Multiple coexistence equilibria in a two parasitoid-one host model

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Abstract

Briggs et al. (1993) introduced a host-parasitoid model for the dynamics of a system with two parasitoids that attack different juvenile stages of a common host. Their main result was that coexistence of the parasitoids is only possible when there is sufficient variability in the maturation delays of the host juvenile stages. Here we analyse the phenomenon of coexistence in that model more deeply. We show that with some distribution families for the maturation delays, the coexistence equilibrium is unique, while with other distributions multiple coexistence equilibria can be found. In particular we find that stable coexistence does not necessarily require mutual invasibility.

Keywords: Population dynamics, Parasitoid-Host Interaction, Delay Differential Equations, Multiplicity of coexistence equilibria
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1. Introduction

It is known that parasitoid species of the same host can coexist (Force, 1970; Price, 1970; Harvey et al., 2009). This observation seems to contradict a principle in ecology which predicts that competing species cannot coexist on the same limiting resource (Gause and Witt, 1935), though it has been shown

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that the principle holds under very stringent equilibrium conditions (Chesson and Case, 1986) and that competitors can coexist on the same biological resource along periodic solutions (Hsu et al., 1977; Armstrong and McGehee, 1980). Parasitoid species are a particularly interesting case, as various mechanisms that can promote parasitoid coexistence on the same host have been suggested (Price, 1970; Lane et al., 2006; Hackett-Jones et al., 2009). Briggs (1993) started to investigate under which conditions parasitoids can coexist when they attack different juvenile stages of a common host. This investigation was continued by Briggs et al. (1993), who found that in their model coexistence at equilibrium is possible only when there is sufficient variability in the maturation delays of the juvenile stages. They suggested that when the variability is large enough, different host individuals can be interpreted as different resources: individuals with a relatively long egg phase support the egg parasitoid, and individuals with a relatively long larva phase support the larva parasitoid. In the present paper we re-analyse the model by Briggs et al. (1993) and find more complex patterns than those already identified: there may be multiple coexistence equilibria, and, contrary to conventional wisdom, stable coexistence does not require mutual invasibility. The model is presented in Section 2. In Sections 3, 4 and 5 we formulate the original results in our somewhat different notation and in Section 6 show that coexistence equilibria are not unique for many distributions of the maturation delays. Finally, in Section 7 we set our results in the context of other works, discuss their relevance for biological pest control, and propose questions for further investigation. A general introduction to parasitoid-host systems can be found, for instance, in the text book by Godfray (1994).

2. The model

The model describes a host with two juvenile stages E and L, and an adult stage A. We refer to the first juvenile stage as eggs and to the second juvenile stage as larvae but they can also represent other developmental stages as pupae or different instars. The egg stage is attacked by an egg parasitoid (whose density is denoted by P) while the larva stage is attacked by a larva parasitoid (density denoted by Q) with attack rates a_P and a_Q respectively. Non-infected host juveniles have random maturation delays which are distributed with probability density functions w_E and w_L. Infected hosts do not progress to the next stage but give rise to new parasitoids a constant time T_{JP} or T_{JQ} after the infection. Unlike the original paper, we

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do not explicitly introduce survival probabilities for the juvenile parasitoids, since these can be absorbed in the parameters c_P and c_Q for the expected number of parasitoids emerging from an infected host. All other host and parasitoid stages have constant (background) death rates d_E, d_L, d_A, d_P and d_Q. Adult hosts have a life time fecundity ρ (so ρd_A is the rate with which an adult produces offspring).

The population dynamics is described by delay differential equations shown below. We adopt the notation used in the original paper but extend it when needed. For simplicity, the term maturing is used for eggs transforming to larvae as well as for larvae transforming to adults, although for eggs the term hatching might be more appropriate. The balance equations for the population densities are

$$
\begin{cases}
\frac{dE(t)}{dt} &= R_E(t) - M_E(t) - a_P P(t)E(t) - d_E E(t) \\
\frac{dL(t)}{dt} &= M_E(t) - M_L(t) - a_Q Q(t)L(t) - d_L L(t) \\
\frac{dA(t)}{dt} &= M_L(t) - d_A A(t) \\
\frac{dP(t)}{dt} &= a_P c_P E(t - T_{JP})P(t - T_{JP}) - d_P P(t) \\
\frac{dQ(t)}{dt} &= a_Q c_Q L(t - T_{JQ})Q(t - T_{JQ}) - d_Q Q(t)
\end{cases}
\tag{1}
$$

