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BEYOND VOLTERRA-LOTKA: PREDATION, DEFENSE COALITIONS, AND CANNIBALISM IN LADYBUG, APHID AND ANT ECOSYSTEMS

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Abstract. The dynamics of the ladybug, aphid, and ant interactions are driven by ladybug-aphid predation, ladybug-ant inter-species competition (aphid-ant symbiosis/ mutualism in defense to ladybugs), and ladybug-ladybug intra-species competition (cannibalism). With this, the ladybug, aphid, and ant dynamics are far richer than typical Volterra-Lotka predator-prey models; though also less studied. Here, we are presenting a two-fold approach to modeling and analyzing the interaction dynamics further. First, we give a two-dimensional accumulated Ordinary Differential Equation Model for the ladybug-aphid interactions (where ants occur as a function of the number of aphids) with saturation terms. The mathematical analysis of this model exhibits a trans-critical bifurcation such that for certain values of the parameters an asymptotically stable mixed-species equilibrium exists with aphid numbers well below those without ladybug presence. Moreover, the non-existence of periodic orbits is shown analytically.

1. Introduction

"Ladybugs are predators both as adults and larvae, and are capable of consuming about 50 aphids daily."[1] Both nymph and adult aphids feed on the plant, adult aphids have wings and can escape predation, and, most importantly, ants serve as protectors for aphids fighting ladybugs. Furthermore, when food supply is rare (or competition too high) ladybugs will cannibalize other ladybugs (may it be eggs, larvae, or adults). Fig. 1 captures these ladybug, aphid, and ant interactions schematically.

When observing the advanced infestation by aphids, it seems that the relevant parts of the plants are completely covered by aphids allowing us to assume that spatial effects can be neglected and Ordinary Differential Equations (ODEs) are justified to model the overall population (amount) dynamics. Moreover, we may assume a total mixing of the aphids and ladybugs in the sense that each experience a quite similar (statistical) local environment with respect to the amounts of the involved species wherever they are at the plant. This is another important justification for the use of ODEs. The ant-ladybug interaction may be different as one may assume that ants hunt ladybugs in groups implying some spatial accumulation of ants towards areas of high ladybug densities.

There are several contributions to the ladybug-aphid-ants interactions in terms of higher-dimensional ODE systems. Ref. [1] introduces a four differential mathematical model describing the within-season population dynamics in an ecological patch of a system composed by aphids, ants, and ladybugs. There, besides the three insect population the time evolution of the cumulative density of aphids is utilized as a regulatory term for aphids, instead of the instantaneous density. The right-hand side equations incorporate carrying capacities of the ecosystem as well as saturation effects for predation. After motivating the ODE model it is discredited to a four-dimensional difference equation model that is analyzed mathematically in terms of fixed points, there stability, and overall dynamical effects. Simulations round-up the presentation. Ref. [1] focuses on the possibility of pest control, i.e. the extinction of aphid populations, by paying attention to the mutualistic relationship between ants and aphids. It shows that initial conditions most realistic from an ecological point of view lead to a steady-state, characterized by a collapsed colony of aphids and ladybirds and a constant population of ants. Dynamically, starting with sufficiently large initial populations, the populations of aphids

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[1]see `https://www.thebuglady.ca/aphid-control`.

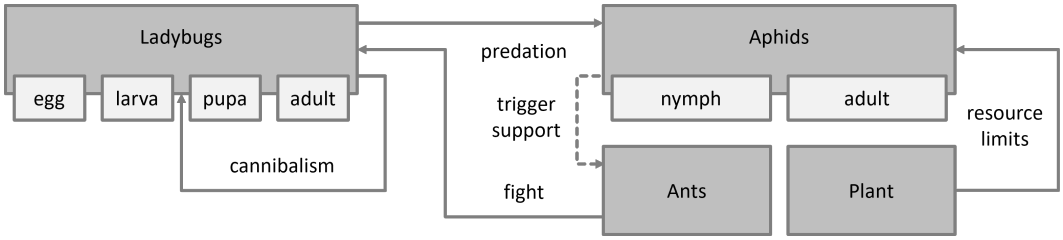

FIGURE 1. Illustration of the ladybug, aphid, and ant interactions.

and ladybugs reach a maximum and then collapse according to the described steady-state population densities.

