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MODELING THE INSECT-VECTORS-MEDIATED PHYTOPLASM TRANSMISSION IN AGROECOSYSTEMS

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Two models for the herbivore-insects-plants interactions are formulated, differing in the way the farmer's behavior is accounted for. In the first one the farmer regularly checks the crop and possibly removes infected plants, reimplanting new healthy ones in their place. The second one instead considers a large crop where this behavior is not possible and where therefore the infection may propagate freely in it, via the action of insect vectors. Effector proteins are known to affect the insect-plant dynamics and their influence is here investigated. Although they cannot influence the ultimate ecosystem behavior, they do impact the speed at which the equilibria are attained, in some fortunate cases favoring a faster infection eradication.

1. Introduction

The aim of this paper is to formulate and analyze particular insects-plants interactions, with the former being often harmful for crops, [1]. Specifically, we consider a leafhopper vector that introduces pathogenic phytoplasma into a susceptible population of seasonal plants. The agroecosystem is assumed to be possibly infected by different phytoplasma strains. The latter differ only by the presence or the absence of a specific effector protein, whose effect renders infected plants more palatable to the insect vector, that are assumed not to have alternative food sources. Indeed, it is known

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that the insect herbivores behavior towards plants can be mediated by molecular interactions, [3,9]. The model is conceived to forecast the effect of this protein on the pathogen spread among the plant and insect populations. We envisage a closed epidemiological system with no insect migrations and consider only a fixed strain of phytoplasma.

Models for this situation have already appeared in the literature, [6]. Also, the presence of effector proteins in agriculture has been demonstrated, [2,4,5,8], and can be used in various situations, [7].

Two different scenarios are presented. In the first one we assume that the farmer regularly checks the crop, so that to control the spread of the pathogen, "infected" plants are possibly removed and replaced by healthy ones. Thus the total seasonal plant population is fixed in time. In the second one, this last restriction is removed and the infection may propagate freely among the plants, via the action of insect vectors.

In particular, we would like to elucidate the role played by the effector proteine in the agroecosystem dynamics.

In the next section we introduce the system controlled by the farmer, and analyze it assessing its equilibria and their stability. Section 3 contains the second situation, with a nonconstant plant population. A final discussion on the role of the effector proteins concludes the paper.

2. The model incorporating the farmer's behavior

2.1. *Model assumptions*

As mentioned, here the number of plants in the agrosystem is fixed: each diseased plant that dies or is discovered by the farmer is removed and is replaced with a new susceptible healthy plant. This assumption also allows us to disregard possible vertical phytoplasma transmission in the plant population.

Demographics is instead considered for the insect vector population. This is motivated by the fact that during the good season, while plants grow and produce fruits and seeds for the next year, insects instead experience generally several reproduction times. It is not uncommon that during the spring and summer, three or more generations are found, with average insects lifetimes spanning around a few weeks. No farmer's control action on the insects diffusion and their damages is assumed to occur. Also, here we allow the pathogen to be possibly vertically transmitted. The assumption however could be easily removed by setting the corresponding parameter to zero, in case it is found not to hold for specific species.

2.2. *Model setup*

Let S represent the susceptible plants population, I represent the one of infected plants, U stand for the susceptible insects and V for those infected. Further, let C denote the whole plants population in the agroecosystem,

$$C = S + I. \tag{1}$$

The model under consideration consists of two simple equations for the susceptible and infected plants and another similar two for the insects. They are connected by the fact that each infected subpopulation is recruited via susceptible interactions with infected of the other subpopulation.

Susceptible plants become indeed infected when bitten by an insect-vector able to transmit the phytoplasma. Let us define a as the preferential attraction probability of insects towards infected plants. Let also λ be the phytoplasma transmission rate. Now the term $(1-a)\lambda VS$ represents the rate at which vectors are attracted by, bite and transmit the phytoplasma to susceptible plants and therefore infect them. Note that in this term, no role is exerted by the healthy insects, because at least in this context, they do not harm the plants. In reality, they suck sap, therefore they damage the plants, but do not transmit the pathogenic phytoplasma, and this is what is of interest here. Furthermore, we model the farmers' behavior, who removes at rate μ the infected plants and replaces them by new susceptible ones. The plants dynamics is therefore captured by the following equations:

$$\frac{dS}{dt} = \mu I - (1-a)\lambda VS, \quad \frac{dI}{dt} = (1-a)\lambda VS - \mu I. \tag{2}$$

Insects are subject to demographics, with birth rate b, natural mortality n and subject to intraspecific competition. However, since they are partitioned among carriers and susceptibles, we must distinguish between their relative influences. We denote by c_{XY}, $X, Y \in \{U, V\}$ the negative action exerted by the subpopulation Y on the subpopulation X. As for the phytoplasma vertical transmission, we allow it, denoting by p the fraction of insect offsprings generated by carrier parents of the previous generation. Thus these new insects bear the phytoplasma since egg disclosure. Adult insects phytoplasma transmission occurs via biting of an infected plant. In this case we must take into account both plant subpopulations, because if a healthy insect bites a susceptible plant, it does not become infected. Let the plant-insect phytoplasma transmission be denoted by σ. This must be a function of susceptible insects and infected plants, thus $\sigma = \sigma(I, U)$. Now the insect has the choice of the plant to bite, and thus the rate at which it finds an infected plant depends on the latter abundance in the whole plant population. The fraction IC^{-1} gives the probability of picking one infected plant among all plants. We also denote by β the phytoplasma acquisition rate. Further, because phytoplasma cannot be transmitted in the absence of plants, we set the transmission to zero if $C = 0$. Overall, the pathogenic phytoplasma transmission from plant to insect is modeled via the function

$$\sigma(I, U) = \begin{cases} \beta \dfrac{IU}{C}, & C \neq 0 \\ 0 & C = 0 \end{cases} . \tag{3}$$

To complete the insects infection process, we need to take into account also their preferential attraction toward infected plants, a. We also assume that phytoplasma carrying does not alter insect natural mortality. Combining all these features and (3), we thus obtain for $C \neq 0$

$$\frac{dU}{dt} = b(1-p)V + bU - a\beta \frac{IU}{C} - c_{UU}U^2 - c_{UV}UV - nU, \tag{4}$$

$$\frac{dV}{dt} = bpV + a\beta \frac{IU}{C} - c_{VV}V^2 - c_{VU}VU - nV. \tag{5}$$

Remark 1. Note that for $C = 0$, the equations (2) are trivial, plants vanish, $S = I = 0$, and only the subsystem (4)-(5) remains, that will be analysed in detail below.

The complete model is made by equations (2), (4), (5), where all the parameters are assumed to be nonnegative. Further restrictions, in view of what we have discussed above, are $a \in (0, 1)$, $p \in [0, 1]$, these parameters being probabilities. Note that for the former the particular cases $a = 0$ and $a = 1$ are excluded, because the protein cannot render the infected or healthy plants entirely appetizing or unappetizing for the insect. The former conditions are supplemented by the following assumptions: healthy insects are more competitive than sick ones, thus some coefficients c_{XY} are comparable; namely,

$$c_{UV} \leq c_{VU}, \quad c_{UV} \leq c_{UU}, \quad c_{VV} \leq c_{VU}. \tag{6}$$

Also, the insect birth rate exceeds their mortality rate, i.e.

$$b \geq n; \tag{7}$$

indeed, if this were not the case, by adding the equations (4) and (5) we find that the whole insect population would vanish. In fact its dynamics would become

$$\frac{d(U+V)}{dt} = b(V+U) - n(V+U) - c_{UU}U^2 - c_{UV}UV - c_{VV}V^2 - c_{VU}VU < 0.$$

A complete list of the parameters is given in Table 1.

