phase plane, i.e. to an equilibrium in which the prey thrives, though at very low values, together with infected predators of just one disease which becomes pandemic in the predators population, while the second one is eradicated and with it also the healthy predators' population, see Figure 3. This is quite a different feature exhibited by model (27) in contrast to the simplified version (4). In fact such an equilibrium is impossible in model (4), since the equilibrium equation for the healthy predators is not satisfied if $V \neq 0$.

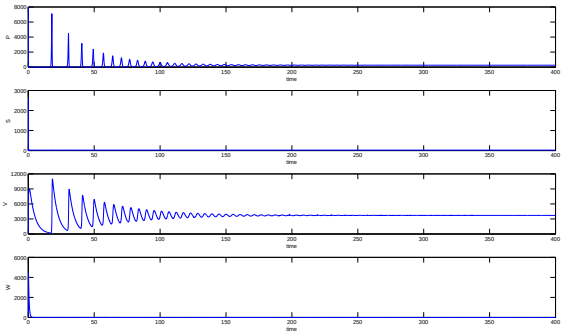

Figure 3: Top to bottom, $P$, $S$, $V$, $W$; the equilibrium consisting of only prey and one strain of the disease is reached for the parameter values $a = 0.02$, $\beta = 0.02$, $e = 0.7$, $\Phi = 2$, $\gamma = 8$, $k = 50000$, $\lambda = 0.4$, $m = 0.05$, $r = 6$, $\nu = 0.4$, $\mu = 0.25$, $b = 0.0015$, $c = 0.6$, $f = 0.55$, $g = 0.012$.

# 12 Discussion

We have introduced a two-strain ecoepidemic model. It is the first model of this kind in the context of ecoepidemiology, in which the diseases affect one population. The simple model without vertical transmission has been extensively analysed. Our results thus indicate that the system (4) has several configurations that are impossible. They are listed in what follows.

The diseased predators of one or the other disease cannot survive alone in the ecosystem, nor can both diseased predators thrive together, neither can only the healthy predators. In absence of prey, healthy predators cannot survive together with the diseased ones, neither those with one of the diseases, nor with both kinds of sick ones.

The prey can neither thrive with either one of the diseased predators, nor with both diseased predators together.

Instead, the model allowing vertical transmission, (27) admits an equilibrium with one disease invading the whole predators' population, while also the prey thrive and the other disease together with the healthy predators are wiped out.

Among the positive findings, the whole ecosystem cannot disappear altogether.

We have answered other relevant questions. The prey alone survive at their carrying capacity if the latter is bounded above by the ratio of the predators'

natural mortality $m$ and their reproduction rate $ea$, a condition which is summarized by the new parameter $A$, see (10). This means also that if $k_P$ exceeds $m(ae)^{-1}$, or equivalently $A > 1$, then the predators, either sound or infected or both, invade the environment. Thus $A$ can be characterized as the predators' environment invasion coefficient.

Both diseases can be eradicated from the predators, while healthy predators survive. For this to be true, the condition (11), namely the opposite condition of (10) must obviously hold, since the healthy predators must be present in the environment. We also need either (13)-(15) to be verified with (12), i.e. (16), or (17) together with (13)-(14). In summary, to have the disease eradicated, the predators' invasion coefficient must be larger than one but also suitably bounded above, as follows

$$1 < A < \min\left\{\frac{\lambda r}{\lambda r - a(\gamma+\mu)}, \frac{\beta r}{\beta r - a(\Phi+\nu)}\right\}.$$

For the model with vertical transmission, a number of sufficient cases on the system's parameters leading to the boundedness result have been investigated.

For two-dimensional classical competition models it is known that only one of the two populations survives. But for ecoepidemic systems, the wiping out of one of the two competitors is not automatic, in fact both can survive in presence of a disease affecting one of them, [29]. In this two-strain model, only one disease can thrive in the ecosystem, thus giving a standard ecoepidemic model with the disease in the predators, see e.g. [28, 30]. The question can be also raised, as to which of the two diseases does indeed survive, and what factors in the system influence this outcome. A partial answer can be obtained by looking at the mutually exclusive conditions (22) and (24). In fact we can define the new quantity

$$B \equiv \frac{B_V}{B_W}, \quad B_V \equiv \frac{\lambda}{\mu+\gamma}, \quad B_W \equiv \frac{\beta}{\varphi+\nu}, \quad (28)$$

we see that $B < 1$ entails that the $W$ strain prevails, while on the contrary for $B > 1$ the disease $V$ outcompetes the other one. Of course the result depends also on the other eigenvalues that cannot be easily assessed analytically. But the quantity $B$ becomes another threshold, which allows to determine the prevailing strain, if any does indeed survive; we know in fact that predators invade the environment only if $A > 1$, see (11). A closer examination of (28) shows that $W$ is the outcome if its activity $B_W$, defined as the ratio between its recuitment rate due to "successful" contacts and the combined outgoing rates given by mortality and recovery rates, exceeds the same quantity for $V$, $B_V$.

The outcome of the system is however clearly determined also by its initial conditions as the phase space may be partitioned into domains of attraction for each equilibrium point, when multiple ones coexist. In practical applications for this situation it would be interesting to be able to determine these domains, in order to establish which one of the two alternative mutually exclusive outcomes arises in a dynamical system. We remark the following result on this issue, aimed at assessing the basins of attraction of each equilibrium point, [7], for bidimensional systems. Work in progress will extend the result to higher dimensional systems.

In general instead both the ecoepidemic systems (4) and (27) with two strains quite surprisingly cannot be sustained at a stable coexistence equilibrium. Thus in the ecoepidemic case, under these assumptions, the two-strain situation cannot be held, as it is customary in standard epidemic models, [1, 2, 5, 6, 9, 19, 20].

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