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Modelling the spiders ballooning effect on the vineyard ecology

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Abstract

We consider an ecosystem in which spiders may be transported by the wind from vineyards into the surrounding woods and vice versa. The model takes into account this tranport phenomenon without building space explicitly into the governing equations. The equilibria of the dynamical system are analyzed together with their stability, showing that bifurcations may occur. Then the effects of indiscriminated spraying to keep pests under control is also investigated via suitable simulations.

Keywords: predator-prey models, spiders, ballooning, generalist predators, equilibria, coexistence, stability, bifurcations, insecticide spraying.

1. Introduction

The importance of generalist predators has received increasing awareness, e.g. [15]. Spiders are among the most ubiquitous and numerous generalist predators in agroecosystems [9, 13] and along with other generalists are thought to be important in reducing and preventing pest outbreaks [11, 14]. One of the key factors for the evolutionary success of spiders is ballooning. Most of the ballooners are immature instars under 1.0 mg although many of the smaller Linyphiids, which are the most frequent long-range dispersers, balloon as adults [1]. Dispersal characterizes the first few days of most spiders although the youngsters may drift on their silken threads to sites more distant than a meter away. Only a fashionable minority makes romantic journeys to unknown niches in distant continents or remote volcanic islands [24]. Selective pressures relating to competition for food, cannibalism, density dependent predation and shortages of suitable web-support structures favoured the evolution of dispersal behaviour. In this sense dispersal can be regarded as an example of an evolved behaviour to avoid competition [24]. Immigration depends both on the dispersal characteristics of the species and the composition of surrounding habitats. Therefore, ballooning-spider population dynamics in a single field not only depends on the immediate surroundings, but on the landscape as a whole [4, 12].

From the individual spider's point of view the landscape consists of a mosaic of patches of varying quality. This landscape structure has to be considered both in spatial and temporal terms [8]. The landscape can be described spatially in terms of patch diversity and heterogeneity. Landscape diversity can be defined as the number of habitat types available to the spiders, and landscape heterogeneity as how intermingled they are. Temporally, the landscape can also be described with respect to disturbance synchronisation, e.g. how large a proportion of the fields are at the same time subject to pesticide application [17]. Hence, the landscape structure is not static, and spatial and temporal diversity and heterogeneity are not independent; they all change with season, management, crop rotation, land use, husbandry, etc. Spider communities are significantly affected by these factors and different agroecosystem dynamics can show different spider assemblages [4]. The population in a single field may need to recover several times every year. This cannot always be achieved by reproduction alone, and thus immigration is important. Consequently, the population dynamics of ballooning spiders, i.e. Linyphiids, cannot be understood without taking their spatial dynamics into account. The problem of investigating the relative importance of these factors is that experiments are very labour intensive and expensive to carry out at landscape scale [23]. Therefore, at this scale, simulation modelling is an appropriate approach to study effects of land use and crop management practices. Several simulation models have suggested that monoculture-dominated homogenous landscapes support fewer spiders than more diverse landscapes and that rotation could be harmful [3, 4, 18]. It has also been suggested that inclusion of less disturbed permanent habitats is beneficial for spider population dynamics, and that field size could play a role for species with poor dispersal abilities [18, 19].

The Langa Astigiana is one of the most important wine producing regions in Italy. Woods and fields have been almost completely removed along the centuries in order to harvest vineyards. Only a few grass patches and sparse groups of trees survive in places and some tree lines mainly as property delimiters. We would like to investigate their role in the ecosystem formed by insects, possible pests of vineyards and their natural predators, spiders.

The model we propose attempts at investigating this situation. From the modelling point of view, the major novelty consists in taking into account the ballooning effect without explicitly introducing spatial dimensions, as for instance in other investigations [3]. The model is described in the next Section, the boundedness of the system's trajectories is studied in Section 3, boundary equilibria with their stability are analyzed in Section 4, the coexistence equilibrium is found in Section 5 and its stability investigated in Section 6. The effects of insecticide spraying are discussed in Section 7 and finally the ecological implications of these findings are summarized in the last Section.

In a related work, [22] a similar model for wandering spiders has been investigated. It differs from the one presented here because the wanderer spider population acts as a predator on the two kinds of prey, the insects living in woods and grass patches which are distinguished from those living and possibly adversely affecting the vineyards. This distinction among prey populations is assumed also in this context, but here we need to distinguish also the spider populations, as being essentially stantial.

2. The proposed model

Let W denote the woods insects carrying capacity, $w(t)$ be the insects population living in woods, V the vineyards insects carrying capacity, with $V >> W$ in the Langhe, $v(t)$ be the insects population living in the vineyards, $s_w(t)$ and $s_v(t)$ represent the spider populations living respectively in the woods and in the vineyards.

The model can then be formulated as follows.

$$\begin{aligned}
\dot{w} &= bw(1-\frac{w}{W}) - \ell w s_w \\
\dot{v} &= av(1-\frac{v}{V}) - kvs_v \\
\dot{s}_w &= -cs_w + s_w[\tilde{\ell}w - \alpha w\tilde{\ell}\frac{V}{V+W}] + s_v\alpha v\tilde{k}\frac{W}{V+W} \\
\dot{s}_v &= -es_v + s_v[\tilde{k}v - \alpha v\tilde{k}\frac{W}{V+W}] + s_w\alpha w\tilde{\ell}\frac{V}{V+W}.
\end{aligned} \tag{2.1}$$

Here the first equation expresses the fact that wood insects reproduce logistically and are subject to predation by the spiders living in the woods. Similarly the second equation states the same for insects and spiders living in the vineyards. The two ecosystems could be considered as separate entities, as the web-making spiders tend to live in the same place, but for the ballooning effect. The transport of the young spiders by the wind is accounted for in the two equations modelling the growth of the spider populations. The third equation gives the dynamics of spiders living in the woods. They die with very low exponential rate c in absence of prey. When a prey is captured, it is turned into newborns with efficiency $\tilde{\ell}$. A fraction α of newborns is carried by the wind into the air and has probability of landing in either woods or surrounding vineyards with probability which we here assume to be proportional to the surface of the two patches. Indeed in practice this surface is related also to their respective carrying capacities. The last two terms in this equation describe then this migration effect, the last one representing immigration from newborns carried into the woods from the vineyards, while the third term represents emigration of wood-born spiders into the surrounding landscape. Notice that the last equation expresses these same concepts in terms of the spider population living in the vineyards, which has predation efficiency $\tilde{k}$. The transport effect of the wind is instead clearly the same for both species, as there is no essential reason for assuming it to be different in the woods than on open land. Notice also that we do not consider the wind transport effect on insects, as they are able to fly on their own and move toward the environment places that they prefer.

3. Boundedness

From the first two equations of (2.1) it is not difficult to show that the two insects populations are bounded above, more precisely

$$\begin{aligned} w(t) &\le \max\{w(0), W\}, \quad \limsup_{t\to\infty} w(t) \le W \\ v(t) &\le \max\{v(0), V\}, \quad \limsup_{t\to\infty} v(t) \le V \end{aligned} \tag{3.1}$$

Moreover, let us define the function $\phi(t) = w + v + s_w + s_v$. Upon summation of the equations (2.1) we find for any arbitrary $\kappa > 0$

$$\begin{aligned} \dot{\phi} + \kappa\phi \le bw(1 - \frac{w}{W}) + av(1 - \frac{v}{V}) - (c-\kappa)s_w - (e-\kappa)s_v \\ -(\ell - \tilde{\ell} - \kappa)s_w - (k - \tilde{k} - \kappa)s_v \\ \le bw(1 - \frac{w}{W}) + av(1 - \frac{v}{V}) \le \frac{1}{4}[bW + aV] \equiv \bar{M} \end{aligned}$$

where we have restricted $\kappa \le \min\{c, e, \ell - \tilde{\ell}, k - \tilde{k}\}$. It follows then that $\dot{\phi} \le -\kappa\phi + \bar{M}$ from which Gronwall's inequality delivers

$$\phi(t) \le \exp(-\kappa t) + \frac{\bar{M}}{\kappa}[1 - \exp(-\kappa t)] \le M. \tag{3.2}$$

Thus every population is bounded for all time.

