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Spiders as biological controllers in the agroecosystem *

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Abstract

In this paper we propose a general model consisting of insects, pests and spiders interacting in an agroecosystem included in a typical homogeneous rural landscape, characterized by a continuous mosaic of cultivated land and a few small patches of grasslands and small woods bounding the fields. The model is general enough to show all the phenomena observed in the agroecosystem. The role of the spider population as a biological controller in the agroecosystem is particularly emphasized. Human intervention by means of pesticide spraying and its relationship with the biological pest controllers is also accounted for.

Keywords: predator-prey model; agroecosystem pest; spiders; ballooning; insecticide spraying, agroecosystems.

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1 Introduction

Spiders have commonly been considered as polyphagous predators [2]. For this reason it has been argued that spiders cannot be efficient in controlling pests [4]. However in China, for example, these invertebrate predators have been actively preserved in order to combat particular pests [24]. In addition it has been demonstrated in Israelian and European apple orchards that they are able to significantly decrease insect damage to harvests, [11, 12]. Marc and Canard, [13] redefined the role of spiders in the agroecosystems, specifying that taking into account their hunting strategies and location in the vegetation they can be regarded as specialist predators. As a consequence, not all species are useful against a particular pest, but preserving their diversity could be important for controlling different pests. Analysis of spider communities in vineyards [7] and in orchards [12] with regard to their different hunting strategies, their biological cycle and their localization in the environment, allows the definition of several functional groups. This is shown to have an effect on the kind of prey consumed. For example concerning tree-dwelling spiders living in orchards, nocturnal wandering spiders, like *Anyphaena accentuata* (Anyphaenidae), *Clubiona brevipes*, *C. corticalis* and *C. leucaspis* (Clubionidae) have been proved to be effective against non-flying Aphids and larvae of Lepidoptera; diurnal wandering species like *Ballus depressus* (Salticidae) against non-flying Aphids and Cicadellidae; ambush species like *Philodromus aureolus* (Philodromidae) and *Diaea dorsata* (Thomisidae) against Hymenoptera and Lepidoptera (adults and larvae). Webweavers have been proved to be effective against several species of potential pests. Examples in this sense are provided by sheet web species like Linyphiids against Cicadellidae, Diptera and Coleoptera, by orb web species like *Araneus diadematus*, *Araniella cucurbitina* and *Nuctenea umbratica* against winged aphids, Lepidoptera and small Hymenoptera [13]. Wandering spiders have been proved to play a very important role in controlling herbivore populations like Cicadellidae, Thysanoptera and Aphididae in agricultural fields [8].

In this paper we consider a general agroecosystem included in a typical homogeneous rural landscape. The land is characterized by a continuous mosaic of cultivated lands in which several small patches of grasslands and small woods bounding the fields are the only elements that enhance diversity. The context of Langa Astigiana, dominated by the vineyard agroecosystem or the context of the Piedmontese flatland nearby the town of Cuneo (NW- Italy),

dominated by fruit orchards, fits perfectly this situation. Arthropod communities (insects and spiders) living in the landscape are considered in the model with a distinction among the insects (pests) living and damaging the agroecosystems (for example vineyards or fruit orchards), and the insects living in the agroecosystems but not damaging the cultivations. We focus moreover on their general predators, namely the spiders, distinguished among wanderers (moving actively in the land mosaic), and webweavers (mostly sit-and-wait strategists). Finally, ballooning behaviour and its influence on population dynamics is duly accounted for in the model. Ballooning is a unique method of aeronautical dispersal adopted by spiders. In general terms it can be defined as a passive sailing through the air by means of silken threads, occurring in special weather conditions, especially when the air layer near the ground is unstable and when wind speed is not exceeding 3 m/s [22]. This method of dispersing explains the quick spiders recolonization of perturbed environments such as agroecosystems after pesticide application. Ballooning can be performed over long or short distances, from a few meters to several hundreds kilometers. It could be supposed that perturbations in agroecosystems should induce ballooning, [14]. Weymann et al. [23] confirmed that severe stress can increase ballooning to very high levels.

Mathematical modelling of the spider population in an agroecosystem has been considered in [5], where specifically a model for spider dispersal in a heterogeneous agricultural landscape is formulated and simulated. The findings demonstrate that the landscape heterogeneity plays a crucial role for survival and abundance of its populations. The inclusion of even a small amount of grasslands, treated as refugia, dramatically increases the spider population. Also the dispersal of the spiders through air transport and the effect of pesticides on the spider population are investigated.

The failures of the chemical method for the control of pests are well documented in the literature. Basically they are mainly due to their adverse effect on pests natural enemies, compounded by increasing development of resistance by pests to pesticides. Furthermore, their adverse effects on human health lead to the urgent need to develop new strategies in fighting pests. The achievement of complete control on pest populations using just their natural enemies represents an ideal goal. In general it represents the most effective single approach to pest management. The application of current ecological knowledge and technology has to be furthered in applied research, by means of modelling and field experiments, to solve the pest problem. The need of accurate simulations for the prediction of any long term effect of large

scale pesticide has been particularly addressed in [4] and [5].

In the present study we also explore an agroecosystem composed of different field types and investigate the role of spiders as bio-controllers in such landscape. Namely, we consider the woods nearby the fields as refugia for the spiders, especially at the times when the fields are sprayed with insecticide. A distinguishing feature of this model compared to [5] is avoidance of using the diffusion equation as basic model, which is mathematically more complex to handle than a simple dynamical system. Nevertheless, in spite of not explicitly building space in the model, we are still able to include in our description the dispersal of the spiders by ballooning. Another feature of the present study consists in partitioning the prey among insects, harmless from the farmer's viewpoint, living in both woods and cultivated land, and pests, whose habitat is only the latter, harmful to crops. As in [5], we also take into account the human intervention through pesticides spraying.

In this paper we describe the development of a mathematical model for the population dynamics of a natural biological controller, namely the spiders, in a rural landscape characterized by a very low habitat diversity. This model is used to examine the crucial role of spiders in controlling pest outbreaks, taking into account the adverse effect of pesticides and the role of spider ballooning as a key factor for spider population survival and related biological control. As such then, this model merges into a larger one several other simpler models, [3, 19, 20, 21], which we investigated separately. The aim is the preparation of a more comprehensive simulation tool.

In [3] two prey, insects in the woods and parasites in the vineyards are considered with wanderer spiders as their predators. The model is analyzed under possible environmental fluctuations.

A four dimensional predator-prey model is studied in [19], with insects living in woods and vineyards as the prey and the webweavers living in the woods and the vineyards as their predator populations. The system accounts for ballooning, this transport phenomenon being modeled without explicitly using space in the governing equations, a feature we retain in the present model as mentioned.

The three dimensional model consisting of prey in open fields, parasites in vineyards and the wanderer spiders moving among these environments is instead considered in [20]. In [21] again a similar model is investigated, in which a satiation effect in the spiders diet is incorporated. Limit cycles are observed for a certain range of parameter values.

Here we integrate all these models into a single larger one which takes into

account the pests, the insects in the woods and vineyards distinguished as two separate populations, the webweavers in the woods and the vineyards, again as different populations, and the wanderer spiders. We study the combined effect of all these interactions, aiming at a more comprehensive description of the ecological situation to reveal the role of spiders as biological controllers in such a complex ecosystem. Human interference is also analyzed, looking at the effect of spraying on these populations. In the discussion we elaborately compare the results of the present model with those of the previously formulated models.

2 The general model

As mentioned in the Introduction, we consider a general agroecosystem in which there are several players. The landscape is formed by two environments, a generally uniform one of cultivated land, and a marginal one constituted by green grass patches and small woods bounding the fields. We consider the insects whose habitat is mainly the latter, those who live in the cultivated land and specifically identify the pests of the cultivations as a class of their own. We moreover focus on their general predators, namely the spiders, distinguished among wanderers, moving freely in search of food between the two landscapes, and the statical webweavers, living essentially in the place where they build their nests.