where

$R_E(t) = \rho d_A A(t)$	host egg recruitment rate
$M_E(t) = \int_0^\infty R_E(t - x_E)S_E(x_E,t)w_E(x_E)dx_E$	host egg maturation rate = host larva recruitment rate
$M_L(t) = \int_0^\infty M_E(t - x_L)S_L(x_L,t)w_L(x_L)dx_L$	host larva maturation rate = host adult recruitment rate

with

$S_E(x_E,t) = \exp\left(-\int_{t-x_E}^t (a_P P(y) + d_E)dy\right)$	probability for host eggs to survive from time $t - x_E$ to t
$S_L(x_L,t) = \exp\left(-\int_{t-x_L}^t (a_Q Q(y) + d_L)dy\right)$	probability for host larvae to survive from time $t - x_L$ to t

parameter	description
ρ	total lifetime fecundity of host adults
d_E	background mortality rate of host eggs
d_L	background mortality rate of host larvae
d_A	background mortality rate of host adults
d_P	background mortality rate of egg parasitoids
d_Q	background mortality rate of larva parasitoids
a_P	egg parasitoid attack rate
a_Q	larva parasitoid attack rate
c_P	expected number of egg parasitoids emerging from infected egg
c_Q	expected number of larva parasitoids emerging from infected larva
T_{JP}	duration of juvenile egg parasitoid stage
T_{JQ}	duration of juvenile larva parasitoid stage

and

function	description
w_E	probability density function for host egg maturation delay
w_L	probability density function for host larva maturation delay

3. Preliminaries

In order to investigate equilibrium states, we introduce some quantities that depend on constant parasitoid densities P and Q. Note first that eggs and larvae can have three different fates: they can die due to the background death rates d_E and d_L, they can be successfully attacked by parasitoids or they can progress to the next stage. We first state the formulae for the transition probabilities between the host stages and the expected durations in the different stages (for the full computations see Appendix A). The probability that a freshly emerged egg hatches into a larva is

$$\Pi_1(P) = \int_0^\infty w_E(\tau) \, e^{-(a_P P + d_E)\tau} \, d\tau \tag{2}$$

and the probability that a freshly hatched larva emerges as an adult is

$$\Pi_2(Q) = \int_0^\infty w_L(\tau) \, e^{-(a_Q Q + d_L)\tau} \, d\tau. \tag{3}$$

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As shown in Appendix A.2, the expected duration of the egg stage is

$$\Gamma_1(P) = \frac{1 - \Pi_1(P)}{a_P P + d_E}, \tag{4}$$

the expected duration of the larva stage (given that this stage is reached) is

$$\Gamma_2(Q) = \frac{1 - \Pi_2(Q)}{a_Q Q + d_L}, \tag{5}$$

and the expected duration of the adult stage (given that this stage is reached) is

$$\Gamma_3 = \frac{1}{d_A}. \tag{6}$$

We now can state the following relations, valid when the related population densities are constant:

The rate of eggs emerging, given constant adult density A, is by definition

$$R_E = \rho d_A A. \tag{7}$$

The constant egg density E is the product of the rate of eggs emerging and the expected duration of the egg stage (to verify set $\frac{dE}{dt} = 0$),

$$E = R_E \, \Gamma_1(P). \tag{8}$$

The constant larva density L is the product of three factors, viz., the rate of eggs emerging, the probability for an egg to mature to a larva and the expected duration of the larva stage, given that it is reached (to verify set $\frac{dL}{dt} = 0$),

$$L = R_E \, \Pi_1(P)\Gamma_2(Q). \tag{9}$$

The constant adult density A is the product of four factors, viz., the rate of eggs emerging, the probability for an egg to mature to a larva, the probability for a larva to mature to an adult and the expected life length of an adult (to verify set $\frac{dA}{dt} = 0$),

$$A = R_E \, \Pi_1(P)\Pi_2(Q)\Gamma_3. \tag{10}$$

The average number of offspring from a freshly laid egg (the basic reproduction number of the host) is the product of the average output of an adult ρ and the probability for an egg to mature to an adult,

