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Modelling multispecies interactions and horizontal transmission of aphid bacterial symbionts

Abstract. In this paper we formulate a model for the investigation of the infection of aphids by bacteria that protect them against parasitoid wasps. The model accounts for the possible transmission mechanisms that can originate in the environment. Mathematically, this corresponds to setting up a nonlinear dynamical system comprising all the relevant populations, and describing their possible mutual interactions via ordinary differential equations. A considerable effort is exerted in assessing the system's equilibria for feasibility and stability. The main theoretical result concerns the latter issue, for which the full set of the Routh-Hurwitz conditions are established analytically.

Keywords. Mathematical models, dynamical systems, equilibria, stability, aphids, pests, parasitoid wasps.

Mathematics Subject Classification: 92D40, 92D45, 92D25.

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1 - Introduction

Mathematical population theory dates back to the work of Malthus who was mainly motivated by economic considerations [**11**]. His original model has been criticized and improved by Verhulst [**21**], but it was not until about a hundred years ago that Lotka and Volterra formulated the first dynamical system for population interactions, [**9**, **22**]. Ever since, the use of differential equations for the modeling and understanding of populations mutual relationships has become a common tool in many applications. Its benefits can be observed in ecology, epidemiology and the combinations of the two, ecoepidemiology [**20**].

In this paper we consider an application to sustainable agriculture, where one of the major crop pests, the aphids, need to be controlled. In particular, a biological mechanism is modeled, for which the aphids are parasitized (i.e. ultimately killed) by wasps, but this beneficial action may be reduced by endosymbiotic bacteria in the aphid host that confer resistance to parasitoid wasps [**25**]. In addition, we account for horizontal transmission via another set of generalist natural enemies of aphids (ladybirds) that chew on the aphid body releasing aphid-hemolymph (potentially containing protective bacteria) into the local environment; these bacteria could then infect and protect other aphids in the surrounding colony.

The basic aphids-parasitoids interaction has already been examined in [**27**]. It considers only 3 populations, i.e. the parasitizing wasps and the aphids, distinguished among susceptible and bacteria-infected. We found that a small amount of horizontal transmission via the wasps was required for co-existence of infected and uninfected aphids to be maintained (as observed in natural populations). Here, we significantly extend this to account for a more realistic system where complementary biological control with generalist natural enemies is included. These results begin to identify ways in which horizontal transmission may occur that we have as yet been unable to fully study using whole-organism experiments. Thus, such models allow us to design hypothesis-driven ecological experiments that set out to test the ideas we have explored here. Mathematically, the model proposed in this paper is much more complex than the one of [**27**], as it includes more populations, the bacteria and the aphids predators, namely the ladybirds, and distinguishes whether horizontal transmission of the protective bacteria by the parasitoid wasps or by environmental exposure after ladybird feeding can further explain coexistence of these aphid populations. Often both parasitoid wasps and ladybirds are used in complementary biological control strategies [**16**] and it is important to understand how protective symbionts might alter the effectiveness of these schemes. Overall, there are 7 populations, their mutual relationships being described in Section 3. The corresponding system of ordinary differential equations is analysed to assess its equilibria and their feasibility. A huge effort is also devoted to the stability analysis, providing the full set of Routh-Hurwitz conditions.

This study may have application to many crops and regions, so that we do not specifically focus on a specific type. Rather, it represents a proof-of-concept model with possibly a very broad usage. Recent biological control efforts indeed aim to increase natural diversity as well as abundance, but competition among natural enemies themselves can also reduce the effectiveness of the biocontrol and is one of the motivations of this investigation.

The paper is organized as follows. In the next section we give the relevant biological background. The model is constructed in Section 3 and its equilibria are established in Section 4. Section 5 contains the local stability analysis results, and a final discussion concludes the paper.

2 - Biological background

Aphids are small herbivorous insects that feed on the phloem-sap of herbaceous plants, shrubs and trees. From over 6000 identified aphid species only a few are major crop pests, yet these are agriculturally and economically important as they reduce crop yield through direct feeding and transmit devastating plant viruses [**2**, **18**] Aphids colonise crop plants in spring and early summer where populations can increase exponentially causing pest outbreaks within agricultural landscapes. Generally, chemical pesticides are sprayed to control aphid populations on crop plants, but aphids are evolving resistance to common pesticides worldwide [**10**]. Further, many chemical pesticides are being banned (particularly in Europe) due to their negative effects on non-target insect populations, such as honeybees [**3**].

In natural systems, aphid population growth is controlled by interactions with a diversity of other species, including numerous natural enemies that find the soft-bodied aphids an easy-to-access food resource. Many generalist predators (e.g. ladybirds, lacewings, and syrphid larvae) feed almost exclusively on aphids in summer when population numbers are high. Aphid-specialist natural enemies include parasitic wasps that lay their eggs inside a living aphid where the wasp larva develops, pupates, and emerges as an adult from the dead aphid ‘mummy’, and entomopathogenic fungi that infect the aphid cuticle, invading the haemolymph and internal organs. Together, these different types of natural enemies interact to keep aphid population growth under control [**19**]. In agricultural systems, natural enemy diversity is reduced but the importance of natural enemies species as biological control agents is becoming increasingly apparent and schemes are being implemented to increase natural biodiversity in our managed systems [**17**].

The control of aphid populations by natural enemies is, however, also impeded by the presence of protective bacteria (aphid symbionts) that are hosted by the aphids within specialised cells [**14**]. Aphid symbionts are predominantly vertically transmitted from mother to offspring, but horizontal transmission has been shown to occur at low frequencies during sexual reproduction [**13**], by parasitoids when ovipositing eggs into aphids [**5**], or even through infected honeydew [**4**]. These bacteria can be costly to host by reducing aphid fitness (increased development time, reduced fecundity, and reduced longevity), but they also provide strong survival benefits to the aphid (e.g. resistance to parasitic wasps) [**25**]. In the absence of a protective symbiont, 60% of aphids (averaged across all aphid and bacteria species) will be successfully parasitized (no survival of the aphid) but this drops to 43% when an aphid hosts a bacterial symbiont; however, some combinations of aphid and bacteria will give 100% protection [**25**]. Aphid individuals host an average of 1-2 symbionts in the field (30-50% infection rate within populations), from nine common symbiont species, and symbionts have been identified from over 300 aphid species across the world [**6**,**26**]. While many studies still continue to use experimental work to uncover the mechanisms by which aphids and aphid symbionts interact, there is also a drive to understand the consequences of aphid symbionts in agricultural and natural systems [**12**, **23**, **24**]. In general, aphid symbionts protect against specialist natural enemies (parasitic wasps and entomopathogenic fungi), but there is evidence for this to also influence the general predators [**7**]. Indirect effects on general predators can also occur through predation of aphids that are already infected by parasitic wasps — aphids take a few days to die when parasitized and slower movement may make them easier prey for predators. This could enhance the removal of unprotected aphids (not hosting a symbiont) from the population, leading to higher frequencies of infected aphids in a population.

In previous work, we have shown the importance of a low frequency of parasitoid-mediated horizontal transmission for coexistence of infected and uninfected aphids with the natural enemies in a population similar to levels found in field surveys [**27**]. Here, we explore the impact of introducing a generalist predator (e.g. a ladybird) to the system. We investigate a potential new method of horizontal transmission, whereby as the ladybird feeds on the aphid (chewing) it releases the insides of the aphid (including the symbiotic bacteria) to the surroundings. As ladybirds often feed within aphid colonies, this could expose nearby aphids to the bacterial symbionts; however, as yet this method of transmission has not been experimentally tested.

In this paper, we use a modelling approach to try to investigate the above issues.

The paper is essentially aimed at assessing the theoretical properties of the model proposed. Further ongoing work will be devoted to numerical simulations.

3 - The extended model

We consider wasps Y that are partitioned among bacteria non carriers, W, and carriers, V, free bacteria B in the environment, i.e. the plants, and not attached to other insects, uninfected aphids A and bacteria-infected aphids I and their predators, ladybirds and ladybugs X, which are generalist predators, that can be bacteria-free, Z, or carriers, J. We do not explicitly model the wasp larvae that grow inside the aphids, nor the bacteria that are present and reproduce inside the infected aphids.

A scheme of the situation is contained in Figure 1 and the population interactions are schematized in Figure 2.

The basic mechanisms involved in this rather complex interaction system are outlined in the scheme presented below. Let us introduce some further notation, in which

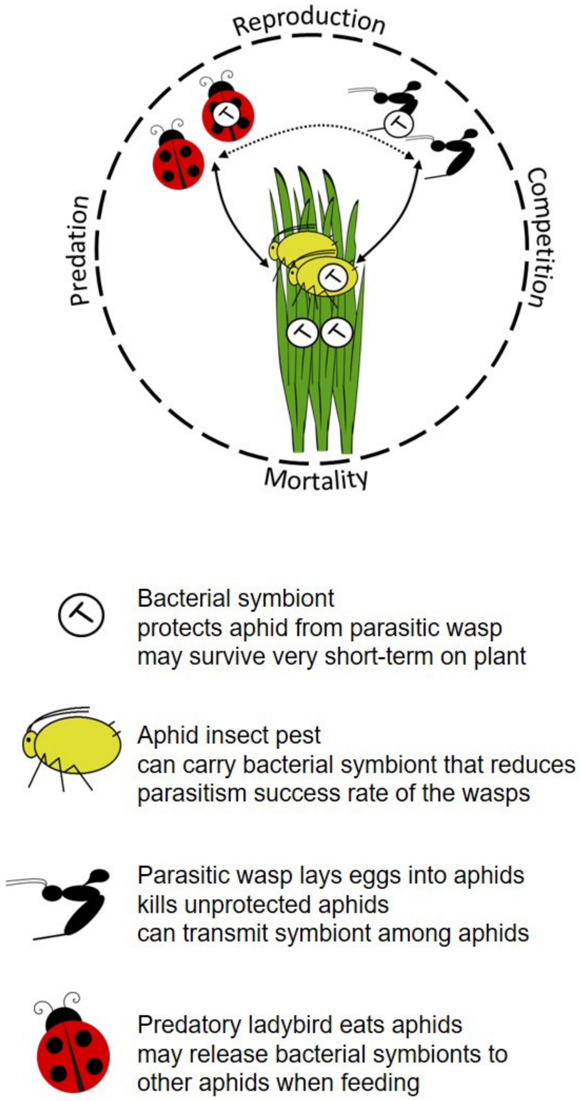

Fig. 1. A schematic picture of the ecosystem whose model is represented by system (3.1).

the relevant populations appear as subscripts. Each such term would be a function of possibly several other populations, that are not explicitly specified in (3.1), but will be duly discussed in the remaining of this Section. Let L denote intraspecific population losses, R reproduction, C^d direct contamination via bacteria, C^v contamination through vectors, P predation by ladybirds, P^i induced losses in the wasp population due to ladybirds predation on aphids carrying the wasp eggs, E aphids losses due to wasps emergence from parasitized aphids, F free bacteria release in the open environ-

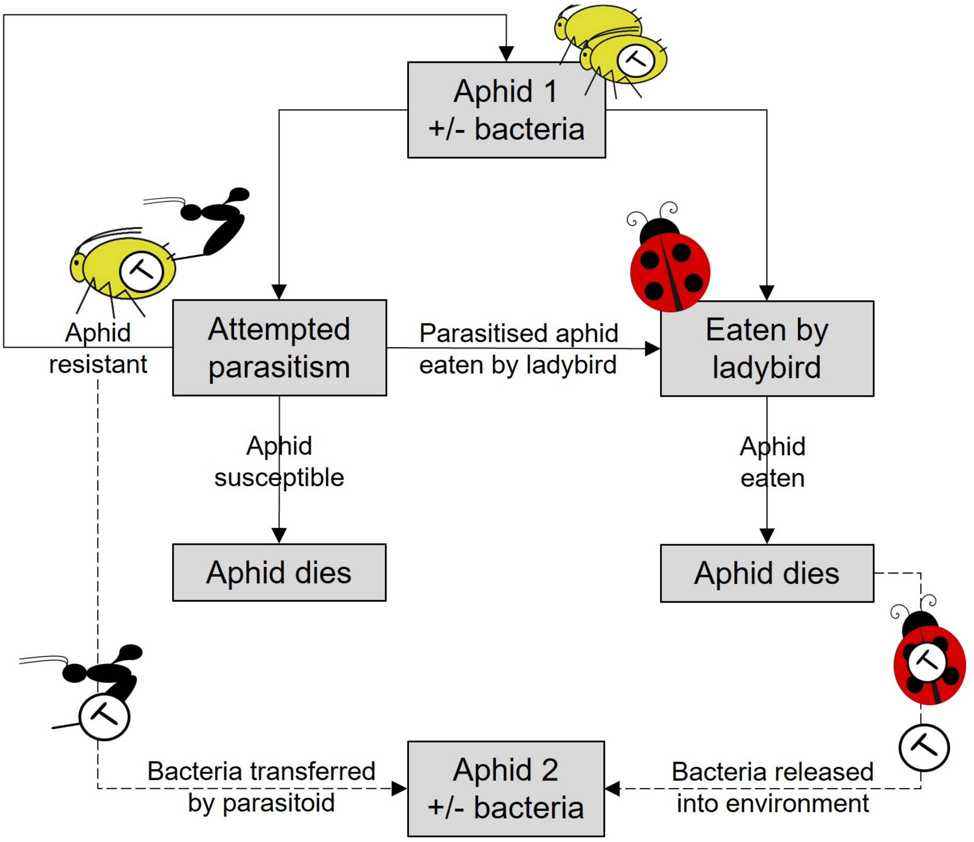

Fig. 2. A schematic representation of the population interactions.

ment by the predations on aphids.

Possible emigrations or immigrations for each population could also be considered including constant inputs $h \in \mathbf{R}$, but are omitted to keep the model tractable. The following equations summarize the interactions:

$$
\begin{aligned}
\frac{dW}{dt} &= R_W - WL_W - C_W^d - C_W^v - P_W^i - P_V^i \\
\frac{dV}{dt} &= -VL_V + C_W^d + C_W^v \\
\frac{dA}{dt} &= R_A - AL_A - C_A^d - C_A^v - E_A - P_A
\end{aligned}
\tag{3.1}
$$

$$\begin{aligned}
\frac{dI}{dt} &= R_I - IL_I + C_A^d + C_A^v - E_I - P_I \\
\frac{dZ}{dt} &= R_Z - C_Z^d - C_Z^v + P_Z + P_J \\
\frac{dJ}{dt} &= R_J + C_Z^d + C_Z^v \\
\frac{dB}{dt} &= F_B - BL_B.
\end{aligned}$$

Note that wasps reproduction occurs via the egg-larva-nimpha-adult stages, for which a good assumption is that if the deposing wasp carries bacteria on her body, the latter are "washed out" in this multiple stage process, so that offsprings emerge as uncontaminated new individuals. This implies to assume $R_V = 0$ in the above V equation. Free bacteria in the open environment cannot thrive, hence we set $R_B = 0$ and do not consider it any longer. Aphids reproduce asexually, with possibly different rates if they are healthy or infected. Also, once infected they cannot get rid of the bacteria within their bodies, so the infection is unrecoverable.

Note that both W and V are the same population Y, in the sense that the demographic parameters must be the same, since carrying or not carrying bacteria on the outside of their bodies does not affect them at all. Wasps are parasitoids, i.e. specialist "predators" of the aphids, in the sense that reproduce only by deposing their eggs inside the aphids. Their larvae feed on the aphids, thus slowly killing them, and finally emerge leaving an empty hull. The deposition rate (birth rate) p is the same for wasps W as well as bacteria-carrying wasps V, while instead $0 \le e \le 1$ is the fraction of the eggs that eventually become adult wasps. In case of an egg deposited in the infected aphids, reproduction is affected by a factor $0 \le f \le 1$, because the emergence rate in the presence of bacteria is much reduced, most likely and possibly even to zero, when the larva is killed inside the host.

Note further that the predation gains for the ladybirds are accounted for in the uncontaminated predators equation via the term P_J as we assume that all the newborns ladybirds do not carry the bacteria on their bodies, for the same reason of the wasps, since also ladybirds reproduce via an egg-larva-nimpha-adult cycle.

We now describe in detail the specific functional forms of the above possible interactions among all the populations involved in this ecosystem.

3.1 - *Demographic losses*

We start from the demographic losses:

$$L_W = L_V = m + aY; \quad L_A = n + gA + \tilde{g}I; \quad L_I = \mu + cI + \tilde{c}A; \tag{3.2}$$

$$L_B = n + \gamma Y + \lambda(A + I) + \phi X.$$

For the wasps, L_W and L_V, which must be the same function as mentioned above, contain the wasps natural mortality m and then the intraspecific competition, at the rate a; the latter also is exerted in the same way by both non-carrier wasps as well as vector wasps, so we take the overall wasp population $Y = W + V$ in it.

For the aphids however, we must distinguish among healthy and parasitized individuals. For the former, L_A contains the natural mortality rate n which instead becomes μ in case of the infected ones, in L_I, and in both functions appear the intraspecific competition rates. In this case, however, the "infected" individuals host within their bodies the wasp larva, which affects them, and we must take this into account. Thus the intraspecific competition rates are modified by the infection, so they are distinguished both for and when due by healthy or infected aphids, with respective rates a, $\widetilde{a}$ and c, $\widetilde{c}$.

Free bacteria, meaning those that are neither inside their aphid hosts, nor those that are attached to the wasps bodies, i.e. just those that are present on the plant, do not survive in the open environment and do not reproduce there, so that they experience a natural mortality rate n. They also disappear from the environment when they are picked up by wasps, both uncontaminated as well as carriers, second term, at rate γ, with the mechanism earlier described. Note further that the contaminated wasps picking up more bacteria does not make them "more infected", thus the equations previously described are not altered, as the V's were and remain carriers. The free bacteria are also picked up by aphids in some way, this being the actual infection mechanism hypothesized in this specific model, at rate λ. Again, when an infected aphid gets infected by one more bacterium, we cannot count one more individual among the I's but we have to subtract a bacterium from the B's. Similarly, bacteria can attach themselves to the ladybirds bodies, which may, J, or may not, Z, already carry some of them, this phenomenon occurring at rate ϕ with the same proviso. Thus our notation in this case is a bit stretched, in the sense that the function L_B here does not really model just intraspecific interactions.

3.2 - *Reproduction*

We now describe each population reproduction function:

$$R_W = W[epA + efpI] + V[epA + efpI]; \quad R_A = rA; \quad R_I = bI; \\ R_Z = uX - vZ - kZX; \quad R_J = -vJ - kJX. \tag{3.3}$$

The deposition rate p is the same for wasps W as well as for bacteria-carrying wasps V, for the reasons already described above, the bacteria attached externally on their bodies do not affect their demographic capacities. We further denote by $0 \le e \le 1$ the fraction of new wasps emerging rate from eggs deposited in a healthy aphid body, which is further reduced by a factor $0 \le f < 1$ if the egg is deposited in an infected aphid. Thus the net birth rate from a healthy aphid is ep, while from an infected one is efp. As all newborn wasps are uncontaminated, these terms appear in the equation for R_W. When the deposing wasp is uncontaminated, the former is expressed by the first term in the bracket, the latter by the second one. For a carrier wasp, the corresponding newborns are modeled via the third and fourth terms, respectively.

For the aphids, we must distinguish among healthy and infected ones, so that the healthy aphids reproduction rate is r, which becomes b for the infected ones.

Finally, reproduction of the predators is modeled via a logistic-like equation, because it is assumed that they have other food sources, with reproduction rate u and natural mortality rate v. Summing the last two equations in (3.3) we obtain indeed a logistic equation with total environmental carrying capacity $(u - v)k^{-1}$. The reproduction rate is split among bacteria-uncontaminated and carriers so that each subpopulation feels the intraspecific pressure k of the whole ladybirds population $X = Z + J$. Furthermore, the whole new generation of the adults appears uncontaminated, because as mentioned they undergo various stages before reaching full maturity, and we assume then that the bacteria, if acquired, are possibly lost before reaching maturity.

3.3 - *Contamination by bacteria*

For the contamination functions we have:

$$C_W^d = \gamma BW; \quad C_A^d = \lambda BA; \quad C_Z^d = \phi BZ; \\ C_A^v = \beta VA; \quad C_W^v = (\omega I + \delta V)W; \quad C_Z^v = (\chi I + \psi J)Z. \tag{3.4}$$

Here the direct contamination rates, as already mentioned in discussing the aphid loss functions, are taken as γ for the wasps, λ for aphids and ϕ for the ladybirds. Recall that the corresponding interaction terms are losses for the bacteria population, as they are removed from the plants. Further these are contamination mechanisms for which the insect that picks up a bacterium leaves the class of uncontaminated population of its respective population and appears in the corresponding carrier population, with a net balance that leaves the whole population size unchanged. If the bacteria are picked up by already contaminated individuals, they are removed from the environment, but do not contribute to new carriers in the respective population. For the indirect contamination, which occurs via another bacteria-affected agent, the basic routes are mainly interspecific. Namely, a new infected aphid is generated during the laying of the wasp egg, at rate β. This term represents the hypothesis investigated already in [**27**]. Then, a new wasp carrier is generated by contact of an healthy wasp with an infected aphid, most likely during ovideposition, at rate ω, and a similar term with rate χ for the ladybirds. Finally, we can also consider intraspecific transmission, assuming that both ladybird-ladybird and wasp-wasp interactions $Z - J$ and $W - I$ are relatively rare, so that such transmissions of bacteria occur at respective rates that are very low, compared to the former ones, namely $\delta << \omega$, $\psi << \chi$.

3.4 - *Parasitization effects*

We next discuss the aphids losses due to emergence of newborn adult wasps from their parasitised bodies:

$$E_A = epWA + epAV; \quad E_I = efpWI + efpIV. \tag{3.5}$$

For an healthy aphid, this can occur via egg deposition from an uncontaminated wasp with subsequent hatching, which occurs at rate ep via the term $epAW$, or when the egg is deposited by a carrier wasp, originating the term $epAV$. Emergence from infected aphids is obtained by similar terms, scaled via the factor f, namely giving $efpWI$, the first term in E_I. If the egg is deposited by a carrier, we have the term $efpIV$, i.e. the second term in E_I.