To be more specific, then let $I_a(t)$ denote the insect population living in the agroecosystems and $I_w(t)$ denote the insect population living in the woods. Let $S_a(t)$ and $S_w(t)$ denote the webweaver spider populations living in the agroecosystems and woods respectively. $W(t)$ denotes the wanderer spider populations which can live and move both in the agroecosystems and woods. Finally, let the harvest pest population be denoted by $P(t)$. We distinguish the insects living in the agroecosystems from the pests, since the latter are considered a nuisance to the culture, while the former are an alternative source of food for the spiders. From the farmer's viewpoint, it is the pests that need to be controlled.

The assumptions leading to the six differential equations below (1) are as follows: the first equation models insects living in the agroecosystems, reproducing according to logistic growth, with carrying capacity K_1 . The function F_1 thus contains a first term denoting logistic growth, and two additional terms with rates α and a_1 , due to predation by webweavers present

in the cultivated land and wanderer spiders. The second equation models insects living in the woods, also reproducing according to logistic growth, first term of F_2 , predated again by webweavers and wanderer spiders, accounted for by the last two terms, at rates respectively β and a_2 . The carrying capacity in this case is instead denoted by K_2 , and assumed to be much smaller than K_1 , in view of the large extension of their environment with respect to the wood, as is the case in the typical landscape of the Langa Astigiana. The third equation models the pest population, which is again growing in logistic fashion. Here it is assumed that pests are present only in the agroecosystem, as they are particularly harmful to this culture. Let the pests agroecosystems carrying capacity be denoted by L and γ and a_3 denote the predation rates of the webweaver and wandering spiders. The function F_3 contains again a logistic term and additional predation terms of the relevant spiders populations. The last three equations model the webweaver spider populations living in the agroecosystem and the wood respectively and lastly the wandering spiders. The two ecosystems in this context could be considered as separate entities, as the web spiders tend to live in the same place and we partitioned the insects according to the environment in which they live, if it were not for two particularities. The first is that wandering spiders freely move across the two habitats in search for food. The second one is a phenomenon occurring to the young spiders. Namely, they release a thread in order to be carried away by the wind. This ballooning effect is also accounted for in the two equations modelling the growth of the web-spiders population. A fraction $0 < \theta < 1$ of the newborns is transported by the wind from its location and lands in the neighboring places. Thus it may remain within the agroecosystem or move to the woods and vice versa. The probability of changing the habitat is assumed to be proportional to the surface of the two patches [19], which in turn is measured by their respective carrying capacities. This migration effect is expressed by the last two terms of F_4 and F_5 in (1), while the first three terms respectively express the gain of predation on insects and prey, when the latter can occur, with conversion rates α' and γ' of agroecosystem webweavers on the insects in the agroecosystems and on the pest, and spiders mortalities δ_a and δ_w respectively. We also let β' denote the conversion rate of wood webweavers on the insects in the woods. Note that the transport effect of the wind is instead clearly the same for both spider groups, as there is no essential reason for assuming it to be different in the woods than on open land. Note that the wind transport effect on insects is disregarded, as we assume that they are able to fly and therefore willingly

move toward the environment place that they prefer, i.e. eventually return to it, [19]. Finally, in the last equation we consider the wandering spiders, which are assumed to move and live anywhere among the two environments. Thus they feed on both the agroecosystem and wood insects with a conversion rate a'_1 and a'_2 respectively, first two terms of F_6 . The last terms indicate predation on the pests with conversion rate a'_3 and natural death rate of the wandering spiders expressed by μ . Finally, note that all the parameters are assumed to be nonnegative.

With the above assumptions, letting $\mathbf{u} = (I_a, I_w, P, S_a, S_w, W)^T$ denote the population vector, we can write the model in compact form as $\dot{\mathbf{u}} = \mathbf{F}(\mathbf{u})$ and explicitly as follows,

$$\begin{aligned}
\frac{dI_a}{dt} &= I_a \left[r_1 \left(1 - \frac{I_a}{K_1} \right) - \alpha S_a - a_1 W \right] \equiv F_1(\mathbf{u}), \\
\frac{dI_w}{dt} &= I_w \left[r_2 \left(1 - \frac{I_w}{K_2} \right) - \beta S_w - a_2 W \right] \equiv F_2(\mathbf{u}), \\
\frac{dP}{dt} &= P \left[q \left(1 - \frac{P}{L} \right) - \gamma S_a - a_3 W \right] \equiv F_3(\mathbf{u}), \\
\frac{dS_a}{dt} &= S_a \left[\alpha' I_a + \gamma' P - \delta_a - \theta K_2 \frac{\alpha' I_a + \gamma' P}{K_1 + K_2} \right] + \frac{\theta K_1 \beta' S_w I_w}{K_1 + K_2} \equiv F_4(\mathbf{u}), \\
\frac{dS_w}{dt} &= S_w \left[\beta' I_w - \delta_w - \beta' I_w \frac{\theta K_1}{K_1 + K_2} \right] + S_a \theta K_2 \frac{\alpha' I_a + \gamma' P}{K_1 + K_2} \equiv F_5(\mathbf{u}), \\
\frac{dW}{dt} &= W [a'_1 I_a + a'_2 I_w + a'_3 P - \mu] \equiv F_6(\mathbf{u}).
\end{aligned} \tag{1}$$

Here for $i = 1, 2, 3$ we assume that

$$K_1 \gg K_2, \quad \alpha \geq \alpha', \quad \beta \geq \beta', \quad \gamma \geq \gamma', \quad a_i \geq a'_i.$$

3 Some analytical results

3.1 Boundedness of the trajectories

In order to begin to investigate the system behavior, let us define an auxiliary variable which can be termed the environment total population

$$Z = I_a + I_w + P + S_a + S_w + W. \tag{2}$$

The time-derivative of (2) along the solutions of (1) is

$$\begin{aligned} \frac{dZ}{dt} = & r_1 I_a \left(1 - \frac{I_a}{K_1}\right) - \alpha S_a I_a - a_1 W I_a + r_2 I_w \left(1 - \frac{I_w}{K_2}\right) - \beta S_w I_w \\ & - a_2 W I_w + qP \left(1 - \frac{P}{L}\right) - \gamma S_a P - a_3 W P + \alpha' I_a S_a + \gamma' P S_a \\ & - \delta_a S_a + \beta' I_w S_w - \delta_w S_w + a'_1 I_a W + a'_2 I_w W + a'_3 P W - \mu W. \end{aligned}$$

Taking $\eta > 0$ we get,

$$\begin{aligned} \frac{dZ}{dt} + \eta Z \leq & r_1 I_a \left(1 - \frac{I_a}{K_1}\right) + r_2 I_w \left(1 - \frac{I_w}{K_2}\right) + qP \left(1 - \frac{P}{L}\right) \\ & - \delta_a S_a - \delta_w S_w - \mu W + \eta (I_a + I_w + P + S_a + S_w + W). \end{aligned}$$

Now if we choose $\eta \leq \min(\delta_a, \delta_w, \mu)$, then

$$\frac{dZ}{dt} + \eta Z \leq \frac{K_1(r_1 + \eta)^2}{4r_1} + \frac{K_2(r_2 + \eta)^2}{4r_2} + \frac{L(q + \eta)^2}{4q},$$

where the quantities on the right hand side represent respectively the maximum values of the functions

$$\eta I_a + r_1 I_a \left(1 - \frac{I_a}{K_1}\right), \quad \eta I_w + r_2 I_w \left(1 - \frac{I_w}{K_2}\right), \quad \eta P + qP \left(1 - \frac{P}{L}\right).$$

Finally, the right-hand side of the above expression is thus bounded by a suitable constant $\ell > 0$, so that

$$\frac{dZ}{dt} + \eta Z \leq \ell.$$

From this differential inequality we obtain

$$\begin{aligned} 0 < Z(I_a(t), I_w(t), P(t), S_a(t), S_w(t), W(t)) &< \frac{\ell}{\eta}(1 - e^{-\eta t}) \\ &+ Z(I_a(0), I_w(0), P(0), S_a(0), S_w(0), W(0))e^{-\eta t}. \end{aligned}$$

Thus as $t \rightarrow \infty$, we have $0 < Z < \frac{\ell}{\eta}$. Hence, all the solutions of (1) with initial values in $\mathbf{R}_{0,+}^6$ are bounded in $\mathbf{R}_{0,+}^6$. This result is not surprising as it constitutes a rather general feature of biological models.