4. Ecosystem's equilibria

We analyze in this Section the possible equilibria of the system. The first one is given by the origin $E^{(1)}$, which is feasible but always unstable, as the eigenvalues of the Jacobian at this point are $a, b, -c, -e$. The second equilibrium point is $E^{(2)} \equiv \left(w^{(2)}, v^{(2)}, s_w^{(2)}, s_v^{(2)}\right)$ $= (W, 0, 0, 0)$. It is easily seen that the second equation for $\dot{v}$ has eigenvalue a, and this is sufficient to conclude that $E^{(2)}$ is always unstable. The the other ones are $-b$, $-e$, $-c + \tilde{\ell}\frac{W}{V+W}(V + W - \alpha V)$.

The point $E^{(3)} \equiv (0, V, 0, 0)$ is the next equilibrium, but here again the linearization of the first equation for $\dot{w}$ gives b as eigenvalue, and the other ones are $-a$, $-c$, $-e + \tilde{k}\frac{V}{V+W}(V + W - \alpha W)$ i.e. again unconditional instability.

We then find $E^{(4)} \equiv (W, V, 0, 0)$. In this case the eigenvalues are $-a, -b$ and the roots of the quadratic equation

$$\lambda^2 + \lambda\left[c - W\tilde{\ell} + e - V\tilde{k} + \frac{\alpha VW(\tilde{\ell}+\tilde{k})}{V+W}\right] + \left(c - W\tilde{\ell} + \frac{\alpha VW\tilde{\ell}}{V+W}\right)\left(e - V\tilde{k} + \frac{\alpha VW\tilde{k}}{V+W}\right) - \frac{V^2W^2\tilde{\ell}\tilde{k}\alpha^2}{(V+W)^2} = 0.$$

The Routh Hurwitz criterion applied to this equation gives the conditions for which $E^{(4)}$ is stable. Sufficient conditions ensuring their satisfaction are given by

$$c > W\tilde{\ell}, \quad e > V\tilde{k} \tag{4.1}$$

The next equilibrium is

$$\begin{aligned} E^{(5)} \equiv & \left(0, \frac{e(V+W)}{\tilde{k}\,(V+W-\alpha W)}, \frac{a}{k}\frac{e\alpha W}{c(W+V-\alpha W)}\left[1 - \frac{e\,(V+W)}{\tilde{k}V\,(V+W-\alpha W)}\right],\right. \\ & \left.\frac{a}{k}\left[1 - \frac{e\,(V+W)}{\tilde{k}V\,(V+W-\alpha W)}\right]\right) \end{aligned} \tag{4.2}$$

The feasibility conditions are two in this case. The first one is $W + V - \alpha W > 0$ which is always satisfied in view of the fact that α is a fraction, i.e. $0 \leq \alpha \leq 1$. The second one is given by

$$\tilde{k}V\,(V+W-\alpha W) > e\,(V+W)\,. \tag{4.3}$$

The next boundary equilibrium is the point

$$\begin{aligned} E^{(6)} \equiv & \left(\frac{c(V+W)}{\tilde{\ell}\,(V+W-\alpha V)}, 0, \frac{b}{\ell}\left(1 - \frac{c(V+W)}{\tilde{\ell}W\,(V+W-\alpha V)}\right),\right. \\ & \left.\frac{b}{\ell}\frac{V\alpha}{e}\left[\frac{c}{W+V-\alpha V}\right]\left[1 - \frac{c\,(V+W)}{\tilde{\ell}W\,(V+W-\alpha V)}\right]\right) \end{aligned} \tag{4.4}$$

which is feasible under the two conditions $W + V - \alpha V > 0$, always satisfied for $0 \leq \alpha \leq 1$, and

$$\tilde{\ell}W\,(V+W-\alpha V) > c\,(V+W)\,. \tag{4.5}$$

The stability analysis for both the above equilibria needs the following Jacobian $J^{(i)} \equiv J(E^{(i)})$

$$\begin{pmatrix} b(1-\frac{2w^{(i)}}{W}) - \ell s_w^{(i)} & 0 & -\ell w^{(i)} & 0 \\ 0 & a(1-\frac{2v^{(i)}}{V}) - ks_v^{(i)} & 0 & -kv^{(i)} \\ (1-\alpha\frac{V}{V+W})\tilde{\ell}s_w^{(i)} & \alpha\frac{W}{V+W}\tilde{k}s_v^{(i)} & (1-\frac{\alpha V}{V+W})\tilde{\ell}w^{(i)} - c & \alpha\frac{W}{V+W}\tilde{k}v^{(i)} \\ \alpha\frac{V}{V+W}\tilde{\ell}s_w^{(i)} & \tilde{k}s_v^{(i)}(1-\alpha\frac{W}{V+W}) & \tilde{\ell}w^{(i)}\alpha\frac{V}{V+W} & \tilde{k}v^{(i)}(1-\frac{\alpha W}{V+W}) - e \end{pmatrix} \tag{4.6}$$

Thus for equilibrium $E^{(5)}$, the eigenvalues are $-c$ and $b - \ell s_w^{(5)}$ and the roots of the quadratic

$$\lambda^2 - \mathrm{tr}(\tilde{J}(E^{(5)}))\lambda + \det(\tilde{J}(E^{(5)})) = 0. \tag{4.7}$$

Here

$$\begin{aligned}\tilde{J}(E^{(5)}) &\equiv \begin{pmatrix} a(1 - 2\frac{v^{(5)}}{V}) - ks_v^{(5)} & -kv^{(5)} \\ \tilde{k}s_v^{(5)}(1 - \alpha\frac{W}{V+W}) & \tilde{k}v^{(5)}(1 - \alpha\frac{W}{V+W}) - e \end{pmatrix} \\ &\equiv \begin{pmatrix} a(1 - 2\frac{v^{(5)}}{V}) - ks_v^{(5)} & -kv^{(5)} \\ \tilde{k}s_v^{(5)}(1 - \alpha\frac{W}{V+W}) & 0 \end{pmatrix}\end{aligned} \tag{4.8}$$

Thus the Routh Hurwitz conditions for stability give $-\mathrm{tr}(J^{(5)}) > 0$ and $\det(J^{(5)}) > 0$, i.e. since $0 \le \alpha \le 1$

$$-\mathrm{tr}(J^{(5)}) \equiv ks_v^{(5)} - a + 2\frac{a}{V}v^{(5)} = ae\frac{V+W}{\tilde{k}V(V+W-\alpha W)} > 0,$$

$$\det(J^{(5)}) \equiv k\tilde{k}v^{(5)}s_v^{(5)}\frac{V+W-\alpha W}{V+W} > 0.$$

Hence the conditions for stability of $E^{(5)}$ reduce to just

$$b < \ell s_w^{(5)}. \tag{4.9}$$

For $E^{(6)}$, we find again explicitly two eigenvalues, $-e$, $a - ks_v^{(6)}$ and then the eigenvalues of

$$\begin{aligned}\tilde{J}(E^{(6)}) &\equiv \begin{pmatrix} b(1 - 2\frac{w^{(6)}}{W}) - \ell s_w^{(6)} & -\ell w^{(6)} \\ \tilde{\ell}s_w^{(6)}(1 - \alpha\frac{V}{V+W}) & \tilde{\ell}w^{(6)}(1 - \alpha\frac{V}{V+W}) - c \end{pmatrix} \\ &\equiv \begin{pmatrix} -\frac{bc(V+W)}{\tilde{\ell}W(V+W-\alpha V)} & -\ell w^{(6)} \\ \tilde{\ell}s_w^{(6)}(1 - \alpha\frac{V}{V+W}) & 0 \end{pmatrix}\end{aligned} \tag{4.10}$$

The Routh Hurwitz criterion on the characteristic equation gives again

$$-\mathrm{tr}(\tilde{J}(E^{(6)})) = \frac{bc(V+W)}{\tilde{\ell}W(V+W-\alpha V)} > 0,$$

$$\det(\tilde{J}(E^{(6)})) = \ell\tilde{\ell}w^{(6)}s_w^{(6)}\frac{V+W-\alpha V}{V+W} > 0,$$

so that the stability of $E^{(6)}$ is ensured just by

$$a < ks_v^{(6)}. \tag{4.11}$$

5. Coexistence

We analyze now the existence of equilibria in the first orthant, with all nonvanishing components, $E^* \equiv E_7 = (w^*, v^*, s_w^*, s_v^*)$. To find sufficient conditions for existence, we solve the first two equations of (2.1) for w and v to get

$$w^* = \frac{W}{b}(b - \ell s_w^*), \qquad v^* = \frac{V}{a}(a - k s_v^*). \tag{5.1}$$