3.5 - *Ladybirds predation*

For the predation by ladybirds, we have to distinguish among two effects, one direct on aphids with population losses and a corresponding advantage for the predators, and an indirect one, as a loss of an aphid that is parasitized by a wasp larva constitutes also a damage for the latter, a population loss in the parasitoids. Again, we remark that whether the ladybirds are contaminated or not does not influence their demographic behavior, in this case specifically the hunting rate. These facts are described as follows:

$$\begin{aligned} P_A &= qA(Z+J); \quad & P_Z &= \widetilde{q}(A+\eta I)Z; \quad & P_W^i &= pqAXY; \\ P_I &= qI(Z+J); \quad & P_J &= \widetilde{q}(A+\eta I)J; \quad & P_V^i &= pqfIXY. \end{aligned} \tag{3.6}$$

Predation on healthy and parasitized aphids is carried out at the same rate q by the whole ladybirds population. These terms constitute instead a gain for each ladybird subpopulation, expressed by the factor $\widetilde{q} < q$, possibly scaled via the factor η for the infected aphids, as the presence of bacteria may alter the nutritional content for the predators. Finally the losses of the wasps larval content in the inoculated aphids corresponds to the predator removal of the fraction of the aphids that contain larvae, that we know has already been denoted by p. In case of infected aphids, this must be further scaled via the fraction f expressing, as we know, the larvae survival rate in the presence of the bacteria in the aphids bodies.

3.6 - *Bacteria release in the environment*

Release of free bacteria from infected aphids occurs when an attacking ladybird chews the aphid, so that part of its bodily content is released in the environment. Let α denote the bacteria liberation rate into the open environment due to this mechanism. In principle one may think that when the aphid dies naturally or by intraspecific competition, expressed by the terms L_I in (3.2), its body decomposes, again releasing in the environment its content. This could be modeled via a different bacteria release rate, $\widetilde{\alpha}$. However, as the bacteria thrive only in the living aphid, in such case they will die together with the aphid. Therefore this possible contribution $\widetilde{\alpha}(\mu + cI + \widetilde{c}A)$ to F_B cannot occur on biological grounds. Finally, mortality can be induced also by the killing of the aphids when the new wasp emerges from them. Release of bacteria in the environment in such case again does not occur as the aphid body at this point has become an empty husk because the wasp larva has eaten all its contents. Therefore also the possible contribution term to F_B, of the type $\alpha epfY$, is not included in the model. The equation then reads:

$$F_B = \alpha qIX. \tag{3.7}$$

Overall, defining the shorthands

$$Y = V + W, \quad X = Z + J, \tag{3.8}$$

we have the following equations

$$\begin{aligned}
\frac{dW}{dt} &= Y[epA + efpI] - W[m + aY + \gamma B] - (\omega I + \delta V)W - pqAXY, \\
\frac{dV}{dt} &= \gamma BW - V[m + aY] + (\omega I + \delta V)W,
\end{aligned} \tag{3.9}$$

$$\frac{dA}{dt} = A[r - n - gA - \tilde{g}I] - \lambda BA - \beta VA - epWA - epAV - qAX,$$

$$\frac{dI}{dt} = I[b-\mu-cI-\tilde{c}A]+\lambda BA+\beta VA-efpWI-efpIV-qIX, \tag{3.10}$$

$$\begin{aligned}\frac{dZ}{dt} &= uX-vZ-kZX-\phi BZ-(\chi I+\psi J)Z+\widetilde{q}(A+\eta I)X,\\ \frac{dJ}{dt} &= -vJ-kJX+\phi BZ+(\chi I+\psi J)Z,\end{aligned} \tag{3.11}$$

$$\frac{dB}{dt} = \alpha qIX-B[n+\gamma Y+\lambda(A+I)+\phi X]. \tag{3.12}$$

4 - Model analysis

To assess the equilibria, we follow a path that allows their determination on the basis of the possibility of each population to appear or not to appear in the corresponding equilibrium configuration. We expose the analysis in full detail, rather than summarize just the points found, for completeness of presentation.

Clearly the origin E_0 is a possible equilibrium, in view of the fact that (3.9)-(3.10)-(3.11)-(3.12) is a homogeneous system.

We discriminate at first on the bacteria population. Initially assume that it is not present, so that $B=0$.

The seventh equilibrium equation, (3.12), implies then that either $I=0$ or $X=0$, i.e. $Z=J=0$, The latter will be denoted as Case (B) and analysed later. For $I=0$, from the second equation in (3.10) we find either $A=0$, that we next investigate, or Case (A), namely $V=0$.

4.1 - *Case* $I=A=0$

In the situation with $I=A=0$, the first equilibrium equation in (3.10) holds, the first (3.9) gives $W=0$, since $W\neq 0$ implies then that a linear combination of populations with positive coefficients gives a negative value, and the second one in turn $V=0$, again because the opposite statement gives a negative value for V. From the second equation in (3.11) we find

$$X=\frac{1}{k}(\psi Z-v).$$

Summing the equations (3.11) instead, we find

$$X=\frac{u-v}{k},$$

which, upon substution into the former one, gives in turn

$$Z_1 = \frac{u}{\psi}, \quad J_1 = \frac{(u-v)\psi - uk}{k\psi} \tag{4.1}$$

which define the equilibrium $E_1 = (0,0,0,0,Z_1,J_1,0)$ or else $J = 0$ and a nonvanishing value for Z, but this will constitute equilibrium E_6 analysed later. E_1 is feasible for

$$u\psi \geq v\psi + uk. \tag{4.2}$$

4.2 - *Case (A)*

We now consider case (A). Here $B = I = V = 0$ and the second equilibrium equations in (3.9) and (3.10) are satisfied. There are four equilibria to consider.

We find at first the point $E_8 = (W^{\Psi}_{8+}, 0, A^{\Psi}_{8+}, 0, Z^{\Psi}_{8+}, J^{\Psi}_{8+}, 0)$, which is fully analysed in the Appendix A. Its feasibility conditions are (6.3), (6.5), (6.6) and (6.7).

4.2.1 - `Equilibria` E_{11} `and` E_{12}

We further discover the equilibrium $E_{11} = (0,0,A_{11},0,Z_{11},0,0)$ with

$$A_{11} = \frac{k(r-n) - q(u-v)}{gk + q\widetilde{q}}, \quad Z_{11} = \frac{(u-v)g + \widetilde{q}(r-n)}{gk + q\widetilde{q}}, \tag{4.3}$$

feasible for

$$rk + qv \geq nk + qu, \quad gu + \widetilde{q}r \geq gv + \widetilde{q}n. \tag{4.4}$$

Further, the situations of simultaneously nonvanishing of the triples A, Z and J, as well as W, A and Z, lead to two additional equilibria, namely $E_{12} = (0,0,A_{12},0,Z_{12}, J_{12},0)$ and E_{14} where for the former we find

$$\begin{aligned} A_{12} &= \frac{k(r-n) - q(u-v)}{gk + q\widetilde{q}}, \quad & X &= \frac{1}{k}(u - v + \widetilde{q}A_{12}), \\ Z_{12} &= \frac{1}{\psi}(u + \widetilde{q}A_{12}), \quad & J_{12} &= \frac{1}{q}(r - n - gA_{12}) - Z_{12}, \end{aligned} \tag{4.5}$$

with feasibility provided by the conditions

$$r \geq n + gA_{12} + \frac{qu}{\psi} + \frac{q\widetilde{q}}{\psi}A_{12}, \quad A_{12} \geq \frac{v-u}{\widetilde{q}}, \tag{4.6}$$

Table 1. *Equilibria of the system* (3.9)*,* (3.10)*,* (3.11)*,* (3.12) *and their feasibility conditions. NI stands for Not Investigated, for the cases that cannot be analytically analysed.*

Equilibrium	Populations	Feasibility
E_0	$(0,0,0,0,0,0,0)$	—
E_1	$(0,0,0,0,Z_1,J_1,0)$	(4.2)
E_2	$(W_2,0,A_2,0,0,0,0)$	(4.7)
E_{3+}	$(W_{3+},V_{3+},0,I_{3+},0,0,0)$	(4.8); sufficient: (4.9)
$E_{3\pm}$	$(W_{3\pm},V_{3\pm},0,I_{3\pm},0,0,0)$	(4.8), (4.10)
E_4	$(0,0,A_4,I_4,0,0,0)$	(4.11) or (4.12)
E_5	$(0,0,0,\frac{b-\mu}{c},0,0,0)$	$b \geq \mu$
E_6	$(0,0,0,0,\frac{u-v}{k},0,0)$	$u \geq v$
E_8	$(W^{\Psi}_{8+},0,A^{\Psi}_{8+},0,Z^{\Psi}_{8+},J^{\Psi}_{8+},0)$	(6.3), (6.5), (6.6), (6.7)
E_{10}	$(0,0,\frac{r-n}{g},0,0,0,0)$	$r \geq n$
E_{11}	$(0,0,A_{11},0,Z_{11},0,0)$	(4.4)
E_{12}	$(0,0,A_{12},0,Z_{12},J_{12},0)$	(4.6)
E_{14}	$(W_{14+},0,A_{14+},0,Z_{14+},0,0)$	(6.10), (6.9)
E_{13}	$(W_{13},V_{13},A_{13},I_{13},0,0,0)$	NI
E_{15}	$(0,0,0,I_{15},Z_{15},J_{15},B_{15},)$	(6.17)
E_{16}	$(0,0,A_{16},I_{16},Z_{16},J_{16},B_{16},)$	(6.20), (6.21) and conic intersections discussed in the text
$E_{9\pm}$	$(W_{9\pm},V_{9\pm},0,I_{9\pm},Z_{9\pm},J_{9\pm},B_{9\pm},)$	(6.25), (6.27), (6.30)
E_7	$(W_7,V_7,A_7,I_7,Z_7,J_7,B_7)$	NI

the latter, once rewritten explicitly, corresponding to the second condition in (4.4).

The last equilibrium is $E_{14} = (W_{14+},0,A_{14+},0,Z_{14+},0,0)$, again analysed in Appendix A. For its feasibity conditions (6.9) and (6.10) must hold.

This concludes the analysis of case (A).

4.3 - *Case (B)*

We now turn to Case (B), where $B = Z = J = 0$. The equilibrium equations (3.11) and (3.12) are satified.

4.3.1 - Equilibria E_2, E_3, E_4

Assume $I = 0$, Case (C). Then either $V = 0$ or $A = 0$. In the latter case, the first equilibrium equation in (3.9) cannot be satisfied. In the former one instead, the second equilibrium equation in (3.9) holds. The first ones in (3.9) and (3.10) yield

$$A_2 = \frac{emp + a(r-n)}{e^2p^2 + ag}, \quad W_2 = \frac{r - n - gA_2}{ep}.$$

Nonnegativity of W_2 requires $ar + emp \geq an$ but this condition is implied by the corresponding one for A_2. Feasibility for $E_2 = (W_2, 0, A_2, 0, 0, 0, 0)$ reduces thus to

$$r \geq n + \frac{gm}{ep}. \tag{4.7}$$

The case $I \neq 0$ and $A = 0$ entails that the first equilibrium equation in (3.10) holds. From the corresponding first equilibrium equation in (3.9) and the second ones in (3.10) and (3.11), the nonvanishing populations are found

$$I_3 = \frac{a(b-\mu) + efmp}{ac + e^e f^2 p^2}, \quad W_3 = \frac{efpI_3V_3}{\omega I_3 + \delta V_3},$$

for the positivity of which we need to require

$$ab + efmp \geq a\mu. \tag{4.8}$$

V_3 is a root of the quadratic $\Gamma(V) = \sum_{k=0}^{2} \pi_k V^k = 0$, with

$$\pi_2 = -a\delta, \quad \pi_1 = \delta(efpI_3 - m) - a\omega I_3 - aefpI_3, \quad \pi_0 = \omega I_3(efpI_3 - m).$$

Now, for a positive root V_{3+} it is sufficient to require $efpI_3 > m$, i.e.

$$befp > efp\mu + cm. \tag{4.9}$$

Instead if $efpI_3 < m$, we need a positive discriminant $\Delta_\Gamma > 0$ to have two positive roots:

$$[\delta(efpI_3 - m) - (a\omega + aefp)I_3]^2 + 4a\omega I_3(a\omega + aefp)\delta > 0. \tag{4.10}$$

Now if $I \neq 0$, $V = 0$ and $A \neq 0$, the equations (3.9) are satisfied if $W = 0$, and then from (3.10) we find $E_4 = (0, 0, A_4, I_4, 0, 0, 0)$ with

$$I_4 = \frac{(b-\mu)g - \widetilde{c}(r-n)}{cg - \widetilde{c}\widetilde{g}}, \quad A_4 = \frac{c(r-n) - \widetilde{g}(b-\mu)}{cg - \widetilde{c}\widetilde{g}},$$

with feasibility conditions given by one of the alternative sets:

$$bg + \widetilde{c}n \geq \mu g + \widetilde{c}r, \quad cr + \widetilde{c}\mu \geq cn + b\widetilde{g}, \quad cg > \widetilde{c}\widetilde{g} \tag{4.11}$$

$$bg + \widetilde{c}n \leq \mu g + \widetilde{c}r, \quad cr + \widetilde{c}\mu \leq cn + b\widetilde{g}, \quad cg < \widetilde{c}\widetilde{g}. \tag{4.12}$$

4.3.2 - `Equilibria` E_5, E_6, E_{10}

Alternatively, the case $I \neq 0$, $V \neq 0$ and $A \neq 0$ implies that the first equation (3.9) if $W = 0$ is impossible. For $B = 0$, $Z = 0$ and $J = 0$, one can also have the one-population equilibria $E_5 = (0, 0, 0, I_5, 0, 0, 0)$ and $E_{10} = (0, 0, A_{10}, 0, 0, 0, 0)$; in this context (which does not really belong to case (B), but is reported here anyway), allowing $Z \neq 0$, we also find $E_6 = (0, 0, 0, 0, Z_6, 0, 0)$, with

$$I_5 = \frac{b - \mu}{c}, \quad A_{10} = \frac{r - n}{g}, \quad Z_6 = \frac{u - v}{k}$$

and feasibility conditions given respectively by

$$(E_5) : \ b \geq \mu, \quad (E_{10}) : \ r \geq n, \quad (E_6) : \ u \geq v. \tag{4.13}$$

Finally, there is the possibility of equilibrium $E_{13} = (W_{13}, V_{13}, A_{13}, I_{13}, 0, 0, 0)$. Again, the feasibility details are reported in Appendix A.

This concludes the analysis of case (B) and therefore, together with case (A), of the whole set of the bacteria-free equilibria. A schematic picture of these equilibria is reported in Figure 3.

4.4 - *Bacteria present in the environment:* $B \neq 0$

We now consider the case in which bacteria are present in the system steady states, $B \neq 0$.

In this condition $I = 0$ cannot occur, because the last equation, (3.12), would not be satisfied, nor for the same reason can X vanish, entailing both $Z = J = 0$. Thus there are three subcases left whenever $X > 0$. But $Z > 0$, $J = 0$ and $Z = 0$, $J > 0$ both cannot occur because the second equation (3.11) would not be satisfied. We are thus reduced to assume

$$I \neq 0, \quad Z \neq 0, \quad J \neq 0, \quad B \neq 0.$$

There are three more equilibria that arise, in addition to E^7, the coexistence of all the ecosystem populations. We find $E_{15} = (0, 0, 0, I_{15}, Z_{15}, J_{15}, B_{15})$, as well as $E_{16} = (0, 0, A_{16}, I_{16}, Z_{16}, J_{16}, B_{16})$ and $E_9 = (W_9, V_9, 0, I_9, Z_9, J_9, B_9)$. In this situation the second equation (3.9) prevents the remaining possible subcases.

Again, the feasibility analysis of all these equilibria is deferred to Appendix A.

Figure 4 represents schematically the bacteria-affected equilibria.

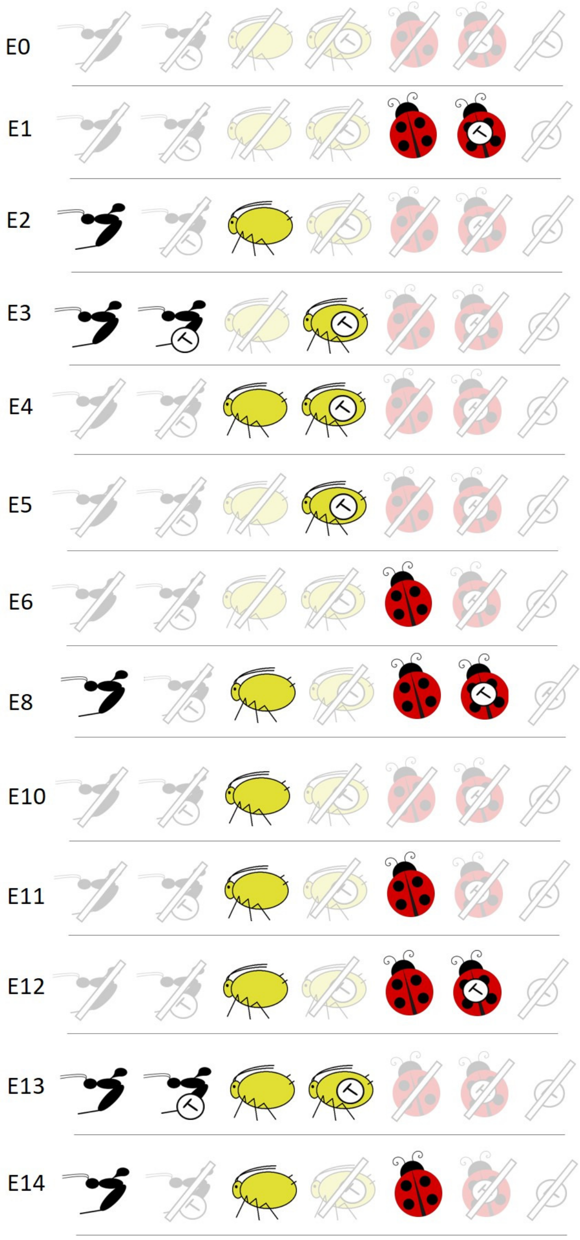

Fig. 3. Picture of the bacteria-free equilibria. Left to right, in each column are shown in color the populations W, V, A, I, Z, J, B that thrive.

5 - Stability

5.1 - *The bacteria-free equilibria*

5.1.1 - `Equilibrium` E_0

At E_0, the Jacobian, fully reported in its general form in Appendix B, becomes a diagonal matrix, from which the eigenvalues are immediately found

$$-m, \quad -m, \quad r-n, \quad b-\mu, \quad u-v, \quad -v, \quad -n$$

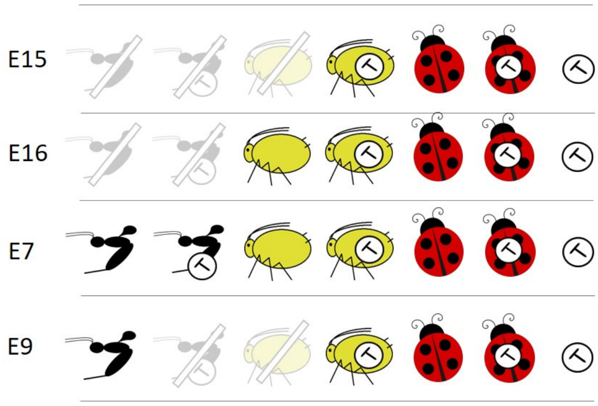

Fig. 4. Picture of the equilibria where bacteria thrive. Left to right, in each column are shown in color the populations W, V, A, I, Z, J, B that thrive.

to give the stability condition

$$b < \mu, \quad r < n, \quad u < v. \tag{5.1}$$

5.1.2 - Equilibrium E_1

For E_1, five eigenvalues are immediate, recalling (3.8)

$$-m, \quad -m, \quad r - n - qX_1, \quad b - \mu - qX_1, \quad -n - \phi X_1,$$

the remaining two arise from a two by two minor $\widehat{J}_{E_1}$, which using the equilibrium equations, has a negative trace and a positive determinant,

$$\begin{aligned}
\operatorname{tr}(\widehat{J}_{E_1}) &= -\left(kZ_1 + u\frac{J_1}{Z_1}\right) - kJ_1 < 0,\\
\det(\widehat{J}_{E_1}) &= \left(kZ_1 + u\frac{J_1}{Z_1}\right) kJ_1 - [u - (k+\psi)Z_1](\psi - k)J_1\\
&= \frac{J_1}{Z_1}[kuJ_1 + u(k-\psi)Z_1 + \psi^2 Z_1^2] = \frac{J_1}{Z_1}\delta_1.
\end{aligned}$$

But the feasibility condition (4.2) implies that $u \geq v$, from which $\delta_1 > 0$ and in turn $\det(\widehat{J}_{E_1}) > 0$, so that it does not contribute to stability. The conditions for its occurrence come from the eigenvalues above, giving

$$r < n + qX_1 = n + q\frac{u-v}{k}, \quad b < \mu + qX_1 = \mu + q\frac{u-v}{k}. \tag{5.2}$$

5.1.3 - Equilibrium E_2

Three eigenvalues are obtained easily for the Jacobian evaluated at E_2,

$$u - v + \widetilde{q}A_2, \quad -v, \quad -n - \lambda A_2 - \gamma W_2 < 0.$$

The remaining part of the matrix factorizes into two minors, both two by two, Δ_2^{13} and Δ_2^{24}, where the superscripts denote the diagonal elements that they contain and the index refers to the equilibrium. The Routh-Hurwitz conditions for the negativity of their eigenvalues are now investigated. Suitably using the equilibrium equations, we find

$$\mathbf{J}_{11}(E_2) = -aW_2 < 0, \quad \mathbf{J}_{33}(E_2) = -gA_2 < 0.$$

For Δ_2^{13} then it follows

$$-\mathrm{tr}\Delta_2^{13} = aW_2 + gA_2 > 0, \quad \det \Delta_2^{13} = (ag + e^2p^2)A_2W_2 > 0$$

so that the conditions are satisfied unconditionally, while for Δ_2^{24} we have instead to require the following conditions

$$\begin{aligned} &\beta + \delta W_2 < m + aW_2 + \mu + \widetilde{c}A_2 + efpW_2, \\ &\beta\omega A_2W_2 + b(m + aW_2) + \delta W_2(\mu + \widetilde{c}A_2 + efpW_2) \\ &\qquad\qquad < \delta bW_2 + (\mu + \widetilde{c}A_2 + efpW_2)(m + aW_2). \end{aligned} \tag{5.3}$$

In addition negativity of the explicitly found eigenvalues is also needed, implying:

$$u + \widetilde{q}A_2 < v. \tag{5.4}$$

5.1.4 - Equilibrium E_3

At the equilibrium E_3 only one eigenvalue can be factorized immediately, $\mathbf{J}_{33}(E_3)$, providing the first stability condition, recalling (3.8)

$$r < n + \widetilde{g}I_3 + \beta V_3 + epY_3. \tag{5.5}$$

Use of the equilibrium equations gives the negative diagonal elements

$$\mathbf{J}_{11}(E_3) = -aW_3 - efp\frac{I_3V_3}{W_3}, \quad \mathbf{J}_{22}(E_3) = -aV_3 - \omega\frac{I_3W_3}{V_3}, \quad \mathbf{J}_{44}(E_3) = -cI_3.$$