3.2 Equilibria and their stability

Before analyzing the system's equilibrium points, we first write down the general structure of the Jacobian of the system (1) at an arbitrary point $(I_a, I_w, P, S_a, S_w, W)$.

$$J \equiv \begin{pmatrix} J_{11} & 0 & 0 & -\alpha I_a & 0 & -a_1 I_a \\ 0 & J_{22} & 0 & 0 & -\beta I_w & -a_2 I_w \\ 0 & 0 & J_{33} & -\gamma P & 0 & -a_3 P \\ \alpha' S_a D_2 & A_2 S_w & \gamma' S_a D_2 & J_{44} & A_2 I_w & 0 \\ A_1 S_a & \beta' S_w D_1 & A_3 S_a & A_1 I_a + A_3 P & J_{55} & 0 \\ a'_1 W & a'_2 W & a'_3 W & 0 & 0 & J_{66} \end{pmatrix}, \quad (3)$$

where $J_{11} = r_1 - \frac{2r_1 I_a}{K_1} - \alpha S_a - a_1 W$, $J_{22} = r_2 - \frac{2r_2 I_w}{K_2} - \beta S_w - a_2 W$, $J_{33} = q - \frac{2qP}{L} - \gamma S_a - a_3 W$, $J_{44} = (\alpha' I_a + \gamma' P) D_2 - \delta_a$, $J_{55} = \beta' I_w D_1 - \delta_w$, $J_{66} = a'_1 I_a + a'_2 I_w + a'_3 P - \mu$, and

$$D_1 = \left(1 - \theta \frac{K_1}{K_1 + K_2}\right) > 0, \quad D_2 = \left(1 - \theta \frac{K_2}{K_1 + K_2}\right) > 0,$$

$$A_1 = \theta \alpha' \frac{K_2}{K_1 + K_2}, \quad A_2 = \theta \beta' \frac{K_1}{K_1 + K_2}, \quad A_3 = \theta \gamma' \frac{K_2}{K_1 + K_2}.$$

Our first result shows that for the system (1), total extinction is not possible. Indeed the eigenvalues of the Jacobian (3) at the origin are r_1 , r_2 , q , $-\delta_a$, $-\delta_w$, $-\mu$, so that the origin is always an unstable equilibrium.

There are a few other boundary equilibria, where one or more populations are extinct. They in general share the same stability property of the origin. More specifically, all the following equilibria are unstable, as the Jacobian evaluated at $(K_1, 0, 0, 0, 0, 0)$, $(0, K_2, 0, 0, 0, 0)$, $(0, 0, L, 0, 0, 0)$, has two positive eigenvalues, while evaluated at $(K_1, K_2, 0, 0, 0, 0)$, $(K_1, 0, L, 0, 0, 0)$, $(0, K_2, L, 0, 0, 0)$ has one positive eigenvalue. Thus all above equilibria must be disregarded, as the system can never approach them.

Instead the equilibrium point $(K_1, K_2, L, 0, 0, 0)$ is conditionally stable,

since its Jacobian (3) reduces to

$$J_1 \equiv \begin{pmatrix} -r_1 & 0 & 0 & -\alpha K_1 & 0 & -a_1 K_1 \\ 0 & -r_2 & 0 & 0 & -\beta K_2 & -a_2 K_2 \\ 0 & 0 & -q & -\gamma K_3 & 0 & -a_3 K_3 \\ 0 & 0 & 0 & (\alpha' K_1 + \gamma' L) D_2 - \delta_a & A_2 K_2 & 0 \\ 0 & 0 & 0 & A_1 K_1 + A_3 L & \beta' K_2 D_1 - \delta_w & 0 \\ 0 & 0 & 0 & 0 & 0 & \bar{J}_{66} \end{pmatrix}, \quad (4)$$

with $\bar{J}_{66} = a'_1 K_1 + a'_2 K_2 + a'_3 L - \mu$. The eigenvalues of (4) are $-r_1$, $-r_2$, $-q$, \bar{J}_{66} and the roots of the quadratic equation,

$$\lambda^2 - \{(\alpha' K_1 + \gamma' L) D_2 + \beta' K_2 D_1 - \delta_a - \delta_w\} \lambda + (\alpha' K_1 + \gamma' L) \beta' K_2 D_1 D_2 + \delta_a \delta_w - (\alpha' K_1 + \gamma' L) D_2 \delta_w - \beta' K_2 D_1 \delta_a - A_1 A_2 K_1 K_2 - A_2 A_3 K_2 L = 0. \quad (5)$$

From Descarte's rule of sign equation (5) has roots with negative real parts if the following conditions hold,

$$\begin{aligned} (\alpha' K_1 + \gamma' L) D_2 + \beta' K_2 D_1 &< \delta_a + \delta_w, & (6) \\ (\alpha' K_1 + \gamma' L) \beta' K_2 D_1 D_2 + \delta_a \delta_w &> (\alpha' K_1 + \gamma' L) D_2 \delta_w + \beta' K_2 D_1 \delta_a \\ &+ A_1 A_2 K_1 K_2 + A_2 A_3 K_2 L. \end{aligned}$$

Thus, the equilibrium $(K_1, K_2, L, 0, 0, 0)$ is locally asymptotically stable if $\mu > a'_1 K_1 + a'_2 K_2 + a'_3 L$ and the conditions (6) are satisfied.

In such case the spiders disappear from the environment, an undesirable result, considering their potential role in controlling the pest.

Remark 1. Note that if the death rates of the spider populations are above a certain critical value then the insect populations and the pest population reach their carrying capacity, while the spider population is washed away from the system. Thus to prevent the outbreak of the pest population and the disappearance of the spider population, the death rates of the spider populations must be kept below a certain critical value. In this context spraying could have adverse effects on the spiders as well, and can thus negatively affect the system, raising the spiders mortality.

The pest-free equilibrium point is $((I_{a_2}, I_{w_2}, 0, S_{a_2}, S_{w_2}, W_2)$. Its Jacobian

(3) becomes

$$J_2 \equiv \begin{pmatrix} -\frac{r_1 I_{a_2}}{K_1} & 0 & 0 & -\alpha I_{a_2} & 0 & -a_1 I_{a_2} \\ 0 & -\frac{r_2 I_{w_2}}{K_2} & 0 & 0 & -\beta I_{w_2} & -a_2 I_{w_2} \\ 0 & 0 & \widetilde{J}_{33} & 0 & 0 & 0 \\ \alpha' S_{a_2} D_2 & A_2 S_{w_2} & \gamma' S_{a_2} D_2 & \widetilde{J}_{44} & A_2 I_{w_2} & 0 \\ A_1 S_{a_2} & \beta' S_{w_2} D_1 & A_3 S_{a_2} & A_1 I_{a_2} & \widetilde{J}_{55} & 0 \\ a'_1 W_2 & a'_2 W_2 & a'_3 W_2 & 0 & 0 & \widetilde{J}_{66} \end{pmatrix}, \quad (7)$$

with $\widetilde{J}_{33} = q - \gamma S_{a_2} - a_3 W_2$, $\widetilde{J}_{44} = \alpha' I_{a_2} D_2 - \delta_a$, $\widetilde{J}_{55} = \beta' I_{w_2} D_1 - \delta_w$, $\widetilde{J}_{66} = a'_1 I_{a_2} + a'_2 I_{w_2} - \mu$.