Feasibility implies that the opposite conditions of (4.9) and (4.11), but both evaluated at E^*, have to be satisfied in order for E^* to be feasible, namely

$$a > k s_v^*, \quad b > \ell s_w^*. \tag{5.2}$$

Substituting (5.1) into the last two equations of (2.1), we obtain the following equations in s_w and s_v. The first one is

$$-A s_w^2 + 2\tilde{B} s_w + 2C s_v - D s_v^2 = 0 \tag{5.3}$$

where $A \equiv \frac{\ell}{b}\tilde{\ell}\frac{W}{V+W}(V + W - \alpha V) > 0$, $\tilde{B} \equiv \frac{1}{2}[\tilde{\ell}\frac{W}{V+W}(V + W - \alpha V) - c] \in \mathbf{R}$, $C \equiv \frac{1}{2}\alpha\tilde{k}\frac{VW}{V+W} > 0$, $D \equiv \frac{k}{a}\frac{VW}{V+W}\tilde{k}\alpha > 0$. The second one instead is

$$-E s_w^2 + 2F s_w + 2\tilde{G} s_v - H s_v^2 = 0 \tag{5.4}$$

where $E \equiv \frac{\ell}{b}\tilde{\ell}\frac{VW}{V+W}\alpha > 0$, $F \equiv \frac{1}{2}\tilde{\ell}\alpha\frac{VW}{V+W} > 0$, $\tilde{G} \equiv \frac{1}{2}[\tilde{k}\frac{V}{V+W}(V + W - \alpha W) - e] \in \mathbf{R}$, $H \equiv \frac{k}{a}\frac{V}{V+W}\tilde{k}(V + W - \alpha W) > 0$.

Both are conic sections, in fact both are ellipses in the $(s_w, s_v) \equiv (x, y)$ plane. Their detailed analysis shows that both cross the origin. Notice that in this context the origin in $\mathbf{R}^2$ gives rise for the whole model to the equilibria we named $E^{(1)}$, $E^{(2)}$ and $E^{(3)}$, which we already analyzed earlier. We concentrate then on the ellipses' possible further intersections.

The first ellipse intersects the positive vertical semiaxis at the point $P \equiv (x_P, y_P) = (0, 2\frac{C}{D})$, and an intersection with the horizontal axis at $Q \equiv (x_Q, y_Q) = (2\frac{\tilde{B}}{A}, 0)$. Also its derivative at the point P is $y_1'(P) = \frac{\tilde{B}}{C}$, while at the origin it is $y_1'(O) = -\frac{\tilde{B}}{C}$. It is then easily seen to have the same sign as the abscissa x_Q at P, while at the origin it has always its opposite sign. The center is located at the point $(\frac{\tilde{B}}{A}, \frac{C}{D})$. The vertices are instead

$$(\frac{\tilde{B}}{A} \pm \frac{1}{AD}\sqrt{\tilde{B}^2 D^2 + AC^2 D}, \frac{C}{D}), \quad (\frac{\tilde{B}}{A}, \frac{C}{D} \pm \frac{1}{AD}\sqrt{A^2 C^2 + A\tilde{B}^2 D}) \tag{5.5}$$

The second one instead has a further intersection with the positive vertical semiaxis at the point $R \equiv (x_R, y_R) = (0, 2\frac{\tilde{G}}{H})$, and an intersection with the horizontal axis at $S \equiv (x_S, y_S) = (2\frac{F}{E}, 0)$. Also its derivative at the point R is $y_2'(R) = \frac{F}{\tilde{G}}$, while at the origin it is $y_2'(O) = -\frac{F}{\tilde{G}}$ It is thus seen to have the same sign as the height y_R when evaluated at R and its opposite sign when evaluated at the origin. The center in this case is the point $(\frac{F}{E}, \frac{\tilde{G}}{H})$. The vertices in this case are

$$(\frac{F}{E}, \frac{\tilde{G}}{H} \pm \frac{1}{EH}\sqrt{\tilde{G}^2E^2 + EF^2H}), \quad (\frac{F}{E} \pm \frac{1}{EH}\sqrt{F^2H^2 + E\tilde{G}^2H}, \frac{\tilde{G}}{H}) \tag{5.6}$$

In view of the above remarks, both ellipses have axes that are parallel to the coordinate axes.

Combining these informations it is now easy to write down sufficient conditions for the existence of E^*. We distinguish four cases.

1A) $\tilde{B} > 0$, $\tilde{G} > 0$; in this case sufficient conditions for the existence and uniqueness of an intersection between y_1 and y_2 in the first quadrant, which might give a feasible E^* if conditions (5.2) are also satisfied, are either

$$CH > D\tilde{G} \text{ and } FA > E\tilde{B} \tag{5.7}$$

or alternatively

$$CH < D\tilde{G} \text{ and } FA < E\tilde{B}. \tag{5.8}$$

1B) $\tilde{B} > 0$, $\tilde{G} < 0$; the conditions reduce just to the following one

$$FA > E\tilde{B}. \tag{5.9}$$

2A) For $\tilde{B} < 0$, $\tilde{G} > 0$ the condition now is

$$CH > D\tilde{G}. \tag{5.10}$$

2B) Finally for $\tilde{B} < 0$, $\tilde{G} < 0$ we need to compare the derivatives of y_1 and y_2 at the origin, namely $y_1'(O) < y_2'(O)$, to impose an intersection in the first quadrant. We thus find

$$FC < \tilde{G}\tilde{B}. \tag{5.11}$$

Direct substitution of the values for $A,\ \tilde{B},\ C, D,\ E,\ F,\ \tilde{G}$ into (5.7) shows that these two conditions are always satisfied, since they are equivalent respectively to $c > 0$ and $e > 0$. Geometrically, they correspond to the requirements $x_S \geq x_Q$ and $y_P \geq y_R$, where equality holds only for the cases $c = 0$ and $e = 0$ respectively. It follows in turn that (5.9) and (5.10) are always satisfied. These conditions must hold together with (5.2), and the latter imply that the intersection E^* of the ellipses must lie within the square with vertices $OPUS$, where $U \equiv (x_S, y_P) \equiv (2\frac{F}{E}, 2\frac{C}{D}) \equiv (\frac{b}{\ell}, \frac{a}{k})$. The first ellipse however circumscribes this square in the cases 1A) and 1B) corresponding to $x_Q > 0$, i.e. $\tilde{G} > 0$. Therefore in such cases E^* will result infeasible since one of the first two coordinates, v, w is negative. In cases 2A) and 2B) the arc OP of the first ellipse not containing Q lies entirely in the square $OPUS$, conditions (5.10) and (5.11) guarantee an intersection so that E^* is always feasible. The case 2A) is graphically illustrated in Figure 1.

To investigate further this phenomenon, we analyze also the particular cases. Notice first of all that for the particular case $e = 0$ new equilibria are found, namely $E_0 \equiv (0, 0, 0, \bar{s}_v)$ for some arbitrary $\bar{s}_v > 0$, which however on further investigation has to be $\bar{s}_v \equiv y_P \equiv \frac{a}{b}$, or also $E_1 \equiv (W, 0, 0, \bar{s}_v)$. Conversely for $c = 0$ we find $E_2 \equiv (0, 0, \bar{s}_w, 0)$ and $E_3 \equiv (0, V, \bar{s}_w, 0)$, where $\bar{s}_w \equiv \frac{b}{\ell}$. It is then easy to study the stability of these points. Substituting into the Jacobian, the eigenvalues $a, b, -c, 0$ for E_0 and $-b, a - k\bar{s}_v \equiv 0, -c + \tilde{\ell}W(1 - \alpha\frac{V}{V+W}), 0$ for E_1 are found. Instability of the former is immediate. The stability condition for the latter is then $\tilde{\ell}W(1 - \alpha\frac{V}{V+W}) < c$, i.e. $\tilde{B} < 0$, or also $x_Q < 0$. In case 2A) E_1 is then stable. For E_2 we find the eigenvalues $b - \ell\bar{s}_w \equiv 0, -a, 0, \tilde{k}\frac{V}{V+W}(V + W - \alpha W) - e$, so that once again it is stable if $\tilde{G} < 0$ i.e. when $y_R < 0$. Thus in case 2A) it results unstable, while in case 2B) it is stable. For E_3 we find instead $0, a, 0, -e$ so that it is always unstable.