$$R_0 = \rho \, \Pi_1(P) \, \Pi_2(Q). \tag{11}$$

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At a nontrivial equilibrium the basic reproduction number R_0 equals one, as can be seen by plugging the definition of R_E into equation (10). The zero growth condition for host eggs (8) and larvae (9) can be combined by eliminating R_E. This yields

$$\frac{\Pi_1(P)\Gamma_2(Q)}{\Gamma_1(P)} = \frac{L}{E}. \tag{12}$$

4. Equilibrium states

4.1. When only the egg parasitoid is present

For the case that only the egg parasitoid is present, its equilibrium density P^* can be determined by plugging $Q = 0$ into the basic reproduction number R_0, which is equal to 1 at equilibrium, i.e. by requiring

$$\rho \, \Pi_1(P^*) \, \Pi_2(0) = 1. \tag{13}$$

Assuming that $R_0 > 1$ for $P = 0$ and $Q = 0$, this equation has a unique root for P^* since R_0 approaches 0 strictly monotonically with increasing P. The equilibrium state for the egg density is determined by the requirement of zero growth rate for (non-trivial) P. This, by setting $dP(t)/dt = 0$ and assuming constant population densities, leads to

$$E_P^* = \frac{d_P}{a_P c_P}. \tag{14}$$

The equilibrium larva density L_P^* in presence of only the egg parasitoid can be calculated from the relation (12),

$$L_P^* = E_P^* \frac{\Pi_1(P^*)\Gamma_2(0)}{\Gamma_1(P^*)}. \tag{15}$$

The host adult density can be obtained for all equilibrium systems by combining (7) and (8).

4.2. When only the larva parasitoid is present

In the same way as for the egg parasitoid, we can derive the equilibrium densities for the case that only the larva parasitoid is present. The equilibrium larva parasitoid density Q^* is determined through the equation

$$\rho \, \Pi_1(0) \, \Pi_2(Q^*) = 1 \tag{16}$$

and again this equilibrium density is unique. The equilibrium larva density is

$$L_Q^* = \frac{d_Q}{a_Q c_Q}, \tag{17}$$

and the equilibrium egg density is

$$E_Q^* = L_Q^* \frac{\Gamma_1(0)}{\Pi_1(0)\Gamma_2(Q^*)}. \tag{18}$$

4.3. When both parasitoids are present

According to equation (11) the host adult density is in equilibrium when the parasitoid densities satisfy

$$Q = \Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right) \tag{19}$$

where Π_2^{-1} is the inverse function of Π_2. Plugging (19) into (12) yields a condition for all host stages to be in equilibrium

$$f(P) = \frac{L}{E} \tag{20}$$

where $f : [0, P^*] \to \mathbb{R}^+$ is defined by

$$f(P) = \frac{\Pi_1(P)}{\Gamma_1(P)}\Gamma_2\left(\Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right)\right). \tag{21}$$

When both parasitoids coexist, the equilibrium egg and larva densities are determined by the requirement of zero growth rate for the egg and larva parasitoid respectively. Hence they are given by E_P^* and L_Q^*, and thus the egg parasitoid coexistence equilibrium P^{**} is determined by the condition

$$f(P^{**}) = \frac{L_Q^*}{E_P^*}. \tag{22}$$

The corresponding larva parasitoid density Q^{**} can be obtained by equation (19).

Note that in the same way one can derive an equivalent function $g(Q) = L/E$

which determines coexistence equilibria by $g(Q^{**}) = \frac{L_Q^*}{E_P^*}$, where

$$
\begin{aligned}
g(Q) &= \frac{\Pi_1\left(\Pi_1^{-1}\left(\frac{1}{\rho \, \Pi_2(Q)}\right)\right)}{\Gamma_1\left(\Pi_1^{-1}\left(\frac{1}{\rho \, \Pi_2(Q)}\right)\right)}\Gamma_2(Q) \\
&= \frac{\Gamma_2(Q)}{\Pi_2(Q)}\frac{1}{\rho \, \Gamma_1\left(\Pi_1^{-1}\left(\frac{1}{\rho \, \Pi_2(Q)}\right)\right)}
\end{aligned}
\tag{23}
$$

with Π_1^{-1} being the inverse function of Π_1. All further analysis could be carried out with either f or g but for simplicity we stick with the function f. Turning back to the function f, we see that the shape of the function contains information on the multiplicity of coexistence equilibria. According to equation (22), multiple coexistence equilibria cannot arise if f is strictly monotonic. If on the other hand for some parameters f is not monotonic, we can always find values of the parameters c_P, c_Q, d_P or d_Q that give rise to multiple coexistence equilibria by shifting the critical horizontal $L_Q^*/E_P^* = d_Q a_P c_P / d_P a_Q c_Q$ until the graph of the function f (which does not depend on those parameters) is intersected multiple times. Each intersection yields a coexistence equilibrium. Similarly, the critical horizontal can be shifted using those parameters until there are no coexistence equilibria.