The coexistence equilibrium $(I_a^*, I_w^*, P^*, S_a^*, S_w^*, W^*)$ at which the whole ecosystem thrives has the following Jacobian, obtained again from some simplifications of (3)

$$J_3 \equiv \begin{pmatrix} -\frac{r_1 I_a^*}{K_1} & 0 & 0 & -\alpha I_a^* & 0 & -a_1 I_a^* \\ 0 & -\frac{r_2 I_w^*}{K_2} & 0 & 0 & -\beta I_w^* & -a_2 I_w^* \\ 0 & 0 & -\frac{q P^*}{L} & -\gamma P^* & 0 & -a_3 P^* \\ \alpha' D_2 S_a^* & A_2 S_w^* & \gamma' D_2 S_a^* & -B_1 S_w^* & B_1 & 0 \\ A_1 S_a^* & \beta' D_1 S_w^* & A_3 S_a^* & B_2 & -B_2 S_a^* & 0 \\ a'_1 W^* & a'_2 W^* & a'_3 W^* & 0 & 0 & 0 \end{pmatrix}, \quad (8)$$

where

$$B_1 = A_2 I_w^*, \quad B_2 = A_1 I_a^* + A_3 P^*.$$

We attempt to localize the eigenvalues of these matrices using the Bauer-Fike theorem, see [1] p. 592. Considering the former, one eigenvalue comes from \widetilde{J}_{33} . The remaining 5×5 matrix \widehat{J}_2 is then split via $\widehat{J}_2 = M + U$ where M and U respectively contain the strict lower and upper triangular parts of \widehat{J}_2 , and where the diagonal of M has the components $-\frac{r_1 I_{a_2}}{K_1}$, $-\frac{r_2 I_{w_2}}{K_2}$, $-\delta_a$, $-\delta_w$, $-\mu$. If λ denotes a generic eigenvalue of \widehat{J}_2 and λ_j is the closest eigenvalue of M , we thus obtain in some matrix norm the estimate

$$|\lambda - \lambda_j| \leq \|P\| \|P^{-1}\| \|U\| \equiv \sigma,$$

where P is the matrix of the eigenvectors of M . Since $\lambda_j < 0$ for all j by construction, it follows $\lambda \leq \sigma + \lambda_j$, so that by requiring

$$\min\left\{\frac{r_1 I_{a_2}}{K_1}, \frac{r_2 I_{w_2}}{K_2}, \delta_a, \delta_w, \mu\right\} > \sigma \quad (9)$$

we find $\lambda < 0$ so that stability of the pest-free equilibrium would be guaranteed. The expression of σ is very complicated, and difficult to examine any further. However some biological interpretation can nevertheless be obtained, as (9) states that in order to achieve stability, “large enough” mortalities would be necessary, in addition to the requirement of the explicit eigenvalue to be negative, i.e. a “low enough” pest birthrate, namely

$$q < \gamma S_{a_2} + a_3 W_2. \quad (10)$$

Note that similar, perhaps cruder, estimates could be obtained also via the Gershgorin theorem, [1] p. 588, but leading anyway to conclusions that do not differ too much from the above ones.

Remark 2. We stress the fact that from the condition (10), to render the system pest-free it is necessary to keep the specific growth rate of the pest population below a certain critical value, although by itself this is certainly not sufficient, as also all the other eigenvalues would need to have negative real parts. If q is large enough instead, the pest-free equilibrium becomes unstable, i.e. it will never be possible to eliminate the pests from the system while at the same time preserving the rest of the ecosystem.

For the interior equilibrium the analysis is more difficult, as explicit eigenvalues do not exist and since $J_{66} = 0$. A similar splitting as above can be used, where now the matrices M and U will be 6×6 . The diagonal of M now contains the elements $-\frac{r_1 I_{a_2}}{K_1}$, $-\frac{r_2 I_{w_2}}{K_2}$, $-\frac{q P^*}{L}$, $-B_1 S_w^*$, $-B_2 S_a^*$, $-H$, for some $H > 0$ and $U_{6,6} = H$. This constant will now appear also in some components of P and P^{-1} and linearly in U . We do not report these expressions in view of their complexity. Thus σ will depend on H . By choosing a suitable matrix norm it might be possible to make $\|P\|$ and $\|P^{-1}\|$ independent of H . Then, taking H small, in the norm of U it will be dominated by other components, so that σ will finally not depend on H . Then the previous estimates for the eigenvalues of J_2 would apply also to this case, leading to very similar conclusions.

Remark 3. These considerations seem to indicate thus that high mortalities apparently are needed to make these equilibria stable, together with large B_1 , B_2 and in turn of A_1 , A_2 , A_3 . The latter can simultaneously be achieved by a large θ , so that a high rate ballooning will also help the stability of the coexistence equilibrium.

However, as seen, to derive more precise analytic conclusions on the stability from (7) and (8) for both equilibria is in general very difficult. We therefore will further investigate their stability numerically.

4 Numerical simulations

With the realistic set of parameter values given in Table 1, in Fig 1 the system is observed to be stable around the coexisting steady state

$$E^* = (11.24, 19.32, 13.6, 78.64, 2.97, 118.2).$$

The main objective of the present study is to make the system free from the pest population. It is observed analytically that the death rates play an important role for the extinction thresholds. Halley et al. [5] observed that high mobility of spiders allows them to escape temporary lethal events by dispersing into refugia. So, in numerical simulations the focus will also be on these two factors, i.e, spider dispersal through ballooning and the presence of woods, on the dynamics of our system. For this, the parameters like μ , the death rate of the wanderers, θ the portion of webweaver that disperse through air, and K_2 , the carrying capacity for the insects living in the woods, are varied, keeping the other parameters fixed as given in Table 1. Decreasing μ to 0.05, with other parameter values fixed, it is observed that the pest population is washed away from the system, see Fig. 2. Thus decrease in the death rate of the wanderer spiders makes the system pest-free, a remarkable consequence. Next decreasing the death rates of the webweavers, it is observed that there is a decrease in the pest population, but it remains in the system (result not reported here). Thus, in conclusion wanderers are more effective in making the system pest-free than the webweavers. The result is very realistic specially if the pest are represented by ground insects, unable to fly.

With $\theta = 0$, retaining the other parameters fixed, i.e., in the absence of the ballooning phenomenon it is observed that the webweavers living in the woods disappear from the ecosystem, Fig. 3. Moreover comparing the values obtained for $\theta = 0$ with the values at E^* , there is an increase in the webweavers living in the agroecosystem (83.32 kg ha^{-1}) but there is also an increase in the pest population (14.6 kg ha^{-1}). Thus ballooning helps in maintaining the population of the webweavers living in the woods, which in turn helps in controlling the pest population. Thus the migration of the newborns by external means plays an important role in the coexistence of all the species and helps spiders to act as a bio-controller.

Finally, increasing the value of K_2 to 70, with other parameter values fixed, the system becomes pest-free, see Fig. 4. Thus we observe that the woods play an important role in maintaining the stability of the ecosystem,

even when the growth rate of the pest population increases. Thus our result supports the observation of Halley et al. [5], that the dispersal of spiders and the presence of woods plays a crucial role in the dynamics of the system.

Note that by allowing the parameter values to range in wider intervals, perhaps outside those observed in field measurements, namely

$$\begin{aligned} r_1 = 1.417, \quad K_1 = 700, \quad \alpha = 0.526, \quad a_1 = 0.03, \quad r_2 = 1, \quad K_2 = 1.35, \\ \beta = 0.65, \quad a_2 = 0.1, \quad q = 1.2, \quad L = 300, \quad \gamma = 0.4, \quad a_3 = 0.05, \\ \alpha' = 0.5, \quad \gamma' = 0.38, \quad \delta_a = 0.07, \quad \beta' = 0.6, \quad \delta_w = 0.3, \quad a'_1 = 0.02, \\ a'_2 = 0.09, \quad a'_3 = 0.03, \quad \mu = 0.07, \quad \theta = 0.35. \end{aligned}$$

and taking as initial value $(0.0519, 0.7318, 0.0448, 2.6895, 0.0092, 4.5118)$, we observe bifurcations of the coexistence equilibrium, see Fig. 7.