It follows that as e grows, the axis intersection between the ellipses moves away from the s_v axis retaining its stability, thus giving rise to a stable manifold, the arc OP of the ellipse not containing the point Q, where E^* is located. Incidentally, it can be shown numerically and proven theoretically that for $e < 0$ this would be the stable branch of a saddle-node bifurcation of an infeasible equilibrium. Similar remarks can be made reversing the stability concepts and exchanging e with c, P with S and Q with R.

Condition (5.11) is equivalent to requiring $y_1'(O) = -\frac{\tilde{B}}{C} < -\frac{F}{\tilde{G}} = y_2'(O)$. It is equivalent to $FACH > E\tilde{B}\tilde{G}D > EFCD$ which gives $\frac{A}{E} > \frac{D}{H}$. Upon substitution of the parameter values and simplifications, we find $(V + W - \alpha V)(V + W - \alpha W) > VW$ and this leads to $(1 - \alpha)(V^2 + W^2) + VW(1 - \alpha)^2 > 0$ which is clearly always satisfied. Thus (5.11) always holds and in case 2B) we thus always have a feasible intersection.

Finally, notice also that $E^{(5)}$ feasible is equivalent to $\tilde{G} \geq 0$, and $E^{(6)}$ feasible is equivalent to $\tilde{B} \geq 0$.

6. The Hopf bifurcation

The Hopf bifurcation arises if and only if we can find purely imaginary eigenvalues, and a kind of transversality condition is satisfied. Since the characteristic polynomial is the quartic in λ,

$$\sum_{i=0}^{4} b_i \lambda^i, \tag{6.1}$$

to have purely imaginary eigenvalues the following condition must hold

$$\sum_{i=0}^{4} b_i \lambda^i = (\lambda^2 + \eta^2)(\lambda^2 + \beta\lambda + \zeta) = 0. \tag{6.2}$$

Long multiplication and comparison of coefficients of like powers gives the conditions

$$b_3 = \beta, \quad b_2 = \zeta + \eta^2, \quad b_1 = \beta\eta^2, \quad b_0 = \eta^2\zeta, \tag{6.3}$$

which in turn can be solved and are equivalent to just the following relationship among the coefficients of (6.1)

$$b_3 b_2 b_1 = b_3^2 b_0 + b_1^2. \tag{6.4}$$

Now notice that the meaning of each such coefficient b_i of (6.1) is as follows. Let us denote the principal minors of order k of the Jacobian by $M_k(J)$. We have then $b_3 = -\mathrm{tr}(J)$, $b_2 = \sum M_2(J)$, $b_1 = -\sum M_3(J)$, $b_0 = \det(J)$, where the sum is meant over all possible principal minors of the given order. Now observe that the parameter e appears only in the element J_{44} with a negative sign. Alternatively one could consider the parameter c appearing only in J_{33} also with negative sign. The above condition (6.4) in view of the meaning of each b_i in terms of the elements of the Jacobian, is therefore a cubic equation in e,

$$b_3 b_2 b_1 - b_3^2 b_0 - b_1^2 \equiv \sum_{i=0}^{3} c_i e^i. \tag{6.5}$$

In order to ensure existence of a real positive root $e^\dagger$, we thus need that the signs of the constant term and of the coefficient of e^3 be opposite.

Explicitly, from (6.4) we have

$$\mathrm{tr}(J) \sum \mathrm{M}_2(J) \sum M_3(J) = (\mathrm{tr}(J))^2 \det(J) + (\sum M_3(J))^2, \tag{6.6}$$

from which we extract the highest order terms containing J_{44} obtaining

$$J_{44} \times J_{44}[J_{11} + J_{22} + J_{33}] \times J_{44}\{\sum M_2[J_{(1:3,1:3)}]\} = [J_{44}]^2 \times J_{44} \det[J_{(1:3,1:3)}],$$

where $M_2[J_{(1:3,1:3)}]$ denotes the principal minors of order two of the submatrix $J(1:3, 1:3)$ of the Jacobian, formed by its first three rows and columns, and $\det[J_{(1:3,1:3)}]$ is the corresponding determinant. Notice that we have excluded the consideration of the last term $(\sum M_3(J))^2$, since it gives only a contribution to the coefficient of J_{44}^2. The coefficient of J_{44}^3 is therefore

$$c_3 \equiv [J_{11} + J_{22} + J_{33}][\sum_i \tilde{M}_2] - \det[J_{(1:3,1:3)}]. \tag{6.7}$$

The term independent of e is instead

$$c_0 \equiv \sum_i M_2[J_{(1:3,1:3)}] \det[J_{(1:3,1:3)}] - [J_{11} + J_{22} + J_{33}][\sum_i (-1)^i \hat{M}_3(J_{i4})], \tag{6.8}$$

where $\hat{M}_3(J_{i4})$ represents the minor corresponding to the element J_{i4} in J. The condition for existence of $e^\dagger > 0$ for which (6.2) is true, is thus given by

$$c_0 c_3 < 0. \tag{6.9}$$

Then only the transversality condition still needs to be satisfied to obtain a Hopf bifurcation. The roots of (6.2) are in general of the form

$$\lambda_1(e) = \xi_1(e) + i\xi_2(e), \quad \lambda_2(e) = \xi_1(e) - i\xi_2(e), \quad \lambda_\pm(e) = \frac{1}{2}\left[-b_3 \pm \sqrt{b_3^2 - \frac{4}{b_1}b_0 b_3}\right] \tag{6.10}$$

Differentiate now the characteristic equation with respect to e, to obtain after some algebra

$$\gamma_{11}\xi_1' - \gamma_{12}\xi_2' = \gamma_{10}, \quad \gamma_{12}\xi_1' + \gamma_{12}\xi_2' = \gamma_{20}$$

where

$$\begin{aligned}
\gamma_{11} &= 4\xi_1^3 - 12\xi_1\xi_2^2 + 3\beta(\xi_1^2 - \xi_2^2) + 2(\eta^2 + \zeta)\xi_1 + \eta^2\beta \\
\gamma_{12} &= 12\xi_1^2\xi_2 - 4\xi_2^3 + 6\beta\xi_1\xi_2 + 2(\eta^2 + \zeta)\xi_2 \\
\gamma_{10} &= \beta'(3\xi_1\xi_2^2 - \xi_1^2) + [(\eta^2)' + \zeta'](\xi_2^2 - \xi_1^2) - \xi_1[(\eta^2)'\beta + (\eta^2)\beta'] - ((\eta^2)'\zeta + \eta^2\zeta') \\
\gamma_{20} &= \beta'(\xi_2^3 - 3\xi_1^2\xi_2) - \xi_1\xi_2((\eta^2)' + \zeta') - \xi_2((\eta^2)'\beta + \eta^2\beta').
\end{aligned}$$

Here the prime denotes derivative with respect to the parameter e. On solving for ξ_1' and ξ_2' the above system, we find

$$\xi_1' = \frac{\gamma_{10}\gamma_{11} + \gamma_{20}\gamma_{12}}{\gamma_{11}^2 + \gamma_{22}^2}, \quad \xi_2' = \frac{\gamma_{20}\gamma_{11} - \gamma_{10}\gamma_{12}}{\gamma_{11}^2 + \gamma_{22}^2}$$

and the transversality condition $\xi_1'(e^\dagger) \neq 0$, in terms of the original entries in the Jacobian matrix, becomes then

$$(d^\dagger + m_2^\dagger)(m_2^\dagger t^\dagger - m_3^\dagger)(t^\dagger)^4 + 2(m_3^\dagger)^4[(t^\dagger)^2 + (m_3^\dagger)^3] \neq 0 \tag{6.11}$$

where we used the shorthand notations

$$\begin{aligned}
m_2^\dagger &= \sum M_2[J_{(1:3,1:3)}(e^\dagger)], \quad m_3^\dagger = \sum M_3[J(e^\dagger)] \\
t^\dagger &= \mathrm{tr}[J(e^\dagger)] \qquad\quad d^\dagger = \det[J(e^\dagger)].
\end{aligned}$$

It appears then far from easy to perform a detailed study providing analytical conditions so that (6.11) is satisfied in terms of the original model parameters. We turned at this point to numerical simulations to show evidence that the Hopf bifurcation does arise and sustained oscillations are indeed possible. Figure 4 supports our statement, a Hopf bifurcation is found for this system, as the simulation reported in it shows indeed the sustained oscillations of all the model populations.