Mutualism in the sense of co-predation of ladybugs and the Pennsylvania ground beetle on aphids is discussed in Ref. [5]. Here it turns out that this kind of cooperation between predators of different species significantly increases the predation success of each species.

Ref. [4] treat both the in-seasonal as well as the inter-seasonal effects of the ladybug and aphid, dynamics taking especially ladybug cannibalism into account. Their conclusions rely on the in-season dynamics (with one 'new' generation of ladybugs) and the carry over of the populations to the next season. The major motivation for Ref. [4] is to study mathematically the observed phenomenon that insect predators are typically less effective in pest control compared to parasitoids.[2] Based on previous works, see Refs. [2, 3], the discussion and simulation in Ref. [4] is based on a three-dimensional ODE model for the cumulative density of the aphids (prey), the density of the aphids and the density of the ladybugs (predators). Again, carrying capacities of the ecosystem and predation saturation effects are included, though, the effect of ants on the ladybug-aphid dynamics are dismissed. Ref. [4] finds that "prey always tends to oscillate from year to year, at least initially, while predator abundance usually monotonously approaches an equilibrium." Moreover, it is pointed out that "in situations where the developmental time of the predator is long relative to that of its prey, predators are unlikely to be effective classical biological control agents. This is because the predator abundance is strongly regulated by cannibalism."

Ref [6] gives a three dimensional model for the ladybug-aphid predator prey interaction by taking into account aphid, ladybug, and hibernating ladybug populations. Impacts of insecticides on the aphid population are included as an additional death rate rate proportional to the aphid population. Again, carrying capacities of the ecosystem (for both species) and predation saturation effects are included and as well the effect of ants on the ladybug-aphid dynamics and ladybug cannibalism are dismissed. The resulting three-dimensional system is discussed by means of dynamical systems theory and phase-space simulations are conducted. Moreover, the underlying control problem of reducing the aphid population most effectively is stated and analyzed.

In this article, we add the following new aspects to the known body of results: In terms of an ODE model, we set-up a two-dimensional interaction model for aphids and ladybugs including a carrying capacity of the ecosystem for the aphid population, cannibalism of ladybugs, predation saturation as well as mutualism (in terms of a reduction of ladybug mortality). Thus, our model is an example for ecosystems beyond the typical predator-prey setting modeled by the classical Volterra-Lotka dynamics. This model is mathematically analyzed by means of dynamical systems techniques. For certain parameter values the pure aphid equilibrium is asymptotically stable (ineffective pest control or, in other words, effective defense of the aphids by the ants). For the remaining values of the parameters, the system exhibits a trans-critical bifurcation such that an asymptotically stable mixed-species equilibrium exists with aphid numbers well below those without ladybug presence (biologically/ evolutionary significant setting). Moreover, the non-existence of periodic orbits is shown analytically. Note, that the existence of periodic orbits is the key result of the Volterra-Lotka dynamics.

[2]Parasitoids are insects whose females lay their eggs in or on the bodies of the host insects. Parasitoid eggs develop into parasitoid larvae at the expense of their host. Hosts that have been parasitized thus give rise to the next generation of parasitoids, while only hosts that are not parasitized will give rise to the next generation of hosts.

2. The Governing Equations of the Ladybug-Aphid- Ants Interactions

The dynamics of the ladybug, aphid, and ant interactions are driven by ladybug-aphid predation, ladybug-ant inter-species competition (aphid-ant symbiosis/ mutualism in defense to ladybugs), and ladybug-ladybug intra-species competition (cannibalism). We assume that there are no seasonal environmental influences.

Let $x(t)$ be the time-dependent amount of aphids (in all live stages) and $y(t)$ that of the ladybugs (in all live stages). We assume, that in the absence of ladybugs the aphid population follows a logistic growth (with growth rate $r > 0$ and carrying capacity $C > 0$) and that the rate of change of the aphid population is negatively influenced by a Monod-type ladybug predation term, i.e.

$$\dot{x} \;=\; rx\left(1-\frac{x}{C}\right) - \frac{d_1 xy}{k+x+y^2}\,, \tag{2.1}$$

where $d_1 > 0$ is a proportionality factor for the ladybug-aphid interactions, $k > 0$ the saturation constant for the ladybugs. The additional term y^2 in the denominator of the ladybug predation term represents saturation due to ladybug cannibalism and thus reduced predation pressure in case of too many ladybugs.