The Jacobian further factorizes into the product of two minors of size three, Δ_3^{124} and Δ_3^{567}. A careful analysis of the latter then shows that it gives an additional negative eigenvalue, $\mathbf{J}_{77}(E_3) = -n - \gamma Y_3 - \lambda I_3 < 0$. The Routh-Hurwitz conditions for the remaining part of the minor, Δ_3^{56}, $-\mathrm{tr}\Delta_3^{56} = -\mathbf{J}_{55}(E_3) - \mathbf{J}_{66}(E_3) > 0$ and $\det \Delta_3^{56} = \mathbf{J}_{55}(E_3)\mathbf{J}_{66}(E_3) - \mathbf{J}_{56}(E_3)\mathbf{J}_{65}(E_3) > 0$ explicitly give

$$u + \widetilde{q}\eta I_3 < 2v + \chi I_3, \quad (v + \chi I_3)v > v(u + \widetilde{q}\eta I_3) + \chi I_3(u + \widetilde{q}\eta I_3). \tag{5.6}$$

For Δ_3^{124} the Routh-Hurwitz conditions require also the calculation of the sum $\Sigma_3^{124} = \Delta_3^{12} + \Delta_3^{14} + \Delta_3^{24}$ of the minors of order two:

$$\begin{aligned}
\Delta_3^{12} &= \mathbf{J}_{11}(E_3)\mathbf{J}_{22}(E_3) - ((a+\delta)W_3 - efpI_3)\left((a-\delta)V_3 - \omega I_3\right), \\
\Delta_3^{14} &= -cI_3\mathbf{J}_{11}(E_3) - efpI_3\left(\omega W_3 - efpI_3(V_3 + W_3)\right), \\
\Delta_3^{24} &= -cI_3\mathbf{J}_{22}(E_3) + efpI_3\omega W_3.
\end{aligned}$$

In addition, we need $-\mathrm{tr}\Delta_3^{124} = -\mathbf{J}_{11}(E_3) - \mathbf{J}_{22}(E_3) - \mathbf{J}_{44}(E_3) > 0$, which is always true by the diagonal elements being negative and $-\det \Delta_3^{124} > 0$. Explicitly:

$$\begin{aligned}
cI_3\Delta_3^{12} + efpI_3\omega W_3 &\left[efpI_3\left(1 + \frac{V_3}{W_3}\right) - \omega\frac{I_3W_3}{V_3} - \omega I_3 - 2\delta W_3\right] \\
&> efpI_3\left(V_3 + W_3\right)\left[\omega\frac{I_3W_3}{V_3} + \omega I_3 + \delta V_3\right].
\end{aligned} \tag{5.7}$$

The final Routh-Hurwitz condition for stability is

$$-\mathrm{tr}\Delta_3^{124}\Sigma_3^{124} > -\det \Delta_3^{124}. \tag{5.8}$$

5.1.5 - Equilibrium E_5

At E_5 three eigenvalues are immediately found, $\mathbf{J}_{77}(E_5) = -n - \lambda I_5 < 0$, $\mathbf{J}_{44}(E_5) = -cI_5 < 0$ and one more from $\mathbf{J}_{33}(E_5)$ that provides the first stability condition

$$r < n + \widetilde{g}I_5. \tag{5.9}$$

There are then two remaining minors of order two, Δ_5^{12} and Δ_5^{56}, for which the Routh-Hurwitz conditions need to be assessed. The condition for Δ_5^{12} on the trace gives $2m + \omega I_5 > efpI_5$, which is implied by the determinant one. A similar situation arises for the trace of Δ_5^{56}, $2v + \chi I_5 > u + \tilde{q}\eta I_5$. Thus stability is regulated only by the conditions on the determinants of Δ_5^{12} and Δ_5^{56}, which respectively read

$$m > efpI_5, \quad v > \tilde{q}\eta I_5. \tag{5.10}$$

5.1.6 - `Equilibrium` E_4

For E_4 the Jacobian splits into three principal minors, the first two of order two, Δ_4^{12} and Δ_4^{34} the last one of order three, Δ_4^{567}, from which however a negative eigenvalue arises immmediately, $\mathbf{J}_{77}(E_4) = -n - \lambda(A_4 + I_4)$. The Routh-Hurwitz conditions on the trace of the minors Δ_4^{12} and Δ_4^{56} are implied by their respective conditions on the determinant, which give:

$$m > ep(A_4 + fI_4), \quad v > u + \widetilde{q}(A_4 + \eta I_4). \tag{5.11}$$

The trace of Δ_4^{34} is instead always negative, $-\mathrm{tr}\Delta_4^{34} = gA_4 + cI_4 > 0$, while the determinant provides the additional stability condition for this equilibrium:

$$cg > \widetilde{c}\widetilde{g}. \tag{5.12}$$

Thus this requirement entails that condition (4.12) gives raise just to an unstable feasible equilibrium.

5.1.7 - `Equilibrium` E_6

At this point all eigenvalues are explicitly known. Four of them are negative, $-m$, double, $\mathbf{J}_{55}(E_6) = -kZ_6$ and $\mathbf{J}_{77}(E_6) = -n - \phi Z_6$, while the remaining three provide the stability conditions:

$$r < n + qZ_6, \quad b < \mu + qZ_6, \quad \psi Z_6 < v + kZ_6. \tag{5.13}$$

5.1.8 - `Equilibrium` E_{10}

At E_{10} the third equilibrium equation gives the eigenvalue $\mathbf{J}_{33}(E_{10}) = -gA_{10} < 0$, three more are negative, $-m$, $-v$, $-n - \lambda A_{10}$ and the remaining ones give the stability conditions:

$$epA_{10} < m, \quad b < \mu + \widetilde{c}A_{10}, \quad u + \widetilde{q}A_{10} < v. \tag{5.14}$$

5.1.9 - `Equilibrium` E_{11}

The equilibrium equations for E_{11} give $\mathbf{J}_{33}(E_{11}) = -gA_{11}$, $\mathbf{J}_{55}(E_{11}) = -kZ_{11}$. One eigenvalue is negative, $-m$, one more is known immediately giving the first stability condition (5.15) below. Expanding the remaining minor $\Delta_{11}^{34567} - \Lambda\mathbf{I_5}$, where $\mathbf{I_5}$ denotes the identity matrix of order 5, it factorizes into the product of the subminor Δ_{11}^{47}, the linear term $\mathbf{J}_{66}(E_{11}) - \Lambda$ that provides the additional eigenvalue

$\mathbf{J}_{66}(E_{11}) = -v - (k - \psi)Z_{11}$, yielding the second stability condition (5.15) and the quadratic $\Lambda^2 + (gA_{11} + kZ_{11})\Lambda + (gk + q\widetilde{q})A_{11}Z_{11} = 0$, which has negative roots or roots with negative real part.

$$epA_{11} < m + pqA_{11}Z_{11}, \quad \psi Z_{11} < v + kZ_{11}. \tag{5.15}$$

The Routh-Hurwitz conditions applied to the minor Δ_{11}^{47}, $-\text{tr}(\Delta_{11}^{47}) > 0$ and $\det(\Delta_{11}^{47}) > 0$, give the remaining stability conditions:

$$\begin{gathered} b < n + \mu + (\widetilde{c} + \lambda)A_{11} + (q + \phi)Z_{11}, \\ (\mu - b + \widetilde{c}A_{11} + qZ_{11})(n + \lambda A_{11} + \phi Z_{11}) > \alpha\lambda qA_{11}Z_{11}. \end{gathered} \tag{5.16}$$

The details for the remaining equilibria, E_{12}, E_8, E_{14} and E_{13} are deferred to Appendix B.

5.2 - *Equilibria with the presence of bacteria*

For equilibria E_{15} and E_9, we state here only the stability conditions that can easily be established, reporting the more complicated ones in Appendix B, together with the analysis of the point E_{16}.

5.2.1 - `Equilibrium` E_{15}

Here we find that one eigenvalue is J_{33} which gives the stability condition

$$n + \widetilde{g}I_{15} + \lambda B_{15} + q(A_{15} + J_{15}) > r. \tag{5.17}$$

5.2.2 - `Equilibrium` E_9

Here the situation is even more difficult, as only one eigenvalue can be evaluated, and furthermore the remaining minor of order six cannot be factorized. The stability condition arising from the eigenvalue $\mathbf{J}_{33}(E_9)$ reads

$$r < n + \widetilde{g}I_9 + \lambda B_9 + epW_9 + qX_9. \tag{5.18}$$

6 - Discussion

The aim of this model is the investigation of the aphids infection process by bacteria that can protect them from wasp parasitoids. In this context, we should recall that

Table 2. *Equilibria of the system* (3.9), (3.10), (3.11), (3.12) *and their stability conditions. NI stands for Not Investigated, for the cases that cannot be analytically analysed.*

Equilibrium	Populations	Stability
E_0	$(0,0,0,0,0,0,0)$	(5.1)
E_1	$(0,0,0,0,Z_1,J_1,0)$	(5.2)
E_2	$(W_2,0,A_2,0,0,0,0)$	(5.3), (5.4)
E_3	$(W_3,V_3,0,I_3,0,0,0)$	(5.5), (5.6), (5.7), (5.8)
E_4	$(0,0,A_4,I_4,0,0,0)$	(5.11), (5.12)
E_5	$(0,0,0,\frac{b-\mu}{c},0,0,0)$	(5.9), (5.10)
E_6	$(0,0,0,0,\frac{u-v}{k},0,0)$	(5.13)
E_8	$(W_{8+}^{\Psi},0,A_{8+}^{\Psi},0,Z_{8+}^{\Psi},J_{8+}^{\Psi},0)$	(6.38), (6.40), (6.39), (6.41)
E_{10}	$(0,0,\frac{r-n}{g},0,0,0,0)$	(5.14)
E_{11}	$(0,0,A_{11},0,Z_{11},0,0)$	(5.15), (5.16)
E_{12}	$(0,0,A_{12},0,Z_{12},J_{12},0)$	(6.34), (6.35), (6.36), (6.37)
E_{14}	$(W_{14},0,A_{14},0,Z_{14},0,0)$	(6.42), (6.43), (6.44)
E_{13}	$(W_{13},V_{13},A_{13},I_{13},0,0,0)$	(6.46), (6.47), (6.48)
E_{15}	$(0,0,0,I_{15},Z_{15},J_{15},B_{15},)$	(5.17), (6.49), (6.50)
E_{16}	$(0,0,A_{16},I_{16},Z_{16},J_{16},B_{16},)$	(6.51), (6.52)
$E_{9\pm}$	$(W_{9\pm},0,0,I_{9\pm},Z_{9\pm},J_{9\pm},B_{9\pm},)$	(5.18), (6.53)
E_7	$(W_7,V_7,A_7,I_7,Z_7,J_7,B_7)$	NI

infecting bacteria are a nuisance, because they protect aphids from parasitoid wasps and reduce the effectiveness of biological control efforts. The model accounts for all the possible mechanisms that contribute to the infection.

By examining the equilibria of the model, it is immediately apparent that the presence of free bacteria in the environment, i.e. $B \neq 0$, entails also the presence of the infected aphids, compare equilibria E_{15}, E_{16} and E_9 in Table 1. On the other hand, the equilibria that one would strive to obtain are those in which no aphids are present, while possibly the remaining environmental populations still thrive. It should be clearly stated that these equilibria are ecologically very difficult, to achieve in the field, if not impossible. In fact, here we considered a closed system, where no immigrations are possible.

Equilibrium E_1 is not of this type, because together with the aphids also the parasitoids vanish, but this could be a price that can be willingly accepted, if the aphids population can be eradicated. In order to achieve it, both the feasibility (4.2) and the stability (5.2) conditions must be ensured. In these stability conditions, the reproduction r, b and mortality n, μ rates of uninfected and infected aphids appear. As the latter are usually smaller than the former, the quantity $qk^{-1}(u-v)$ should be large enough so that (5.2) is satisfied. In turn, this implies that the aphids' predators reproduce fast (high u) and die slowly (small v), and/or that their intraspecific competition rate k is small, and/or that their hunting rate on aphids q is large. On the other hand, to ensure feasibility, the ladybirds carrying capacity $(u-v)k^{-1}$ should exceed the ratio of reproduction u and transmission of bacteria ψ rates.

Equilibrium E_2 contains both wasps and uninfected aphids, at nonzero levels. It is therefore questionable if it is a target to be aimed at, as aphids are prone to be parasitized, but still they thrive in the environment, damaging the crops. In case this is found as an acceptable cost, assuming as mentioned above that aphids reproduce already fast enough, $r > n$, for its achievement the parameters g and m should be low, while e and p large, to ensure feasibility. The converse conditions would of course be required if this equilibrium should instead be avoided. In the former case, a low wasp mortality m is needed, as well as a low healthy aphids intraspecific competition g, and/or high wasp maturation e and deposition p rates. The stability conditions involve the equilibrium population values and therefore are more involved to interpret ecologically.

Equilibria E_3, E_4, E_5, E_{13} and E_9 contain the infected aphids population and therefore should be avoided as these are resistant to the parasitic wasps. Interestingly, note that the first four equilibria contain the bacteria thriving only inside the aphids' bodies, but not in the environment. This is possible clearly due to the reproduction mechanism of the aphids described in the model formulation, because there is vertical transmission of the bacteria. In order to achieve this aim, the feasibility or stability conditions must be violated. An easy way of obtaining this result for E_3 is via a large infected aphids mortality μ, compare conditions (4.8) and (4.9), but this may be difficult to hold, as in general their reproductive rate exceeds the mortality, $b > \mu$. But if for instance the parameters $\widetilde{g}$, β and ep are low enough, it may be possible to invalidate the stability condition (5.5). Thus for this to occur, a low wasp effective reproduction rate, as well as low intraspecific contacts among healthy and infected aphids and wasp carriers V would be needed.

To avoid equilibrium E_4 for instance one could try see if the stability condition (4.12) can be violated. This entails that the ratio of the intraspecific competition among healthy aphids and of healthy and infected aphids, $g\widetilde{g}^{-1}$, should not exceed the corresponding ratio of the intraspecific competition between infected and healthy aphids with the one pertaining only to infected aphids, $\widetilde{c}c^{-1}$. Note also, that perhaps paradoxically, a high level of aphids may entail that the stability condition (5.11) is violated, if the right hand sides of one of the inequalities exceeds the wasp, m, or the ladybirds, v, mortality rates. Similar considerations hold for the equilibrium E_5, compare (5.10). On the other hand, a low number of infected aphids may help in violating the first stability condition (5.9). For E_{13}, in view of the fact that the feasibility are not explicitly known, we focus only on stability. For instance, condition (6.47) would be violated for a low enough v, the ladybirds natural mortality. Note that a negative statement can also follow from this remark. For instance, the use of chemicals or other agents that indiscriminately kill insects would artificially increase v, and are therefore likely to favor the insurgence of equilibrium E_{13}.

At E_{10} only healthy aphids thrive. But from the stability analysis, it turns out easily that a low enough wasp mortality m coupled with a high effective reproduction rate of theirs, ep, renders this point unstable, compare the first condition in (5.14).

Susceptible aphids can thrive with their predators, whether only not carriers, point E_{11}, or also including the carrier ones, E_{12}. In both cases it is observed that a high value of the parameter e, the wasp emergence rate from larvae implanted in the aphids, may help in destabilizing these equilibria, compare (5.15) and (6.34). A high contagion rate ψ of healthy wasps from carrier wasps may achieve the same result for the point E_{11}, when combined with low wasp mortality and intraspecific competition rates. A high aphids population level coupled with a relatively low reproduction rate may instead render the point E_{12} unfeasible, see the first condition in (4.6). The equilibrium E_{14} can instead be destabilized by a high bacteria transmission rate among healthy and carriers ladybirds, ϕ, combined with their low mortality and intraspecific competition rates, see (6.42).

Equilibrium E_6 contains only the predators. If we are willing to sacrifice the parasitoid population, it can be achieved if the ladybirds population is high enough. This can certainly be obtained by an artificial enrichment of the environment of such predators, and indicates that at least in principle, biological control could be viable.

The above considerations are relevant, especially because some of the indicated measures to achieve or avoid some equilibria involve insects intrinsic parameters, but perhaps they could be acted upon by suitable external human actions. These could represent viable indications for the field workers, suggesting possible strategies for the biological control of these infestants.

6.1 - *Comparison with the earlier, reduced model*

Note that in the previous investigation [**27**] only four equilibria were found other than the origin and coexistence. The infected-aphids-only point of [**27**] corresponds to the equilibria E_5 and E_{15} of this paper. The former has only the infected aphids as nonvanishing populations, the latter also free bacteria and ladybirds. For E_5 the feasibility conditions are the same as in [**27**], while for E_{15} they can be relaxed or strenghtened depending on the sign and magnitude of the quantity $q(v - u)k^{-1}$. If positive, the aphids birth rate can be lowered perhaps even below the mortality level, without affecting the equilibrium feasibility, and conversely a large ladybirds net birth rate $u - v$ would render this equilibrium unfeasible. For stability of E_5, condition (5.9) is the same as found in [**27**]. But now two more are necessary for stability, (5.10), on which to act to prevent this equilibrium to arise. In particular, the wasps m and ladybirds v natural mortalities, if low enough, would respectively drop below the thresholds $efb(b - \mu)c^{-1}$ and $\widetilde{q}\eta(b - \mu)c^{-1}$. In this situation a high infected aphids mortality c would also be of help. Therefore the enlarged model at hand here, shows that there are further tools available for controlling these pests, than those found in [**27**].

In [**27**] another one-population equilibrium is the susceptible-aphids-only point. It corresponds here to the points E_{10}, E_{11} and E_{12}. The feasibility condition $r \geq n$ for which the susceptible aphids net birth rate is positive arises also here at E_{10} but it is relaxed for E_{11} and E_{12} where similar considerations as in the previous case of E_{15} can be made. These equilibria could be rendered unfeasible by suitably playing with the ladybirds net birth rate, for instance for E_{11}. Also in this case the stability conditions for the three points E_{10}, E_{11} and E_{12} provide more options for their destabilization than those found for the correspoding equilibrium in [**27**]. For instance, a very high transmission rate ψ among ladybirds destabilizes E_{11}, but with the most likely result that the system settles to E_{12} where the two ladybirds populations are present, together with aphids. Instead, a low wasp mortality rate m helps in destabilizing both E_{11} and E_{12}, see the first condition in (5.15) as well as (6.34).

When both susceptible and infected aphids are the only populations present, in [**27**] the feasibility conditions are a bit more involved. This equilibrium corresponds here to the points E_4 and E_{16}. For the latter we do not have equilibrium values, but discussed its feasibility through analytical means, and stability is even more complicated. But with numerical information on the model parameters, in a specific situation, the conditions could be used to destabilize the equilibrium. The feasibility conditions for E_4 are exactly the same as found in the former investigation. The stability condition also coincides, but here one more is found. The point thus can be destabilized simply if the ladybirds birth rate exceeds their mortality, see the second inequality in (5.11).

Wasps and infected aphids can also coexist, in the absence of susceptible aphids, in [**27**]. Here this is expressed by the point E_3 where also carrier wasps are present, as well as E_{13} and E_9. It is interesting that the two feasibility conditions found in [**27**] appear here split among E_3, see (4.8), and (4.9), both scaled via the fraction p. Again here the stability conditions are more elaborated and provide additional possible tools for the destabilization of this point, the simplest and most usable being (6.47) already described above. This is further enhanced in the analysis of E_9, which is the coexistence point that thus contains also the healthy aphids, where for feasibility also the parameters related to ladybirds and wasps appear, see (6.25), (6.27), (6.30). The first stability condition (5.18), which is the same as the first one for E_3, (5.5), can be satisfied more easily than in the restricted model of [**27**]. But the additional Routh-

Hurwitz conditions (6.53) make the stability requirements more stringent. The same holds true for E_3, where for instance low ladybirds mortality v and transmission rates χ will help in the destabilization process, compare the first inequality in (6.53).

6.2 - *Ecological considerations*

The major result of this investigation, however, is that in [**27**] no point exists where the aphids disappear, unless also the wasps are wiped out. Here this fact occurs as well, but aphids can vanish leaving ladybirds thriving, at equilibria E_1 and E_6. Thus disappearance of aphids entails the disappearance of their specialist parasitoids, a fact that should be expected. Biological control in closed systems can potentially avoid this by providing additional non-pest aphids on banker plants [**1**]. This maintains the parasitic wasp populations when pest aphids are removed from the system, and keep them available in case of reintroduction of the pest aphid.

A few points that can be raised by ecologists in this context are whether predation by generalist natural enemies can alter the aphid-wasp interaction. We have positively answered this issue in the discussion above and this is relevant for exploration of complementary biological control strategies [**16**]. As for the mechanism responsible for the alteration, it may be likely that the reason might be related to the aphids exposure to the bacteria, increasing the proportion of infected aphids that are resistant to the wasps, as well as increasing wasp losses by predation of parasitized aphids, reducing the impact of wasps on the aphid population. Equilibrium E_{15} might be an answer to the former statement, where healthy aphids vanish, and only infected thrive, as well as ladybirds. Such a situation would be feasible only if the ladybirds were able to maintain low levels of aphids in the population. Combined with a reduced reproduction rate of infected aphids [**25**], this could be a viable control strategy where protective bacterial symbionts are fixed in the population. On the other hand, equilibria E_{15} and E_{16} may also be in support of the wasp pressure reduction, as also wasps vanish there. Finally, the ecologists may argue that with two types of natural enemies there are always some infected and uninfected aphids in a population, i.e. always a polymorphism, no fixed type. This is not necessarily true, because there are equilibria, whenever their feasibility and stability conditions are verified, where infected aphids disappear, for instance E_2, or healthy ones vanish, E_3 for instance.

In reality, we find that the proportion of aphids hosting protective bacteria is dynamic across a growing season [**15**]. (Smith et al 2015). A system therefore might move between a number of these different states until a more constant environment is experienced upon which the equilibrium may be achieved. Even in closed systems, a change in the temperature or available host plant could disrupt the equilibrium, while in the field many more factors might affect the interactions. Indeed, all these changes will be reflected into and will affect the model parameters and therefore may ultimately lead to equilibria shifts. As we have seen, the addition of a further natural enemy leads to more potential outcomes. But the latter would eventually be influenced by yet untested abiotic and biotic factors.

So, overall, this theoretical analysis, although heavy at times and with conditions that might in practice be difficult to interpret and use, is still worthy because it provides some extra light on additional means to fight aphids in nature.

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References

[1] M. V. BALZAN, *Flowering banker plants for the delivery of multiple agroecosystem services*, Arthropod-Plant Interactions **11** (2017), 743–754.

[2] R. L. BLACKMAN and V. F. EASTOP, *Aphids on the world's herbaceous plants and shrubs*, John Wiley & Sons, London, 2006.

[3] D. J. N. BUTLER, *EU expected to vote on pesticide ban after major scientific review*, Nature **555** (2018), 150–151.