5. Invasibility of stable equilibria

When in the absence of parasitoids $R_0 > 1$, either parasitoid can establish a population. Often, a stable host-parasitoid equilibrium will be reached with R_0 set at 1 (Murdoch et al., 1987) and we follow Briggs et al. (1993) in examining when this equilibrium can be invaded by the other parasitoid. A case where the host and parasitoid populations settle into a periodic solution is examined numerically in the next Section.

It is not difficult to show that a stable equilibrium population with only the larva parasitoid can be invaded by the egg parasitoid when the egg parasitoid alone reduces the egg density more than the larva parasitoid alone, that is when

$$
E_P^* < E_Q^*.
\tag{24}
$$

To demonstrate this, we compute the Malthusian parameter $\lambda = \lambda_P(E)$ for the egg parasitoid at constant egg density E. Namely, we linearise system

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162 (1) around the equilibrium, obtaining

$$\frac{dP(t)}{dt} = a_P c_P E P(t - T_{JP}) - d_P P(t) \tag{25}$$

163 where $E = E_Q^*$. We then assume

$$P(t) = e^{\lambda t} P(0) \tag{26}$$

164 and obtain

$$\lambda P(t) = a_P c_P E P(t) e^{-\lambda T_{JP}} - d_P P(t)$$
$$\lambda = E a_P c_P e^{-\lambda T_{JP}} - d_P. \tag{27}$$

165 The egg parasitoid can invade a stable equilibrium community of the larva
166 parasitoid and the host when this equation has a positive real root for
167 $E = E_Q^*$, that is $\lambda_P(E_Q^*) > 0$. The claim that this requires $E_P^* < E_Q^*$
168 follows because the unique real root $\lambda_P(E)$ increases strictly monotonically
169 with E and $\lambda_P(E_P^*) = 0$. (Note that we do not have to consider complex
170 roots for λ since their real parts cannot exceed the real root.)
171 In the same way it can be seen that the larva parasitoid can invade a stable
172 equilibrium population with only the egg parasitoid when

$$L_Q^* < L_P^*. \tag{28}$$

173 We speak of mutual invasibility of stable equilibria when

$$E_P^* < E_Q^* \text{ and } L_Q^* < L_P^*. \tag{29}$$

174 The value of the function f defined in (21) at the boundary of its domain, rel-
175 ative to the right hand side of (22), turns out to be related to the invasibility
176 conditions. Indeed,

$$\begin{aligned}
f(0) &= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \, \Pi_1(0)} \right) \right) \\
&= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left(\Pi_2^{-1} \left(\Pi_2(Q^*) \right) \right) \\
&= \frac{\Pi_1(0)}{\Gamma_1(0)} \Gamma_2 \left(Q^* \right) \\
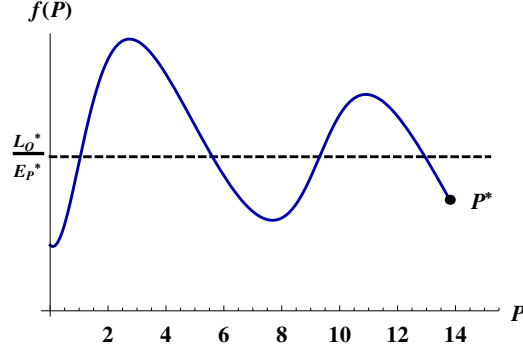&= \frac{L_Q^*}{E_Q^*}
\end{aligned} \tag{30}$$