Table 1. Description, dimensions and basic assumptions about the parameters, assumed to be all positive.

	Description	Dimension	Assumptions
a	insects preferential attraction rate toward infected plants	-	$a \in (0,1)$
b	insects natural birth rate	$\frac{1}{[t]}$	$b \geq n$
c_{XY}	intraspecific competition rate of class X individuals over class Y individuals, $[X, Y \in \{U, V\}]$	$\frac{1}{[t]}$	$c_{UV} < c_{VU}$ $c_{UV} < c_{UU}$ $c_{VV} < c_{VU}$
C	number of plants, fixed	-	$C = S + I > 0$
n	insects natural mortality rate	$\frac{1}{[t]}$	
p	probability of insects vertical phytoplasma transmission	-	$p \in [0,1]$
β	phytoplasma acquisition rate for insects from plants	$\frac{1}{[t]}$	
λ	phytoplasma transmission rate for plants from insects	$\frac{1}{[t]}$	
μ	infected plants mortality rate and replanting rate of susceptible plants	$\frac{1}{[t]}$	

2.3. *Equilibria Analysis*

2.3.1. *The insect-only subsystem*

For $C = 0$, from (4)-(5) we obtain the equilibria $P_0 = (0,0)$, $P_1 = (U_1, 0)$, $P_* = (U_*, V_*)$, with

$$U_1 = \frac{b-n}{c_{UU}}; \qquad V_* = \frac{1}{c_{VV}}(bp - c_{VU}U_* - n),$$

while U_* is a positive root of the quadratic $\sum_{k=0}^{2} a_k U^k = 0$ with

$$a_2 = \frac{c_{UV}c_{VU}}{c_{VV}} - c_{UU}, \quad a_0 = \frac{b(1-p)}{c_{VV}}(bp-n),$$
$$a_1 = b - n - \frac{c_{UV}}{c_{VV}}(bp-n) - \frac{c_{VU}}{c_{VV}}b(1-p),$$

which also must satisfy, to ensure nonnegativity of V_*,

$$U_* \leq \frac{bp-n}{c_{VU}}. \tag{8}$$

To be fulfilled, this implies also

$$bp \geq n \tag{9}$$

which in turn gives $a_0 \geq 0$. Thus by Descartes' rule, a positive root U_* is obtained by requiring also $a_2 > 0$ or $a_1 > 0$. In summary, feasibility of P_* is ensured by (9) and at least one of the following conditions

$$bc_{VV} \leq nc_{VV} + c_{UV}(bp - n) + c_{VU}b(1-p), \quad c_{UV}c_{VU} \leq c_{VV}c_{UU}. \tag{10}$$

Feasibility for P_1 holds unconditionally, being ensured by (7).

The Jacobian of (4)-(5) is

$$\widehat{\boldsymbol{J}} = \begin{bmatrix} b - n - 2c_{UU}U - c_{UV}V & b(1-p) - c_{UV}U \\ -c_{VU}V & bp - 2c_{VV}V - c_{VU}U - n \end{bmatrix},$$

At the origin its eigenvalues would give the stability condition $b < n$, which cannot hold in view of (7), so that it is always unstable.

For P_1 we find instead $n < b$, ensured by (7), and

$$(bp - n)c_{UU} < (b - n)c_{VU}. \tag{11}$$

At P_*, we apply the Routh-Hurwitz conditions. The trace condition is always satisfied,

$$c_{VV}U_*V_* + c_{UU}U_*^2 + b(1-p)V_* > 0.$$

Stability is thus ruled only by the sign of the determinant; stable coexistence of healthy and infected insects occurs for

$$V_* > \frac{U_*}{b(1-p)c_{VV}}[U_*(c_{VU}c_{UV} - c_{UU}c_{VV}) - c_{VU}b(1-p)]. \tag{12}$$

2.3.2. *The complete model*

In view of the parameter assumptions, specifically here $\lambda, \mu > 0$ and $a \neq 1$, from (2) note that $I = 0$ implies $S = 0$ or $V = 0$. Thus the search for the system's equilibria is somewhat eased. We find the points

$$\widehat{E}_1 = (C, 0, 0, 0), \quad \widehat{E}_2 = \left(C, 0, \frac{b-n}{c_{UU}}, 0\right), \quad \widehat{E}_3 = \left(C - \widehat{I}_3, \widehat{I}_3, 0, \frac{b-n}{c_{VV}}\right),$$

where the latter exists only in the very special case of full vertical phytoplasma transmission:

$$p = 1, \tag{13}$$

and where

$$\widehat{I}_3 = \frac{(1-a)\lambda(b-n)C}{c_{VV}\mu + (1-a)\lambda(b-n)}.$$

The equilibrium $\widehat{E}_1$ corresponds to the insect-and-disease-free equilibrium, with the whole plantation being healthy and insects-free, while $\widehat{E}_2$ instead represents the disease-free point with both plants and insects thriving. Note also that equilibria with $S = 0$, while the other populations do not vanish, cannot occur in this situation, because the new susceptible plants are always introduced in the field by the farmer, to replace the diseased ones that he removes.

We now investigate the coexistence equilibrium. Combining the constraint equation (1) with the equation of the infected plants, we find

$$I = \frac{(1-a)\lambda C V}{\mu + (1-a)\lambda V}.$$

By substitution into the equilibrium equations obtained from (4) and (5), we find the following non-linear system:

$$c_{UU}U^2 + \frac{a(1-a)\beta\lambda}{\mu + (1-a)\lambda V}UV + c_{UV}UV + (n-b)U + b(p-1)V = 0,$$
$$c_{VV}V^2 - \frac{a(1-a)\beta\lambda}{\mu + (1-a)\lambda V}VU + c_{VU}VU + (n-bp)V = 0.$$

It turns out that this system is of order three, which makes an analytical study essentially impossible.

Alternatively, the coexistence point $\widehat{E}_4 = (C - \widehat{I}_4, \widehat{I}_4, \widehat{U}_4, \widehat{V}^*)$ has the population values

$$\widehat{I}_4 = \frac{(1-a)\lambda C \widehat{V}^*}{\mu + (1-a)\lambda \widehat{V}^*}$$
$$\widehat{U}_4 = \frac{(bp-n)\mu - (1-a)c_{VV}\lambda \widehat{V^*}^2 - [c_{VV}\mu + (1-a)(n-bp)\lambda]\widehat{V^*}}{(1-a)c_{VU}\lambda \widehat{V^*} + c_{VU}\mu + a(1-a)\beta\lambda},$$

with feasibility condition obtained by imposing the numerator of U_4 to be positive, namely

$$(bp-n)\mu \geq (1-a)c_{VV}\lambda \widehat{V^*}^2 + [c_{VV}\mu + (1-a)(n-bp)\lambda]\widehat{V^*} \qquad (14)$$

and where $\widehat{V^*}$ is a positive root of the fifth order algebraic equation

$$a_5V^5 + a_4V^4 + a_3V^3 + a_2V^2 + a_1V + a_0 = 0$$

whose coefficients depend on the model parameters. Note also that the condition $\widehat{I}_4 < C$ is easily seen to be always satisfied.

Both these analytic approaches essentially fail and we need to investigate this point numerically.