Next, we assume that the ladybug population grows according to the preyed aphids (with some conversion factor $v \in (0,1)$ that describes the efficiency in biomass uptake) and declines with respect to the amount of interactions with other ladybugs around (with a proportionality factor $d_2 > 0$) as well as with ants, i.e.

$$\dot{y} \;=\; \frac{v d_1 xy}{k+x+y^2} - d_2 y^2 - d_3 xy\,, \tag{2.2}$$

where the ant population is taken as proportional to the aphid population and $d_3 > 0$ is the joint proportionality factor for this ant-aphid relation and the ant-ladybug interaction.[3]

We conduct a coordinate transformation to reduce the number of parameters from 7 to 5. We, define $\xi := c^{-1}x$, $\eta := r^{-1}d_2 y$, and $\tau = rt$, then (2.1)-(2.2) becomes

$$\tfrac{\mathrm{d}}{\mathrm{d}\tau}\,\xi \;=\; \xi(1-\xi) - \frac{\delta_1 \xi\eta}{\kappa+\xi+\beta\eta^2} \quad \text{and} \quad \tfrac{\mathrm{d}}{\mathrm{d}\tau}\,\eta \;=\; \frac{\alpha\xi\eta}{\kappa+\xi+\beta\eta^2} - \eta^2 - \delta_2\xi\eta\,,$$

where $\kappa := c^{-1}k$, $\beta = (cd_2^2)^{-1}r^2$, $\delta_1 = (cd_2)^{-1}d_1$, $\alpha = r^{-1}vd_1$, and $\delta_2 = r^{-1}cd_2$. Finally, with a slight misuse of notation, we write this system as

$$\dot{x} \;=\; x(1-x) - \frac{\delta_1 xy}{\kappa+x+\beta y^2} \;=\; x\left(1-x-\frac{\delta_1 y}{\kappa+x+\beta y^2}\right)\,, \tag{2.3}$$

$$\dot{y} \;=\; \frac{\alpha xy}{\kappa+x+\beta y^2} - \delta_2 xy - y^2 \;=\; y\left(\frac{\alpha x}{\kappa+x+\beta y^2} - \delta_2 x - y\right)\,. \tag{2.4}$$

Fig. 2 illustrates these dynamics for three different sets of parameters by displaying the underlying vector field (arrows), the null-clines (thin lines), the equilibria (encircled stars), as well as selected integral curves/ trajectories (thick lines). In sub-figure (a) we have $\alpha = 1$, $\beta = 1$, $\delta_1 = 1$, $\delta_2 = 1$, and $\kappa = 10$. These vales of the parameter give rise to an asymptotically stable pure aphid equilibrium. I.e., pest control does not really work out; on the contrary the predator population dies out. In sub-figure (b) we have $\alpha = 50$, $\beta = 4$, $\delta_1 = 20$, $\delta_2 = 1$, and $\kappa = 10$. Here, integral curves/ trajectories seem to spiral into an asymptotically stable mixed-species equilibrium at an aphid-coordinate relatively smaller than that of the pure aphid population equilibrium (here shown as an unstable equilibrium on the abscissa axis). One tempted to interpret this as an effective continuous pest control. Finally, in sub-figure (c) we have $\alpha = 50$, $\beta = 4$, $\delta_1 = 1$, $\delta_2 = 1$, and $\kappa = 10$. For these parameter values we also obtain an asymptotically stable mixed-species equilibrium. This time, its aphid-coordinate is quite close to that of the pure aphid population such that it seems that the predation effect on aphids is not so pronounced or the guarding effect of ants is quite substantial.

[3]This inclusion of the effect of the ant population by means of the aphid population as a proxy is a simplification to keep the species number at two. Here, we include, in a sense of the equations, a kind of 'predation' of the aphids on the ladybugs which increases the richness of the mathematical phase space compared to typical predator-prey situations where no 'fighting back' of the prey is typically observed.