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Figure 1: The graph of the function f which intersects the level L_Q^*/E_P^* when the egg parasitoid density corresponds to a coexistence equilibrium. The maturation delays are distributed with two discrete values each (see Appendix B.2). Parameter values are $T_{E_1} = 0.2$, $T_{E_2} = 1.35$, $T_{L_1} = 0.75$, $T_{L_2} = 5$, $r_E = 0.5$, $r_L = 0.3$, $a_P = 2$, $a_Q = 0.2$, $d_E = 0$, $d_L = 0$, $\rho = 500$, $d_P = 8$, $d_Q = 0.175$, $c_P = 0.5$ and $c_Q = 0.5$

and

$$
\begin{aligned}
f(P^*) &= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left(\Pi_2^{-1} \left(\frac{1}{\rho \, \Pi_1(P^*)} \right) \right) \\
&= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left(\Pi_2^{-1} \left(\Pi_2(0) \right) \right) \\
&= \frac{\Pi_1(P^*)}{\Gamma_1(P^*)} \Gamma_2 \left(0 \right) \\
&= \frac{L_P^*}{E_P^*},
\end{aligned}
\tag{31}
$$

which implies that the egg parasitoid can invade a stable equilibrium with the larva parasitoid alone when $f(0) < L_Q^*/E_P^*$ and the larva parasitoid can invade a stable equilibrium with the egg parasitoid alone when $f(P^*) > L_Q^*/E_P^*$.

6. Applying distributions for the maturation delays

We apply several distributions for the maturation delays in order to analyze their influence on the multiplicity of coexistence equilibria. Among those are the constant-duration distribution, (shifted) exponential distribution and (shifted) gamma distribution, which have been introduced in the original paper of Briggs et al. (1993). Here the term 'shifted' refers to including minimal

values for the maturation delays. Additionally we introduce a two-value distribution where the maturation delays assume one of two discrete values with certain probabilities.

It turns out that, among these distributions, only the constant-duration and the (non-shifted) exponential distribution yield at most one coexistence equilibrium. For those two distributions the function f is monotonic and therefore the critical horizontal L_Q^*/E_P^* can be crossed at most once. Elementary representations for f in those cases are shown in Appendix B. For the case of constant maturation delays, f is decreasing and hence there is a coexistence equilibrium only if $f(0) > L_Q^*/E_P^* > f(P^*)$, implying that neither parasitoid can invade a stable equilibrium of the other parasitoid and the host. For the case of exponentially distributed maturation delays, f is increasing and hence, in the other way around, there must be mutual invasibility of stable equilibria for a coexistence equilibrium to exist.

For all the other distributions (two-value distribution, shifted exponential distribution and (normal or shifted) gamma distribution), we could numerically find parameters so that the graph of f crosses the critical horizontal line multiple times, giving rise to multiple equilibria. Fig. 1 shows an example where the graph of f crosses the critical horizontal line four times with two-value distributions for the maturation delays (see caption).

6.1. Simulations and stability

To see how the system behaves after a small perturbation from an equilibrium, we computed time plots with the software *Mathematica* shown in Fig. 2. The plots reveal that coexistence equilibria can be stable or unstable, possibly giving rise to oscillations around the equilibrium after perturbation. Bifurcation diagrams are shown in Fig. 3. The left panel shows how the parameter a_P shifts the horizontal in Fig. 1 without changing the function f, and thus we can observe how coexistence equilibria appear and disappear in pairs when changing the parameter. The right panel shows how the adult mortality d_A affects stability without changing the equilibrium values (since this parameter does not occur in the function f or in the level of the critical horizontal line). Low values for d_A seem to stabilize some equilibria while high values for d_A appear to destabilize all equilibria.