[4] A. C. DARBY and A. E. DOUGLAS, *Elucidation of the transmission patterns of an insect-borne bacterium*, Appl. Environ. Microbiol. **69** (2003), 4403–4407.

[5] L. GEHRER and C. VORBURGER, *Parasitoids as vectors of facultative bacterial endosymbionts in aphids*, Biol. Lett. **8** (2012), 613–615.

[6] J. GUO, S. HATT, K. HE, J. CHEN, F. FRANCIS and Z. WANG, *Nine facultative endosymbionts in aphids. A review*, J. Asia Pac. Entomol. **20** (2017), 794–801.

[7] J. L. KOVACS, C. WOLF, D. VOISIN and S. WOLF, *Evidence of indirect symbiont conferred protection against the predatory lady beetle* Harmonia axyridis *in the pea aphid*, BMC ecology **17** (2017), art. 26.

[8] M. KWIATKOWSKI and C. VORBURGER, *Modeling the ecology of symbiont-mediated protection against parasites*, The American Naturalist **179** (2012), 595–605.

[9] A. J. LOTKA, *Elements of mathematical biology*, Dover Publications, New York, 1958.

[10] G. MALLOCH, J. PICKUP, F. HIGHET, S. FOSTER, M. WILLIAMSON and B. FENTON, *Assessment of the spread of pyrethroid resistant* Sitobion avenae *in the*

UK and an update on changes in the population structure of Myzus persicae *in Scotland*, Proceedings Crop Protection in Northern Britain 2016, 223–228.

[**11**] T. R. MALTHUS, *An essay on the principle of population*, J. Johnson, London, 1798.

[**12**] A. H. C. MCLEAN, B. J. PARKER, J. HRČEK, L. M. HENRY and H. C. J. GODFRAY, *Insect symbionts in food webs*, Philos. Trans. R. Soc. Lond. B Biol. Sci. **371** (2016), 20150325.

[**13**] N. A. MORAN and H. E. DUNBAR, *Sexual acquisition of beneficial symbionts in aphids*, Proc. Natl. Acad. Sci. USA **103** (2006), 12803–12806.

[**14**] K. M. OLIVER, A. H. SMITH and J. A. RUSSELL, *Defensive symbiosis in the real world - advancing ecological studies of heritable, protective bacteria in aphids and beyond*, Functional Ecology **28** (2014), 341-355.

[**15**] A. H. SMITH, P. ŁUKASIK, M. P. O'CONNOR, A. LEE, G. MAYO, M. T. DROTT, S. DOLL, R. TUTTLE, R. A. DISCIULLO, A. MESSINA, K. M. OLIVER and J. A. RUSSELL, *Patterns, causes and consequences of defensive microbiome dynamics across multiple scales*, Mol. Ecol. **24** (2015), 1135–1149.

[**16**] W. E. SNYDER, S. N. BALLARD, S. YANG, G. M. CLEVENGER, T. D. MILLER, J. J. AHN, T. D. HATTEN and A. A. BERRYMAN, *Complementary biocontrol of aphids by the ladybird beetle* Harmonia axyridis *and the parasitoid* Aphelinus asychis *on greenhouse roses*, Biological Control **30** (2004), 229–235.

[**17**] L. SUTTER, M. ALBRECHT and P. JEANNERET, *Landscape greening and local creation of wildflower strips and hedgerows promote multiple ecosystem services*, J. Appl. Ecol. **55** (2018), 612–620.

[**18**] H. F. VAN EMDEN, R. HARRINGTON, eds., *Aphids as crop pests*, Cabi, UK, 2017.

[**19**] F. J. F. VAN VEEN, C. B. MÜLLER, J. K. PELL and H. C. J. GODFRAY, *Food web structure of three guilds of natural enemies: predators, parasitoids and pathogens of aphids*, J. Anim. Ecol. **77** (2008), 191–200.

[**20**] E. VENTURINO, *Ecoepidemiology: a more comprehensive view of population interactions*, Math. Model. Nat. Phenom. **11** (2016), 49–90.

[**21**] P. F. VERHULST, *Recherches mathématiques sur la loi d'accroissement de la population*, Nouveaux mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles **18** (1845), 14–54.

[**22**] V. VOLTERRA and U. D'ANCONA, *La concorrenza vitale tra le specie dell'ambiente marino*, VIIe Congr. Int. acquicult et de pêche, Paris 1931, 1–14.

[**23**] C. VORBURGER, *Symbiont-conferred resistance to parasitoids in aphids–Challenges for biological control*, Biological Control **116** (2018), 17–26.

[**24**] S. E. ZYTYNSKA and S. T. MEYER, *Effects of biodiversity in agricultural landscapes on the protective microbiome of insects – a review*, Entomol. Exp. Appl. **167** (2019), 2–13.

[**25**] S. E. ZYTYNSKA, K. TIGHIOUART and E. FRAGO, *Benefits and costs of hosting facultative symbionts in plant-sucking insects: A meta-analysis*, Mol. Ecol. **30** (2021), 2483–2494.

[**26**] S. E. Zytynska and W. W. Weisser, *The natural occurrence of secondary bacterial symbionts in aphids*, Ecol. Entomol. **41** (2016), 13–26.

[**27**] S. E. Zytynska and E. Venturino, *Modelling the role of vector transmission of aphid bacterial endosymbionts and the protection against parasitoid wasps*, in "Trends in biomathematics: mathematical modeling for health, harvesting, and population dynamics", Selected works presented at the BIOMAT Consortium Lectures, Morocco 2018, Rubem P. Mondaini, ed., Springer, Cham, 2019, 209–230.

Appendix A - Feasibility details

Equilibrium E_8

From the second equation in (3.11), we find

$$\psi ZJ = J(kX + v)$$

which upon substitution into the first (3.11) gives

$$X = \frac{1}{k}(u - v + \widetilde{q}A) \tag{6.1}$$

that can be used in the first equation in (3.9) to yield

$$W = \tfrac{1}{a}\Phi(A), \quad \Phi(A) = \textstyle\sum_{i=0}^{2} a_i A^i, \tag{6.2}$$

$$a_2 = -\frac{pq\widetilde{q}}{ak} < 0, \quad a_1 = \frac{p}{a}\left[e - q\frac{u-v}{k}\right], \quad a_0 = -\frac{m}{a} < 0.$$

This parabola has the roots $\Phi_\pm$ and admits a feasible portion only if

$$\Delta = a_1^2 - 4a_0a_2 > 0. \tag{6.3}$$

From the first equation in (3.10) we obtain

$$W = \mathcal{L}(A) = b_0 - b_1 A, \quad b_0 = \frac{1}{ekp}[k(r-n) - q(u-v)], \tag{6.4}$$

$$b_1 = \frac{gk + q\widetilde{q}}{ekp} \geq 0.$$

The straight line $\mathcal{L}$ has a negative slope, so that also to have a feasible portion, the following requirement must hold

$$b_0 > 0. \tag{6.5}$$

Four situations may then arise, based on the position of the zero of $\mathcal{L}$, $A_0 = b_0 b_1^{-1}$. No intersection between the straight line (6.4) and $\Phi(A)$ exists if $A_0 < \Phi_-$. One intersection exists for $\Phi_- < A_0 < \Phi_+$, two arise if $\Phi_+ < A_0$ for a slope of $\mathcal{L}$ sufficiently large in absolute magnitude, but these disappear through a saddle-node bifurcation if the slope becomes too close to zero. Thus the alternative requirements, loosely stated, are

$$\Phi_- < A_0 < \Phi_+; \qquad \Phi_+ < A_0, \quad gk + q\widetilde{q} >> ekp. \tag{6.6}$$

These intersections give $A^{\Psi}_{8\pm}$ as well as $W^{\Psi}_{8\pm}$ and in turn we obtain $X^{\Psi}_{8\pm}$ upon substitution into (6.1). From the second equation in (3.11) in turn

$$Z^{\Psi}_{8\pm} = \frac{1}{\psi}[v + kX^{\Psi}_{8\pm}], \quad J^{\Psi}_{8\pm} = X^{\Psi}_{8\pm} - A^{\Psi}_{8\pm}.$$

Note that the latter is ensured to be nonnegative if the following condition holds

$$u + (\widetilde{q} - k)A^{\Psi}_{8\pm} \geq v. \tag{6.7}$$

Thus for the equilibrium $E_8 = (W^{\Psi}_{8+}, 0, A^{\Psi}_{8+}, 0, Z^{\Psi}_{8+}, J^{\Psi}_{8+}, 0)$, the feasibility conditions are (6.3), (6.5), (6.6) and (6.7).

Equilibrium E_{14}

For E_{14}, the first equations in (3.10) and (3.11) yield the equations of two planes:

$$\pi_1: \quad gA + qZ + epW = r - n, \quad \pi_2 : kZ - \widetilde{q}A = u - v. \tag{6.8}$$

These intersect on the coordinate planes respectively at the points

$$\begin{gathered}\pi_1: \quad \widetilde{P}_W = (\widetilde{W}_0, 0, 0), \quad \widetilde{P}_A = (0, \widetilde{A}_0, 0), \quad \widetilde{P}_Z = (0, 0, \widetilde{Z}_0), \\ \widetilde{W}_0 = \frac{r-n}{ep}, \quad \widetilde{A}_0 = \frac{r-n}{g}, \quad \widetilde{Z}_0 = \frac{r-n}{q}; \\ \pi_2: \quad \widetilde{Q} = (0, \widehat{A}_1, 0), \quad \widehat{Q} = (0, 0, \widehat{Z}_1), \qquad \widehat{A}_1 = \frac{v-u}{k}, \quad \widehat{Z}_1 = \frac{u-v}{k}.\end{gathered}$$

Note that surely one of $\widetilde{Q}$ or $\widehat{Q}$ is admissible. For feasibility of $\widetilde{P}$, the first of the following conditions is required, while to ensure that $\pi_1 \cap \pi_2 \neq \varnothing$, one of the last two is necessary:

$$r \geq n; \quad 0 \leq \widehat{A}_1 \leq \widetilde{A}_0, \quad 0 \leq \widehat{Z}_1 \leq \widetilde{Z}_0. \tag{6.9}$$

The intersection of π_1 and π_2 on the plane $W = 0$ is the point $\overline{P}_1 = (0, \overline{A}_1, \overline{Z}_1)$, the one on $Z = 0$ is the point $\overline{P}_2 = (\overline{W}_2, \overline{A}_2, 0)$, and the one on $A = 0$ is the point $\overline{P}_3 = (\overline{W}_3, 0, \overline{Z}_3)$ where

$$\overline{A}_1 = \frac{k(r-n) + q(v-u)}{kg + q\widetilde{q}}, \quad \overline{Z}_1 = \frac{u - v + \widetilde{q}\overline{A}_1}{k}; \quad \overline{A}_2 = \frac{v-u}{\widetilde{q}},$$

$$\overline{W}_2 = \frac{r-n-g\overline{A}_2}{ep}; \qquad \overline{W}_3 = \frac{r-n-q\overline{Z}_3}{ep}, \quad \overline{Z}_3 = \frac{u-v}{k}.$$

These points are feasible under the conditions (6.9). In such case, the segment S joining $\overline{P}_1$ with $\overline{P}_2$, when $v > u$, or alternatively joining $\overline{P}_1$ with $\overline{P}_3$ is feasible. Note that the first equation in (3.9) gives the degenerate quadric surface

$$\Phi(W, A, Z) = epA - aW - pqAZ - m = 0.$$

In order that the segment S intersects the quadric Φ, this intersection providing the required equilibrium, the above two points must lie in the opposite half spaces into which Φ partitions $\mathbf{R}^3$, i.e. respectively one of the following conditions must hold,

$$\Phi(\overline{P}_1)\Phi(\overline{P}_2) < 0, \quad \Phi(\overline{P}_1)\Phi(\overline{P}_3) < 0. \tag{6.10}$$

Feasibity for E_{14} thus requires (6.9) and (6.10).

Equilibrium E_{13}

In this case the equations (3.9) and (3.10) can be reworked to yield two conic sections. Summing the two equations of (3.9) we obtain

$$Y_{13} \equiv Y(A, I) = \frac{1}{a}[ep(A + fI) - m].$$

Substituting this into the equations (3.10) and summing the two equations we find

$$\begin{aligned} \Theta(A, I) &= A^2(e^2p^2 + ag) + AI(a\tilde{c} + 2e^2p^2f + a\tilde{g}) \\ &+ I^2(ac + e^2p^2f^2) - A[epm + a(r-n)] - I[epmf + a(b-\mu)] = 0. \end{aligned} \tag{6.11}$$

On the other hand, solving the second equation in (3.9),

$$V = \frac{1}{\beta}\widetilde{H}_V, \quad \widetilde{H}_V = r - n - gA - \tilde{g}I - epY, \tag{6.12}$$

and substituting into the first of (3.10), we find the convex parabola

$$\Lambda_V(V) = \delta V^2 + H_V V - \omega IY = 0, \quad H_V = aY + m + \omega I - \delta Y, \tag{6.13}$$

which, because $\Lambda_V(0) = -\omega IY < 0$, has a unique positive root,

$$V_+ = \frac{1}{2\delta}\left[\sqrt{H_V^2 + 4\delta\omega IY} - H_V\right].$$

Substitution into (6.12) produces

$$\frac{\delta}{\beta^2}\widetilde{H}_V^2 + \frac{1}{\beta} H_V \widetilde{H}_V = \omega I Y,$$

which, in expanded form, reads $\Pi(A, I) = \sum_{i,k=0}^{2} \pi_{i,k} A^i I^k = 0$, with

(6.14)

$$\begin{aligned}
\pi_{2,0} &= (ag + e^2p^2)[\delta(ag + e^2p^2) - \beta(a - \delta)ep], \\
\pi_{1,1} &= \{[2\delta(a\widetilde{g} + e^2p^2 f) - \beta((a - \delta)epf + a\omega)](ag + e^2p^2) \\
&\quad -(a\widetilde{g} + e^2p^2 f)(a - \delta)ep - ep\beta^2 a\omega\} \\
\pi_{0,2} &= \{(a\widetilde{g} + e^2p^2 f)[\delta(a\widetilde{g} + e^2p^2 f) - \beta((a - \delta)epf + a\omega)] - aefp\beta^2\omega\} \\
\pi_{1,0} &= \{[a(r - n) + emp][\beta ep(a - \delta) - 2\delta(ag + e^2p^2)] - \beta\delta m(ag + e^2p^2)\} \\
\pi_{0,1} &= \{[a(r - n) + emp][\beta(epf(a - \delta) + a\omega) - 2\delta(a\widetilde{g} + e^2p^2 f)] \\
&\quad +a^2\beta^2\omega m - \beta\delta m(a\widetilde{g} + e^2p^2 f)\} \\
\pi_{0,0} &= \delta[a(r - n) + emp][a(r - n) + emp + \beta m].
\end{aligned}$$

But neither the invariants, respectively

$$\Delta_\Theta = [(ep)^2 + ag][ac + (epf)^2] - \frac{[a\widetilde{c} + 2(ep)^2 f + a\widetilde{g}]^2}{4}; \; \Delta_\Pi = \pi_{2,0}\pi_{0,2} - \frac{1}{4}\pi_{1,1}^2$$

nor the intersections with the coordinate axes, can have a sure sign. The latter are respectively the origin and the points $(A_\Theta, 0)$, $(0, I_\Theta)$, $(A_\Pi, 0)$, $(0, I_\Pi)$, where

$$A_\Theta = \frac{epm + a(r - n)}{e^2p^2 + ag}, \quad I_\Theta = \frac{epmf + a(b - \mu)}{ac + e^2p^2f^2},$$

while A_Π and I_Π are respectively the roots of the two quadratic equations

$$\sum_{k=0}^{2} \pi_{k,0} A^k = 0, \quad \sum_{k=0}^{2} \pi_{0,k} I^k = 0.$$

Here again the signs of all the coefficients are not determined, giving rise to every possible alternative. Therefore in this situation all the possible cases can arise, giving more possibilities than the ones arising for equilibrium E_{16} listed below. Hence, we do not pursue this case any further.

Equilibrium E_{15}

In case of E_{15}, the equations (3.9) and the first one in (3.10) are satisfied. Solving the second one in (3.11) for BZ and substituting into the first one gives

$$X = \frac{1}{k}(u - v + \widetilde{q}\eta I), \tag{6.15}$$

and the latter into the second one of (3.10), provides

$$I_{15} = \frac{k(b-\mu) - q(u-v)}{ck + \eta q\widetilde{q}} \tag{6.16}$$

from which the value of X_{15} is then obtained plugging (6.16) into (6.15). Nonnegativity of these quantities requires

$$kb + qv \geq k\mu + qu, \quad u + \widetilde{q}\eta I_{15} \geq v. \tag{6.17}$$

Substituting further (6.15) into (3.12), in view of (6.17) the nonnegative bacteria population level is then obtained

$$B_{15} = \frac{\alpha q I_{15}(u - v + \eta\widetilde{q} I_{15})}{nk + \lambda k I_{15} + \phi(u - v + \eta\widetilde{q} I_{15})} \geq 0.$$

Using (6.15) into the second equation of (3.11) yields

$$Z_{15} = J\frac{v + kX_{15}}{\psi J_{15} + \phi B_{15} + \chi I_{15}} = J\frac{u + \widetilde{q}\eta I_{15}}{\psi J_{15} + \phi B_{15} + \chi I_{15}} \geq 0$$

where the value of J is the positive root J_{15} of the quadratic $\sum_{k=0}^{2} \beta_k J^k = 0$ obtained combining (6.15) and (6.16). The existence of such a feasible J_{15} is always guaranteed in view of the opposite signs of $\beta_0 = -X_{15}(\phi B_{15} + \chi I_{15}) < 0$ and $\beta_2 = \psi > 0$, while $\beta_1 = v + (k - \psi)X_{15} + \phi B_{15} + \chi I_{15}) \in \mathbf{R}$. Feasibility thus requires only (6.17).

Equilibrium E_{16}

For E_{16} we substitute the value of BZ from the second equilibrium equation of (3.11) into the first one to find X, which differs from (6.15), here being

$$X = \frac{1}{k}[u - v + \widetilde{q}(A + \eta I)]. \tag{6.18}$$

From (3.12) we then obtain

$$B = \frac{\alpha q I[u - v + \widetilde{q}(A + \eta I)]}{nk + \lambda k(A + \eta I) + \phi[u - v + \widetilde{q}(A + \eta I)]}. \tag{6.19}$$

Feasibility for X, which also gives $B_{16} \geq 0$, entails

$$u + \widetilde{q}(A + \eta I) \geq v. \tag{6.20}$$

Using (6.19) into the equilibrium equations (3.10), two conic sections in A and I, $\Xi(A, I)$ and $\widetilde{\Omega}(A, I)$, are obtained:

$$\Xi = (r - n - gA - \widetilde{g}I - qX)[nk + \lambda k(A + \eta I) + \phi kX] - k\alpha\lambda qIX = 0,$$
$$\widetilde{\Omega} = k\alpha\lambda qAX + (b - \mu - cI - \widetilde{c}A - qX)[nk + \lambda k(A + \eta I) + \phi kX] = 0.$$

We study Ξ, which can be written as $\Xi(A, I) = \sum_{i,k=0}^{2} y_{ik}A^i I^k$ with

$$\begin{aligned}
y_{20} &= (kg + q\widetilde{q})(k\lambda + \phi\widetilde{q}), \quad y_{02} = (k\widetilde{g} + q\widetilde{q}\eta)(k\lambda + \phi\widetilde{q}\eta) + k\alpha\lambda q\widetilde{q}\eta, \\
y_{11} &= (kg + q\widetilde{q})(k\lambda + \phi\widetilde{q}\eta) + (k\widetilde{g} + q\widetilde{q}\eta)(k\lambda + \phi\widetilde{q}) + k\alpha\lambda q\widetilde{q}\eta, \\
y_{10} &= (kg + q\widetilde{q})[nk + \phi(u - v)] - (k\lambda + \phi\widetilde{q})[k(r - n) - q(u - v)], \\
y_{01} &= k\alpha\lambda q(u - v) + (k\widetilde{g} + q\widetilde{q}\eta)[nk + \phi(u - v)] \\
&\quad -(k\lambda + \phi\widetilde{q}\eta)[k(r - n) - q(u - v)], \\
y_{00} &= -[k(r - n) - q(u - v)][nk + \phi(u - v)].
\end{aligned}$$

Assuming nondegeneracy, the sign of its invariant $\delta_\Xi = y_{20}y_{02} - \frac{1}{4}y_{11}^2$ cannot be determined unambigously:

$$\begin{aligned}
\delta_\Xi = {} & (kg + q\widetilde{q})(k\lambda + \phi\widetilde{q})k\alpha\lambda q\widetilde{q}\eta \\
& - \frac{1}{4}[(kg + q\widetilde{q})(k\lambda + \phi\widetilde{q}\eta) - (k\widetilde{g} + q\widetilde{q}\eta)(k\lambda + \phi\widetilde{q})]^2 \\
& - \frac{1}{4}k\alpha\lambda q\widetilde{q}[k\alpha\lambda q\widetilde{q} + 2(kg + q\widetilde{q})(k\lambda + \phi\widetilde{q}\eta) + 2(k\widetilde{g} + q\widetilde{q}\eta)(k\lambda + \phi\widetilde{q})],
\end{aligned}$$

so the nature of the conic could be both an ellipse, for $\delta_\Xi > 0$ or a hyperbola for $\delta_\Xi < 0$. But its intersections with the axis $I = 0$ are

$$A_{(1)} = \frac{k(r - n) - q(u - v)}{kg + q\widetilde{q}}, \quad A_{(2)} = \frac{\phi(v - u) - nk}{kg + q\widetilde{q}} < 0,$$

the inequality coming from (6.20). Those with $A = 0$ are the roots of the quadratic $\sum_{k=0}^{2} y_{0,k}I^k = 0$. Now, if $k(r - n) < q(u - v)$, we have $y_{0,0} > 0$ and noting that $u \geq v$ from (6.20), also $y_{0,1} > 0$. These results combined with $y_{0,2} > 0$ imply that both roots are negative, $I_\pm < 0$, and further also $A_{(1)} < 0$. Hence the hyperbola has four negative intersections with the axes so that no feasible branch can exist. Thus in such case E_{16} is unfeasible. Therefore assume

$$k(r - n) > q(u - v), \tag{6.21}$$

so that $y_{0,0} < 0$ and $I_+ > 0$, $A_{(1)} > 0$.

$$I_+ > 0 > I_-, \quad A_{(1)} > 0 > A_{(2)}. \tag{6.22}$$

There are instead only three possible situations for the graph of $\Xi(A,I)$ in the first quadrant, that for our purposes reduce to two. If is a hyperbola, one alternative is that the two points $Q_{\Xi,A1} = (A_{(1)},0)$ and $Q_{\Xi,I+}(0,I_+)$ lie on different branches, being respectively connected with the points $Q_{\Xi,I-}(0,I_-)$ and $Q_{\Xi,A2} = (A_{(2)},0)$. Thus the two branches emanating from these two points lie in part in the first quadrant. Alternatively, whether it is a hyperbola or an ellipse, the branch joining the two points $Q_{\Xi,A} = (A_{(1)},0)$ and $Q_{\Xi,I}(0,I_+)$ lies in the first quadrant. In summary:

- Case ($\mathcal{H}_\Xi$): two feasible branches emanate respectively from $Q_{\Xi,A1} = (A_{(1)},0)$ and $Q_{\Xi,I+}(0,I_+)$;
- Case ($\mathcal{E}_\Xi$): the branch joining the two points $Q_{\Xi,A} = (A_{(1)},0)$ and $Q_{\Xi,I}(0,I_+)$ lies in the first quadrant.