7. Spraying Effects

We investigate in this Section the results of insecticide spraying. We remark that in general the vineyard is assumed to be sprayed from planes flying not too high above the ground and aiming at the vineyards, but due to the wind effect the insecticide may land on the woods as well. Also the poison is meant to act on the insects and pests of the vineyards, but it may very well affect the spiders too. Letting t_i denote the instants in time when the spraying occurs, we thus obtain the modified model

$$\begin{aligned}
\dot{w} &= w\left[b\left(1-\frac{w}{W}\right)-\ell s_w\right]-h\left(1-q\right)\delta\left(t_i\right) \qquad (7.1)\\
\dot{v} &= v\left[a\left(1-\frac{v}{V}\right)-ks_v\right]-hq\delta\left(t_i\right)\\
\dot{s_w} &= s_w\left[-c+\tilde{\ell}w\left(1+\alpha\left(-\frac{V}{V+W}\right)\right)\right]+\frac{W}{V+W}\tilde{k}vs_v\alpha-K\left(1-q\right)\delta\left(t_i\right)\\
\dot{s_v} &= s_v\left[-e+\tilde{k}v\left(1+\alpha\left(-\frac{W}{V+W}\right)\right)\right]+\frac{V}{V+W}\tilde{\ell}ws_w\alpha-Kq\delta\left(t_i\right)
\end{aligned}$$

where q represents the fraction of insecticide falling on the vineyards, h and K represent its efficacy on insects and spiders respectively, $\delta\left(t\right)$ is the Dirac delta function,

$$\delta\left(t\right)=\begin{cases}1 & \text{for } t=t_i\\ 0 & \text{for } t\neq t_i\end{cases}.$$

The effect of the Dirac delta function is to suddenly push downward the solutions at the instants t_i, so that if the perturbation is large enough and if another basin of attraction of some other stable equilibrium exists, the effect of spraying may result in a move of the system toward this alternative equilibrium instead of letting the trajectories tend to the previous one.

8. Ecological consequences

The model we presented shows the following features. Among the equilibria which may be stable, $E^{(5)}$ contains no wood insects. Its occurrence leads then to loss of diversity and therefore is not to be desired. $E^{(4)}$ instead is a spider-free equilibrium, in our settings thus a very bad situation, since it leads to predator loss and survival only of possibly harmful insects. $E^{(6)}$ has instead no vineyard-living prey. Finally at $E^{*}\equiv E^{(7)}$ the whole ecosystem thrives, a plus from the environmental biodiversity point of view.

The stability of the equilibria $E^{(4)}$-$E^{(7)}$ is always conditional. While for $E^{(4)}$ it reduces to upper bounds on the woods and vineyard insects carrying capacities, for $E^{(5)}$ and $E^{(6)}$ we find instead that stability is ensured by keeping both spider populations at a sufficiently high level.

The ecological coexistence equilibrium $E^{*}\equiv E^{(7)}$ analyzed in Sections 5 and 6 shows a Hopf bifurcation, which is obtained also by numerical simulations, see Figure 4, the resulting oscillations being sustained in time for all the model populations.

The implications of the Hopf bifurcation are to be taken seriously into account, as they involve the sudden shift of an apparently stable equilibrium where the whole ecosystem coexists to fluctuating population values. If the latter become too large, due to for instance to some external unpredictable circumstances, such as fast climatic variations, resulting in a change of the spiders death rate, the large oscillations may hit the coordinate axes and lead to disappearance of the limit cycle. The ecosystem would then be seriously affected since at least one of its populations vanishes.

Finally the effect of spraying has also been simulated. Other that in adverse circumstances spraying may lead to environmental ecological damages, the main conclusion we can draw here is that a further investigation of the basins of attractions of each stable equilibria would be necessary in case the simulations were concerning a real application. Indeed the spraying effect changes suddenly the trajectories behavior, so that if they are moved to a different basin, the outcome of the dynamics may very well be much different than expected.

Several studies have confirmed that pesticide spraying induces an increase in the density of some pest populations. For instance, in [2, 10] it is found that phytophagous pests had economically important demographical outbreaks after treatments with pesticides. According to the authors, these outbreaks of pest populations after chemical treatment were induced as a result of reduction of predators, particularly spiders. Indeed, spiders seem to be more sensitive to pesticides compared with many phytophagous pests [7]; in consequence, the decrease in spider populations leads to a reduction in the predation pressure, thus favouring the outbreak of some pests.

Many studies all over the world have shown that the use of chemicals decreases the diversity and density of spiders. In [6] it is reported that the spider population in sprayed orchard was affected by pesticide treatments and was often eliminated altogether. However, the spiders reappeared in the orchard when the interval between the applications was long enough. Application of insecticides several times in the season or at high dosages usually destroys spider communities [6]. The same study showed a similar decrease in the specific diversity.

Much richer and much more complex computer models for the spider evolution in a heterogeneous landscape have been proposed in the literature, see [16–19, 21] for instance. Mainly, they are aimed at simulating the Danish farmland, by using a very extensive grid of cells each modelling a possibly different habitat and introducing in each patch a spider population composed of individuals in various states of development. The general algorithm is described in detail in [20]. These simulations aim at providing insights into the management of sustainable agricultural systems, in which natural predators constitute a major component of pest control. In particular the numerical experiments attempt at forecasting what are the consequences of varying the agricultural field sizes and at studying spatial heterogeneity, aiming at determining the various local conditions within a complex landscape structure. Meteorological and farming data are used for the dispersal model, which are in support also of our assumptions. Indeed under suitable good weather conditions, ballooning can disperse the spiders up to 30 km downwind in just a few hours, [16].

Our is rather an analytical, “global” model with much more contained goals, but a first step in the same direction. By combining indeed this approach with the results of [4], in future works we plan to investigate the potential that spiders offer to control the pests that affect the vineyards in Piemonte, the first wine producing region in the world.

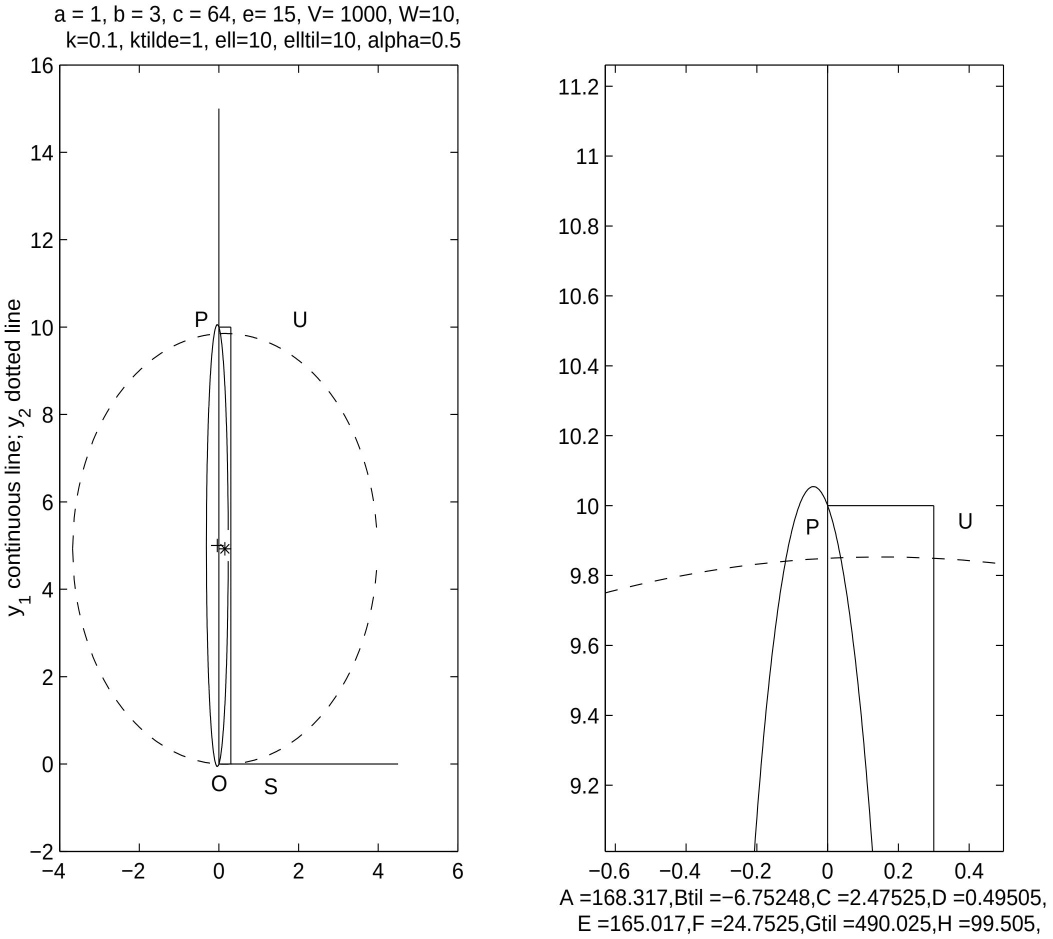

Figure 1: Case 2A) of Section 5: illustration of the feasible ellipses intersections. On the right a blowing up of a particular of the left picture.