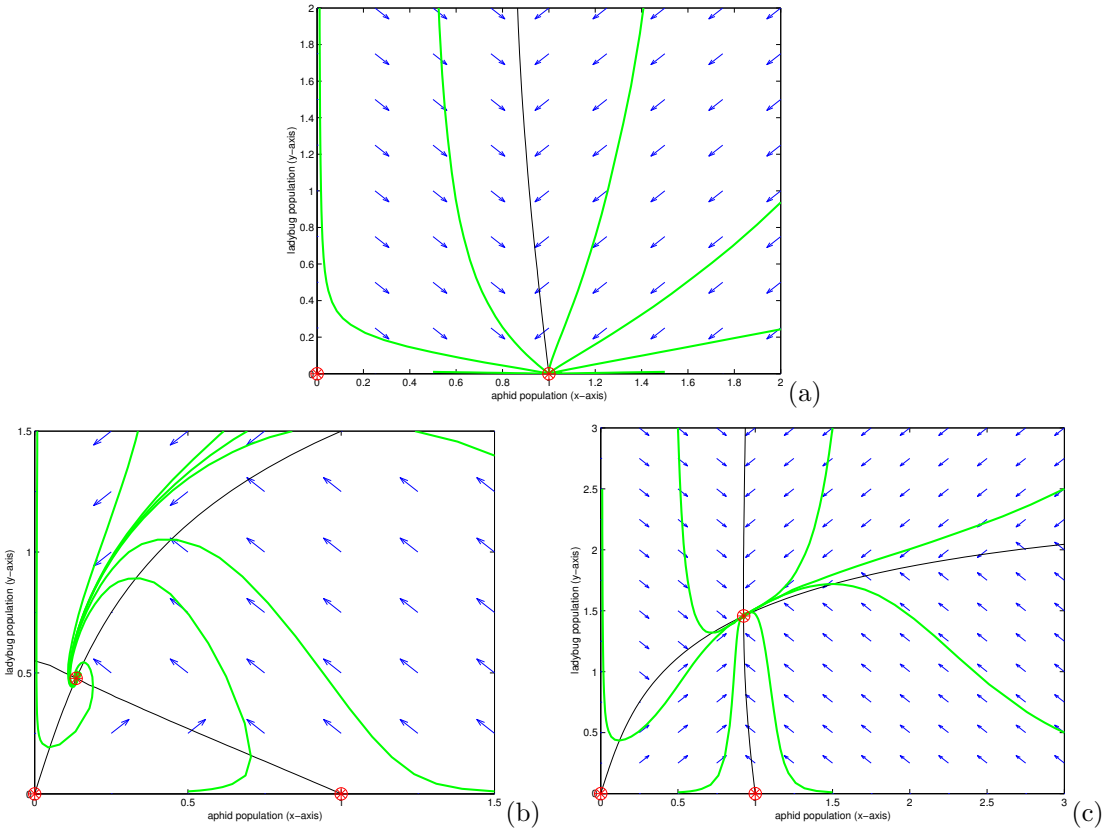

FIGURE 2. Illustration of the dynamics induced by (2.3)-(2.4) for different values of the parameters α, β, δ_1, δ_2, and κ. Shown are the vector field (arrows), the null-clines (thin lines), examples of integral curves (thick lines), and the equilibria (encircled stars).

The varying effectiveness of ladybug predation seem to be related to the slope of the null-cline passing through the single-species aphid equilibrium. A more in depth discussion of this relation is postponed to later works.

Let us proceed with a rigorous analysis: The dynamics induced by (2.3)-(2.4) leave the non-negative quadrant $\{(x,y) \in \mathbb{R}^2 : x, y \geq 0\}$ invariant and are such that the origin $(0,0)$ is an equilibrium point (extinction equilibrium). For $x = 0$, we have $\dot{x} = 0$ and $\dot{y} < 0$, and for $y = 0$, we have $\dot{y} = 0$ whereas $x(t)$ follows logistic growth on the x-axis. Thus $(0,0)$ is a saddle point with the y-axis being an attractive direction and the x-axis being a repulsive direction.

The point $(1,0)$ is a single-species equilibrium (pure aphid population). Confined to the x-axis $(1,0)$ is asymptotically stable due to the logistic growth dynamics. Though $(1,0)$ considering the full two-dimensional dynamics, we have that the Jacobian matrix $J(1,0)$ about $(1,0)$ reads

$$\begin{aligned} J(1,0) &= \begin{pmatrix} 1-2x-\frac{\delta_1 y(\kappa+\beta y^2)}{(\kappa+x+\beta y^2)^2} & -\frac{\delta_1 x(\kappa+x-\beta y^2)}{(\kappa+x+\beta y^2)^2} \\ \frac{\alpha y(\kappa+\beta y)}{(\kappa+x+\beta y^2)^2} - \delta_2 y & \frac{\alpha x(\kappa+x-\beta y^2)}{(\kappa+x+\beta y^2)^2} - \delta_2 x - 2y \end{pmatrix}\Bigg|_{x=1,y=0} \\ &= \begin{pmatrix} -1 & -\frac{\delta_1}{\kappa+1} \\ 0 & \frac{\alpha}{\kappa+1} - \delta_2 \end{pmatrix}. \end{aligned}$$