5 Spraying effect

The spray of insecticide is here modelled by a mortality-like function, active at particular instants in time, but whose effects last in time. Let

$$\psi(t_i) = \begin{cases} 0, & t_i > t \\ e^{-\rho(t-t_i)}, & t_i \leq t, \end{cases}$$

$i = 1, 2, \dots, N$, be the spraying instants.

Then model (1) gets modified as follows

$$\begin{aligned} \frac{dI_a}{dt} &= F_1 - nu \sum_{i=1}^N \psi(t_i), & \frac{dI_w}{dt} &= F_2 - n(1-u) \sum_{i=1}^N \psi(t_i), & (11) \\ \frac{dP}{dt} &= F_3 - Nu \sum_{i=1}^N \psi(t_i), & \frac{dS_a}{dt} &= F_4 - mu \sum_{i=1}^N \psi(t_i), \\ \frac{dS_w}{dt} &= F_5 - m(1-u) \sum_{i=1}^N \psi(t_i), & \frac{dW}{dt} &= F_6 - m \sum_{i=1}^N \psi(t_i). \end{aligned}$$

The meaning of the new parameters is the following one: u denotes the portion of insecticide sprayed directly on the agroecosystems, $(1-u)$ the portion instead that is accidentally dispersed in the woods, n and N its effectiveness against the insects and the pests respectively, with the assumption that $N > n$, and finally m represents the effectiveness against the spiders.

Here note that the right hand side of the equation (11) is now discontinuous, but to model “instantaneous” processes like the spraying of the insecticides we have to use the semi-continuous model. A similar semi-continuous model was already used to observe the effects of insecticide spraying in some of our previous works, see [3, 21].

The numerical simulation reported in Fig. 1 is related to Fig. 5 when spraying is administered, with constants $n = 0.01$, $N = 0.04$, $m = 0.008$, $u = 0.9$ and $\rho = 0.1$. The interspraying time was taken to be 20 week^{-1} , since the range given in Halley et al. [5] is $15\text{-}30 \text{ week}^{-1}$. The impact of spraying is immediately evident, as the agroecosystem pests are wiped out, but so are also the spiders, although the spraying effectiveness level on the latter is extremely low, see Fig. 5. The spiders living in the woods take more time for extinction than those living in the agroecosystem. The insects living in the woods escape the spraying effect. Thus the woods present in the system play an important role for the survival of the bio-controller specially when the system is affected by spraying. This is in agreement with the observations of Halley et al. [5] who concluded that the landscape heterogeneity increases survival and abundance of the species.

It is observed that during the spraying the predation rate of the spiders decreases [16]. Thus next decrease the predation rates with $\alpha = 0.001$, $a_1 = 0.0025$, $\beta = 0.00015$, $a_2 = 0.001$, $\gamma = 0.001$, $a_3 = 0.002$ with other parameter values as in Fig. 5, and observe that the webweavers go to extinction while the spiders remain in the system, see Fig. 6. This result is also according to the finding of Halley et al. [5] who observe that spraying reduces the spider population and may lead to their extinction. This is a disaster from the farmer’s point of view, see Fig. 6.

6 Discussion

We have presented a very general model to describe the possible interactions among the most relevant populations present in an agroecosystem. The model is moderately complex, being made by six such populations, accounting for different spider and insect populations living in a agroecosystem and in the surrounding woods. Our investigation mainly focuses on the role of spiders as bio-controllers and on the importance of landscape heterogeneity for the survival and abundance of these bio-controllers. We incorporated the ballooning effect of the spiders in the model description. We also investigated

the effect of spraying of pesticides on the system. Some of these studies were also performed by Halley et al. [5], but using different mathematical tools, namely diffusion equations, and without considering environment pests and insects.

We determined the system's equilibria and performed the stability analysis of most of them. For the intractable ones, we turned to numerical simulations, to assess their stability for some parameter ranges. It is interesting to compare the nature of the equilibrium points of the present paper with the previous works. The first results of this investigation show that all the solutions of the system are bounded and total extinction will never occur. Also, the equilibria with one or two prey populations and no spider populations are all unstable. That is, in the absence of the spiders it will never happen that one or two prey populations alone remain in the system. We observe the same result in [3, 19, 20, 21]. On the other hand, all the three insects populations survive in the ecosystem in absence of spiders, if the death rate of the latter is higher than a certain critical value. In such case indeed the spider-free equilibrium point is stable, i.e. as mentioned, spiders are wiped out and the insects and the pests reach their carrying capacities. The role of spiders in controlling the pest population is thus confirmed. We observe a similar result in [3, 19], but in [20, 21] this kind of equilibrium does not exist. Also, if the specific growth rate of the pest population is below another certain critical value then the system can be made pest-free by the presence of the spider population. This is according to the results of [3, 20, 21], where we observe that the vineyard insects-free equilibrium is stable if the specific growth rate of the vineyard insects is below a certain critical value. Extinction criteria in the system are very important to establish. Recall indeed that one of the aims of these studies is to render the system pest-free without harming the other ecosystem components, in particular the extinction of the other population should be prevented. Halley et al. [5] also investigated the extinction and found that the extinction thresholds often depend on the carrying capacity. Our simulations show that stability of extinction equilibrium points also depends on the carrying capacity, in agreement also with the findings of [3, 20, 21]. There, the vineyard insects-free equilibrium is observed to be stable if the specific growth rate of the vineyard insects lies below a certain critical value.

Our numerical simulations are aimed at analyzing the effects of the different model parameters on the solutions. They substantiate the theoretical result that the system can be made pest-free by a decrease in the death rate

of the wanderer spiders. On the other hand external influences like sudden weather instabilities may alter the ecosystem populations, increasing death rates of spider populations, [10, 14]. Also the wind-induced migration of the newborns plays a relevant role for the coexistence of all the species in the ecosystem. This is a very important factor together with the presence of refugia such as woods for the survival of the bio-controllers. At times of emergency like spraying of insecticides, since these green patches are spared from insecticide, they can harbor spiders fleeing from the sprayed cultures and therefore save them from local extinction.

As discussed in the Introduction some instances of the present general picture have already appeared in the literature. These works also take into account the effect of spraying of insecticides in such systems. For example in [19] an ecosystem in which webweaver spiders may be transported by the wind from agroecosystems into the surrounding woods and vice versa has been considered. The effect of human activities in the ecosystem, by considering insecticide spraying was built into the model, as well as in the case of wanderer spiders, [20]. The effects of the insecticide were assumed to be instantaneous and the conclusions indicated that the populations could recover after spraying if the atmospheric and environmental conditions were not too much adverse. In practice the effect of the insecticide tend to last in time so that an exponential decay was then assumed in [21], as more realistic, and retained in the present model. Here also the human intervention through spraying has been simulated. Many field studies show that the use of chemicals decreases the diversity and density of spiders and correspondingly an outbreak of nuisance insects, [6, 4, 10]. Our simulation also supports the above result. If the insecticide is used at moderate concentrations and sprayed very frequently, there is a high chance for the spider populations to get extinct. We observe indeed that even spraying very low effective pesticides has a damaging effect on the spider populations as well as on the pests, as already remarked in [21]. The reduction in the predation rate due to spraying effects causes extinction of the webweavers, while pests survive in the ecosystem. This is in agreement with field studies, [5]. These remarks clearly show that the spraying of chemicals has a direct effect on the biodiversity of the agroecosystems and of the surrounding woods, the role of insecticides having been considered in detail by Halley et al. [5]. They present a table showing the intensity of the toxicities and the timings and frequency of application. Their final results are very similar to our conclusions.

Since the use of chemicals has in general been shown to have negative effect on the coexistence of the different species, an alternative ecofriendlier way to control the pest is provided by the use of spiders. This strategy would also help to maintain the diversity of the agroecosystem. Our theoretical analysis is then in agreement with field studies indicating the positive role spiders play as biological controllers in rice fields and fruit orchards, [13, 15, 17], in which the method of spider augmentation led up to 60% reduction of pesticide use [10] without harming the final production.