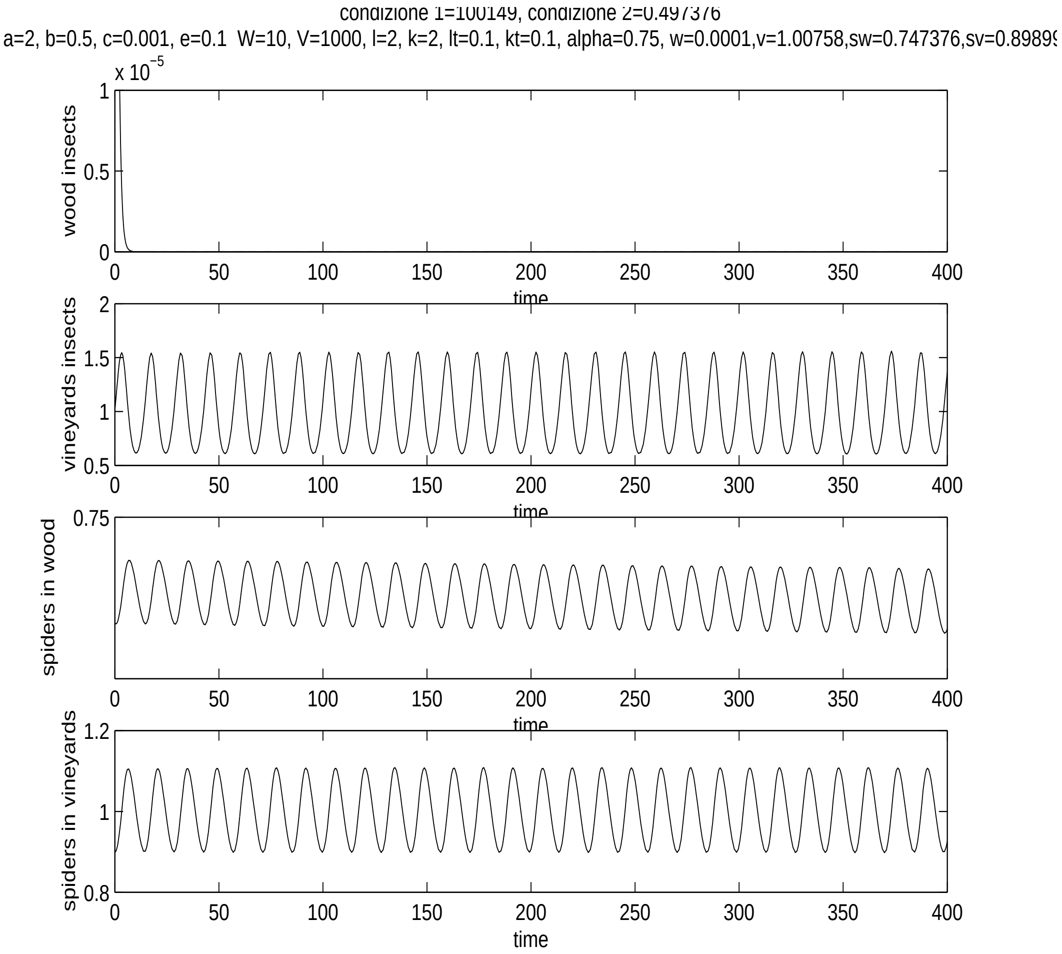

Figure 2: Stability conditions for $E^{(5)}$ are verified but we get an unstable behavior, in fact w vanishes and the other populations show sustained oscillations. Perhaps this indicates that the basin of attraction of equilibrium $E^{(5)}$ is extremely small.

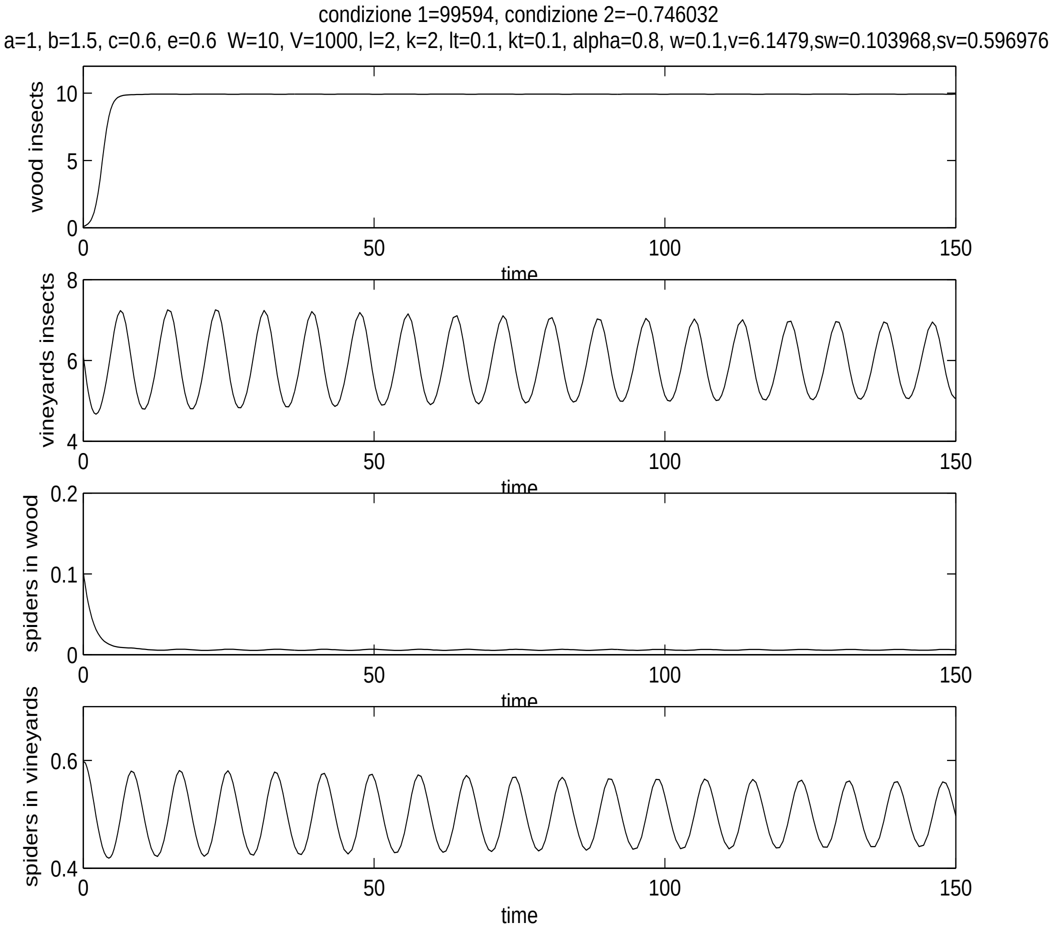

Figure 3: Instability of equilibrium $E^{(5)}$, initial conditions close to it, stability conditions not verified. Neutral cycles in a plane parallel to the s_v-v phase plane, wood insects rather attain their carrying capacity value.