Thus, for $\frac{\alpha}{\kappa+1} - \delta_2 > 0$ the single-species equilibrium is a saddle point, for $\frac{\alpha}{\kappa+1} - \delta_2 = 0$ it is linearly Lyapunov stable (as the eigenvalue 0 is semi-simple), and for $\frac{\alpha}{\kappa+1} - \delta_2 < 0$ it is asymptotically stable. Therefore, we expect a bifurcation to happen at $\frac{\alpha}{\kappa+1} - \delta_2 = 0$ where stability gets exchanged

with another (mixed-species) equilibrium or a another asymptotically stable structure occurs (e.g. a periodic orbit).

Moreover, we immediately have as well:

Lemma 1 (No Unbounded Population Growth)**.** *For all admissible values of the parameters, neither of the two species grows beyond all bounds.*

Proof. For all admissible values of the parameters and $x, y > 0$ we first have that the right-hand side of (2.3) is negative whenever $x \geq 1$ and, second, that the right-hand side of (2.4) is also negative for y large enough. Let $y^b < \infty$ be such a bound where the right-hand side of (2.4) is negative for all $y > y^b$. Then, under the dynamics induced by (2.3)-(2.4), any initial condition outside the phase space rectangle $\{(x, y) \in \mathbb{R}^2 : 0 < x < 1, 0 < y < y^b\}$ will eventually enter this strip and stay there forever. □

Thus, the interesting dynamics are taking place in the phase space rectangle $\{(x, y) \in \mathbb{R}^2 : 0 < x < 1, 0 < y < y^b\}$ for some large enough values of y^b such that the right hand side of (2.4) remains negative for all $y > y^b$.

3. A Simplified Model (No Saturation)

For simplicity we assume that no saturation is present, i.e. the parts $\frac{xy}{\kappa+x+\beta y^2}$ in (2.3)-(2.4) become xy and, in (2.4), we additionally combine the ladybug-aphid and ladybug-ant interaction terms. In this way, we obtain

$$\dot{x} \;=\; x(1-x) - dxy \qquad \text{and} \qquad \dot{y} \;=\; axy - y^2\,, \tag{3.1}$$

with suitable parameters $d > 0$ and $a \in \mathbb{R}$ where $a < 0$ indicates a net pressure of the ants on the ladybug population (decline) and $a > 0$ a net growth due to ladybug-aphid interaction. The dynamics induced by the system (3.1) leave the non-negative quadrant $\{(x, y) \in \mathbb{R}^2 : x, y \geq 0\}$ invariant.

From a broader perspective system (3.1) is a modified predator-prey model for $a > 0$ and a competition model for $a < 0$. Though, the case $a < 0$ is not very interesting as $\dot{y} < 0$ for all $y > 0$ indicating the eventual dying out of species y (only x survives at the value of the carrying capacity $x = 1$). For $a > 0$, we have

Proposition 1 (Equilibria of the Simplified Model)**.** *Let $a > 0$, then system* (3.1) *has exactly three equilibrium points in the non-negative quadrant:*

- *the extinction equilibrium* $(0, 0)$ *which is a saddle point,*
- *the single-species equilibrium* $(1, 0)$ *which is a saddle point, and*
- *the mixed-species equilibrium* $(\frac{1}{1+ad}, \frac{a}{1+ad}) \in (0, 1) \times (0, a)$ *which is asymptotically stable.*

Proof. Existence and type of the extinction $(0, 0)$ and single-species equilibrium $(1, 0)$ follow as in our previous discussion for the complete model (2.3)-(2.4). In particular, the corresponding Jacobi matrices $J(0, 0)$ of (3.1) about $(0, 0)$ and $J(1, 0)$ about $(1, 0)$ are

$$J(0,0) \;=\; \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix} \qquad \text{and} \qquad J(1,0) \;=\; \begin{pmatrix} -1 & -d \\ 0 & a \end{pmatrix}.$$

$J(1, 0)$ immediately displays the saddle character of $(1, 0)$. When confining the dynamics to the y-axis, we get, as previously, the saddle character of $(0, 0)$ as well. Equating $\dot{x} = 0$ and $\dot{y} = 0$ in (3.1) shows that the only remaining further solution is the mixed species equilibrium $(x^*, y^*) = (\frac{1}{1+ad}, \frac{a}{1+ad})$. There are no further equilibrium points.