2.4. *Local stability analysis*

The Jacobian matrix associated with the model (2), (4), (5) is

$$\widehat{\boldsymbol{J}} = \begin{bmatrix} -(1-a)\lambda V & \mu & 0 & -(1-a)\lambda S \\ (1-a)\lambda V & -\mu & 0 & (1-a)\lambda S \\ 0 & -a\beta\dfrac{U}{C} & \widehat{\boldsymbol{J}}_{3,3} & \widehat{\boldsymbol{J}}_{3,4} \\ 0 & a\beta\dfrac{U}{C} & \widehat{\boldsymbol{J}}_{4,3} & \widehat{\boldsymbol{J}}_{4,4} \end{bmatrix},$$

with

$$\begin{aligned} \widehat{\boldsymbol{J}}_{3,3} &= b - a\beta\frac{I}{C} - 2c_{UU}U - c_{UV}V - n\,, \\ \widehat{\boldsymbol{J}}_{3,4} &= b(1-p) - c_{UV}U\,, \\ \widehat{\boldsymbol{J}}_{4,3} &= a\beta\frac{I}{C} - c_{VU}V\,, \\ \widehat{\boldsymbol{J}}_{4,4} &= bp - 2c_{VV}V - c_{VU}U - n\,. \end{aligned}$$

Because the first two rows of $\widehat{\boldsymbol{J}}$ are linearly dependent, at least one of the eigenvalues of $\widehat{\boldsymbol{J}}$ vanishes. Thus no equilibrium is asymptotically stable, but at most it can only be stable.

At $\widehat{E}_1$ the nonvanishing eigenvalues are $-\mu$, $b-n$, $bp-n$, but in view of (7) the second one is always positive, implying that this equilibrium is unconditionally unstable, unless $b-n$ in which case it is stable but not asymptotically.

At $\widehat{E}_2$ one eigenvalue is zero and another one is immediate, $n-b<0$. We then apply the Routh-Hurwitz criterion for the remaining minor of order two to respectively obtain, for the trace and the determinant,

$$\mu - \left[\left(p - \frac{c_{VU}}{c_{UU}}\right)b - \left(1 - \frac{c_{VU}}{c_{UU}}\right)n\right] > 0; \qquad (15)$$

$$\mu\left[\left(p - \frac{c_{VU}}{c_{UU}}\right)b - \left(1 - \frac{c_{VU}}{c_{UU}}\right)n\right] + (1-a)a\beta\lambda\frac{b-n}{c_{UU}} < 0. \qquad (16)$$

Now (15) follows if the bracket is negative, which is ensured by

$$(pc_{UU} - c_{VU})b < (c_{UU} - c_{VU})n. \qquad (17)$$

Similarly, (16) can be ensured if in addition to (17) we require also

$$(pc_{UU} - c_{VU})b < (c_{UU} - c_{VU})n - (1-a)a\beta\lambda\frac{b-n}{\mu}. \qquad (18)$$

At $\widehat{E}_3$ all the eigenvalues of the Jacobian are explicitly known, two of which are always negative, in view of (7)

$$n - b < 0, \quad -\left[(1-a)\lambda\frac{b-n}{c_{VV}} + \mu\right] < 0.$$

Thus the remaining nonzero one alone determines the stability of this equilibrium:

$$\frac{1}{c_{VV}}\left(\frac{(1-a)a\beta\lambda}{\mu + (1-a)\lambda\frac{b-n}{c_{VV}}} + c_{UV}\right) < 1. \tag{19}$$

Coexistence is investigated numerically.

Table 2 summarizes the findings.

Table 2. Feasibility and local stability conditions for the system (2), (4), (5) equilibria.

Equilibria	Feasibility	Stability
$\widehat{E}_1 = (C, 0, 0, 0)$	—	for $b > n$ unstable; for $b = n$ stable but not asymptotically stable
$\widehat{E}_2 = (C, 0, \frac{b-n}{c_{UU}}, 0)$	$b > n$	(15), (16); sufficient: (18)
$\widehat{E}_3 = (C - \widehat{I}_3, \widehat{I}_3, 0, \frac{b-n}{c_{VV}})$	$p = 1$, $b > n$	(19)
$\widehat{E}_4 = (C - \widehat{I}_4, \widehat{I}_4, \widehat{U}_4, \widehat{V}^*)$	$\widehat{V}^* > 0$, $U_4(\widehat{V}^*) > 0$	numerical

From Table 2 a transcritical bifurcation is observed for which $\widehat{E}_2$ emanates from $\widehat{E}_1$ as soon as b increases past n. In Figures 1 and 2 a transcritical bifurcation relating equilibria $\widehat{E}_4$ and $\widehat{E}_2$ is shown to occur in terms of the bifurcation parameters β and λ respectively. The other parameter values for these figures are

$$\begin{gathered} a = 0.5, \quad b = 9, \quad c_{UU} = 0.15, \quad c_{UV} = 0.10, \\ c_{VU} = 0.25, \quad c_{VV} = 0.20, \quad n = 6, \quad \mu = 7. \end{gathered} \tag{20}$$

Also, the chosen initial conditions are

$$S_0 = 300, \quad I_0 = 0, \quad U_0 = 150, \quad V_0 = 1. \tag{21}$$

3. The model with variable plant population

In this second formulation, we account for plants intra-species competition, birth rate and natural mortality. Using the same variables already defined in equations (2), (4), (5) but introducing some new parameters in addition

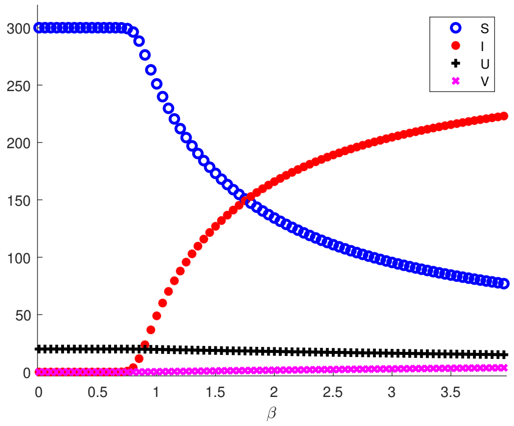

Figure 1. Transcritical bifurcation from $\widehat{E}_4$ to $\widehat{E}_2$ as the bifurcation parameter β decreases below the threshold $\widehat{\beta} \approx 0.75$. The other parameter values are given in (20), with additionally $p = 0.5$ and $\lambda = 11$. Initial conditions given by equation (21).

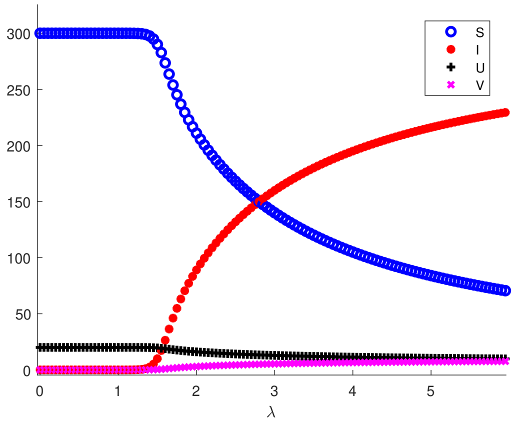

Figure 2. Transcritical bifurcation from $\widehat{E}_4$ to $\widehat{E}_2$ as the bifurcation parameter λ decreases below the threshold $\widehat{\lambda} \approx 1.25$. The other parameter values are given in (20), with additionally $p = 1$ and $\beta = 2$. Initial conditions given by equation (21.)

to the ones previously used, the current model becomes:

$$\frac{dS}{dt} = rS + rI - (1-a)\lambda VS - c_{SI}SI - c_{SS}S^2 - mS \tag{22}$$

$$\frac{dI}{dt} = (1-a)\lambda VS - c_{IS}IS - c_{II}I^2 - (\mu + m)I \tag{23}$$

$$\frac{dU}{dt} = b(1-p)V + bU - a\beta\frac{IU}{S+I} - c_{UU}U^2 - c_{UV}UV - nU \tag{24}$$

$$\frac{dV}{dt} = bpV + a\beta\frac{IU}{S+I} - c_{VV}V^2 - c_{VU}VU - nV. \tag{25}$$

In the equation (22), r represents the plants reproduction rate, and m their natural mortality. Note that the following assumption is necessary,

$$r > m, \tag{26}$$

because otherwise, summing equations (22) and (23) we would obtain

$$\frac{d(S+I)}{dt} = (r-m)(S+I) - c_{SI}SI - c_{SS}S^2 - c_{IS}IS - c_{II}I^2 - \mu I < 0$$

and the whole plant population would vanish, making the model useless.