We further analyzed the dynamics for low values of host adult death rate d_A. We show some simulations for that case in the (P, Q)-plane in Fig. 4. There we see that the population densities lie on the curve of equation
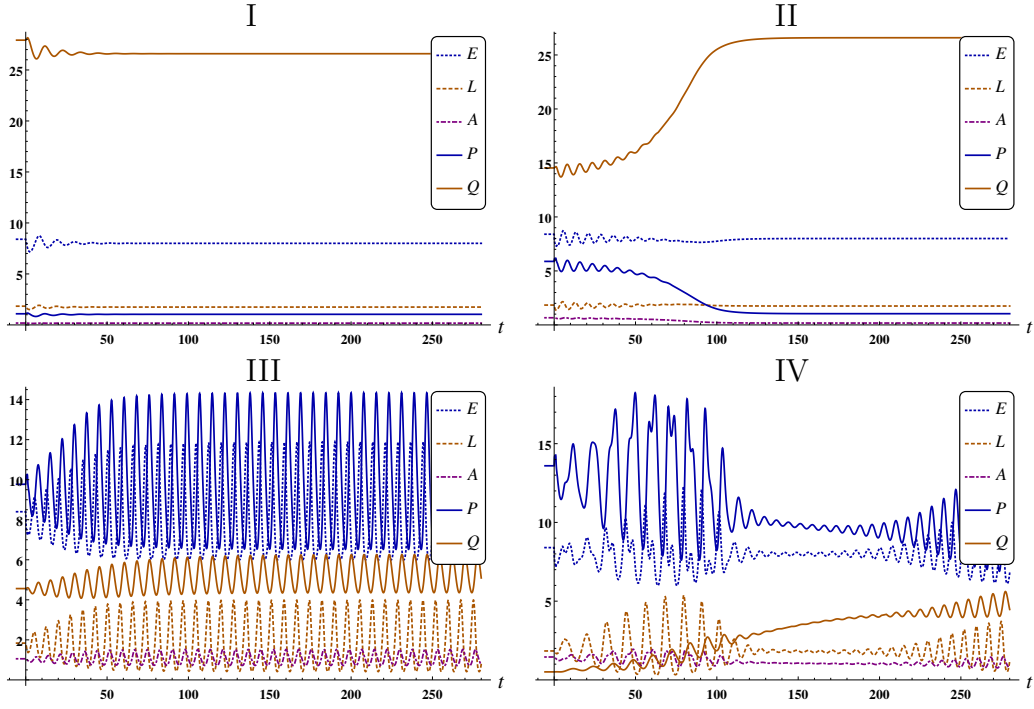
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Figure 2: Time plots of population dynamics after small perturbations from equilibrium densities. The initial densities for $t \leq 0$ are constant and correspond to perturbations from the equilibrium densities indicated by the first (I), second (II), third (III) and forth (IV) intersection of the graph of f with the critical horizontal in Fig. 1. The perturbations consist of increasing all equilibrium densities by 5%. Note that in plot (IV) the same attractor as in plot (III) seems to be approached. Distributions and parameter values are the same as in Fig. 1. Additionally $T_{JP} = 1$, $T_{JQ} = 1$ and $d_A = 0.3$

$\Pi_1(P)\dfrac{\Gamma_2(Q)}{\Gamma_1(P)} = \dfrac{L_Q^*}{E_P^*}$ and move in a direction depending on the relative po-sition of this curve and the curve $\rho\Pi_1(P)\Pi_2(Q) = 1$. This can be justified through a time-scale argument that we just sketch here, leaving details to future work. For the argument note that $A(t)$ is a slow variable when d_A is low, what can be seen from the models definition (1); thus in the fast time-scale $E(t)$, $L(t)$, $P(t)$ and $Q(t)$ will evolve under a constant value for the rate of eggs emerging, see equation (7). Numerical evidence suggests that this reduced system always quickly converges to its (quasi)-equilibrium, where $E = E_P^*$, $L = L_Q^*$ and equations (8) and (9) hold, corresponding to the solid curve in the (P, Q)-plane in Fig. 4. Thus, on the slow time-scale,
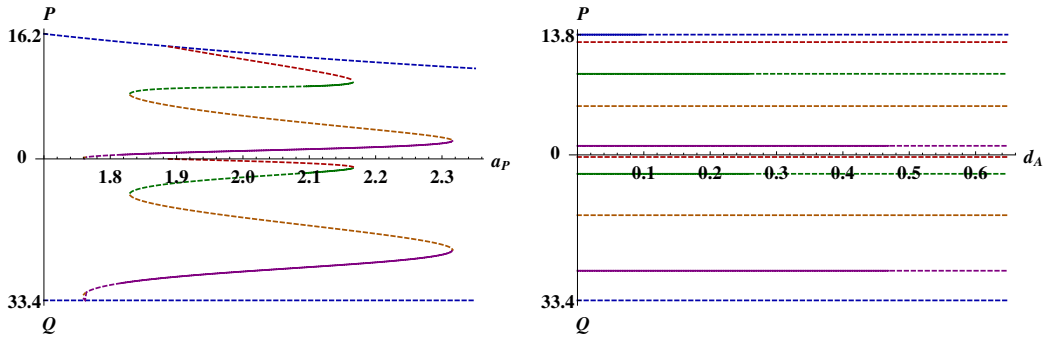
Figure 3: Bifurcation diagrams showing the equilibrium values for both parasitoid species. The upper vertical axis represents values for P and the lower vertical axis represents values for Q. The outermost lines represent equilibria with only one parasitoid species while the inner equilibria are true coexistence equilibria. Values for P and Q corresponding to the same coexistence equilibrium are drawn with the same color in the online version of the article. Stability is indicated by solid (stable) and dashed (unstable) lines. For the stability analysis the eigenvalues of the characteristic equation were calculated with the MATLAB package eigAM/eigTMN by Breda et al. (2014). Parameter values are the same as in Fig. 1 and Fig. 2 (except axis parameters)