The Jacobi matrix $J(x^*, y^*)$ of (3.1) about the mixed species equilibrium (x^*, y^*) reads

$$J(x^*, y^*) \;=\; \begin{pmatrix} 1-2x-dy & -dx \\ ay & ax-2y \end{pmatrix}\Big|_{x=x^*, y=y^*} \;=\; \frac{1}{1+ad}\begin{pmatrix} -1 & -d \\ a^2 & -a \end{pmatrix},$$

with characteristic polynomial $\chi_{J(x^*,y^*)}(\lambda) = \lambda^2 + \frac{1+a}{1+ad}\lambda + a$. Its Hurwitz matrix $H_{J(x^*,y^*)}$ and principal minors Δ_1 and Δ_2 are

$$H_{J(x^*,y^*)} \;=\; \begin{pmatrix} \frac{1+a}{1+ad} & 0 \\ 1 & a \end{pmatrix}, \quad \Delta_1 \;=\; \frac{1+a}{1+ad} \;>\; 0\,, \quad \text{and} \quad \Delta_2 \;=\; \frac{a+a^2}{1+ad} \;>\; 0\,.$$

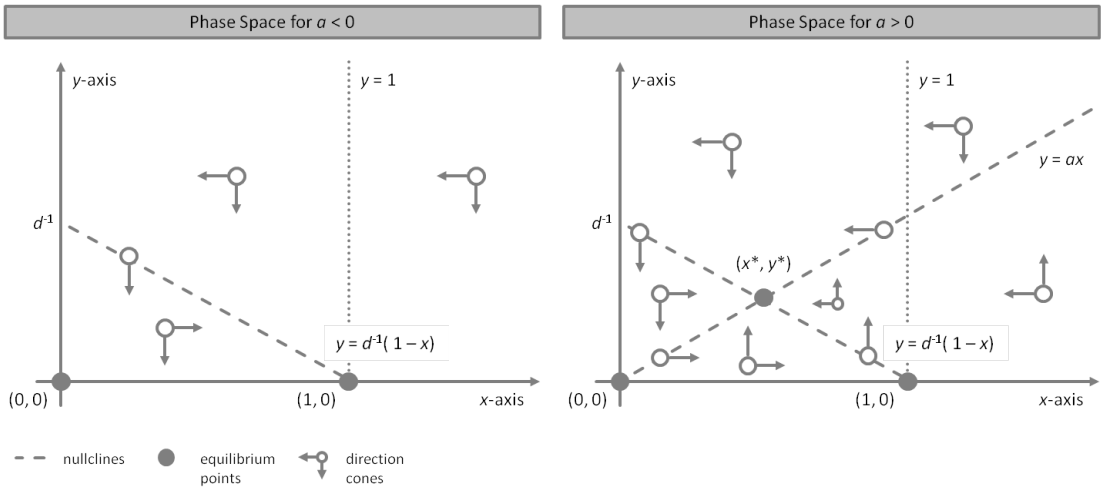

FIGURE 3. Illustration of the phase-space dynamics in the simplified model for $a < 0$ (left-hand side) and $a > 0$ (right-hand side).

Hence, all eigenvalues of $J(x^*, y^*)$ have strictly negative real part and thus (x^*, y^*) is asymptotically stable.