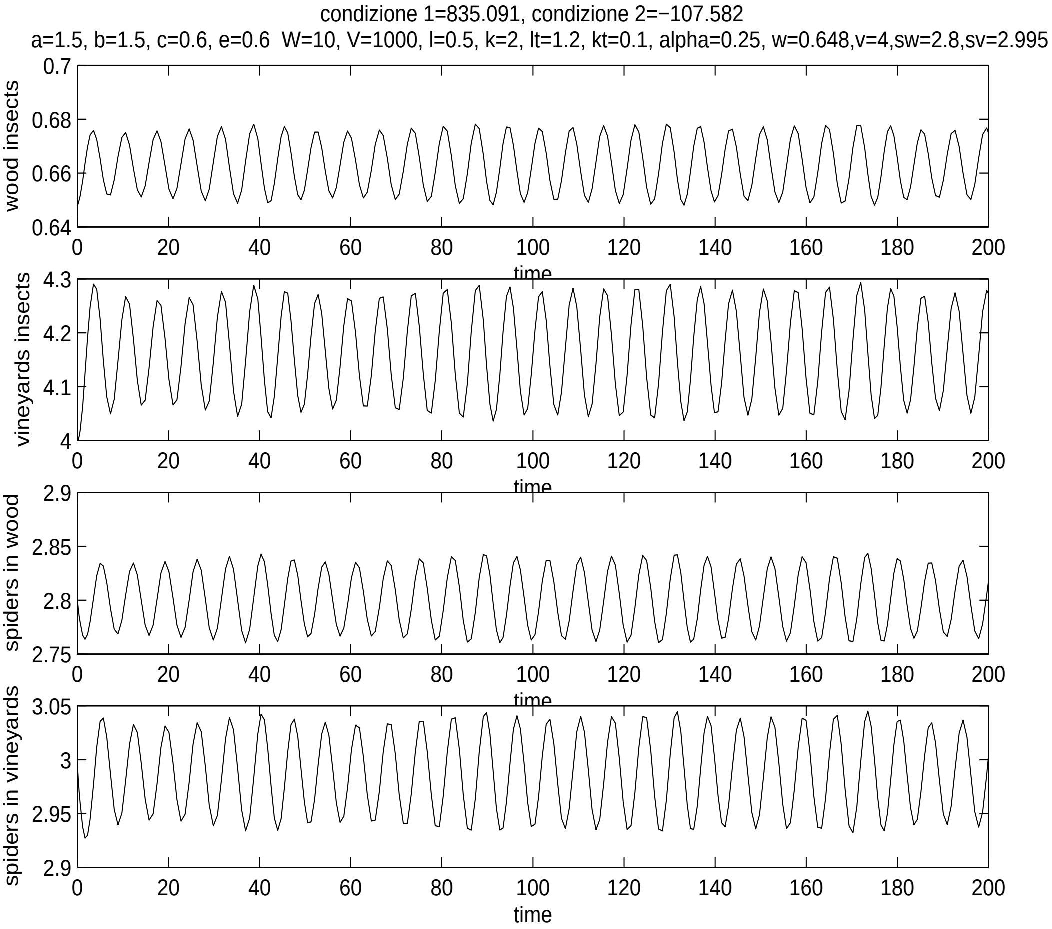

Figure 4: Sustained cycles for all populations

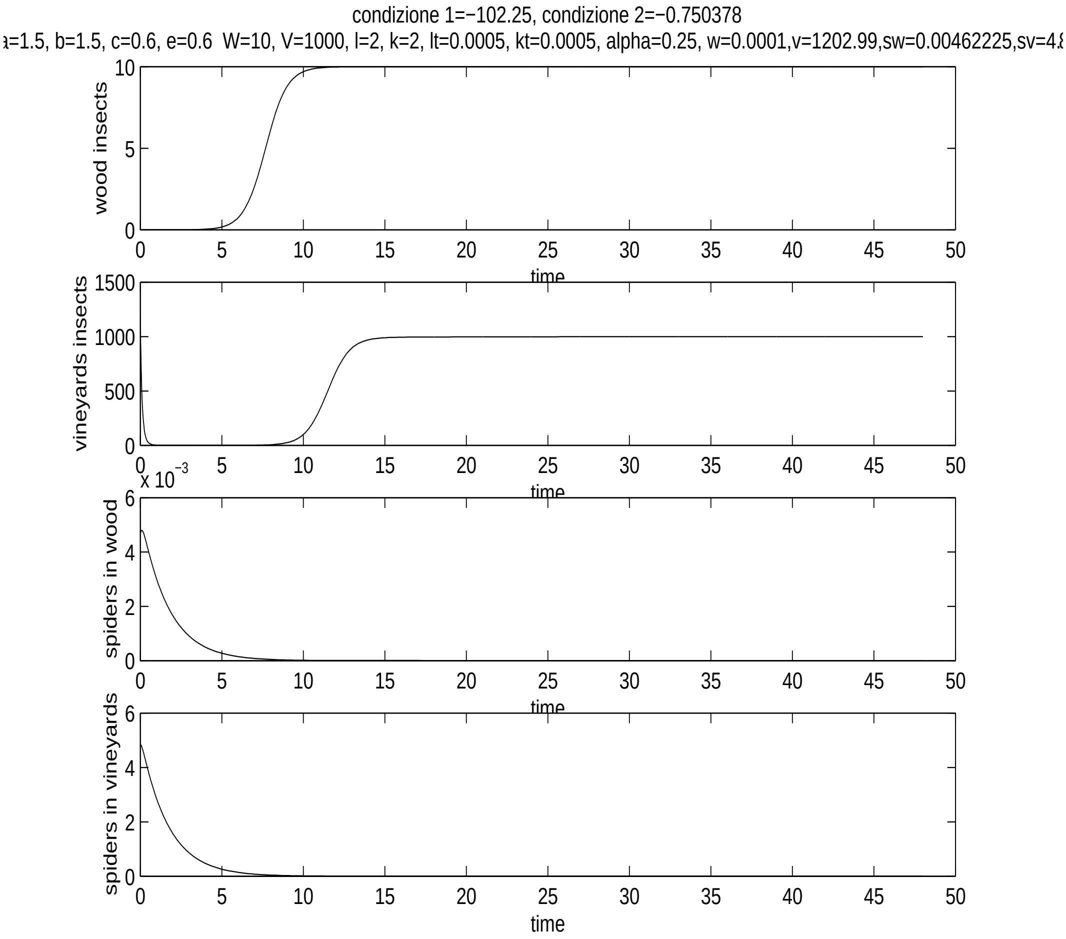

Figure 5: Reference simulation for the spraying effects of the next picture.