In addition, c_{SI} represents the intraspecific pressure exerted by infected over susceptible plants, while c_{SS} is the corresponding pressure due to healthy plants on other healthy ones. In equation (23), corresponding terms are c_{IS} denoting the pressure of susceptibles over infected plants, and c_{II} the intraspecific pressure of infected over other infected plants. The remaining equations (24) and (25) for insect vectors are the same as in the previous model, namely equations (4) and (5), with the only change due to the fact that now in the standard incidence term, the total plant population C is no longer constant, but must be replaced by $S + I$.

Assumptions similar to (6) on the new coefficients are made, namely

$$c_{SI} < c_{IS}, \quad c_{SI} < c_{SS}, \quad c_{II} < c_{IS}. \tag{27}$$

The newly introduced parameters, their meaning, units of measurement and assumptions are also reported in Table 3.

Table 3. Additional parameters in model (22)-(25) and related assumptions.

	Description	Units	Assumptions
c_{XY}	intraspecific competition coefficient of Y over X, with $X, Y \in \{S, I\}$	$\frac{1}{[t]}$	$c_{XY} > 0$ $c_{SI} < c_{IS}$ $c_{SI} < c_{SS}$ $c_{II} < c_{IS}$
m	natural plants death rate	$\frac{1}{[t]}$	$m > 0$
r	natural plants birth rate	$\frac{1}{[t]}$	$r > m$

3.1. *Equilibria feasibility*

Because equations (24)-(25) are the same as for (4)-(5), apart from the replacement of C with $S + I$, the plant free case $S = I = 0$ has been already discussed in Section 2.3.1 and therefore is no longer considered in what follows.

The points that are possible equilibria for the system (22)-(25) are

$$E_1 = \left(\frac{r-m}{c_{SS}}, 0, 0, 0\right), \quad E_2 = \left(\frac{r-m}{c_{SS}}, 0, \frac{b-n}{c_{UU}}, 0\right)$$

the former being unconditionally feasible in view of (26), the latter also, using both (26) and (7). In addition, the particular healthy-insects-free case $E_3 = (S_3, I_3, 0, V_3)$ can be obtained, by assuming perfect vertical transmission

$$p = 1. \tag{28}$$

Easily from (24)-(25), $U_3 = 0$, $V_3 = V_2 = (b-n)c_{VV}^{-1}$. The plants populations can be obtained from (22)-(23). From the latter,

$$S = \Phi(I) = \frac{c_{II}I + \mu + m}{c_{IS}(I^\infty - I)} I, \quad I^\infty = \frac{(1-a)\lambda(b-n)}{c_{IS}c_{VV}}. \tag{29}$$

Thus $\Phi(I)$ has a negative zero and crosses the origin raising up to infinity at I^∞, this representing its only feasible branch, while for $I > I^\infty$ it is negative. Further, its derivative at the origin is positive,

$$\Phi'(0) = c_{VV} \frac{\mu + m}{(1-a)\lambda(b-n)} > 0. \tag{30}$$

Also, by adding the equilibrium equations corresponding to (22) and (23), we obtain a conic section

$$\Psi(I,S) = c_{II}I^2 + c_{SS}S^2 + (c_{IS}+c_{SI})SI - (r-m-\mu)I - (r-m)S = 0. \tag{31}$$

Discarding the degenerate cases, from its invariants, we observe that Ψ is an ellipse in case $4c_{II}c_{SS} > c_{IS} + c_{SI}$ and a hyperbola conversely. This conic goes through the origin and crosses the axes at the points $Q^I = (I^0, 0)$ and $Q^S = (0, S^0)$ with:

$$S^0 = \frac{r-m}{c_{SS}}, \quad I^0 = \frac{r-m-\mu}{c_{II}}.$$

Now, $S_0 > 0$ in view of (26), while the sign of I^0 is not determined. Note that if we try to assess the sign of the slope at the points at which the conic intersects the axes, by implicit differentiation, we find

$$\frac{dS}{dI} = \frac{2c_{II}I + (c_{IS}+c_{SI})S - (r-m-\mu)}{r-m-2c_{SS}S - (c_{IS}+c_{SI})I},$$

so that

$$\frac{dS}{dI}|_{Q^I} = \frac{c_{II}I^0}{r-m-(c_{IS}+c_{SI})I^0}, \quad \frac{dS}{dI}|_{Q^S} = 1 - \frac{\mu + (c_{IS}+c_{SI})S^0}{r-m} < 1,$$

while at the origin we find

$$\Psi'(O) = \frac{dS}{dI}|_O = \frac{\mu}{r-m} - 1 > -1.$$

In spite of these calculations, the signs of the derivatives, although still useful to discard some possible situations arising below, are not enough to discriminate between the two possible types of conic sections. Therefore we must examine them both. Further implicit differentiation produces, after evaluation at the origin,

$$\frac{d^2S}{dI^2}|_O = -\frac{2}{2c_{SS}+r-m}\left[(c_{SS}+c_{IS}+c_{SI})\frac{dS}{dI}|_O + c_{II}\right].$$

Remark 2. From this expression, if $S'(0) > 0$ it follows $S''(0) < 0$. Thus at the origin, a positive slope must be coupled with a negative curvature.

Case A : Suppose Ψ is an ellipse: there are two cases:

(a) $r > m + \mu$ for which $I^0 > 0$; the feasible part of Ψ consists just of an arc in the first quadrant joining the points Q^I and Q^S;
(b) $r < m + \mu$ for which $I^0 < 0$; the feasible part of Ψ consists just of an arc the origin and the point Q^I;

Case B : Suppose Ψ is a hyperbola: there are six cases:

1. $I^0 > 0$, $\Psi'(O) < 0$ and $\Psi''(O) < 0$: the feasible part of Ψ consists just of a convex arc in the first quadrant joining the points Q^I and Q^S;
2. $I^0 > 0$, $\Psi'(O) > 0$ and $\Psi''(O) < 0$: the feasible part of Ψ consists just of an arc joining the origin and the point Q^I and a convex arc emanating from Q^S;
3. $I^0 < 0$, $\Psi'(O) > 0$ and $\Psi''(O) < 0$: the feasible part of Ψ consists just of a concave arc emanating from the origin and a convex arc emanating from Q^S;
4. $I^0 < 0$, $\Psi'(O) < 0$ and $\Psi''(O) > 0$: the feasible part of Ψ consists just of a concave arc emanating from Q^S;
5. $I^0 < 0$, $\Psi'(O) < 0$ and $\Psi''(O) < 0$: the feasible part of Ψ consists just of a convex arc emanating from Q^S;
6. finally, $I^0 > 0$, $\Psi'(O) > 0$ and $\Psi''(O) > 0$: the feasible part of Ψ consists of an arc joining the origin and the point Q^S and a concave arc emanating from Q^I; however, in view of Remark 2 this case cannot arise.