Moreover, the discriminant D of $\chi_{J(x^*,y^*)}(\lambda)$ reads

$$\begin{aligned} D &= \left(\frac{1+a}{1+ad}\right)^2 - 4a = \frac{1}{(1+ad)^2}\left(1+2a+a^2-4a(1+2ad+a^2d^2)\right) \\ &= \frac{1}{(1+ad)^2}\left((1-a)^2-4a^2d(2+ad)\right) . \end{aligned}$$

If $D \geq 0$, i.e. $(1-a)^2 \geq 4a^2d(2+ad)$, then we have (with multiplicity) two real roots, whereas for $D < 0$, i.e. $(1-a)^2 < 4a^2d(2+ad)$, then we have two complex conjugate roots. □

The parameter a gives rise to a trans-critical bifurcation from the single-species equilibrium $(1, 0)$, which is asymptotically stable for $a < 0$, to the mixed-species equilibrium (x^*, y^*) for $a > 0$. For $a > 0$, the mixed-species equilibrium is asymptotically stable while the single-species equilibrium becomes unstable.

Fig. 3 illustrates the governing dynamics in the phase space of our simplified model (3.1) for $a < 0$ (left-hand side) and $a > 0$ (right-hand side).

For $a > 0$, all three equilibrium points are contained in $\mathscr{R} = [0, 1] \times [0, a]$.

Lemma 2 (A Forward Invariant Compact Set)**.** *Let $a > 0$. The compact phase space-rectangle $\mathscr{R} := [0, 1] \times [0, a] \subset \mathbb{R}^2$ is positively invariant under the dynamics induced by* (3.1).

Proof. $\mathscr{R}$ is compact. We already discussed the dynamics confined to the x-axis (i.e. those on $[0, 1]\times 0$) and on the y-axis (i.e. those on $0 \times [0, a]$) such that we know that every trajectory starting in $[0, 1] \times 0$ or $0 \times [0, a]$, respectively, stays there for all times.

For initial conditions in $1 \times [0, a]$ we have $\dot{x} < 0$ and $\dot{y} = y(a - y) \geq 0$ with $\dot{y} = 0$ for $(x, y) = (1, a)$. I.e., trajectories starting on $1 \times [0, a]$ point towards the interior of $\mathscr{R}$.

Last, for initial conditions on $[0, 1] \times a$, we have $\dot{y} = a^2(x - 1) \leq 0$ with $\dot{y} = 0$ for $x = 1$ and $\dot{x} = x(1 - x - ad)$. If $x \geq 1 - ad$ or $x < 1 - ad$ it follows $\dot{x} \leq 0$ or $\dot{x} > 0$, respectively. I.e., trajectories starting on $[0, 1] \times a$ point towards the interior of $\mathscr{R}$.

Thus, $\mathscr{R}$ is positively invariant. □

Next, we go beyond the local information obtained from the stability of the equilibria and discuss the non-existence of periodic orbits around the mixed-species equilibrium (as they would be present in the traditional Lotka-Volterra model).

Proposition 2 (Non-Existence of a Period Orbit in a Vicinity of the Mixed-Species Equilibrium)**.** *Let $a > 0$. There is no periodic orbit lying entirely in the interior of $\mathscr{R}$.*

Proof. The set $(0,1) \times (0,a)$, i.e. the interior of $\mathscr{R}$, is simply connected and the function $\phi(x,y) := x^{-1}y^{-1}$ is continuously differentiable there. For $(x,y) \in (0,1) \times (0,a)$, we have

$$\begin{aligned} \operatorname{div} \begin{pmatrix} \phi(x,y) \cdot \dot{x} \\ \phi(x,y) \cdot \dot{y} \end{pmatrix} &= \partial_x \left(x^{-1}y^{-1}\dot{x} \right) + \partial_y \left(x^{-1}y^{-1}\dot{y} \right) \\ &= \partial_x \left(y^{-1} - xy^{-1} - d \right) + \partial_y \left(a - yx^{-1} \right) \; = \; -y^{-1} - x^{-1} \; < \; 0. \end{aligned}$$

Hence, with the Bendixon-Dulac criterion, we conclude that there is no periodic orbit lying entirely within the interior of $\mathscr{R}$. □

4. On the Phase-Space Dynamics of the Complete Model

We first detail the previously discussed the phase space rectangle $\{(x,y) \in \mathbb{R}^2 : 0 < x < 1, 0 < y < y^b\}$ by actually showing that $[0,1] \times [0,\alpha]$ is positively invariant under the dynamics induced by our system (2.3)-(2.4).