Now, instead of studying $\widetilde{\Omega}$, we take the combination

$$\Omega(A,I) = I\widetilde{\Omega}(A,I) + A\Xi(A,I) = -k^{-1}\textstyle\sum_{i,k=0}^{2} \kappa_{i,k}A^iI^k = 0,$$

$$\kappa_{20} = gk + q\widetilde{q}, \quad \kappa_{02} = ck + q\widetilde{q}\eta, \quad \kappa_{11} = \frac{1}{2}\left[\widetilde{c}k + \widetilde{g}k + q\widetilde{q}(1+\eta)\right],$$

$$\kappa_{10} = -\frac{1}{2}[k(r-n) - q(u-v)], \quad \kappa_{01} = -\frac{1}{2}[k(b-\mu) - q(u-v)], \quad \kappa_{00} = 0.$$

Its invariant

$$\begin{aligned}\mathcal{I} = cgk^2 + gkq\widetilde{q}\eta + ckq\widetilde{q} \\ - \frac{1}{4}[(\widetilde{c}^2 + \widetilde{g}^2)k^2 + q^2\widetilde{q}^2(1-\eta)^2 + 2(\widetilde{c} + \widetilde{g} + g)kq\widetilde{q}(1+\eta)]\end{aligned}$$

however has no definite sign, so that Ω is either an ellipse for $\mathcal{I} > 0$, or a hyperbola, conversely. The conic goes through the origin, and further intersects the axes at

$$A^+ = \frac{k(r-n) - q(u-v)}{gk + q\widetilde{q}} > 0, \quad \widetilde{I} = \frac{k(b-\mu) - q(u-v)}{ck + kq\widetilde{q}\eta}.$$

Note that the inequality follows from (6.21). If it is an ellipse and $\widetilde{I} > 0$, the arc joining $Q_{\Omega,A} = (A^+,0)$ and $Q_{\Omega,I}(0,\widetilde{I})$ lies in the first quadrant, Case ($\mathcal{E}_{\Omega+}$). Else if $\widetilde{I} < 0$ the arc joining the origin and $Q_{\Omega,A} = (A^+,0)$ is in the first quadrant, Case ($\mathcal{E}_{\Omega-}$). Thus:

- Case ($\mathcal{E}_\Omega^+$): the arc joining $Q_{\Omega,A} = (A^+,0)$ and $Q_{\Omega,I}(0,\widetilde{I})$ lies in the first quadrant;
- Case ($\mathcal{E}_\Omega^-$): the arc joining the origin and $Q_{\Omega,A} = (A^+,0)$ is feasible.

If Ω instead is a hyperbola and $\widetilde{I} > 0$, there are four subcases:

- Case $(\mathcal{H}^+_{\Omega 1})$: two feasible branches emanate respectively from $Q_{\Omega,A} = (A^+, 0)$ and $Q_{\Omega,I}(0, \widetilde{I})$;
- Case $(\mathcal{H}^+_{\Omega 2})$: a feasible branch emanates from $Q_{\Omega,A} = (A^+, 0)$ and the arc joining the origin and $Q_{\Omega,I}(0, \widetilde{I})$ is feasible;
- Case $(\mathcal{H}^+_{\Omega 3})$: a feasible branch emanates from $Q_{\Omega,I}(0, \widetilde{I})$ and the arc joining the origin and $Q_{\Omega,A} = (A^+, 0)$ is feasible;
- Case $(\mathcal{H}^+_{\Omega 4})$: the arc joining $Q_{\Omega,A} = (A^+, 0)$ and $Q_{\Omega,I}(0, \widetilde{I})$ is feasible.

If Ω is a hyperbola and instead $\widetilde{I} < 0$, there are three subcases, as two can be merged together, their difference being in the unfeasible region and in the curvature of the feasible branch:

- Case $(\mathcal{H}^-_{\Omega 1})$: the arc joining the origin and $Q_{\Omega,A} = (A^+, 0)$ is feasible;
- Case $(\mathcal{H}^-_{\Omega 2})$: a feasible branch emanates from $Q_{\Omega,A} = (A^+, 0)$ (concave or convex);
- Case $(\mathcal{H}^-_{\Omega 3})$: two feasible branches emanate respectively from the origin and $Q_{\Omega,A} = (A^+, 0)$.

Note that, qualitatively, cases $(\mathcal{E}^+_{\Omega})$ and $(\mathcal{H}^+_{\Omega 4})$ are the same, except for the curvature of the arc. Similarly cases $(\mathcal{E}^-_{\Omega})$ and $(\mathcal{H}^-_{\Omega 1})$ are the same from the qualitative point of view. Therefore, in the discussion that follows, the elliptic cases for Ω are omitted, as they can be assimilated to the above mentioned hyperbolic situations.

We now discuss the possible intersections of Ξ and Ω by combining the various cases.

- $(\mathcal{E}_{\Xi})$ and $(\mathcal{H}^+_{\Omega 1})$: if satisfied, each one of the following two conditions gives raise to one feasible intersection: $I_+ < \widetilde{I}$; $A_{(1)} < A^+$;
- $(\mathcal{H}_{\Xi})$ and $(\mathcal{H}^+_{\Omega 1})$: if satisfied, each one of the following two conditions gives raise to one feasible intersection: $I_+ > \widetilde{I}$; $A_{(1)} > A^+$;
- $(\mathcal{E}_{\Xi})$ and $(\mathcal{H}^+_{\Omega 2})$: if satisfied, each one of the following two conditions gives raise to one feasible intersection: $I_+ < \widetilde{I}$; $A_{(1)} > A^+$;
- $(\mathcal{H}_{\Xi})$ and $(\mathcal{H}^+_{\Omega 2})$: one intersection guaranteed by $I_+ < \widetilde{I}$; another one on the other branches depends on the respective curvatures of Ξ and Ω;

- ($\mathcal{E}_\Xi$) and ($\mathcal{H}^+_{\Omega 3}$): one intersection guaranteed by $I_+ > \widetilde{I}$; in this case there could be two more, giving rise also to a saddle-node bifurcation, if $A_{(1)} > A^+$, or one more if $A_{(1)} < A^+$; alternatively, one intersection guaranteed by $A_{(1)} < A^+$ and $I_+ < \widetilde{I}$;
- ($\mathcal{H}_\Xi$) and ($\mathcal{H}^+_{\Omega 3}$): one intersection guaranteed by $A_{(1)} < A^+$; another one on the other branches depends on the respective curvatures of Ξ and Ω;
- ($\mathcal{E}_\Xi$) and ($\mathcal{H}^+_{\Omega 4}$): one intersection guaranteed by $A_{(1)} > A^+$ and $I_+ < \widetilde{I}$, or else by $A_{(1)} < A^+$ and $I_+ > \widetilde{I}$;
- ($\mathcal{H}_\Xi$) and ($\mathcal{H}^+_{\Omega 4}$): if satisfied, each one of the following two conditions gives raise to one feasible intersection: $I_+ < \widetilde{I}$; $A_{(1)} < A^+$;
- ($\mathcal{E}_\Xi$) and ($\mathcal{H}^-_{\Omega 1}$): one intersection guaranteed by $A_{(1)} < A^+$; two could arise in the opposite case through a saddle-node bifurcation, but this depends on the curvatures of the branches;
- ($\mathcal{H}_\Xi$) and ($\mathcal{H}^-_{\Omega 1}$): one intersection guaranteed by $A_{(1)} < A^+$; in this case there could be two more, giving rise also to a saddle-node bifurcation, depending on the curvatures of the branches;
- ($\mathcal{E}_\Xi$) and ($\mathcal{H}^-_{\Omega 2}$): one intersection guaranteed by $A_{(1)} > A^+$;
- ($\mathcal{H}_\Xi$) and ($\mathcal{H}^-_{\Omega 2}$): the intersection depends on the curvatures of the curves; if the branch of Ω is convex, it occurs for $A_{(1)} < A^+$, but two could instead arise through a saddle-node bifurcation if $A_{(1)} > A^+$;
- ($\mathcal{E}_\Xi$) and ($\mathcal{H}^-_{\Omega 3}$): one intersection is always guaranteed, one more exists if $A_{(1)} > A^+$;
- ($\mathcal{H}_\Xi$) and ($\mathcal{H}^-_{\Omega 3}$): the occurrence of the intersections depends on the curvatures of the curves.

This summarizes the cases in which feasible values of A_{16} and I_{16} arise. To complete the analysis of this equilibrium, observe that X and B_{16} can now be obtained respectively from (6.18) and (6.19). Using the first equation in (3.11) we find

$$Z = X\frac{u + \widetilde{q}(A_{16} + \eta I_{16})}{v + kX + \phi B_{16} + \chi I_{16} + \psi J}. \tag{6.23}$$

Using the definition of X and substituting into it (6.23), we are led to

$$X\frac{u + \widetilde{q}(A_{16} + \eta I_{16})}{v + kX + \phi B_{16} + \chi I_{16} + \psi J} + J = X,$$

which gives the quadratic in J

$$\Gamma(J) = \sum_{i=0}^{2} \gamma_i J^i = 0, \quad \gamma_2 = \psi > 0$$

$$\begin{aligned}
\gamma_1 &= v + kX_{16} + \psi B_{16} + \chi I_{16} + \frac{\psi}{k}[u - v + \widetilde{q}(A_{16} + \eta I_{16})], \\
\gamma_0 &= X_{16}[u + \widetilde{q}(A_{16} + \eta I_{16}) - [v + kX_{16} + \psi B_{16} + \chi I_{16}] \\
&= -X_{16}[\psi B_{16} + \chi I_{16}] < 0.
\end{aligned}$$

Thus a positive root exists giving J_{16} and in turn Z_{16} can be obtained from (6.23).

Equilibrium E_9

Finally we consider E_9. The second equation in (3.11) gives now

$$X = \frac{1}{k}(u - v + \widetilde{q}\eta I), \tag{6.24}$$

for the nonnegativity of which we need:

$$u + \widetilde{q}\eta I_9 \geq v. \tag{6.25}$$

On using (6.24) into the second (3.10) we also find

$$Y = \frac{1}{efkp}\left[k(b - \mu - cI) - q(u - v + \widetilde{q}\eta I)\right], \tag{6.26}$$

entailing the feasibility condition

$$I_9 \leq \frac{k(b - \mu) - q(u - v)}{ck + q\widetilde{q}\eta}. \tag{6.27}$$

Using (6.26) in (3.12), we obtain

$$B = \frac{\alpha q(u - v + \widetilde{q}\eta I)I}{kn + k\gamma Y + \lambda kI + \phi(u - v + \widetilde{q}\eta I)}, \tag{6.28}$$

which is nonnegative in view of (6.25). An expression of Y can also be found by adding the equations (3.9), obtaining $efpI - (m + aY) = 0$, which matched with (6.26) produces

$$I_9 = \frac{efmp + a[k(b - \mu) - q(u - v)]}{e^2f^2p^2 + a(ck + q\widetilde{q}\eta)}. \tag{6.29}$$

It also allows the evaluation of Y from (6.26) and then the one of B_9 from (6.28). Note that condition (6.27) is satisfied if

$$k(b-\mu)-q(u-v)\geq \frac{m}{efp}(ck+q\widetilde{q}\eta), \tag{6.30}$$

which in turn implies the nonnegativity of I_9. Finally from the second (3.11), using (6.24), (6.28) and (6.29) a hyperbola is found:

$$Z(J)=J\frac{u+\widetilde{q}\eta I_9}{\phi B_9+\chi I_9+\psi J}. \tag{6.31}$$

Because it is concave and crosses the origin, an intersection with the straight line defined by (6.24), is always guaranteed, providing the values of J_9 and Z_9. Note that the straight line, namely $k(Z+J)=u-v+\widetilde{q}\eta I_9$, has a nonnegative right hand side because (6.25) holds.

Finally from the second equation in (3.9) we find another hyperbola

$$W=V\frac{m+aY}{\gamma B_9+\omega I_9+\delta V} \tag{6.32}$$

which has always an intersection with the straight line provided by (6.26), namely $efkp(V+W)=k(b-\mu-cI)-q(u-v+\widetilde{q}\eta I)$, which lies in the first quadrant in view of (6.27), giving the values of W_9 and V_9. Hence, the feasibility conditions for E_9 are just (6.25), (6.27) and (6.30).

Appendix B - Stability details

The Jacobian **J** of the system (3.9)-(3.10)-(3.11)-(3.12) has the following entries:

$$
\begin{aligned}
&\mathbf{J}_{11} = (A + fI)ep - (m + aV + \gamma B) - 2aW - (\omega I + \delta V) - pqAX,\\
&\mathbf{J}_{12} = (A + fI)ep - (a + \delta)W - pqAX,\\
&\mathbf{J}_{13} = Y[ep - pqX], \quad \mathbf{J}_{14} = epfY - \omega W,\\
&\mathbf{J}_{15} = \mathbf{J}_{16} = -pqAY, \quad \mathbf{J}_{17} = -\gamma W, \quad \mathbf{J}_{21} = \gamma B - aV + \omega I + \delta V,\\
&\mathbf{J}_{22} = -(m + aW + 2aV) + \delta W, \quad \mathbf{J}_{24} = \omega W, \quad \mathbf{J}_{27} = \gamma W,\\
&\mathbf{J}_{31} = -epA, \quad \mathbf{J}_{32} = -\beta A - epA, \quad \mathbf{J}_{34} = -\widetilde{g}A, \quad \mathbf{J}_{35} = \mathbf{J}_{36} = -qA,\\
&\mathbf{J}_{33} = r - n - 2gA - \widetilde{g}I - \lambda B - \beta V - epY - qX, \quad \mathbf{J}_{37} = -\lambda A,\\
&\mathbf{J}_{41} - efpI, \quad \mathbf{J}_{42} = \beta A - efpI, \quad \mathbf{J}_{43} = \lambda B + \beta V - \widetilde{c}I,\\
&\mathbf{J}_{45} = \mathbf{J}_{46} = -qI,\\
&\mathbf{J}_{44} = b - \mu - \widetilde{c}A - 2cI - efpY - qX, \quad \mathbf{J}_{47} = \lambda A,\\
&\mathbf{J}_{53} = \widetilde{q}X, \quad \mathbf{J}_{54} = \widetilde{q}\eta X - \chi Z, \quad \mathbf{J}_{56} = u - kZ - \psi Z + \widetilde{q}(A + \eta I),\\
&\mathbf{J}_{55} = u - v - 2kZ - kJ - \phi B - \chi I - \psi J + \widetilde{q}(A + \eta I), \quad \mathbf{J}_{57} = -\phi Z,\\
&\mathbf{J}_{64} = \chi Z, \quad \mathbf{J}_{65} = -kJ + \phi B + \chi I + \psi J,\\
&\mathbf{J}_{66} = -v - k(Z + 2J) + \psi Z, \quad \mathbf{J}_{67} = \phi Z, \quad \mathbf{J}_{71} = \mathbf{J}_{72} = -\gamma B,\\
&\mathbf{J}_{73} = -\lambda B, \quad \mathbf{J}_{74} = -\lambda B + \alpha qX,\\
&\mathbf{J}_{75} = \mathbf{J}_{76} = \alpha qI - \phi B, \quad \mathbf{J}_{77} = -[n + \gamma Y + \lambda(A + I) + \phi X].
\end{aligned}
\tag{6.33}
$$

while all the remaining ones vanish.

Equilibrium E_{12}

One eigenvalue is negative also for E_{12}, namely $\mathbf{J}_{22}(E_{12}) = -m < 0$, another one is $\mathbf{J}_{11}(E_{12})$ that gives

$$
epA_{12} < m + pqA_{12}X_{12}. \tag{6.34}
$$

The remaining part of the Jacobian factorizes into the product of the two minors Δ_{12}^{47} and Δ_{12}^{356}. From the third, fifth and sixth equilibrium equations, we find

$$
\mathbf{J}_{33}(E_{12}) = -gA_{12}, \quad \mathbf{J}_{55}(E_{12}) = -kZ_{12} - (u + \widetilde{q}A_{12})\frac{J_{12}}{Z_{12}}, \quad \mathbf{J}_{66}(E_{12}) = -kJ_{12}.
$$

The Routh-Hurwitz conditions $-\text{tr}(\Delta_{12}^{47}) > 0$, $\det(\Delta_{12}^{47}) > 0$ imply

$$
\begin{gathered}
\mu + (\widetilde{c} + \lambda)A_{12} + (q + \phi)X_{12} + n > b,\\
[\mu + \widetilde{c}A_{12} + qX_{12} - b][n + \lambda A_{12} + \phi X_{12}] > q\alpha\lambda A_{12}X_{12}.
\end{gathered}
\tag{6.35}
$$

The Routh-Hurwitz conditions for Δ_{12}^{356} need the sum of the minors of order two

$\Sigma_{12}^{356} = \Delta_{12}^{35} + \Delta_{12}^{36} + \Delta_{12}^{56}$, with

$$\Delta_{12}^{35} = gA_{12}\left[kZ_{12} + (u + \widetilde{q}A_{12})\frac{J_{12}}{Z_{12}}\right] + q\widetilde{q}A_{12}X_{12}, \quad \Delta_{12}^{36} = gkA_{12}J_{12},$$

$$\Delta_{12}^{56} = kJ_{12}\left[kZ_{12} + (u + \widetilde{q}A_{12})\frac{J_{12}}{Z_{12}}\right] + (k - \psi)J_{12}[u - (k + \psi)Z_{12} + \widetilde{q}A_{12}].$$

The condition on the trace holds:

$$-\text{tr}(\Delta_{12}^{356}) = gA_{12} + kZ_{12} + (u + \widetilde{q}A_{12})\frac{J_{12}}{Z_{12}} + kJ_{12} > 0.$$

The determinant instead gives the following stability condition

$$\begin{aligned}(6.36)\quad \det\Delta_{12}^{356} = q\widetilde{q}(\psi - k)J_{12}A_{12}^2 - q\widetilde{q}A_{12}X_{12}kJ_{12}&\\ - gA_{12}\left[kZ_{12} + (u + \widetilde{q}A_{12})\frac{J_{12}}{Z_{12}}\right]kJ_{12}&\\ + gA_{12}(\psi - k)J_{12}(u - kZ_{12} + \widetilde{q}A_{12} - \psi Z_{12}) > 0&\end{aligned}$$

and then the following additional condition must be satisfied:

$$(6.37)\qquad -\text{tr}\Delta_{12}^{356}\Sigma_{12}^{356} > -\det\Delta_{12}^{356}.$$

Equilibrium E_8

The diagonal elemements of the Jacobian that simplify are in this case

$$\mathbf{J}_{11}(E_8) = -aW_8, \quad \mathbf{J}_{33}(E_8) = -gA_8,$$

$$\mathbf{J}_{55}(E_8) = -kZ_8 - (u + \widetilde{q}A_8)\frac{J_8}{Z_8}, \quad \mathbf{J}_{66}(E_8) = -kZ_8.$$

Further, the Jacobian splits into two minors, Δ_8^{1356} and Δ_8^{247}. The condition on the trace holds unconditionally for the former, $-\text{tr}\Delta_8^{1356} = aW_8 + gA_8 + \mathbf{J}_{55}(E_8) + kZ_8 > 0$, while for the latter the following stability condition arises, $-\text{tr}\Delta_8^{247} > 0$, which explicitly reads:

$$(6.38)\qquad m + aW_8 > \delta W_8 + \mathbf{J}_{44}(E_8) + \mathbf{J}_{77}(E_8).$$

From the conditions on the determinants $\det\Delta_8^{1356} > 0$ and $-\det\Delta_8^{247} > 0$ we respectively obtain the further conditions

$$\begin{aligned}aW_8\Delta_8^{356} + ep^2A_8^2q\widetilde{q}W_8X_8[kZ_8 - (\psi - k)J_8] < ep^2A_8(e - qX_8)W_8\Delta_8^{56},&\\ (6.39)\quad [\delta W_8 - (m + aW_8)]\mathbf{J}_{44}(E_8)\mathbf{J}_{77}(E_8) + \alpha\beta\gamma qA_8W_8X_8&\\ < [\delta W_8 - (m + aW_8)]\alpha\lambda qA_8X_8 + \beta\omega A_8W_8\mathbf{J}_{77}(E_8).&\end{aligned}$$

Then we calculate the sums of the minors of order 2, where the relevant minors are listed in the Appendix C,

$$\begin{aligned}\Sigma_8^{1356} &= \Delta_8^{13} + \Delta_8^{15} + \Delta_8^{16} + \Delta_8^{35} + \Delta_8^{36} + \Delta_8^{56},\\ \Sigma_8^{247} &= [\delta W_8 - (m + aW_8)][\mathbf{J}_{44}(E_8) - \mathbf{J}_{77}(E_8)]\\ &\quad + \mathbf{J}_{44}(E_8)\mathbf{J}_{77}(E_8) - \beta\omega A_8 W_8 - \alpha\lambda q A_8 X_8.\end{aligned}$$

and for Δ_8^{1356} also of those of order 3 that provide the condition

$$\Theta_8^{1356} = \Delta_8^{135} + \Delta_8^{136} + \Delta_8^{156} + \Delta_8^{356} < 0. \tag{6.40}$$

Finally the following additional stability conditions must be satified:

$$\begin{gathered}-\mathrm{tr}\Delta_8^{247}\Sigma_8^{247} > -\det\Delta_8^{247};\\ \mathrm{tr}\Delta_8^{1356}\Sigma_8^{1356}\Theta_8^{1356} > (\Theta_8^{1356})^2 + \det\Delta_8^{1356}(\mathrm{tr}\Delta_8^{1356})^2.\end{gathered} \tag{6.41}$$

Equilibrium E_{14}

Here the diagonal elements that simplify upon use of the equilibrium equations are

$$\mathbf{J}_{11}(E_{14}) = -aW_{14}, \quad \mathbf{J}_{33}(E_{14}) = -gA_{14}, \quad \mathbf{J}_{55}(E_{14}) = -kZ_{14}.$$