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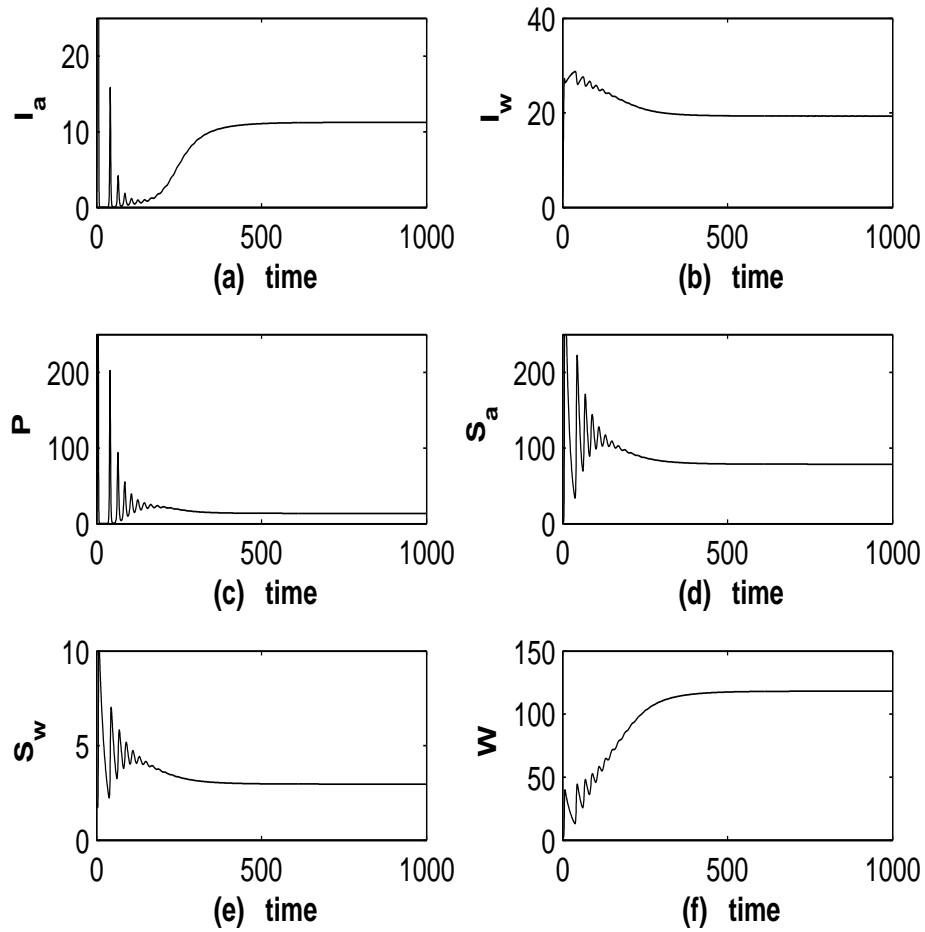


Figure 1: The coexistence steady state is locally asymptotically stable.

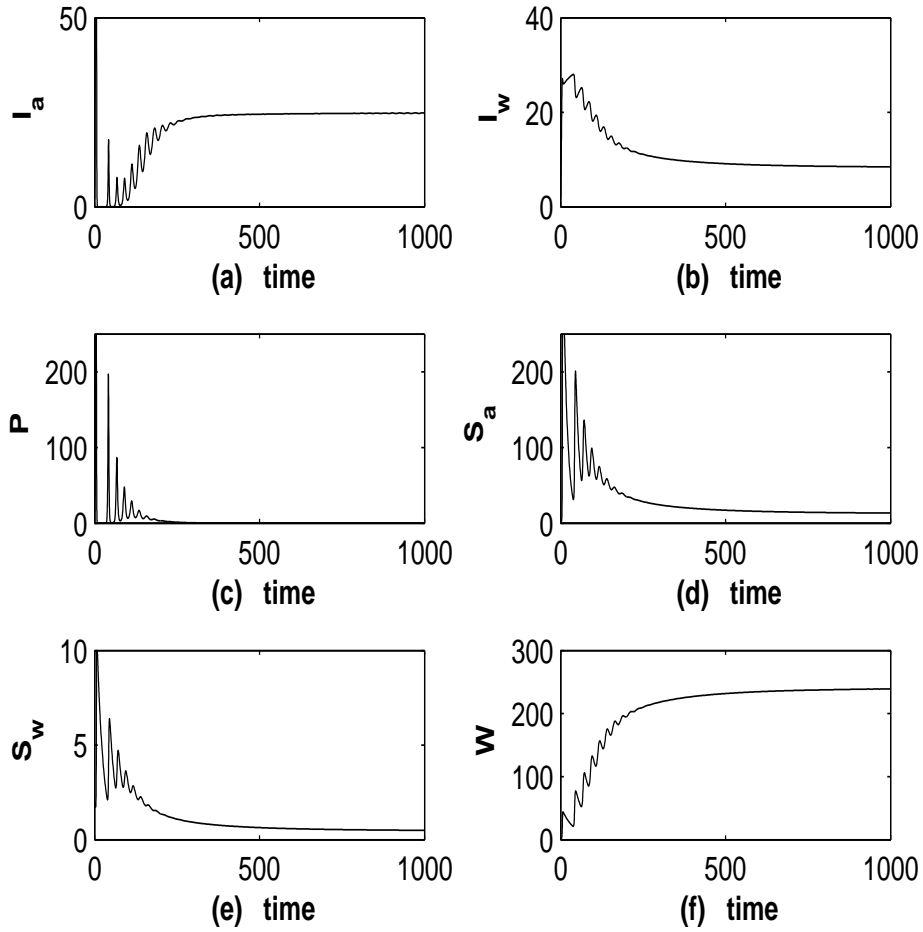


Figure 2: The pest population is washed away while all other populations coexist in the system. This is obtained for $\mu = 0.05$, with the same other parameter values as given in Table 1.

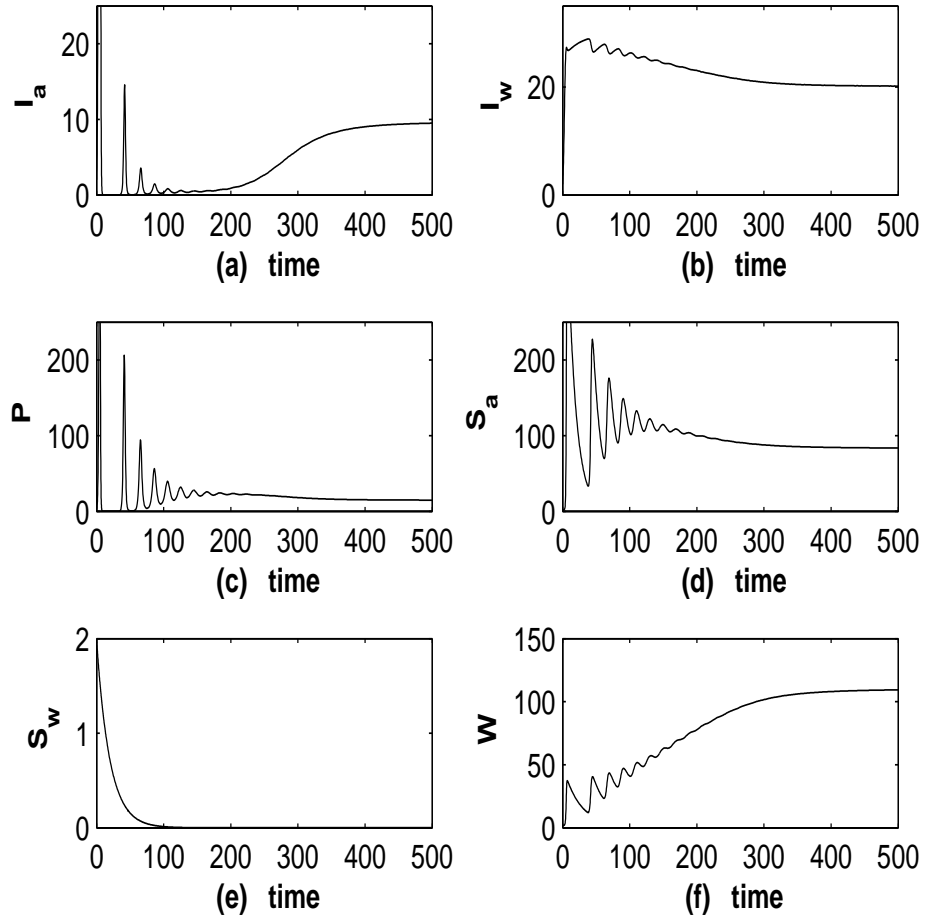


Figure 3: The webweavers living in the agroecosystem become extinct from the system for $\theta = 0$, i.e. in absence of ballooning. The other parameter values are the same as in Table 1.