The susceptible S_3 and infected I_3 populations at equilibrium E_3 are obtained by the intersections of Ψ and Φ lying in the first quadrant. Examining the various situations, we are led to the following conclusions:

Case A : Ψ is an ellipse:

- (a) the feasible intersection with Φ is always guaranteed;
- (b) the feasible intersection with Φ is guaranteed if and only if $\Phi'(0) > \Psi'(O)$.

Case B : Ψ is a hyperbola:

- (1) here $\Psi'(O) < 0 < \Phi'(0)$; exactly one intersection of $\Phi(I)$ and Ψ is guaranteed;
- (2) (i) if $\Phi'(0) < \Psi'(O)$, given that Φ has the vertical asymptote, two intersections between Φ and the two feasible branches of Ψ are always guaranteed;
  - (ii) if $\Phi'(0) > \Psi'(O)$, given that Φ has the vertical asymptote, exactly one intersection of $\Phi(I)$ with the branch of Ψ emanating from Q^S exists;
- (3) (i) if $\Phi'(0) < \Psi'(O)$, given that Φ has the vertical asymptote, two intersections between Φ and the two feasible branches of Ψ are always guaranteed;
  - (ii) if $\Phi'(0) > \Psi'(O)$, given that Φ has the vertical asymptote, exactly one intersection of $\Phi(I)$ with the branch of Ψ emanating from Q^S exists;
- (4) here $\Psi'(O) < 0 < \Phi'(0)$; in this case there is always one feasible intersection between Φ and Ψ;
- (5) here $\Psi'(O) < 0 < \Phi'(0)$; in this case there is always one feasible intersection between Φ and Ψ.

The coexistence equilibrium $E^* = (S^*, I^*, U^*, V^*)$ is investigated numerically.

3.2. *Equilibria stability*

The Jacobian matrix $\boldsymbol{J}$ associated with the model (22)-(25) is the following:

$$\begin{bmatrix} \boldsymbol{J}_{1,1} & r - c_{SI}S & 0 & (a-1)\lambda S \\ -c_{IS}I - (a-1)\lambda V & \boldsymbol{J}_{2,2} & 0 & -(a-1)\lambda S \\ a\beta\frac{IU}{(S+I)^2} & a\beta\frac{IU}{(S+I)^2} - a\beta\frac{U}{S+I} & \boldsymbol{J}_{3,3} & \boldsymbol{J}_{3,4} \\ -a\beta\frac{IU}{(S+I)^2} & a\beta\frac{U}{S+I} - a\beta\frac{IU}{(S+I)^2} & \boldsymbol{J}_{4,3} & \boldsymbol{J}_{4,4} \end{bmatrix},$$

with

$$\begin{aligned}
\boldsymbol{J}_{1,1} &= r - m - c_{SI}I - 2c_{SS}S + \lambda(a-1)V\,,\\
\boldsymbol{J}_{2,2} &= -m - \mu - 2c_{II}I - c_{IS}S\,,\\
\boldsymbol{J}_{3,3} &= b - n - 2c_{UU}U - c_{UV}V - a\beta\frac{I}{S+I}\,,\\
\boldsymbol{J}_{3,4} &= -c_{UV}U - b(p-1),\\
\boldsymbol{J}_{4,3} &= a\beta\frac{I}{S+I} - c_{VU}V,\\
\boldsymbol{J}_{4,4} &= bp - c_{VU}U - 2c_{VV}V - n.
\end{aligned}$$

For the equilibrium E_1, we find the eigenvalues

$$m - r < 0, \quad \frac{c_{IS}(m-r)}{c_{SS}} - \mu - m < 0, \quad b - n \geq 0, \quad bp - n \leq 0$$

so that it is unstable, unless $b = n$, in which case we obtain stability but not asymptotic stability.

Two eigenvalues of the Jacobian evaluated at E_2 are explicitly found, $m - r < 0$ and $n - b < 0$ both negative in view of (26) and (7). Using the Routh-Hurwitz criterion on the remaining minor of order two, we are led to the stability conditions

$$(bp - n) - (\mu + m) - \frac{c_{IS}}{c_{SS}}(r - m) - \frac{c_{VU}}{c_{UU}}(b - n) < 0, \quad (32)$$

$$\left(\frac{c_{IS}}{c_{SS}}(r-m) + \mu + m\right)\left(bp - n - \frac{c_{VU}}{c_{UU}}(b-n)\right) < \frac{\lambda\beta a(a-1)(b-n)}{c_{UU}}. (33)$$

Further, estimating the second term on the left of condition (33) as follows

$$\begin{aligned}
bp - n - \frac{c_{VU}}{c_{UU}}(b-n) &= b\left[p - \frac{n}{b} - \frac{c_{VU}}{c_{UU}}(1 - \frac{n}{b})\right]\\
= b\left(p - \frac{n}{b}\right)\left[1 - \frac{c_{VU}}{c_{UU}}\frac{1-\frac{n}{b}}{p-\frac{n}{b}}\right] &> b\left(p - \frac{n}{b}\right)\left[1 - \frac{c_{VU}}{c_{UU}}\right]
\end{aligned}$$

the condition (33) can be rewritten as

$$bc_{UU}\left(1 - \frac{c_{VU}}{c_{UU}}\right)\left(p - \frac{n}{b}\right) < -\frac{\lambda\beta a(1-a)(b-n)c_{SS}}{c_{IS}(r-m) + c_{SS}(\mu+m)}\,.$$

Remark 3. Now (32) holds if

$$p < \frac{n}{b} < 1 \quad (34)$$

by (7) and (26). Conversely, using

$$bp - n - \frac{c_{VU}}{c_{UU}}(b-n) < (b-n)\left(1 - \frac{c_{VU}}{c_{UU}}\right) < 0,$$

it also holds if

$$\frac{n}{b} < p < 1, \quad c_{VU} > c_{UU}. \tag{35}$$

Remark 4. This last condition is certainly not met if either one of the following sets of inequalities hold:

$$\frac{n}{b} < p, \quad c_{VU} < c_{UU}; \qquad p < \frac{n}{b} < 1, \quad c_{VU} > c_{UU}. \tag{36}$$

Therefore, in such case, E_2 is certainly unstable.