The Jacobian splits into the product of two minors of order 3 and 4, respectively Δ_{14}^{135} and Δ_{14}^{2467}, but from the latter the eigenvalue $\mathbf{J}_{66}(E_{14})$ factorizes giving the first stability condition

$$\phi Z_{14} < v + kZ_{14}. \tag{6.42}$$

The traces of the first minor is negative,

$$\mathrm{tr}\Delta_{14}^{135} = -(aW_{14} + gA_{14} + kZ_{14}) < 0,$$

while the correspoding one of Δ_{14}^{247} provides the second stability condition

$$\begin{aligned}m + \mu + n + (\widetilde{c} + \lambda)A_{14} + (a + efp + \gamma)W_{14}&\\ + (q + \phi)Z_{14} > \delta W_{14} + b.&\end{aligned} \tag{6.43}$$

The sums of the minors of order two are

$$\begin{aligned}\Sigma_{14}^{135} &= a(g + k)A_{14}W_{14} + ep^2 A_{14}W_{14}(e - qZ_{14}) + (gk + q\widetilde{q})A_{14}Z_{14},\\ \Sigma_{14}^{247} &= [(\delta - a)W_{14} - m][b - \mu - \widetilde{c}A_{14} - efpW_{14} - qZ_{14}]\\ &- [(\delta - a - efp)W_{14} - m + b - \mu - \widetilde{c}A_{14} - qZ_{14}](n + \lambda A_{14} + \phi Z_{14} + \gamma W_{14})\\ &- \lambda\alpha q A_{14}Z_{14} - \beta A_{14}W_{14},\end{aligned}$$

while the determinants $\det\Delta_{14}^{135}$ and $\det\Delta_{14}^{247}$ respectively provide the stability conditions

$$
\begin{aligned}
(6.44)\quad & ep^2\widetilde{q}qA_{14}^2W_{14}^2Z_{14} < a(gk+q\widetilde{q})A_{14}W_{14}Z_{14} + ekp^2A_{14}W_{14}Z_{14}(e-qZ_{14}),\\
& \beta A_{14}\omega W_{14}(n+\lambda A_{14}+\phi Z_{14}+\gamma W_{14}) + \beta A_{14}\alpha qZ_{14}\gamma W_{14}\\
& \qquad < [(\delta-a)W_{14}-m][\alpha\lambda qA_{14}Z_{14}\\
& \qquad + (b-\mu-\widetilde{c}A_{14}-efpW_{14}-qZ_{14})(n+\lambda A_{14}+\phi Z_{14}+\gamma W_{14})].
\end{aligned}
$$

In addition the following conditions, which we do not write explicitly, must hold:

$$
(6.45)\qquad -\mathrm{tr}\Delta_{14}^{135}\Sigma_{14}^{135} > -\det\Delta_{14}^{135},\quad -\mathrm{tr}\Delta_{14}^{247}\Sigma_{14}^{247} > -\det\Delta_{14}^{247}.
$$

Equilibrium E_{13}

At E_{13} the Jacobian factorizes into two minors, Δ_{13}^{1234} and Δ_{13}^{567}, the latter giving immediately the negative eigenvalue $\mathbf{J}_{77}(E_{13}) = -n-\gamma Y_{13}-\lambda A_{13}$. The Routh-Hurwitz conditions on Δ_{13}^{56} give the first set of stability conditions:

$$
\begin{aligned}
(6.46)\qquad & b_{13} < 2v+\chi I_{13},\quad b_{13} = u+\widetilde{q}(A_{13}+\eta I_{13}) > 0,\\
& v[u-v-\chi I_{13}+\widetilde{q}(A_{13}+\eta I_{13})] + \chi I_{13}[u+\widetilde{q}(A_{13}+\eta I_{13})] < 0.
\end{aligned}
$$

Noting that the latter is a concave parabola in v with a positive value at $v=0$, the inequality holds for $v > v_+$, where

$$
v_+ = \frac{1}{2}\left[b_{13}-\chi I_{13}+\sqrt{(b_{13}-\chi I_{13})^2+4b_{13}\chi I_{13}}\right] = b_{13}
$$

denotes the largest of its roots. Thus (6.46) are equivalent to

$$
(6.47)\qquad v > \max\left\{b_{13}, \frac{1}{2}(b_{13}-\chi I_{13})\right\}.
$$

Further, the diagonal elements that simplify using the equilibrium equations are

$$
\begin{aligned}
\mathbf{J}_{11}(E_{13}) &= -aW_{13}-ep\frac{V_{13}}{W_{13}}(A_{13}+fI_{13}),\quad \mathbf{J}_{22}(E_{13}) = -aV_{13}-\omega\frac{I_{13}}{V_{13}},\\
\mathbf{J}_{33}(E_{13}) &= -gA_{13},\quad \mathbf{J}_{44}(E_{13}) = -cI_{13}-\beta\frac{A_{13}V_{13}}{I_{13}}.
\end{aligned}
$$

Thus the trace condition is seen immediately to hold $-\mathrm{tr}(\Delta_{13}^{1234}) > 0$. For the remaining Routh-Hurwitz conditions, we find

$$
\begin{aligned}
\Sigma_{13}^{1234} &= \Delta_{13}^{12}+\Delta_{13}^{13}+\Delta_{13}^{14}+\Delta_{13}^{24}+\Delta_{13}^{34}+\mathbf{J}_{22}(E_{13})\mathbf{J}_{33}(E_{13}),\\
\Theta_{13}^{1234} &= \Delta_{13}^{123}+\Delta_{13}^{124}+\Delta_{13}^{134}+\Delta_{13}^{234}.
\end{aligned}
$$

The final conditions to hold are thus

$$\det \Delta_{13}^{1234} > 0, \quad \Theta_{13}^{1234} < 0, \qquad (6.48)$$
$$\text{tr}\Delta_{13}^{1234}\Sigma_{13}^{1234}\Theta_{13}^{1234} > (\Theta_{13}^{1234})^2 + \det \Delta_{13}^{1234}(\text{tr}\Delta_{13}^{1234})^2.$$

Equilibrium E_{15}

By the equilibrium equation, we obtain the simplifications along the Jacobian's diagonal

$$\mathbf{J}_{44}(E_{15}) = -cI_{15}, \quad \mathbf{J}_{55}(E_{15}) = -\tfrac{J_{15}}{Z_{15}}(u + \widetilde{q}\eta I_{15}) - kZ_{15},$$
$$\mathbf{J}_{66}(E_{15}) = -\frac{Z_{15}}{J_{15}}(\phi B_{15} + \chi I_{15}) - kJ_{15}, \quad \mathbf{J}_{77}(E_{15}) = -\alpha q\frac{I_{15}X_{15}}{B_{15}}.$$

The remaining minor splits into the product of Δ_{15}^{12} and Δ_{15}^{4567}. The Routh-Hurwitz conditions on the former yield the stability conditions

$$2m + \gamma B_{15} + \omega I_{15} > +efpI_{15}, \qquad (6.49)$$
$$\mathbf{J}_{11}(E_{15})\mathbf{J}_{22}(E_{15}) > efpI_{15}(\gamma B_{15} + \omega I_{15}).$$

For Δ_{15}^{4567} the condition on the trace holds,

$$-\text{tr}\Delta_{15}^{4567} = cI_{15} + (u + \widetilde{q}\eta I_{15})\frac{J_{15}}{Z_{15}} + (\phi B_{15} + \chi I_{15})\frac{Z_{15}}{J_{15}} + \left(k + \alpha q\frac{I_{15}}{B_{15}}\right)X_{15} > 0.$$

To assess the stability conditions, we need the sums of minors of various orders. They are explicitly listed in the Appendix, as well as the determinant.

We then obtain the sums

$$\Sigma_{15}^{4567} = \Delta_{15}^{45} + \Delta_{15}^{46} + \Delta_{15}^{47} + \Delta_{15}^{56} + \Delta_{15}^{57} + \Delta_{15}^{67},$$
$$\Theta_{15}^{4567} = \Delta_{15}^{456} + \Delta_{15}^{457} + \Delta_{15}^{467} + \Delta_{15}^{567}.$$

The final conditions to hold are

$$-\text{tr}\Delta_{15}^{247}\Sigma_{15}^{247} > -\det \Delta_{15}^{247}, \quad \det \Delta_{15}^{4567} > 0, \qquad (6.50)$$
$$\text{tr}\Delta_{15}^{4567}\Sigma_{15}^{4567}\Theta_{15}^{4567} > (\Theta_{15}^{4567})^2 + \det \Delta_{15}^{4567}(\text{tr}\Delta_{15}^{4567})^2, \quad \Theta_{15}^{4567} < 0.$$

Equilibrium E_{16}

The diagonal entries of the Jacobian that simplify are in this case

$$\mathbf{J}_{22} = -m, \quad \mathbf{J}_{33} = -gA_{16}, \quad \mathbf{J}_{44} = -\left(cI_{16} + \lambda\frac{A_{16}}{I_{16}}B_{16}\right),$$

$$\mathbf{J}_{55} = -\left(kZ_{16} + [\widetilde{q}(A_{16} + \eta I_{16}) + u]\frac{J_{16}}{Z_{16}}\right),$$
$$\mathbf{J}_{66} = -\left(kJ_{16} + [\phi B_{16} + \chi I_{16}]\frac{Z_{16}}{J_{16}}\right), \quad \mathbf{J}_{77} = -\alpha q I_{16}\frac{Z_{16} + J_{16}}{B_{16}}.$$

We find the splitting into the minors Δ_{16}^{12} and Δ_{16}^{34567}. For the former, the Routh-Hurwitz conditions give

$$(6.51)\quad \begin{aligned} -\mathrm{tr}\Delta_{16}^{12} &= 2m + \gamma B_{16} + \omega I_{16} + pqA_{16}X_{16} - ep(A_{16} + fI_{16}) > 0,\\ \det\Delta_{16}^{12} &= (\gamma B_{16} + \omega I_{16})[pqA_{16}X_{16} - ep(A_{16} + fI_{16})] - m\mathbf{J}_{11} > 0. \end{aligned}$$

For Δ_{16}^{34567} we need the minors and their sums from order two up to order four, respectively Σ_{16}^{34567}, Θ_{16}^{34567} and Ω_{16}^{34567}. The minors are listed in the Appendix C. For their sums, we have

$$\begin{aligned} \Sigma_{16}^{34567} &= \Delta_{16}^{34} + \Delta_{16}^{35} + \Delta_{16}^{36} + \Delta_{16}^{37} + \Delta_{16}^{45} + \Delta_{16}^{46} + \Delta_{16}^{47} + \Delta_{16}^{56} + \Delta_{16}^{57} + \Delta_{16}^{67},\\ \Theta_{16}^{34567} &= \Delta_{16}^{345} + \Delta_{16}^{346} + \Delta_{16}^{347} + \Delta_{16}^{356} + \Delta_{16}^{357} + \Delta_{16}^{367} + \Delta_{16}^{456} + \Delta_{16}^{457}\\ &\quad + \Delta_{16}^{467} + \Delta_{16}^{567}, \quad \Omega_{16}^{34567} = \Delta_{16}^{3456} + \Delta_{16}^{3457} + \Delta_{16}^{3467} + \Delta_{16}^{3567} + \Delta_{16}^{4567}. \end{aligned}$$

Finally there is the determinant, $\det\Delta_{16}^{34567}$. The full Routh-Hurwitz conditions that must be satified are

$$(6.52)\quad \begin{aligned} &-\mathrm{tr}\Delta_{16}^{34567} > 0, \quad -\det\Delta_{16}^{34567} > 0,\\ &D_{(2),16}^{34567} = \Theta_{16}^{34567} - \mathrm{tr}\Delta_{16}^{34567}\Sigma_{16}^{34567} > 0,\\ &D_{(3),16}^{34567} = \mathrm{tr}\Delta_{16}^{34567}[\det\Delta_{16}^{34567} - \mathrm{tr}\Delta_{16}^{34567}\Omega_{16}^{34567}] - \Theta_{16}^{34567}D_{(2),16}^{34567} > 0,\\ &D_{(4),16}^{34567} = \Omega_{16}^{34567}D_{(3),16}^{34567} + \det\Delta_{16}^{34567}[\mathrm{tr}\Delta_{16}^{34567}\Omega_{16}^{34567}\\ &\qquad + \Sigma_{16}^{34567}\Theta_{16}^{34567} - \mathrm{tr}\Delta_{16}^{34567}(\Sigma_{16}^{34567})^2 - \det\Delta_{16}^{34567}] > 0. \end{aligned}$$

Equilibrium E_9

The diagonal elements of the Jacobian that simplify are

$$\mathbf{J}_{11}(E_9) = -aW_9, \quad \mathbf{J}_{22}(E_9) = -m - (a - \delta)W_9, \quad \mathbf{J}_{44}(E_9) = -cI_9,$$
$$\mathbf{J}_{55}(E_9) = -kZ_9 - (u + \widetilde{q}\eta I_9)\frac{J_9}{Z_9}, \quad \mathbf{J}_{66}(E_9) = -kJ_9 - (\phi B_9 + \chi I_9)\frac{Z_9}{J_9},$$
$$\mathbf{J}_{77}(E_9) = -\alpha q\frac{I_9}{B_9}X_9.$$

Define the sums of the minors of the various orders as follows, which are explicitly listed in the Appendix:

$$\Sigma_9^{124567} = \sum_{i<j=1}^{6} \Delta_9^{ij}, \qquad \Theta_9^{124567} = \sum_{i<j<k=1}^{6} \Delta_9^{ijk},$$

$$\Omega_9^{124567} = \sum_{i<j<k<m=1}^{6} \Delta_9^{ijkm}, \quad \Xi_9^{124567} = \sum_{i<j<k<m<n=1}^{6} \Delta_9^{ijkmn}.$$

Then the Routh-Hurwitz conditions for stability can be written as

$$\begin{aligned}
&-\mathrm{tr}\Delta_9^{124567} > 0, \quad D_{(2),9}^{124567} = -\mathrm{tr}\Delta_9^{124567}\Sigma_9^{124567} + \Theta_9^{124567} > 0,\\
&D_{(3),9}^{124567} = -\Theta_9^{124567} D_{(2),9} + \mathrm{tr}\Delta_9^{124567}[\Xi_9^{124567} - \mathrm{tr}\Delta_9^{124567}\Omega_9^{124567}] > 0,\\
&D_{(4),9}^{124567} = \Omega_9^{124567} D_{(3),9}^{124567} - \Sigma_9^{124567}[\mathrm{tr}\Delta_9^{124567}\Sigma_9^{124567}\Xi_9^{124567}\\
&\qquad - (\mathrm{tr}\Delta_9^{124567})^2 \det \Delta_9^{124567} - \Theta_9^{124567}\Xi_9^{124567}]\\
&\qquad + \mathrm{tr}\Delta_9^{124567}[\Omega_9^{124567}\Xi_9^{124567} - \Theta_9^{124567} \det \Delta_9^{124567}] - (\Xi_9^{124567})^2 > 0,\\
&D_{(5),9}^{124567} = -\Xi_9^{124567} D_{(4),9}^{124567} - \det \Delta_9^{124567}[-\Theta_9^{124567} D_{(3),9}^{124567}\\
&\qquad + \mathrm{tr}\Delta_9^{124567}(+\mathrm{tr}\Delta_9^{124567}\Sigma_9^{124567}\Xi_9^{124567}\\
&\qquad - (\mathrm{tr}\Delta_9^{124567})^2 \det \Delta_9^{124567} - \Theta_9^{124567}\Xi_9^{124567})] > 0.
\end{aligned} \tag{6.53}$$

Appendix C

Minors of Equilibrium E_8

Recalling (3.8), we now calculate the minors of order 2

$$\begin{aligned}
&\Delta_8^{13} = [ag + ep^2(e - qX_8)]A_8W_8, \quad \Delta_8^{15} = -aW_8\mathbf{J}_{55}(E_8), \quad \Delta_8^{16} = akW_8Z_8,\\
&\Delta_8^{35} = q\widetilde{q}A_8X_8 - gA_8\mathbf{J}_{55}(E_8), \qquad \Delta_8^{36} = gkA_8Z_8,\\
&\Delta_8^{56} = (k - \psi)J_8[u - (k + \psi)Z_8 + \widetilde{q}A_8] - kZ_8\mathbf{J}_{55}(E_8),
\end{aligned}$$

and those of order 3

$$\begin{aligned}
&\Delta_8^{135} = \Delta_8^{13}\mathbf{J}_{55}(E_8) - \widetilde{X}_8(a - ep^2A_8)qA_8W_8, \qquad \Delta_8^{136} = -kZ_8\Delta_8^{13},\\
&\Delta_8^{156} = -aW_8\Delta_8^{56}, \qquad \Delta_8^{356} = -\{g\Delta_8^{56} + q\widetilde{q}X_8[(\psi - k)J_8 - kZ_8]\}A_8.
\end{aligned}$$

Minors of Equilibrium E_{13}

We have here

$$\mathbf{J}_{12}(E_{13}) = ep(A_{13} + fI_{13}) - (a+\delta)W_{13}, \quad \mathbf{J}_{21}(E_{13}) = \omega I_{13} + (\delta - a)V_{13}.$$

Then we can write the minors of order 2

$$\begin{aligned}
\Delta_{13}^{12} &= \mathbf{J}_{11}(E_{13})\mathbf{J}_{22}(E_{13}) - \mathbf{J}_{12}(E_{13})\mathbf{J}_{21}(E_{13}),\\
\Delta_{13}^{13} &= \mathbf{J}_{11}(E_{13})\mathbf{J}_{33}(E_{13}) + e^2p^2A_{13}Y_{13},\\
\Delta_{13}^{14} &= \mathbf{J}_{11}(E_{13})\mathbf{J}_{44}(E_{13}) - efpI_{13}(efpY_{13} - \omega W_{13}),\\
\Delta_{13}^{24} &= \mathbf{J}_{22}(E_{13})\mathbf{J}_{44}(E_{13}) - (\beta A_{13} - efpI_{13})\omega W_{13},\\
\Delta_{13}^{34} &= \mathbf{J}_{33}(E_{13})\mathbf{J}_{44}(E_{13}) + \widetilde{g}A_{13}(\beta V_{13} - \widetilde{c}I_{13}),
\end{aligned}$$

and those of order 3

$$\begin{aligned}
\Delta_{13}^{123} &= \mathbf{J}_{33}(E_{13})\Delta_{13}^{12} + epY_{13}[epA_{13}\mathbf{J}_{22}(E_{13}) - \mathbf{J}_{21}(E_{13})(\beta + ep)A_{13}],\\
\Delta_{13}^{124} &= \mathbf{J}_{44}(E_{13})\Delta_{13}^{12} - \omega W_{13}[\mathbf{J}_{11}(E_{13})(\beta A_{13} - epfI_{13}) - epfI_{13}\mathbf{J}_{12}(E_{13})]\\
&\quad + (efpY_{13} - \omega W_{13})[(\beta V_{13} - \widetilde{c}I_{13})\mathbf{J}_{21}(E_{13}) - \mathbf{J}_{22}(E_{13})efpI_{13}],\\
\Delta_{13}^{134} &= \mathbf{J}_{33}(E_{13})\Delta_{13}^{14} - epY_{13}[\mathbf{J}_{21}(E_{13})\mathbf{J}_{44}(E_{13}) - \omega W_{13}efpI_{13}]\\
&\quad + (\widetilde{c}I_{13} - \beta V_{13})[epA_{13}(efpY_{13} - \omega W_{13}) - \widetilde{g}A_{13}\mathbf{J}_{11}(E_{13})]\\
\Delta_{13}^{234} &= \mathbf{J}_{22}(E_{13})\Delta_{13}^{34}\\
&\quad + \omega W_{13}[(efpI_{13} - \beta A_{13})\mathbf{J}_{33}(E_{13}) - (\beta + ep)A_{13}(\beta V_{13} - \widetilde{c}I_{13})].
\end{aligned}$$

Finally,

$$\begin{aligned}
\det \Delta_{13}^{1234} &= \mathbf{J}_{33}(E_{13})\Delta_{13}^{124} + epY_{13}\{epA_{13}\Delta_{13}^{24} - \mathbf{J}_{21}(E_{13})[\mathbf{J}_{44}(E_{13})(\beta + ep)A_{13}\\
&\quad - \widetilde{g}A_{13}(\beta A_{13} - efpI_{13})] + efpI_{13}A_{13}[\mathbf{J}_{22}(E_{13})\widetilde{g} + \omega W_{13}(\beta + ep)]\}\\
&\quad + (\widetilde{c}I_{13} - \beta V_{13})\{(\beta + ep)A_{13}[epA_{13}(efpY_{13} - \omega W_{13}) - \widetilde{g}A_{13}\mathbf{J}_{11}(E_{13})]\\
&\quad - \widetilde{g}A_{13}\Delta_{13}^{12} - epA_{13}[\omega W_{13}\mathbf{J}_{12}(E_{13})] - \mathbf{J}_{22}(E_{13})(efpY_{13} - \omega W_{13})\}.
\end{aligned}$$

Minors of Equilibrium E_{15}

Observe that in this case we have

$$\mathbf{J}_{56}(E_{15}) = u - (k + \psi)Z_{15} + \widetilde{q}\eta I_{15}, \quad \mathbf{J}_{65}(E_{15}) = (\psi - k)J_{15} + \phi B_{15} + \chi I_{15}.$$