$A(t)$ changes according to the third equation of the system (1) with all other state variables at the quasi-equilibrium. It can be easily verified that $A(t)$ will increase or decrease according to whether the basic reproduction number R_0 from equation (11) is greater or smaller than 1, thus according to whether (P, Q) is above or below the dashed curve in Fig. 4. As at the quasi-equilibrium A and P are related by relation (8) with $E = E_P^*$, an increase [decrease] of $A(t)$ corresponds to an increase [decrease] of $P(t)$. This explains why the dynamics in the (P, Q)-plane is towards the right when the dashed curve is above the solid curve ($R_0 > 1$) and towards the left when the dashed curve is below. Since the intersections between the two curves correspond to values of (P, Q) where all state variables are at equilibrium, the previous graphical argument shows that, in the limit of $d_A \to 0$, an equilibrium is stable when the dashed curve crosses the solid curve from above, while it is unstable when the curves cross in the opposite way.

These findings can be transferred to the shape of the function $f(P)$. Indeed, it can be easily verified that the solid curve is below the dashed curve if and only if $f(P)$ is below L_Q^*/E_P^*. Therefore the findings above imply that coexistence equilibria are stable, for d_A sufficiently small, when $f'(P^{**}) > 0$,
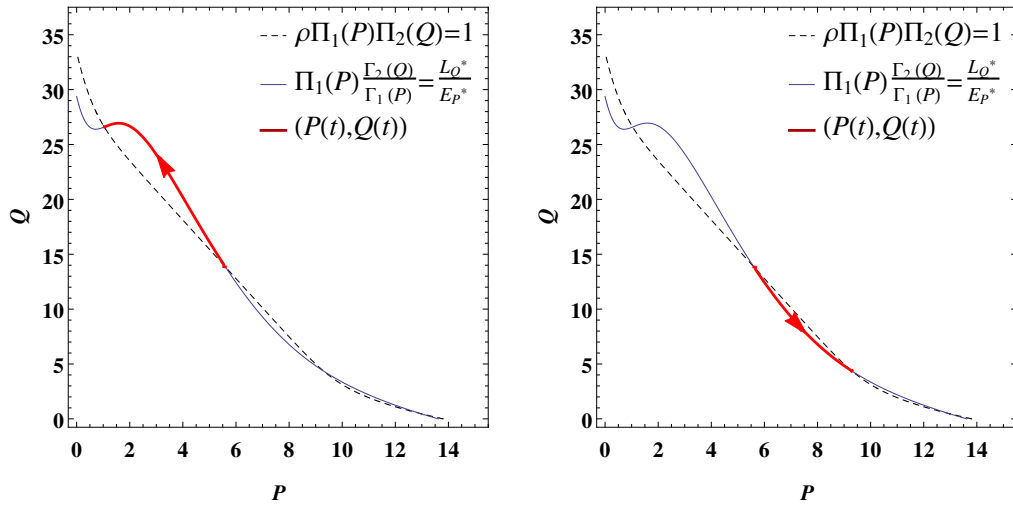
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Figure 4: Parasitoid phase plane with time dynamics. Initial population densities (for $t \leq 0$) correspond to the second coexistence equilibrium from left in Fig. 1. Perturbation is introduced via the host adult densities, which are respectively to its equilibrium value decreased by 1% in the left panel and increased by 1% in the right panel. Host adult mortality rate is very low, $d_A = 0.001$. All other parameter values are as in Fig. 1 and 2

while they are unstable when $f'(P^{**}) < 0$. The second statement appears to be true for all $d_A > 0$ but we give a formal proof only for the scenario with constant maturation delays in Appendix C.2.