At E_3 the characteristic equation factorizes into the product of two quadratic equations, stemming each from a suitable minor of order 2. We can apply once more the Routh-Hurwitz conditions to these submatrices, to find two sets of stability conditions, namely

$$\begin{aligned} \boldsymbol{J}(E_3)_{1,1} + \boldsymbol{J}(E_3)_{2,2} < 0, \quad (37)\\ \boldsymbol{J}(E_3)_{1,1}\boldsymbol{J}(E_3)_{2,2} + \left(c_{IS}I_3 + \frac{\lambda(b-n)(a-1)}{c_{VV}}\right)(r - c_{SI}S_3) > 0, \end{aligned}$$

where

$$\begin{aligned} \boldsymbol{J}(E_3)_{1,1} &= r - m - c_{SI}I_3 - 2c_{SS}S_3 + \frac{\lambda(b-n)(a-1)}{c_{VV}}, \\ \boldsymbol{J}(E_3)_{2,2} &= -m - \mu - 2c_{II}I_3 - c_{IS}S_3 \end{aligned}$$

and

$$\boldsymbol{J}(E_3)_{3,3} + n - 2b + bp < 0, \quad \boldsymbol{J}(E_3)_{3,3}(n - 2b + bp) > \boldsymbol{J}(E_3)_{4,3}b(1-p) \tag{38}$$

with

$$\boldsymbol{J}(E_3)_{3,3} = b - n - \frac{c_{UV}(b-n)}{c_{VV}} - \frac{a\beta I^*}{S_3 + I^*}, \quad \boldsymbol{J}(E_3)_{4,3} = \frac{a\beta I^*}{S_3 + I^*} - \frac{c_{VU}(b-n)}{c_{VV}}.$$

Coexistence is shown numerically to be stable, for suitable parameter choices.

We also show transcritical bifurcations arising for the pair of equilibria E_4 to E_2 as the bifurcation parameters β (Figure 3) and λ (Figure 4) vary. The remaining parameter values used in these figures are

$$\begin{gathered} a = 0.5, \quad b = 19, \quad c_{UU} = 0.1, \quad c_{UV} = 0.2, \quad c_{VU} = 0.4, \\ c_{VV} = 0.3, \quad c_{SS} = 0.014, \quad c_{SI} = 0.023, \quad c_{IS} = 0.042, \\ c_{II} = 0.035, \quad n = 15, \quad m = 0.5, \quad r = 4, \quad \mu = 0.3. \end{gathered} \tag{39}$$

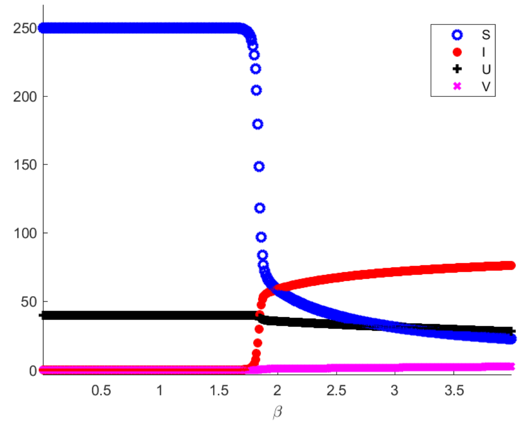

Figure 3. Transcritical bifurcation from E_4 to E_2 as the bifurcation parameter β decreases below the threshold $\widehat{\beta} \approx 1.75$. The other parameter values are given by (39) and $p = 0.5$ and $\lambda = 12$. Initial conditions given below by equation (21).

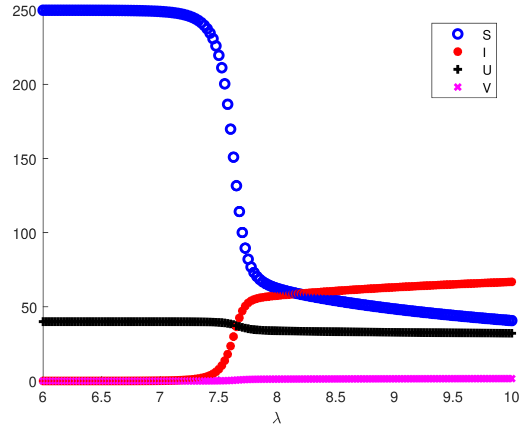

Figure 4. Transcritical bifurcation from E_4 to E_2 as the bifurcation parameter λ decreases below the threshold $\widehat{\lambda} \approx 7.25$. The other parameter values are are given by (39) and $p = 1$ and $\beta = 3$. Initial conditions given below by equation (21).

4. The effector protein action on the ecosystem

For the model (2), (4), (5), we use the following reference parameter values:

$$b = 9, \quad c_{UU} = 0.15, \quad c_{UV} = 0.10, \quad c_{VU} = 0.25, \quad c_{VV} = 0.20, \qquad (40)$$
$$n = 9, \quad p = 0.5, \quad \beta = 12, \quad C = 300, \quad \lambda = 11, \quad \mu = 7.$$

For model (22)-(25) the same initial conditions (21) are used, but the reference parameter values are

$$\begin{gathered}
b = 19, \quad c_{UU} = 0.1, \quad c_{UV} = 0.2, \quad c_{VU} = 0.4, \quad c_{VV} = 0.3, \\
c_{SS} = 0.014, \quad c_{SI} = 0.023, \quad c_{IS} = 0.042, \quad c_{II} = 0.035, \quad n = 19, \\
m = 0.5, \quad p = 0.5, \quad r = 4, \quad \beta = 11, \quad \lambda = 12, \quad \mu = 0.3.
\end{gathered} \tag{41}$$

Figures 6-10 contain the simulations for model (2), (4), (5). In particular, Figure 6 shows the solutions behavior in the particular case of $b = n$, while in all the other ones $b > n$. Note that all the possible system's equilibria are shown to arise, for suitable parameter choices. Clearly, the parameter a does not influence the final outcome, in the sense that changing it does not alter the point that is ultimately achieved. It does affect however the speed at which the equilibrium is reached. Although in the transient phase there might be some slight differences, compare the frame for V in Figure 6, in general a higher value of a helps in removing faster the infected and boosts the susceptible plants growth; these remarks hold in a lesser way for insects. An exception for the infected insects is however given by the coexistence equilibrium $\widehat{E}_4$ of Figure 9, their number being increased by a larger value of the effector protein.

Completely similar remarks hold for the simulations involving model (22)-(25), Figures 11-16. Again, Figure 11 shows the particular case $b = n = 19$, while the remaining ones assume $b > n$.

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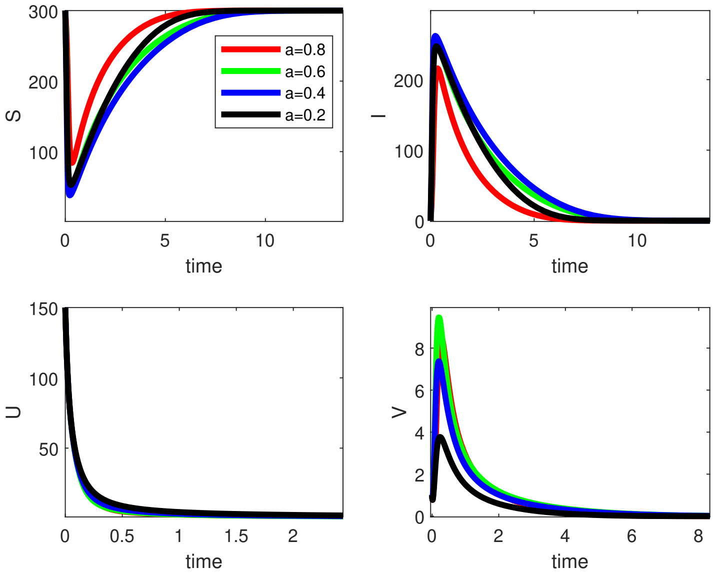

Figure 5. Model (2), (4), (5): Equilibrium $\widehat{E}_1$ obtained with parameter values (40) and initial conditions (21).