Recalling (3.8), we now calculate the minors of order 2,

$$\begin{aligned}
\Delta_{15}^{45} &= cI_{15}\left[(u+\widetilde{q}\eta I_{15})\frac{J_{15}}{Z_{15}}+kZ_{15}\right]+qI_{15}(\widetilde{q}\eta X_{15}-\chi Z_{15}),\\
\Delta_{15}^{46} &= cI_{15}\mathbf{J}_{65}(E_{15})+\chi qI_{15}Z_{15},\quad \Delta_{15}^{47}=cI_{15}^{2}\alpha q\frac{X_{15}}{B_{15}},\\
\Delta_{15}^{56} &= +\left[kJ_{15}+(u+\widetilde{q}\eta I_{15})\frac{J_{15}}{Z_{15}}\right]\left[kJ_{15}+(\phi B_{15}+\chi I_{15})\frac{Z_{15}}{J_{15}}\right]\\
&\quad -\mathbf{J}_{56}(E_{15})\mathbf{J}_{65}(E_{15}),\\
\Delta_{15}^{57} &= \left[kJ_{15}+(u+\widetilde{q}\eta I_{15})\frac{J_{15}}{Z_{15}}\right]\alpha q\frac{I_{15}}{B_{15}}X_{15}+\phi Z_{15}(\alpha qI_{15}-\phi B_{15}),\\
\Delta_{15}^{67} &= \left[kJ_{15}+(\phi B_{15}+\chi I_{15})\frac{Z_{15}}{J_{15}}\right]\alpha q\frac{I_{15}}{B_{15}}X_{15}-\phi Z_{15}(\alpha qI_{15}-\phi B_{15})
\end{aligned}$$

and those of order 3

$$\begin{aligned}
\Delta_{15}^{456} &= -cI_{15}\Delta_{15}^{56}-qI_{15}\chi Z_{15}[\mathbf{J}_{56}(E_{15})-\mathbf{J}_{55}(E_{15})]\\
&\quad +qI_{15}(\widetilde{q}\eta X_{15}-\chi Z_{15})[\mathbf{J}_{66}(E_{15})-\mathbf{J}_{65}(E_{15})]\\
\Delta_{15}^{457} &= \mathbf{J}_{44}(E_{15})\Delta_{15}^{57}+qI_{15}[\mathbf{J}_{77}(E_{15})(\widetilde{q}\eta X_{15}-\chi Z_{15})+\phi Z_{15}(\alpha qX_{15}-\lambda B_{15})]\\
\Delta_{15}^{467} &= -cI_{15}\Delta_{15}^{67}-qI_{15}\left[\chi\alpha q\frac{I_{15}}{B_{15}}X_{15}+\phi Z_{15}(\alpha qX_{15}-\lambda B_{15})\right]\\
\Delta_{15}^{567} &= \mathbf{J}_{55}(E_{15})\Delta_{15}^{67}-\mathbf{J}_{56}(E_{15})[\mathbf{J}_{65}(E_{15})\mathbf{J}_{77}(E_{15})-\phi Z_{15}(\alpha qI_{15}-\lambda B_{15})]\\
&\quad -\phi Z_{15}(\alpha qI_{15}-\lambda B_{15})[\mathbf{J}_{65}(E_{15})-\mathbf{J}_{66}(E_{15})].
\end{aligned}$$

Finally, the determinant is

$$\begin{aligned}
\det\Delta_{15}^{4567} &= -cI_{15}\Delta_{15}^{567}+qI_{15}\left\{(\widetilde{q}\eta X_{15}-\chi Z_{15})\Delta_{15}^{67}\right.\\
&-\chi Z_{15}\left[\phi Z_{15}(\alpha qX_{15}-\lambda B_{15})-\alpha q\frac{I_{15}}{B_{15}}X_{15}\mathbf{J}_{56}(E_{15})\right]\\
&+(\alpha qX_{15}-\lambda B_{15})\phi Z_{15}\left[\mathbf{J}_{56}(E_{15})+\mathbf{J}_{66}(E_{15})\right]\\
&-(\widetilde{q}\eta X_{15}-\chi Z_{15})\left[\alpha q\frac{I_{15}}{B_{15}}X_{15}\mathbf{J}_{65}(E_{15})-\phi B_{15}(\alpha qI_{15}-\phi B_{15})\right]-\chi Z_{15}\Delta_{15}^{57}\\
&\left.+(\alpha qX_{15}-\lambda B_{15})\phi Z_{15}\left[\mathbf{J}_{55}(E_{15})+\phi B_{15}+\psi(I_{15}+J_{15})-kJ_{15}\right]\right\}.
\end{aligned}$$

Minors of Equilibrium E_{16}

Observing that

$$\mathbf{J}_{56}=\phi B_{16}+\chi I_{16}+\psi J_{16}-kJ_{16},\quad \mathbf{J}_{65}=u+\widetilde{q}(A_{16}+\eta I_{16})-(k+\psi)Z_{16}$$

and recalling (3.8), the minors of order 2 are:

$$
\begin{aligned}
\Delta_{16}^{34} &= \mathbf{J}_{33}(E_{16})\mathbf{J}_{44}(E_{16}) - (\widetilde{c}I_{16} - \lambda B_{16})\widetilde{g}A_{16},\\
\Delta_{16}^{35} &= \mathbf{J}_{33}(E_{16})\mathbf{J}_{55}(E_{16}) - q\widetilde{q}A_{16}X_{16}, \quad \Delta_{16}^{36} = \mathbf{J}_{33}(E_{16})\mathbf{J}_{66}(E_{16}),\\
\Delta_{16}^{37} &= \mathbf{J}_{33}(E_{16})\mathbf{J}_{77}(E_{16}) - \lambda^2 A_{16}B_{16},\\
\Delta_{16}^{45} &= \mathbf{J}_{44}(E_{16})\mathbf{J}_{55}(E_{16}) - [\chi Z_{16} - \widetilde{q}\eta X_{16}]qI_{16},\\
\Delta_{16}^{46} &= \mathbf{J}_{44}(E_{16})\mathbf{J}_{66}(E_{16}) + q\chi Z_{16}I_{16},\\
\Delta_{16}^{47} &= \mathbf{J}_{44}(E_{16})\mathbf{J}_{77}(E_{16}) + \lambda A_{16}[\lambda B_{16} - \alpha q X_{16}],\\
\Delta_{16}^{56} &= \mathbf{J}_{55}(E_{16})\mathbf{J}_{66}(E_{16}) - \mathbf{J}_{56}(E_{16})\mathbf{J}_{65}(E_{16}),\\
\Delta_{16}^{57} &= \mathbf{J}_{55}(E_{16})\mathbf{J}_{77}(E_{16}) - \phi Z_{56}(\phi B_{16} - \alpha q I_{16}),\\
\Delta_{16}^{67} &= \mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16}) + \phi Z_{56}(\phi B_{16} - \alpha q I_{16}),
\end{aligned}
$$

so that

$$\Sigma_{16}^{34567} = \sum_{i<j=3}^{7} \Delta_{16}^{ij}.$$

The minors of order 3:

$$
\begin{aligned}
\Delta_{16}^{345} &= \mathbf{J}_{33}(E_{16})\mathbf{J}_{44}(E_{16})\mathbf{J}_{55}(E_{16}) + \widetilde{g}A_{16}[\mathbf{J}_{55}(E_{16})(\lambda B_{16} - \widetilde{c}I_{16}) + q\widetilde{q}I_{16}X_{16}]\\
&\quad - qA_{16}[(\widetilde{c}I_{16} - \lambda B_{16})(\chi Z_{16} - \widetilde{q}\eta X_{16}) - \widetilde{q}X_{16}\mathbf{J}_{44}(E_{16})],\\
\Delta_{16}^{346} &= \Delta_{16}^{34}\mathbf{J}_{66}(E_{16}) + \chi Z_{16}[\mathbf{J}_{33}(E_{16})qI_{16} - qA_{16}(\lambda B_{16} - \widetilde{c}I_{16})],\\
\Delta_{16}^{347} &= \Delta_{16}^{34}\mathbf{J}_{77}(E_{16}) + [\lambda B_{16} - \alpha q X_{16}]\lambda A_{16}[\mathbf{J}_{33}(E_{16}) - \widetilde{c}I_{16} + \lambda B_{16}]\\
&\quad + \lambda^2 A_{16}B_{16}[\widetilde{g}A_{16} - \mathbf{J}_{44}(E_{16})],\\
\Delta_{16}^{356} &= \Delta_{16}^{56}\mathbf{J}_{33}(E_{16}) - \widetilde{q}qX_{16}A_{16}[\mathbf{J}_{56}(E_{16}) - \mathbf{J}_{66}(E_{16})],\\
\Delta_{16}^{357} &= \Delta_{16}^{57}\mathbf{J}_{33}(E_{16}) + \widetilde{q}A_{16}X_{16}[q\mathbf{J}_{77}(E_{16}) + \lambda(\phi B_{16} - \alpha q I_{16})]\\
&\quad - \lambda B_{16}A_{16}[q\phi Z_{16} + \lambda \mathbf{J}_{55}(E_{16})],\\
\Delta_{16}^{367} &= \Delta_{16}^{37}\mathbf{J}_{66}(E_{16}) - \phi Z_{16}[\mathbf{J}_{33}(E_{16})(\alpha q I_{16} - \phi B_{16}) - \lambda q A_{16}B_{16}],\\
\Delta_{16}^{456} &= \Delta_{16}^{56}\mathbf{J}_{44}(E_{16}) + qI_{16}[\mathbf{J}_{66}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) - \chi Z_{16}\mathbf{J}_{56}(E_{16})\\
&\quad - \mathbf{J}_{65}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) + \chi Z_{16}\mathbf{J}_{55}(E_{16})],\\
\Delta_{16}^{457} &= \Delta_{16}^{57}\mathbf{J}_{44}(E_{16}) + qI_{16}[\mathbf{J}_{77}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) + \phi Z_{16}(\alpha q I_{16} - \lambda B_{16})]\\
&\quad + \lambda A_{16}[(\alpha q I_{16} - \phi B_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) + \mathbf{J}_{55}(E_{16})(\lambda B_{16} - \alpha q X_{16})],\\
\Delta_{16}^{467} &= \Delta_{16}^{67}\mathbf{J}_{44}(E_{16}) + qI_{16}[\mathbf{J}_{77}(E_{16})\chi Z_{16} - \phi Z_{16}(\alpha q X_{16} - \lambda B_{16})]\\
&\quad + \lambda A_{16}[\chi Z_{16}(\alpha q I_{16} - \phi B_{16}) - \mathbf{J}_{66}(E_{16})], \qquad \Delta_{16}^{567} = \Delta_{16}^{56}\mathbf{J}_{77}(E_{16})\\
&\quad - \phi Z_{16}(\alpha q I_{16} - \phi B_{16})[\mathbf{J}_{55}(E_{16}) - \mathbf{J}_{56}(E_{16}) - \mathbf{J}_{65}(E_{16}) + \mathbf{J}_{66}(E_{16})].
\end{aligned}
$$

The minors of order 4:

$$\begin{aligned}
&\Delta_{16}^{3456} = \mathbf{J}_{66}(E_{16})\Delta_{16}^{345} - \mathbf{J}_{65}(E_{16})\{\mathbf{J}_{56}(E_{16})\Delta_{16}^{34} + qI_{16}\mathbf{J}_{33}(E_{16})[(\widetilde{q}\eta X_{16}\\
&- \chi Z_{16}) + \widetilde{g}\widetilde{q}X_{16}A_{16}] - \widetilde{q}A_{16}[(\lambda B_{16} - \widetilde{c}I_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) - \widetilde{q}X_{16}\mathbf{J}_{44}(E_{16})]\}\\
&+ \chi Z_{16}\{\mathbf{J}_{56}(E_{16})[qA_{16}(\lambda B_{16} - \widetilde{c}I_{16}) - cI_{16}J_{33}(E_{16})] + qI_{16}\Delta_{16}^{35}\\
&- qA_{16}[\mathbf{J}_{55}(E_{16})(\lambda B_{16} - \widetilde{c}I_{16}) + q\widetilde{q}I_{16}X_{16}\},
\end{aligned}$$

$$\begin{aligned}
&\Delta_{16}^{3457} = \mathbf{J}_{77}(E_{16})\Delta_{16}^{345} + \phi Z_{16}[\mathbf{J}_{33}(E_{16})\mathbf{J}_{44}(E_{16})(\alpha qI_{16} - \phi B_{16})\\
&- \widetilde{g}A_{16}qI_{16}\lambda B_{16} - qA_{16}(\widetilde{c}I_{16} - \lambda B_{16})(\lambda B_{16} - \alpha qX_{16}) - \lambda B_{16}\mathbf{J}_{44}(E_{16})qA_{16}\\
&+ (\alpha qX_{16} - \lambda B_{16})qI_{16}\mathbf{J}_{33}(E_{16}) - (\widetilde{c}I_{16} - \lambda B_{16})\widetilde{g}A_{16}(\phi B_{16} - \alpha qI_{16})]\\
&+ \lambda A_{16}\{\mathbf{J}_{33}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16})(\alpha qI_{16} - \phi B_{16}) + \lambda B_{16}\widetilde{g}A_{16}\mathbf{J}_{55}(E_{16})\\
&- \widetilde{q}X_{16}(\alpha qX_{16} - \lambda B_{16})qA_{16} - \lambda qA_{16}B_{16}(\widetilde{q}\eta X_{16} - \chi Z_{16})\\
&- \mathbf{J}_{55}(E_{16})\mathbf{J}_{33}(E_{16})(\alpha qX_{16} - \lambda B_{16}) + \widetilde{q}\widetilde{g}X_{16}A_{16}(\alpha qI_{16} - \phi B_{16})\\
&- (\widetilde{c}I_{16} - \lambda B_{16})(\alpha qI_{16} - \phi B_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) - \widetilde{q}qX_{16}I_{16}(\alpha qX_{16} - \lambda B_{16})\\
&- \mathbf{J}_{55}(E_{16})\mathbf{J}_{44}(E_{16})\lambda B_{16} - \lambda B_{16}qI_{16}(\widetilde{q}\eta X_{16} - \chi Z_{16})\\
&- (\lambda B_{16} - \alpha qX_{16})\mathbf{J}_{55}(E_{16})(\widetilde{c}I_{16} - \lambda B_{16}) - \widetilde{q}X_{16}\mathbf{J}_{44}(E_{16})(\alpha qX_{16} - \phi B_{16})\},
\end{aligned}$$

$$\begin{aligned}
&\Delta_{16}^{3467} = \mathbf{J}_{33}(E_{16})\Delta_{16}^{467} + (\widetilde{c}I_{16} - \lambda B_{16})[(\chi Z_{16}\lambda A_{16} + \phi Z_{16}\widetilde{g}A_{16})(\phi B_{16}\\
&- \alpha qI_{16}) - \widetilde{g}A_{16}\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16}) - (\phi qA_{16}Z_{16} + \lambda A_{16}\mathbf{J}_{66}(E_{16}))(\alpha qX_{16}\\
&- \lambda B_{16}) + \chi Z_{16}qA_{16}\mathbf{J}_{77}(E_{16})] + \lambda B_{16}[\mathbf{J}_{66}(E_{16})\lambda\widetilde{g}A_{16}^2 + \mathbf{J}_{44}(E_{16})qA_{16}\phi Z_{16}\\
&- \mathbf{J}_{44}(E_{16})\mathbf{J}_{66}(E_{16})\lambda A_{16} - \chi Z_{16}qI\lambda A_{16} + \widetilde{g}A_{16}qI_{16}\phi Z_{16} - q\lambda A_{16}^2\chi Z_{16}],
\end{aligned}$$

$$\begin{aligned}
&\Delta_{16}^{3567} = \mathbf{J}_{33}(E_{16})\Delta_{16}^{567} - \widetilde{q}X_{16}\{qA_{16}\mathbf{J}_{65}(E_{16})\mathbf{J}_{77}(E_{16}) - [\phi Z_{16}qA_{16}\\
&+ \phi Z_{16}qA_{16} + \mathbf{J}_{66}(E_{16})\lambda A_{16} - \mathbf{J}_{65}(E_{16})\lambda A_{16}](\phi B_{16} - \alpha qI_{16})\\
&- qA_{16}\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16})] + \lambda B_{16}[-qA_{16}\mathbf{J}_{56}(E_{16})\phi Z_{16} + \mathbf{J}_{65}(E_{16})qA_{16}\phi Z_{16}\\
&- \lambda A_{16}\Delta_{16}^{56} + (\mathbf{J}_{55}(E_{16}) - \mathbf{J}_{66}(E_{16}))qA_{16}\phi Z_{16}\},
\end{aligned}$$

$$\begin{aligned}
&\Delta_{16}^{4567} = \mathbf{J}_{44}(E_{16})\Delta_{16}^{567}\\
&+ qI_{16}[\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) - (\lambda B_{16} - \alpha qX_{16})(\mathbf{J}_{56}(E_{16})\\
&+ \mathbf{J}_{66}(E_{16}))\phi Z_{16} + (\phi B_{16} - \alpha qI_{16})[\chi\phi Z_{16}^2 - \phi Z_{16}(\widetilde{q}\eta X_{16} - \chi Z_{16})\\
&- \chi Z_{16}\mathbf{J}_{56}(E_{16})\mathbf{J}_{77}(E_{16}) + \mathbf{J}_{65}(E_{16})(\lambda B_{16} - \alpha qX_{16})\phi Z_{16}\\
&+ \chi Z_{16}\mathbf{J}_{55}(E_{16})\mathbf{J}_{77}(E_{16})\\
&+ (\phi B_{16} - \alpha qI_{16})\phi Z_{16}(\chi Z_{16} - \widetilde{q}\eta X_{16}) + (\chi Z_{16} - \widetilde{q}\eta X_{16})\mathbf{J}_{65}(E_{16})\mathbf{J}_{77}(E_{16})\\
&+ \chi Z_{16}\mathbf{J}_{55}(E_{16})(\lambda B_{16} - \alpha qX_{16}) - \chi\phi Z_{16}^2(\phi B_{16} - \alpha qI_{16})]\\
&+ \lambda A_{16}\{(\phi B_{16} - \alpha qI_{16})[(\chi Z_{16} - \widetilde{q}\eta X_{16})\mathbf{J}_{66}(E_{16}) - \chi Z_{16}\mathbf{J}_{55}(E_{16})]\\
&+ \boldsymbol{\Delta}_{16}^{56}(\lambda B_{16} - \alpha qX_{16}) - [(\chi Z_{16} - \widetilde{q}\eta I_{16})\mathbf{J}_{65}(E_{16})\\
&- \chi Z_{16}\mathbf{J}_{56}(E_{16})](\phi B_{16} - \alpha qI_{16})\}.
\end{aligned}$$

Finally there is the determinant:

$$
\begin{aligned}
&\Delta_{16}^{34567} = \mathbf{J}_{33}(E_{16})\Delta_{16}^{4567} + (\widetilde{c}I_{16} - \lambda B_{16})\{\mathbf{J}_{56}(E_{16}) - \mathbf{J}_{66}(E_{16}) \\
&\quad - \widetilde{g}A_{16}[\mathbf{J}_{55}(E_{16})\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16}) \\
&\quad + (\phi B_{16} - \alpha q I_{16})\phi Z_{16}(\mathbf{J}_{65}(E_{16}) - \mathbf{J}_{56}(E_{16})) \\
&\quad - \mathbf{J}_{65}(E_{16})\mathbf{J}_{56}(E_{16})\mathbf{J}_{77}(E_{16})] + qA_{16}[\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16})(\widetilde{q}\eta X_{16} - \chi Z_{16}) \\
&\quad - \chi Z_{16}\mathbf{J}_{56}(E_{16})\mathbf{J}_{77}(E_{16}) + (\mathbf{J}_{56}(E_{16}) + \mathbf{J}_{66}(E_{16}))\phi Z_{16}(\lambda B_{16} - \alpha q X_{16}) \\
&\quad - \phi Z_{16}(\phi B_{16} - \alpha q I_{16})(\chi Z_{16} - \widetilde{q}\eta I_{16})] - qA_{16}[\chi\phi Z_{16}^{2}(\phi B_{16} - \alpha q I_{16}) \\
&\quad - (\chi Z_{16} - \widetilde{q}\eta X_{16})\mathbf{J}_{65}(E_{16})\mathbf{J}_{77}(E_{16}) - \mathbf{J}_{55}(E_{16})\phi Z_{16}(\lambda B_{16} - \alpha q X_{16}) \\
&\quad - \phi Z_{16}\mathbf{J}_{65}(E_{16})(\lambda B_{16} - \alpha q X_{16}) - \phi Z_{16}(\phi B_{16} - \alpha q I_{16})(\chi Z_{16} - \widetilde{q}\eta X_{16}) \\
&\quad - \chi Z_{16}\mathbf{J}_{55}(E_{16})\mathbf{J}_{77}(E_{16})] - \lambda A_{16}[\chi Z_{16}(\phi B_{16} - \alpha q I_{16})(\mathbf{J}_{56}(E_{16}) - \mathbf{J}_{55}(E_{16})) \\
&\quad + \mathbf{J}_{55}(E_{16})\mathbf{J}_{66}(E_{16})(\lambda B_{16} - \alpha q X_{16}) - (\lambda B_{16} - \alpha q X_{16})\mathbf{J}_{56}(E_{16})\mathbf{J}_{65}(E_{16}) \\
&\quad - (\chi Z_{16} - \widetilde{q}\eta X_{16})(\mathbf{J}_{65}(E_{16}) - \mathbf{J}_{66}(E_{16}))(\phi B_{16} - \alpha q I_{16})]\} \\
&\quad + \widetilde{q}X_{16}\{-\widetilde{g}A_{16}[-qI_{16}\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16}) + qI_{16}\mathbf{J}_{77}(E_{16})\mathbf{J}_{65}(E_{16}) \\
&\quad + \lambda A_{16}(\mathbf{J}_{66}(E_{16}) - \mathbf{J}_{65}(E_{16}))(\phi B_{16} - \alpha q I_{16})] \\
&\quad + qA_{16}[\mathbf{J}_{44}(E_{16})\mathbf{J}_{66}(E_{16})\mathbf{J}_{77}(E_{16}) + (\phi B_{16} - \alpha q I_{16})(\phi Z_{16}\mathbf{J}_{44}(E_{16}) \\
&\quad - \chi Z_{16}\lambda A_{16}) + \chi Z_{16} q I_{16}\mathbf{J}_{77}(E_{16}) + (\lambda B_{16} - \alpha q I_{16})(\phi Z_{16} q I_{16} \\
&\quad - \lambda A_{16}\mathbf{J}_{66}(E_{16}))] - qA_{16}[\mathbf{J}_{44}(E_{16})\mathbf{J}_{65}(E_{16})\mathbf{J}_{77}(E_{16}) \\
&\quad + (qI_{16}\phi Z_{16} + \lambda A_{16}\mathbf{J}_{65}(E_{16}))(\lambda B_{16} - \alpha q X_{16}) \\
&\quad - (\phi B_{16} - \alpha q I_{16})(\phi Z_{16}\mathbf{J}_{44}(E_{16}) - \lambda A_{16}\chi Z_{16}) + \chi Z_{16} q I_{16}\mathbf{J}_{77}(E_{16})] \\
&\quad + \lambda A_{16}[\mathbf{J}_{44}(E_{16})(\mathbf{J}_{66}(E_{16}) - \mathbf{J}_{65}(E_{16}) + \chi Z_{16} q I_{16})(\phi B_{16} - \alpha q I_{16}) \\
&\quad + (\lambda B_{16} - \alpha q X_{16}) q I_{16}(\mathbf{J}_{66}(E_{16}) - \mathbf{J}_{65}(E_{16}))]\} \\
&\quad - \lambda B_{16}\{\widetilde{g}A_{16}[qI_{16}\phi Z_{16}(\mathbf{J}_{65}(E_{16}) - \mathbf{J}_{56}(E_{16}) + \mathbf{J}_{55}(E_{16}) - \mathbf{J}_{66}(E_{16})) \\
&\quad + \lambda A_{16}\Delta_{16}^{56}] - qA_{16}[qI_{16}\phi\chi Z_{16}^{2} + \mathbf{J}_{44}(E_{16})\mathbf{J}_{56}(E_{16})\phi Z_{16} \\
&\quad - (\chi Z_{16} - \widetilde{q}\eta X_{16})(\lambda A_{16}\mathbf{J}_{66}(E_{16}) + \phi Z_{16} q I_{16}) \\
&\quad + \chi Z_{16}\lambda A_{16}\mathbf{J}_{56}(E_{16}) + \phi Z_{16}\mathbf{J}_{66}(E_{16})\mathbf{J}_{44}(E_{16})] + qA_{16}[(qI_{16}\chi Z_{16} \\
&\quad + \mathbf{J}_{44}(E_{16})\mathbf{J}_{55}(E_{16}))\phi Z_{16} - (\lambda A_{16}\mathbf{J}_{65}(E_{16}) + qI_{16}\phi Z_{16})(\chi Z_{16} - \widetilde{q}\eta X_{16}) \\
&\quad - \chi Z_{16}\lambda A_{16}\mathbf{J}_{55}(E_{16}) + \mathbf{J}_{65}(E_{16})\chi Z_{16}\mathbf{J}_{44}(E_{16})] - \lambda A_{16}[\mathbf{J}_{44}(E_{16})\Delta_{16}^{56} \\
&\quad - \chi Z_{16} q I_{16}(\mathbf{J}_{55}(E_{16}) - \mathbf{J}_{56}(E_{16})) - qI_{16}(\mathbf{J}_{65}(E_{16}) \\
&\quad + \mathbf{J}_{66}(E_{16}))(\chi Z_{16} - \widetilde{q}\eta X_{16})]\}.
\end{aligned}
$$