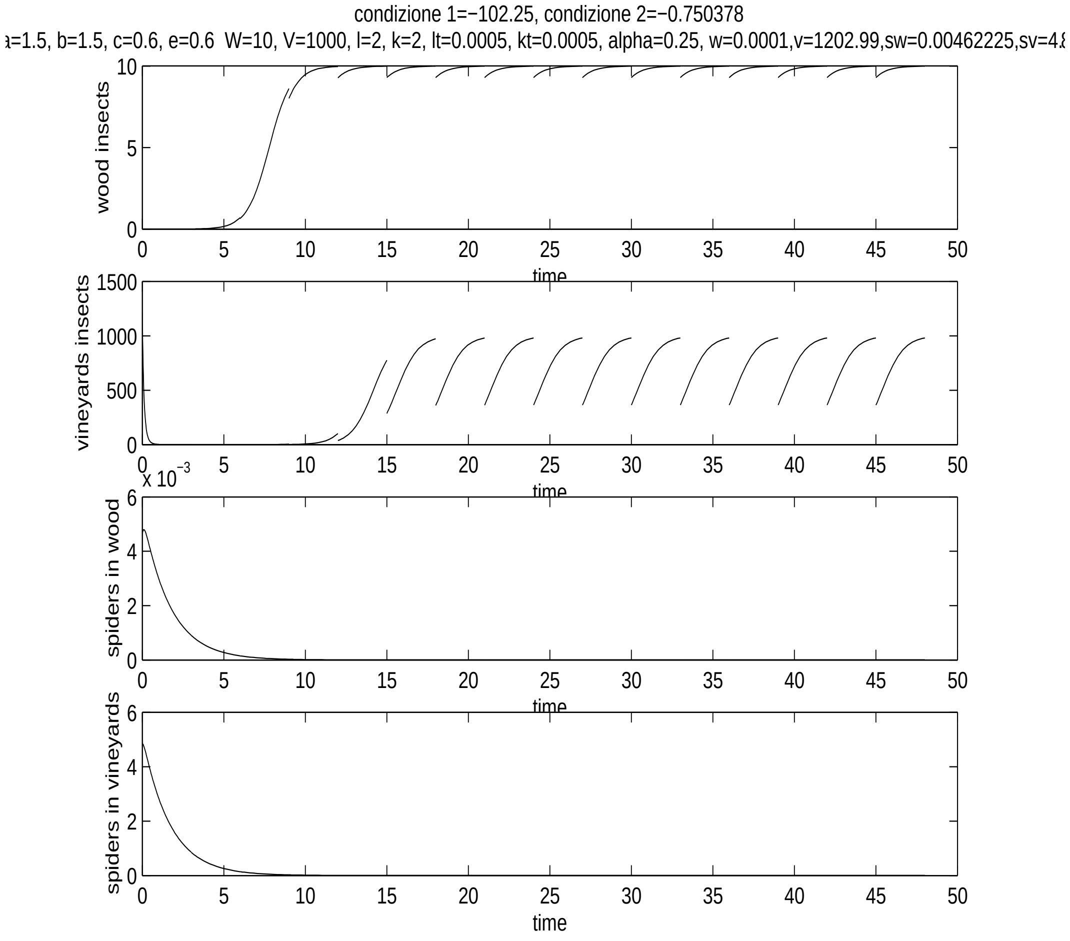

Figure 6: Spraying effects: the interspraying time is 3, a temporary decrease of the insects is obtained, but they will tend to the carrying capacities anyway in the long run.

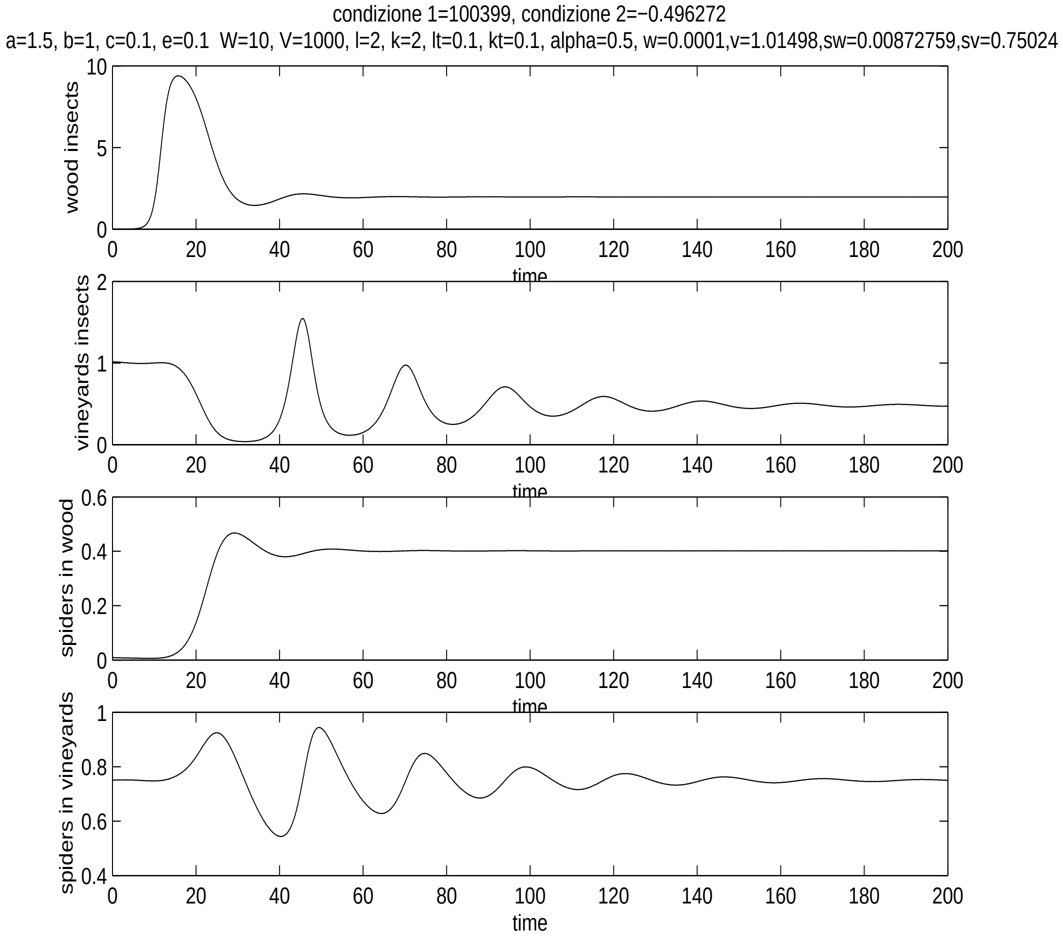

Figure 7: Coexistence equilibrium. It is also a reference simulation for the spraying effects of the next picture.

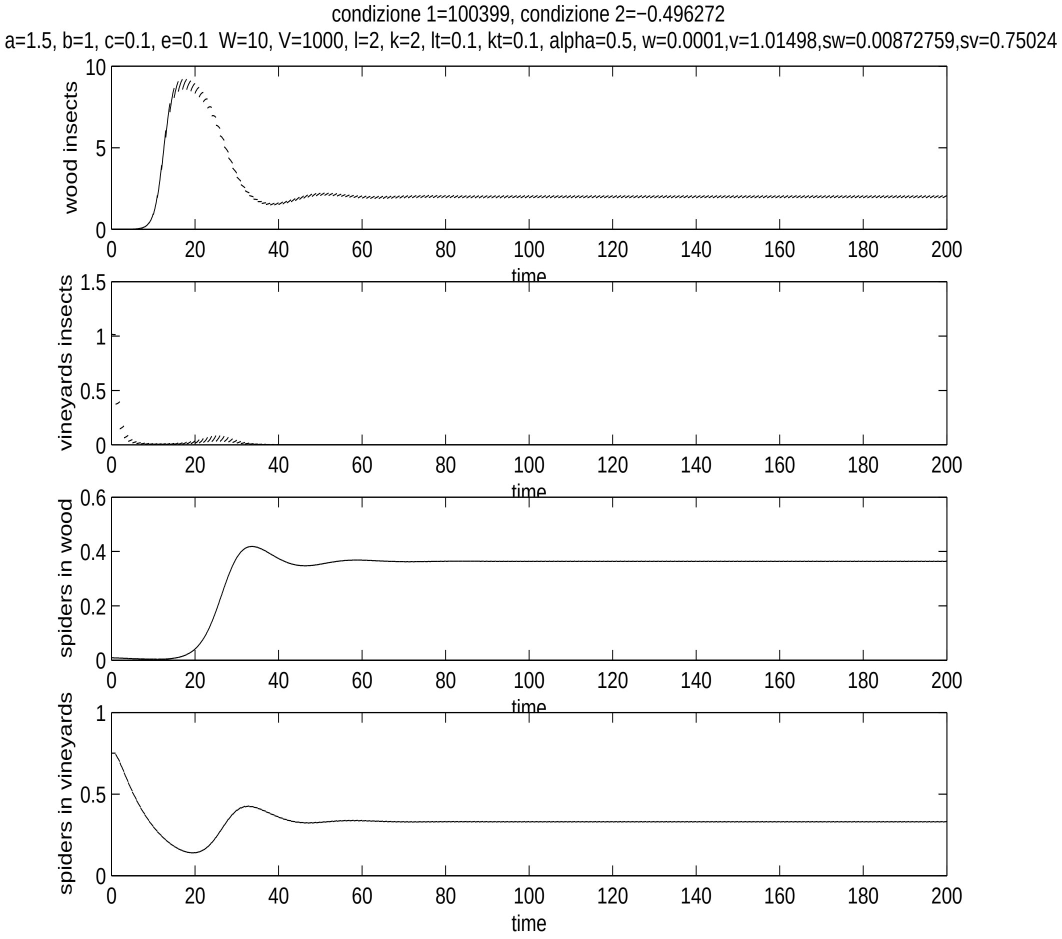

Figure 8: Here the spraying effects seem to wipe out the oscillations in the populations living in vineyards, thus affecting also the spiders. They survive, although harmed, while the spraying seems to control the vineyard insects. The interspraying time is 1.

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