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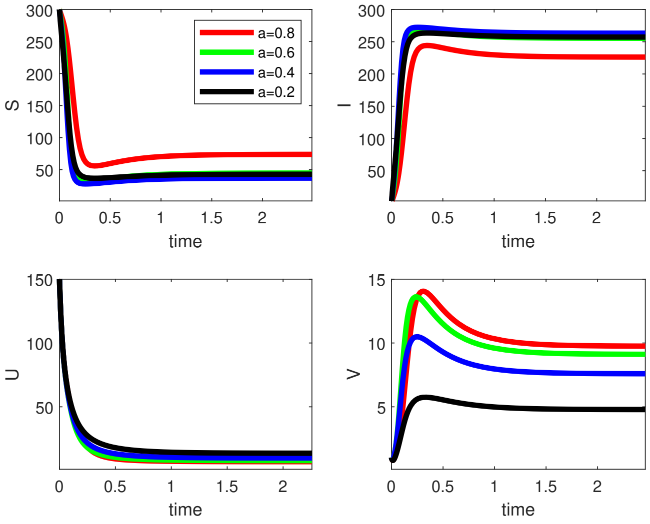

Figure 6. Model (2), (4), (5): Equilibrium $\widehat{E}_4$ obtained with parameter values (40), but for $n = 6 < b$, and initial conditions (21).

Table 4. Feasibility and local stability conditions for the system (22)-(25) equilibria, where the assumptions on the parameters (7) and (26) are implicitly used.

Equilibria	Feasibility	Stability
$E_1 = (\frac{r-m}{c_{SS}}, 0, 0, 0)$	—	unstable if $b > n$ simply stable if $b = n$
$E_2 = (\frac{r-m}{c_{SS}}, 0, \frac{b-n}{c_{UU}}, 0)$	—	(32), (33); sufficient (34), (35)
$E_3 = (S_3, I_3, 0, \frac{b-n}{c_{VV}})$	(28), see text: Cases A and B for $I_3 > 0$ and $S_3 > 0$	numerical
$E_4 = (S^*, I^*, U^*, V^*)$	numerical	numerical

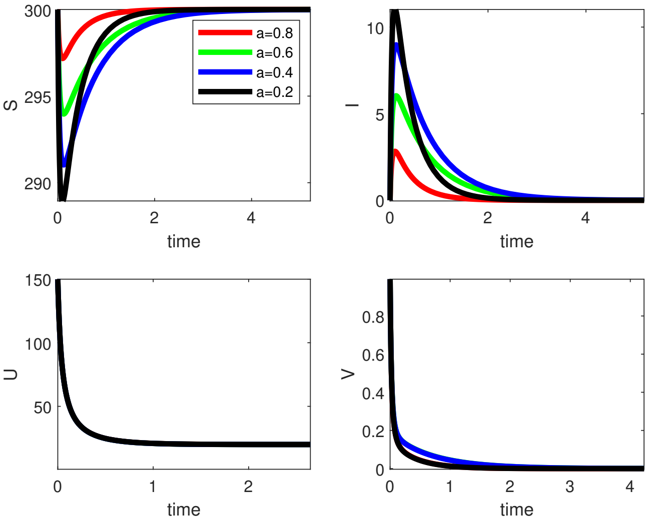

Figure 7. Model (2), (4), (5): Equilibrium $\widehat{E}_2$ obtained with parameter values (40), but for $n = 6 < b$, $\beta = 3$, $\lambda = 2$ and initial conditions (21).

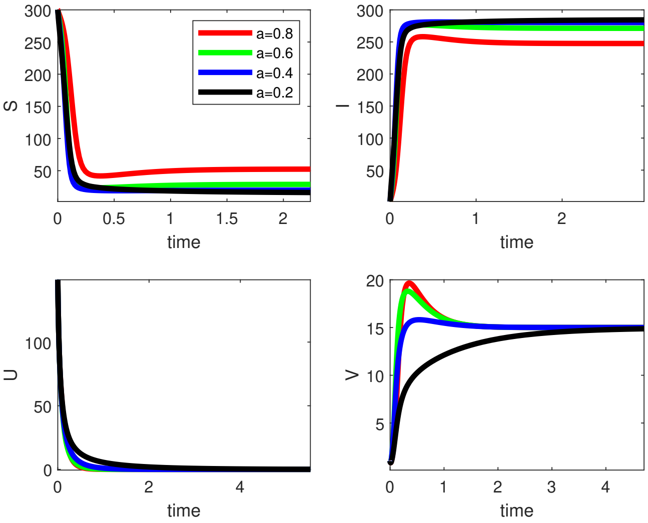

Figure 8. Model (2), (4), (5): Equilibrium $\widehat{E}_3$ obtained with parameter values (40), but for $n = 6 < b$, $p = 1$ and initial conditions (21).

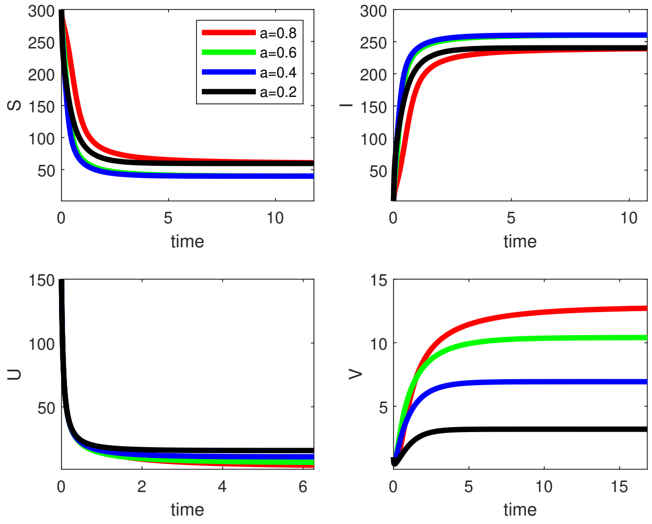

Figure 9. Model (2), (4), (5): Equilibrium $\widehat{E}_4$ obtained with parameter values (40), but for $n = 6 < b$, $p = 1$, $\beta = 2$ and initial conditions (21).

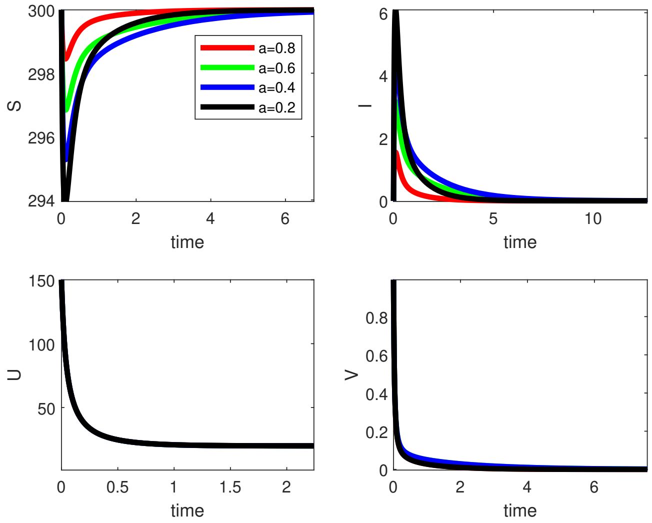

Figure 10. Model (2), (4), (5): Equilibrium $\widehat{E}_2$ obtained with parameter values (40), but for $n = 6 < b$, $p = 1$, $\beta = 2$, $\lambda = 1$ and initial conditions (21).