Lemma 3 (A Forward Invariant Compact Set)**.** *The compact phase space-rectangle $\mathscr{Q} := [0,1] \times [0,\alpha] \subset \mathbb{R}^2$ is positively invariant under the dynamics induced by our system* (2.3)-(2.4)*.*

Proof. Our line of argumentation is analogous to the proof of Lemma 2: $\mathscr{Q}$ is compact and we already discussed the dynamics confined to the x-axis (i.e. those on $[0,1] \times 0$) and on the y-axis (i.e. those on $0 \times [0,\alpha]$). Hence, every trajectory starting in $[0,1] \times 0$ or $0 \times [0,\alpha]$, respectively, stays there for all times.

For initial conditions in $1 \times [0,\alpha]$ we have $\dot{x} < 0$. If $y \in [0,\alpha]$ is small then, depending on the parameters, $\dot{y}$ may take any sign, in particular $\dot{y} = 0$ for $y = 0$. Though, if $y \in [0,\alpha]$ is close to α then $\dot{y} < 0$ as $\alpha(\kappa + 1 + \beta y^2) < \alpha$. I.e., trajectories starting on $1 \times [0,\alpha]$ point towards the interior of $\mathscr{Q}$.

Last, for initial conditions on $[0,1] \times \alpha$, we first have

$$\begin{aligned} \frac{\dot{y}}{y} &= \frac{\alpha x}{\kappa + x + \beta\alpha^2} - \delta_2 x - \alpha \; = \; \frac{\alpha(x - \kappa - x - \beta\alpha^2}{\kappa + x + \beta\alpha^2)} - \delta_2 x \\ &= -\frac{\alpha(\kappa + \beta\alpha^2}{\kappa + x + \beta\alpha^2)} - \delta_2 x \; < \; 0\,, \end{aligned}$$

for all $x \in [0,1]$ and, second, $\dot{x} = 0$ for $x = 0$ as well as $\dot{x} < 0$ for $x = 1$, respectively. I.e., trajectories starting on $[0,1] \times \alpha$ point towards the interior of $\mathscr{Q}$.

Thus, $\mathscr{Q}$ is positively invariant. □

Next, in complete analogy to Proposition 2, we show that there are no periodic orbits in $\mathscr{Q}$.

Proposition 3 (Non-Existence of a Period Orbits Lying Completely in $\mathscr{Q}$)**.** *Let $1 + \frac{1}{\alpha} - \frac{\delta_1}{\kappa} > 0$. Then there is no periodic orbit lying entirely in the interior of $\mathscr{Q}$.*

Proof. The set $(0,1) \times (0,\alpha)$, i.e. the interior of $\mathscr{Q}$, is simply connected and the function $\phi(x,y) := x^{-1}y^{-1}$ is continuously differentiable there. For $(x,y) \in (0,1) \times (0,\alpha)$, we have

$$\begin{aligned} \operatorname{div} \begin{pmatrix} \phi(x,y) \cdot \dot{x} \\ \phi(x,y) \cdot \dot{y} \end{pmatrix} &= \partial_x \left(\frac{1}{y} - \frac{x}{y} - \frac{\delta_1}{\kappa + x + \beta y^2} \right) + \partial_y \left(\frac{\alpha}{\kappa + x + \beta y^2} - \delta_2 - \frac{y}{x} \right) \\ &= -\frac{1}{x} - \frac{1}{y} - \frac{2\alpha\beta y - \delta_1}{(\kappa + x + \beta y^2)} \; \leq \; -1 - \frac{1}{\alpha} + \frac{\delta_1}{\kappa} \; < \; 0\,. \end{aligned}$$

Hence, with the Bendixon-Dulac criterion, we conclude that there is no periodic orbit lying entirely within the interior of $\mathscr{Q}$. □

Together with the change of stability of the single-species equilibrium $(1,0)$, the Poincare-Bendixon criterion now allows us to conclude the existence of a mixed-species equilibrium in the interior of $\mathscr{Q}$.

5. Summary

Based on first principles, we set-up a coupled continuous-time ODE model for the interactions of ladybugs, aphids, and ants (in terms of a virtual quantity proportional to the amount of aphids present). Due to the combined predation, cannibalism, and mutualism effects these models are richer than usually used Volterra-Lotka predation-prey only models. Depending on the parameters used in the ODE model, we observe the occurrence of a complete extinction of the ladybug and aphid populations (effective pest control), the extinction of the ladybug population (failed pest control due to ant impact), and the co-existence of the ladybug and aphid populations (ineffective pest control). Such co-existence states are typically linked to evolutionary survival of the involved species.

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