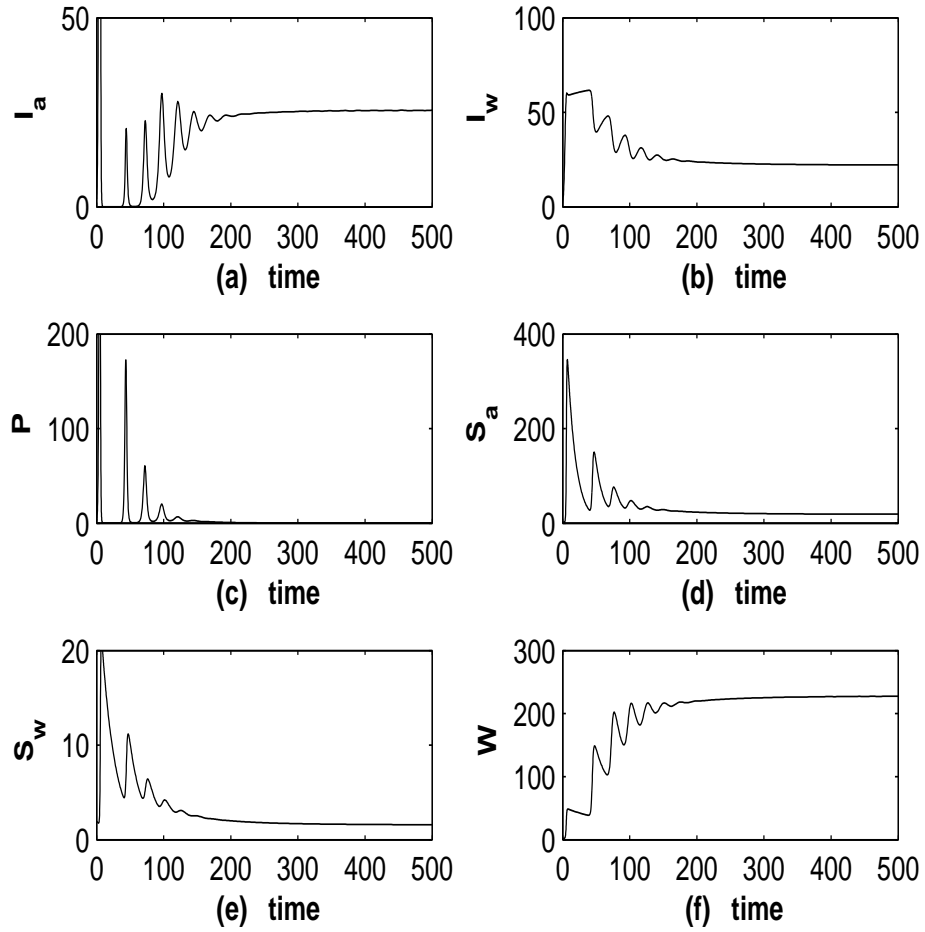


Figure 4: The pest population becomes extinct for $K_2 = 70$, while other parameter values retain the values of Table 1. All other populations coexist in the system.

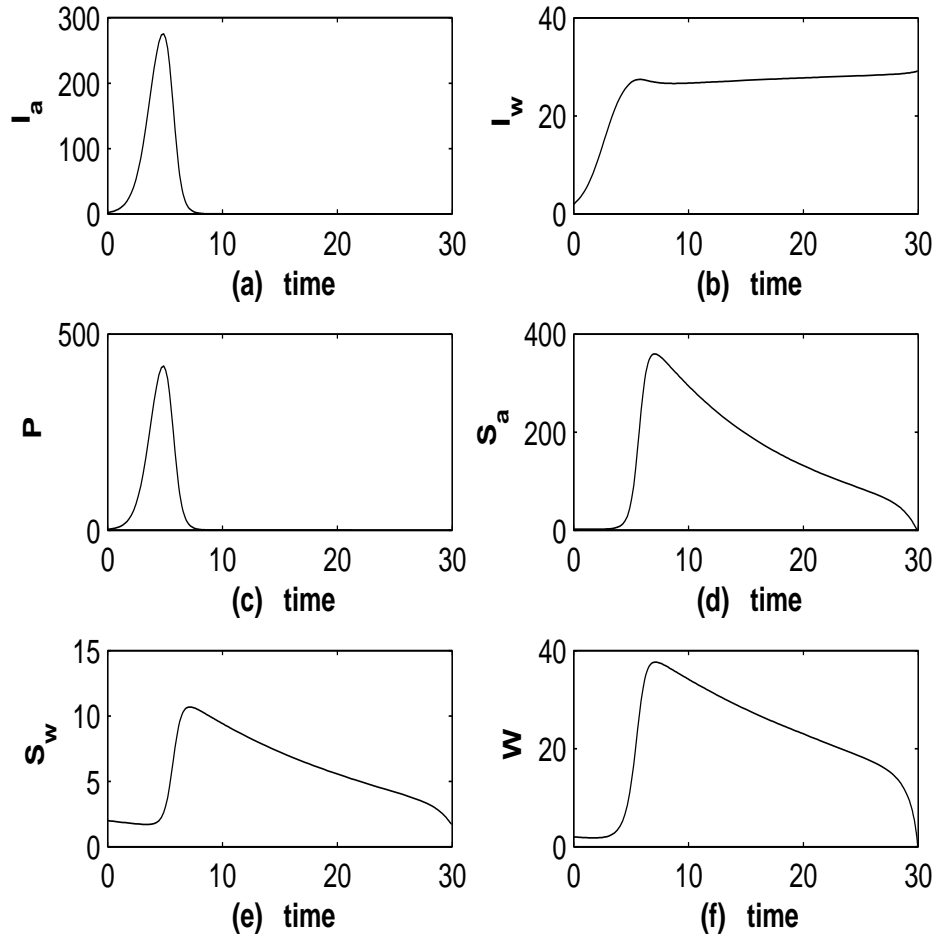


Figure 5: The model with spraying effects: with an interspraying time of 20, the spider population in the agroecosystem goes to extinction together with the pest population. The parameter values are those of Table 1.