Minors of Equilibrium E_9

Recalling (3.8), the minors of order 2 of Δ_9^{124567} are:

$$
\begin{aligned}
&\Delta_9^{12} = -aW_9\mathbf{J}_{22}(E_9) - \mathbf{J}_{12}(E_9)(\gamma B_9 + \omega I_9), \quad \Delta_9^{15} = -aW_9\mathbf{J}_{55}(E_9),\\
&\Delta_9^{14} = -aW_9\mathbf{J}_{44}(E_9) + efpI_9W_9(efp - \omega), \quad \Delta_9^{16} = -aW_9\mathbf{J}_{66}(E_9),\\
&\Delta_9^{17} = -aW_9\mathbf{J}_{77}(E_9) - \gamma^2 B_9W_9, \quad \Delta_9^{24} = \mathbf{J}_{22}(E_9)\mathbf{J}_{44}(E_9) + efpI_9\omega W_9,\\
&\Delta_9^{25} = \mathbf{J}_{22}(E_9)\mathbf{J}_{55}(E_9), \quad \Delta_9^{27} = \mathbf{J}_{22}(E_9)\mathbf{J}_{77}(E_9) + \gamma^2 B_9W_9,\\
&\Delta_9^{26} = \mathbf{J}_{22}(E_9)\mathbf{J}_{66}(E_9), \quad \Delta_9^{45} = \mathbf{J}_{44}(E_9)\mathbf{J}_{55}(E_9) + qI_9(\widetilde{q}\eta X_9 - \chi Z_9),\\
&\Delta_9^{46} = \mathbf{J}_{44}(E_9)\mathbf{J}_{66}(E_9) + qI_9\chi Z_9, \quad \Delta_9^{47} = \mathbf{J}_{44}(E_9)\mathbf{J}_{77}(E_9),\\
&\Delta_9^{56} = \mathbf{J}_{55}(E_9)\mathbf{J}_{66}(E_9) - \mathbf{J}_{56}(E_9)\mathbf{J}_{65}(E_9),\\
&\Delta_9^{57} = \mathbf{J}_{55}(E_9)\mathbf{J}_{77}(E_9) + \phi Z_9(\alpha qI_9 - \phi B_9),\\
&\Delta_9^{67} = \mathbf{J}_{66}(E_9)\mathbf{J}_{77}(E_9) - \phi Z_9(\alpha qI_9 - \phi B_9).
\end{aligned}
$$

The minors of order 3 are:

$$
\begin{aligned}
\Delta_9^{124} &= -aW_9\mathbf{J}_{22}(E_9)\mathbf{J}_{44}(E_9) - \mathbf{J}_{12}(E_9)efpI_9\omega W_9\\
&\quad - efpI_9(\gamma B_9 + \omega I_9 - \mathbf{J}_{22}(E_9))W_9(efp - \omega)\\
&\quad - aW_9efpI_9\omega W_9 - (\gamma B_9 + \omega I_9)\mathbf{J}_{12}(E_9)\mathbf{J}_{44}(E_9),\\
\Delta_9^{125} &= \mathbf{J}_{55}(E_9)\Delta_9^{12}, \quad \Delta_9^{126} = \mathbf{J}_{66}(E_9)\Delta_9^{12},\\
\Delta_9^{127} &= -aW_9\Delta_9^{27} - (\gamma B_9 + \omega I_9)(\mathbf{J}_{12}(E_9)\mathbf{J}_{77}(E_9) - \gamma^2 B_9W_9)\\
&\quad - \gamma^2 B_9W_9(\mathbf{J}_{12}(E_9) + \mathbf{J}_{22}(E_9))\\
\Delta_9^{245} &= \mathbf{J}_{55}(E_9)\Delta_9^{24} + qI_9\mathbf{J}_{22}(E_9)(\widetilde{q}\eta X_9 - \chi Z_9),\\
\Delta_9^{246} &= \mathbf{J}_{66}(E_9)\Delta_9^{24} + qI_9\mathbf{J}_{22}(E_9)\chi Z_9,\\
\Delta_9^{247} &= \mathbf{J}_{77}(E_9)\Delta_9^{24} - \omega W_9[efpI_9(q\alpha X_9 - \lambda B_9) + \gamma B_9\mathbf{J}_{44}(E_9)],\\
\Delta_9^{256} &= \mathbf{J}_{22}(E_9)\Delta_9^{56}, \quad \Delta_9^{267} = \mathbf{J}_{22}(E_9)\Delta_9^{67} + \gamma^2 W_9B_9\mathbf{J}_{66}(E_9),\\
\Delta_9^{257} &= \mathbf{J}_{22}(E_9)\Delta_9^{57} + \gamma^2 B_9W_9\mathbf{J}_{55}(E_9),\\
\Delta_9^{456} &= \mathbf{J}_{44}(E_9)\Delta_9^{56} - qI_9[\chi Z_9\mathbf{J}_{56}(E_9) - (\widetilde{q}\eta X_9\\
&\quad - \chi Z_9)(\mathbf{J}_{66}(E_9) - \mathbf{J}_{65}(E_9)) - \chi Z_9\mathbf{J}_{55}(E_9)],\\
\Delta_9^{457} &= \mathbf{J}_{44}(E_9)\Delta_9^{57} + qI_9[\mathbf{J}_{77}(E_9)(\widetilde{q}\eta X_9 - \chi Z_9) + \phi Z_9(\alpha qX_9 - \lambda B_9)],\\
\Delta_9^{467} &= \mathbf{J}_{44}(E_9)\Delta_9^{67} + qI_9[\chi Z_9\mathbf{J}_{77}(E_9) - \phi Z_9(\alpha qX_9 - \lambda B_9)],\\
\Delta_9^{567} &= \mathbf{J}_{55}(E_9)\Delta_9^{67} - \mathbf{J}_{56}(E_9)[\mathbf{J}_{65}(E_9)\mathbf{J}_{77}(E_9)\\
&\quad - \phi Z_9(\alpha qI_9 - \phi B_9)] + \phi Z_9(\alpha qI_9 - \phi B_9)(\mathbf{J}_{65}(E_9) - \mathbf{J}_{66}(E_9)),
\end{aligned}
$$

$$
\begin{aligned}
\Delta_9^{145} &= -aW_9\Delta_9^{45} + W_9(efp-\omega)efpI_9\mathbf{J}_{55}(E_9),\\
\Delta_9^{146} &= -aW_9\Delta_9^{46} + W_9(efp-\omega)efpI_9\mathbf{J}_{66}(E_9),\\
\Delta_9^{147} &= -aW_9\Delta_9^{47} + W_9(efp-\omega)efpI_9\mathbf{J}_{77}(E_9)\\
&\quad -\gamma W_9[\gamma B_9\mathbf{J}_{44}(E_9) + efpI_9(\alpha qX_9 - \lambda B_9)],\\
\Delta_9^{156} &= -aW_9\Delta_9^{56}, \quad \Delta_9^{157} = -aW_9\Delta_9^{57} - \gamma^2 W_9B_9\mathbf{J}_{55}(E_9),\\
\Delta_9^{167} &= -aW_9\Delta_9^{67} - \gamma^2 W_9B_9\mathbf{J}_{66}(E_9),\\
\Delta_9^{247} &= \mathbf{J}_{77}(E_9)\mathbf{J}_{24}(E_9) + \gamma W_9[\gamma B_9\mathbf{J}_{44}(E_9) - efpI_9(\alpha qX_9 - \lambda B_9)].
\end{aligned}
$$

Then we list the minors of order 4:

$$
\begin{aligned}
\Delta_9^{1245} &= \mathbf{J}_{55}(E_9)\Delta_9^{124} + qI_9(\widetilde{q}\eta X_9 - \chi Z_9)\Delta_9^{12},\\
\Delta_9^{1246} &= \mathbf{J}_{66}(E_9)\Delta_9^{124} + qI_9\chi Z_9\Delta_9^{12},\\
\Delta_9^{1247} &= \mathbf{J}_{77}(E_9)\Delta_9^{124} + \gamma W_9[(\alpha qX_9 - \lambda B_9)efpI_9(aW_9 + \mathbf{J}_{12}(E_9))\\
&\quad + \gamma B_9(\Delta_9^{14} - \mathbf{J}_{12}(E_9)\mathbf{J}_{44}(E_9)) + efpI_9W_9(efp-\omega))]\\
&\quad + \gamma W_9\{(\alpha qX_9 - \lambda B_9)efpI_9(\mathbf{J}_{22}(E_9) - \gamma B_9 - \omega I_9)\\
&\quad + \gamma B_9[\mathbf{J}_{44}(E_9)(\gamma B_9 + \omega I_9) + efpI_9\omega W_9] - \gamma B_9\Delta_9^{24}\}\\
\Delta_9^{2456} &= \mathbf{J}_{66}(E_9)\Delta_9^{245} - \mathbf{J}_{65}(E_9)[\mathbf{J}_{56}(E_9)\Delta_9^{24} + qI_9\mathbf{J}_{22}(E_9)(\widetilde{q}\eta X_9 - \chi Z_9)\\
&\quad - \chi Z_9\mathbf{J}_{22}(E_9)(\mathbf{J}_{56}(E_9) - \mathbf{J}_{55}(E_9)),\\
\Delta_9^{2457} &= \mathbf{J}_{55}(E_9)\Delta_9^{247} - (\alpha qI_9 - \phi B_9)[\phi Z_9\Delta_9^{24} + \gamma W_9efpI_9(\widetilde{q}\eta X_9 - \chi Z_9)]\\
&\quad + qI_9[(\widetilde{q}\eta X_9 - \chi Z_9)\Delta_9^{27} + \phi Z_9(\mathbf{J}_{22}(E_9)(\alpha qX_9 - \lambda B_9)\\
&\quad + \gamma\omega B_9W_9], \quad \Delta_9^{2467} = \mathbf{J}_{22}(E_9)\Delta_9^{467} - \omega W_9[qI_9\gamma B_9\phi Z_9 - efpI_9\Delta_9^{67}]\\
&\quad + \gamma W_9\{\gamma B_9\Delta_9^{46} + efpI_9[(\alpha qI_9 - \phi B_9)\chi Z_9 - \mathbf{J}_{66}(E_9)(\alpha qX_9 - \lambda B_9)]\},\\
\Delta_9^{1456} &= -aW_9\Delta_9^{456} + W_9(efp-\omega)efpI_9\Delta_9^{56},\\
\Delta_9^{1457} &= -aW_9\Delta_9^{457} + W_9(efp-\omega)[efpI_9\Delta_9^{57} + \gamma B_9qI_9\phi Z_9]\\
&\quad - \gamma W_9\{efpI_9[(\widetilde{q}\eta X_9 - \chi Z_9)(\alpha qI_9 - \phi B_9)\\
&\quad - (\alpha qX_9 - \lambda B_9)\mathbf{J}_{55}(E_9)] + \gamma B_9\Delta_9^{45}\},\\
\Delta_9^{1467} &= -aW_9\Delta_9^{467} + W_9(efp-\omega)[efpI_9\Delta_9^{67} - \gamma B_9qI_9\phi Z_9]\\
&\quad - \gamma W_9\{efpI_9[\chi Z_9(\alpha qI_9 - \phi B_9) - \mathbf{J}_{66}(E_9)(\alpha qX_9 - \lambda B_9)] + \gamma B_9\Delta_9^{46}\},\\
\Delta_9^{4567} &= \mathbf{J}_{44}(E_9)\Delta_9^{567} + qI_9\{(\widetilde{q}\eta X_9 - \chi Z_9)\Delta_9^{67} - \chi Z_9[\mathbf{J}_{56}(E_9)\mathbf{J}_{77}(E_9)\\
&\quad + \phi Z_9(\alpha qI_9 - \phi B_9)] + (\alpha qX_9 - \lambda B_9)\phi Z_9[\mathbf{J}_{56}(E_9) + \mathbf{J}_{66}(E_9)]\}\\
&\quad - qI_9\{(\widetilde{q}\eta X_9 - \chi Z_9)[\mathbf{J}_{65}(E_9)\mathbf{J}_{77}(E_9) - \phi Z_9(\alpha qI_9 - \phi B_9)] - \chi Z_9\Delta_9^{57}\\
&\quad + (\alpha qX_9 - \lambda B_9)\phi Z_9[\mathbf{J}_{55}(E_9) + \mathbf{J}_{65}(E_9)]\},
\end{aligned}
$$

$$
\begin{aligned}
\Delta_9^{1567} &= -aW_9\Delta_9^{567} - \gamma^2 B_9 W_9 \Delta_9^{56},\\
\Delta_9^{1256} &= \Delta_9^{12}\Delta_9^{56},\\
\Delta_9^{1257} &= \Delta_9^{127}\mathbf{J}_{55}(E_9) + (\alpha q I_9 - \phi B_9)\phi Z_9 \Delta_9^{12},\\
\Delta_9^{1267} &= \Delta_9^{127}\mathbf{J}_{66}(E_9) - (\alpha q I_9 - \phi B_9)\phi Z_9 \Delta_9^{12},\\
\Delta_9^{2567} &= \Delta_9^{567}\mathbf{J}_{22}(E_9) + \gamma^2 B_9 W_9 \Delta_9^{56}.
\end{aligned}
$$

Let us define the following quantities:

$$
\begin{aligned}
\mathcal{L} &= (\widetilde{q}\eta X_9 - \chi Z_9)(\alpha q I_9 - \phi B_9)(\mathbf{J}_{65}(E_9) - \mathbf{J}_{66}(E_9)) + \Delta_9^{56}(\alpha q X_9 - \lambda B_9)\\
&\quad + \chi Z_9(\alpha q I_9 - \phi B_9)(\mathbf{J}_{56}(E_9) - \mathbf{J}_{55}(E_9)),\\
\mathcal{Q} &= q I_9 \phi Z_9(\mathbf{J}_{55}(E_9) + \mathbf{J}_{65}(E_9) - \mathbf{J}_{56}(E_9) - \mathbf{J}_{66}(E_9)),\\
\mathcal{R} &= (\alpha q I_9 - \phi B_9)(\widetilde{q}\eta X_9 - \chi Z_9)(\mathbf{J}_{65}(E_9) - \mathbf{J}_{66}(E_9))\\
&\quad + (\alpha q I_9 - \phi B_9)\chi Z_9(\mathbf{J}_{56}(E_9) - \mathbf{J}_{55}(E_9)) + (\alpha q X_9 - \lambda B_9)\Delta_9^{56}.
\end{aligned}
$$

Next the minors of order 5:

$$
\begin{aligned}
\Delta_9^{12456} &= -aW_9\Delta_9^{2456} - \mathbf{J}_{12}(E_9)[(\gamma B_9 + \omega I_9)\Delta_9^{456} + efpI_9\omega W_9\Delta_9^{56}]\\
&\qquad + W_9(efp - \omega)efpI_9\Delta_9^{56}[\mathbf{J}_{22}(E_9) - (\gamma B_9 + \omega I_9)],\\
\Delta_9^{12457} &= -aW_9\Delta_9^{2457} - \mathbf{J}_{12}(E_9)\{(\gamma B_9 + \omega I_9)\Delta_9^{457} + efpI_9[\omega W_9\Delta_9^{57}\\
&\qquad + \gamma W_9((\widetilde{q}\eta X_9 - \chi Z_9)(\alpha q I_9 - \phi B_9) - (\alpha q X_9 - \lambda B_9)\mathbf{J}_{55}(E_9))]\\
&\qquad + \gamma B_9[\omega W_9 q I_9 \chi Z_9 + \gamma W_9 \mathbf{J}_{44}(E_9)\mathbf{J}_{55}(E_9)] + \gamma W_9 q I_9(\widetilde{q}\eta X_9 - \chi Z_9)]\}\\
&\qquad + W_9(efp - \omega)\{efpI_9\Delta_9^{257} - (\gamma B_9 + \omega I_9)[efpI_9\Delta_9^{57} - \gamma B_9 q I_9 \chi Z_9]\\
&\qquad + \gamma B_9[\mathbf{J}_{22}(E_9) q I_9 \phi Z_9 - efpI_9\gamma W_9\mathbf{J}_{55}(E_9)]\}\\
&\qquad - \gamma W_9\{\mathbf{J}_{55}(E_9)[(\gamma B_9 + \omega I_9)(\mathbf{J}_{44}(E_9)\gamma B_9 - efpI_9(\alpha q X_9 - \lambda B_9)]\\
&\qquad - \mathbf{J}_{22}(E_9)[\gamma B_9\mathbf{J}_{44}(E_9) - efpI_9(\alpha q X_9 - \lambda B_9)]]\\
&\qquad + (\widetilde{q}\eta X_9 - \chi Z_9)[(\gamma B_9 + \omega I_9)[\gamma B_9 q I_9 - efpI_9(\alpha q I_9 - \phi B_9)]\\
&\qquad - \mathbf{J}_{22}(E_9)(q I_9 \gamma B_9 - efpI_9(\alpha q I_9 - \phi B_9)]\},\\
\Delta_9^{12567} &= -aW_9\Delta_9^{2567} - \mathbf{J}_{12}(E_9)[(\gamma B_9 + \omega I_9)\Delta_9^{567} + \gamma^2 B_9 W_9\Delta_9^{56}]\\
&\qquad - \gamma W_9\gamma B_9[\Delta_9^{256} - (\gamma B_9 + \omega I_9)\Delta_9^{56}],\\
\Delta_9^{14567} &= -aW_9\Delta_9^{4567} - W_9(efp - \omega)[\gamma B_9\mathcal{Q} - efpI_9\Delta_9^{567}]\\
&\qquad - \gamma W_9[\gamma B_9\Delta_9^{456} - efpI_9\mathcal{L}],\\
\Delta_9^{24567} &= \mathbf{J}_{22}(E_9)\Delta_9^{4567} + efpI_9[\omega W_9\Delta_9^{567} - \gamma W_9\mathcal{R}] + \gamma B_9[\gamma W_9\Delta_9^{456}\\
&\qquad + \omega W_9 q I_9 \chi Z_9(\mathbf{J}_{56}(E_9) + \mathbf{J}_{66}(E_9) - \mathbf{J}_{55}(E_9) - \mathbf{J}_{65}(E_9))]
\end{aligned}
$$

$$
\begin{aligned}
\Delta_9^{12467} = {} & -aW_9\Delta_9^{2467} - (\gamma B_9 + \omega I_9)\{\mathbf{J}_{12}(E_9)\Delta_9^{467} + efpI_9[W_9(efp-\omega)\Delta_9^{67} \\
& - \gamma W_9(\chi Z_9(\alpha q I_9 - \phi B_9) - \mathbf{J}_{66}(E_9)(\alpha q X_9 - \lambda B_9))] \\
& - \gamma B_9[qI_9\phi Z_9 W_9(efp-\omega) + \gamma W_9\mathbf{J}_{44}(E_9)\mathbf{J}_{66}(E_9) + \chi Z_9 q I_9 \gamma W_9]\} \\
& - efpI_9\{\mathbf{J}_{12}(E_9)[\omega W_9\mathbf{J}_{66}(E_9)\mathbf{J}_{77}(E_9) - (\alpha q X_9 - \lambda B_9)\mathbf{J}_{66}(E_9)\gamma W_9 \\
& + \chi Z_9(\alpha q I_9 - \phi B_9) - \phi Z_9(\alpha q I_9 - \phi B_9)\omega W_9] \\
& - \mathbf{J}_{22}(E_9)[W_9(efp-\omega)(\mathbf{J}_{66}(E_9)\mathbf{J}_{77}(E_9) - (\alpha q I_9 - \phi B_9)\phi Z_9) \\
& - \gamma W_9(\chi Z_9(\alpha q I_9 - \phi B_9) - (\alpha q X_9 - \lambda B_9)\mathbf{J}_{66}(E_9))] \\
& - \mathbf{J}_{66}(E_9)\gamma W_9[(efp-\omega) + \omega W_9]\}.
\end{aligned}
$$

Finally the determinant:

$$
\begin{aligned}
\Delta_9^{124567} = {} & -aW_9\Delta_9^{24567} - (\gamma B_9 + \omega I_9)\{\mathbf{J}_{12}(E_9)\Delta_9^{4567} + efpI_9[\gamma W_9\mathcal{R} \\
& + W_9(efp-\omega)\Delta_9^{567}] + \gamma B_9[\gamma W_9\Delta_9^{456} + W_9(efp-\omega)\mathcal{Q}]\} \\
& + efpI_9\{\mathbf{J}_{12}(E_9)[\omega W_9\Delta_9^{567} - \gamma W_9\mathcal{L}] \\
& - \mathbf{J}_{22}(E_9)[W_9(efp-\omega)\Delta_9^{567} + \gamma W_9\mathcal{L}] \\
& - \gamma B_9 efp\gamma\omega W_9^2\Delta_9^{56}\} + \gamma B_9\{\mathbf{J}_{12}(E_9)[\omega W_9\mathcal{Q} - \gamma W_9\Delta_9^{456}] \\
& - \mathbf{J}_{22}(E_9)[W_9(efp-\omega)\mathcal{Q} + \gamma W_9\Delta_9^{456}] - e^2f^2p^2I_9\gamma W_9^2\Delta_9^{56}\}.
\end{aligned}
$$

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