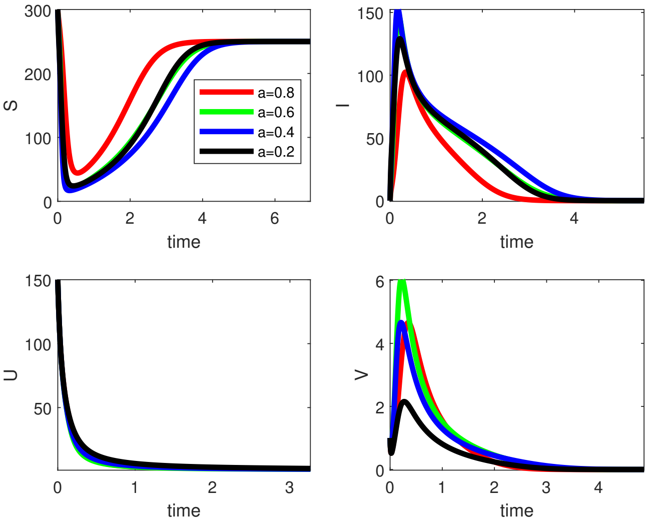

Figure 11. Model (22)-(25): Equilibrium E_1 obtained with parameter values (41) and initial conditions (21).

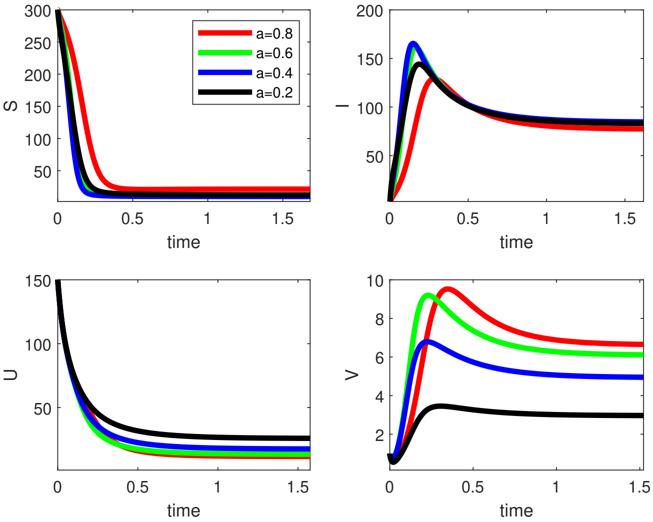

Figure 12. Model (22)-(25): Equilibrium E_4 obtained with parameter values (41) but for $n = 15$ and initial conditions (21).

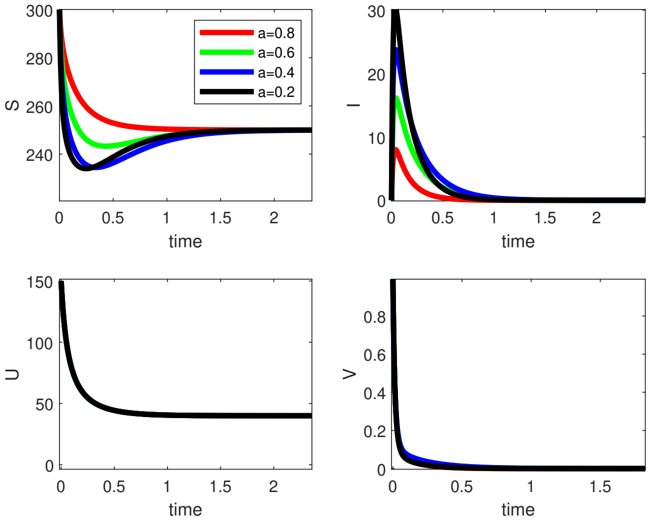

Figure 13. Model (22)-(25): Equilibrium E_2 obtained with parameter values (41) but for $n = 15$, $\beta = 1$ and initial conditions (21).

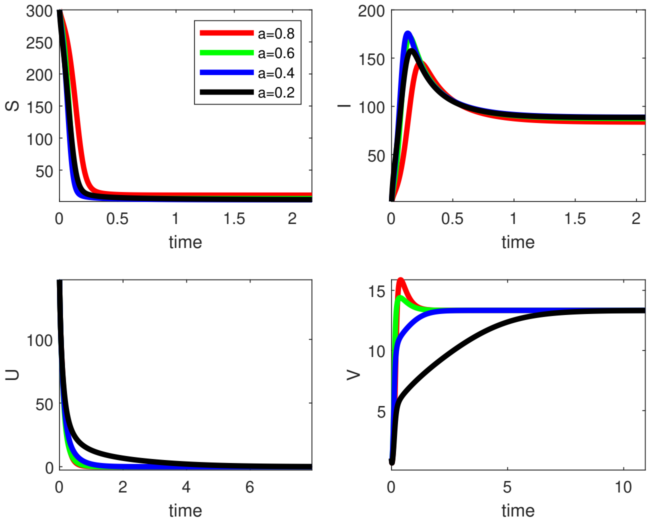

Figure 14. Model (22)-(25): Equilibrium E_3 obtained with parameter values (41) but for $n = 15$, $p = 1$ and initial conditions (21).

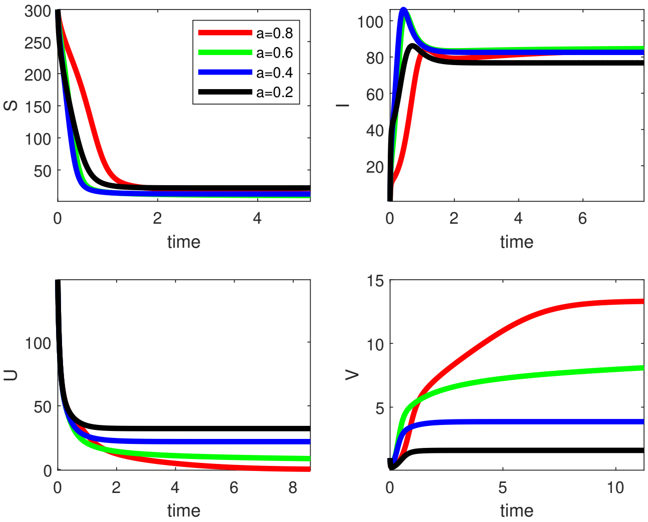

Figure 15. Model (22)-(25): Equilibrium E_4 obtained with parameter values (41) but for $n = 15$, $p = 1$, $\beta = 3$ and initial conditions (21).

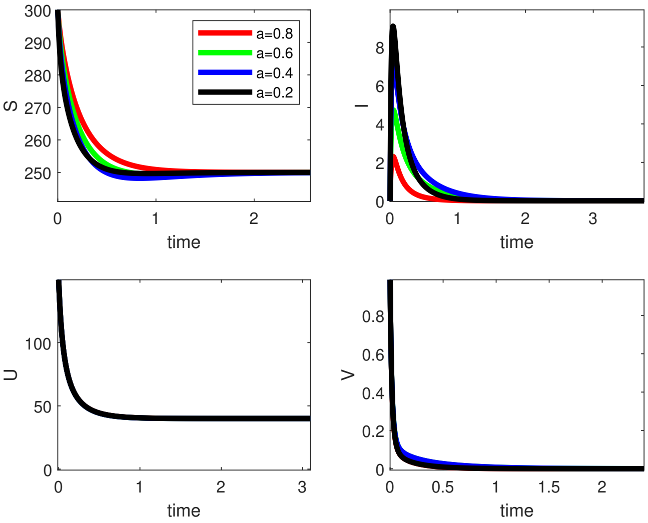

Figure 16. Model (22)-(25): Equilibrium E_2 obtained with parameter values (41) but for $n = 15$, $p = 1$, $\beta = 3$, $\lambda = 3$ and initial conditions (21).