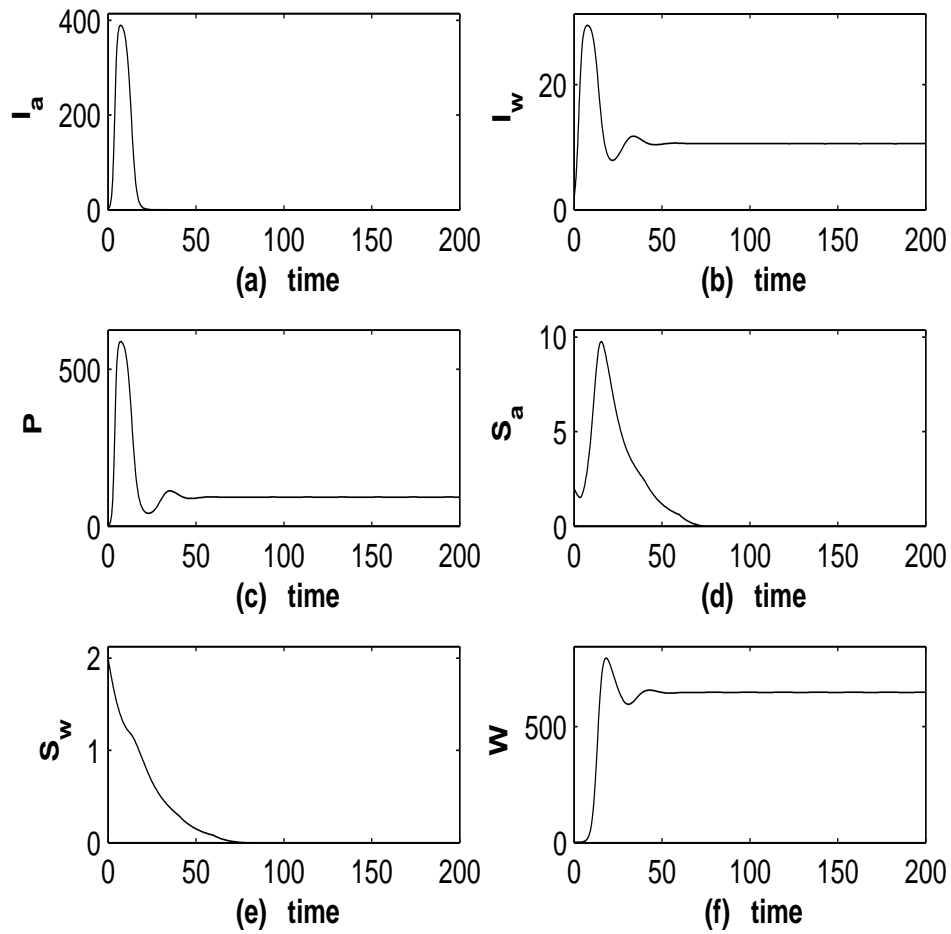


Figure 6: Spraying effects with smaller predation rates and other parameter values are the same as in Fig. 5. In this case the spiders disappear while the pests thrive.

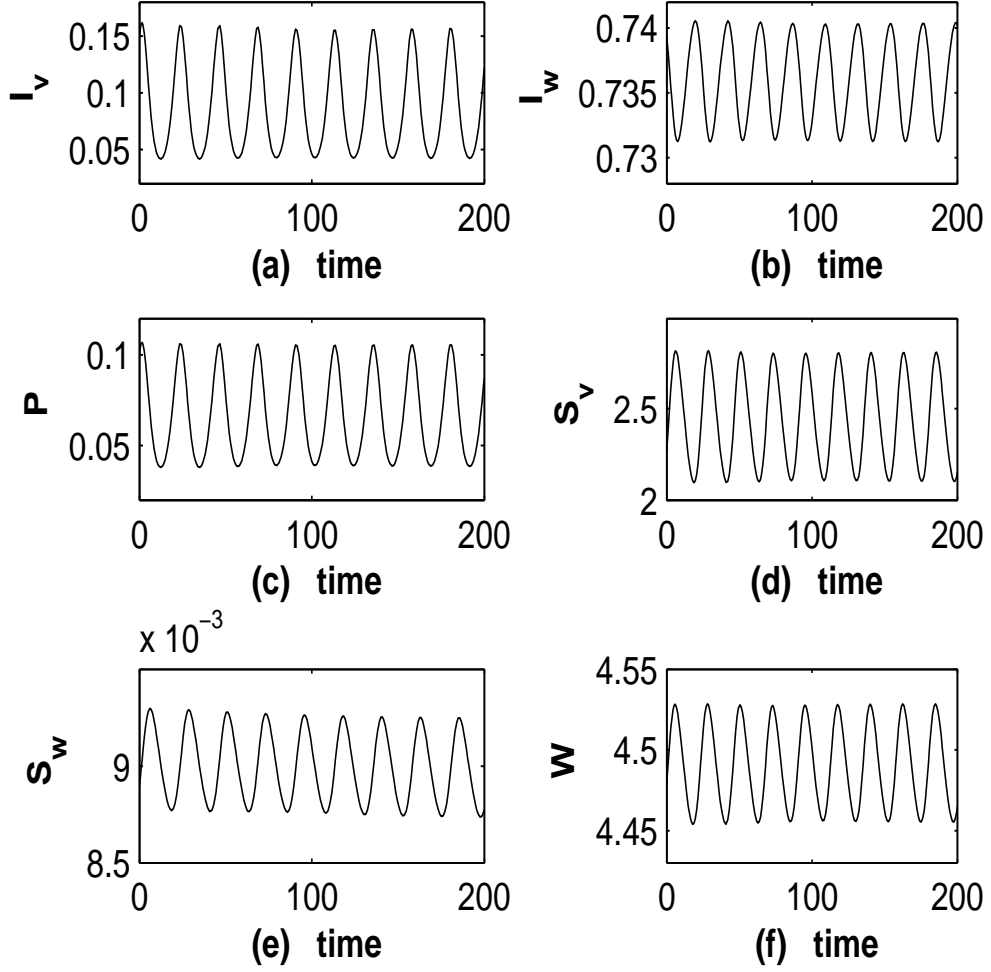


Figure 7: All the populations coexist oscillating in the system for the hypothetical parameter values $r_1 = 1.417$, $K_1 = 700$, $\alpha = 0.526$, $a_1 = 0.03$, $r_2 = 1$, $K_2 = 1.35$, $\beta = 0.65$, $a_2 = 0.1$, $q = 1.2$, $L = 300$, $\gamma = 0.4$, $a_3 = 0.05$, $\alpha' = 0.5$, $\gamma' = 0.38$, $\delta_a = 0.07$, $\beta' = 0.6$, $\delta_w = 0.3$, $a'_1 = 0.02$, $a'_2 = 0.09$, $a'_3 = 0.03$, $\mu = 0.07$, $\theta = 0.35$.

Table 1: The fixed set of parameter values, mostly taken from different available literature. Unit of populations are given by kg ha^{-1} and time t is weeks.

Parameters	Values given in the literature	Values considered in our simulations	Unit
r_1	Generally less than growth rate of the pests	1.417	week^{-1}
K_1	–	400	kg ha^{-1}
α	0.002-0.02 [16]	0.01	$\text{ha kg}^{-1} \text{week}^{-1}$
a_1	0.002-0.02 [16]	0.005	$\text{ha kg}^{-1} \text{week}^{-1}$
r_2	Generally less than growth rate of the pests	1	week^{-1}
K_2	According to model assumption, $K_2 \ll K_1$	30	kg ha^{-1}
β	0.00038-0.00055 [16]	0.0005	$\text{ha kg}^{-1} \text{week}^{-1}$
a_2	approximately 0.002 [16]	0.003	$\text{ha kg}^{-1} \text{week}^{-1}$
q	1.063-2.077 [9]	1.53	week^{-1}
L	Generally greater than the carrying capacity of insects	600	kg ha^{-1}
γ	–	0.01	$\text{ha kg}^{-1} \text{week}^{-1}$
a_3	–	0.006	$\text{ha kg}^{-1} \text{week}^{-1}$
α'	approximately 33% of α [18]	0.0033	$\text{ha kg}^{-1} \text{week}^{-1}$
γ'	approximately 33% of γ [18]	0.0033	$\text{ha kg}^{-1} \text{week}^{-1}$
δ_a	0.02-0.11 [5]	0.08	week^{-1}
β'	approximately 33% of β [18]	0.0002	$\text{ha kg}^{-1} \text{week}^{-1}$
δ_w	0.02-0.11 [5]	0.055	week^{-1}
a'_1	approximately 33% of a_1 [18]	0.0017	$\text{ha kg}^{-1} \text{week}^{-1}$
a'_2	approximately 33% of a_2 [18]	0.0009	$\text{ha kg}^{-1} \text{week}^{-1}$
a'_3	approximately 33% of a_3 [18]	0.002	$\text{ha kg}^{-1} \text{week}^{-1}$
μ	0.02-0.11 [5]	0.064	week^{-1}
θ	not a constant [5]	0.35	–