Further investigations of invasibility are illustrated with time plots in Fig. 5, where the larva parasitoid is introduced at very low density into an equilibrium system of egg parasitoid and host. This numerical example has important implications concerning invasion and coexistence which go beyond what was found by Briggs et al. (1993). One point is that the invasibility criteria stated in Section 5 do hold only for constant equilibria. If a single-parasitoid equilibrium is unstable with respect to the interaction of this parasitoid and the host, it has no sense to investigate its invasibility by the other parasitoid. Instead one should (numerically) find the single parasitoid-host attractor and investigate its invasibility (Metz et al., 1992). One may actually do this in one go by using the introduction of the second parasitoid as a way to perturb the unstable equilibrium as done in Fig. 5. As this figure reveals, oscillations may facilitate successful invasion in the sense that the second parasitoid is successful when the single parasitoid equilibrium is unstable ($d_A = 0.3$), while being unsuccessful in case it is stable ($d_A = 0.05$) since $L_P^* < L_Q^*$. By

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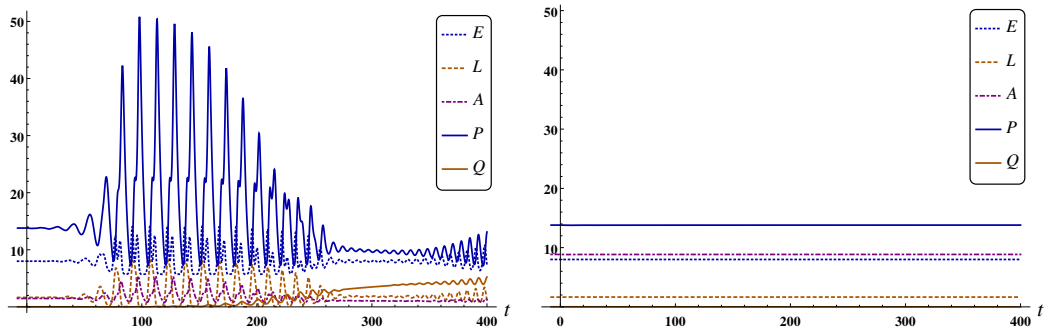
(a) For $d_A = 0.3$ the equilibrium of host and egg parasitoid is unstable and the larva parasitoid can invade through oscillations

(b) For $d_A = 0.05$ the equilibrium of host and egg parasitoid is stable and the larva parasitoid cannot invade

Figure 5: Time plots of population dynamics after introducing the larva parasitoid into an equilibrium system of egg parasitoid and host. The system is started with constant population densities for $t \leq 0$ corresponding to the equilibrium densities of egg parasitoid and host with additional a low density $Q = 0.01$ of the larva parasitoid. Distributions and parameter values are the same as in Fig. 1 and 2 with exception of a lower value for d_A in the right panel

combining Fig. 5b with the right panel of Fig. 3 another conclusion emerges: non-invasibility of a stable single-parasitoid equilibrium does not exclude the possibility of stable equilibrium coexistence of the two parasitoids (indeed, for $d_A = 0.05$ we observe in Fig. 3 that simultaneously the equilibrium with only the egg parasitoid, and two coexistence equilibria are stable).

7. Discussion

We found multiple (non-trivial) coexistence equilibria in a model for the population dynamics of two parasitoids attacking different juvenile stages of a common host. The model was introduced by Briggs et al. (1993) and it involves distributed maturation delays for the host juvenile stages. We have shown that, depending on the distributions of the maturation delays, multiple coexistence equilibria can arise. To our knowledge, this is the first documented example of multiple coexistence equilibria in a parasitoid-host model, as well as the first example for the multiplicity of coexistence equilibria to depend on the distribution of maturation delays.

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Non steady-state attractors in parasitoid-host systems, in contrast, have received considerable attention before. Already the dynamics of the classical discrete-time model by Nicholson and Bailey (1935) are known to be oscillatory: one or both species go extinct after diverging oscillations around the unstable coexistence equilibrium. In a continuous-time parasitoid-host model by Murdoch et al. (1987), stability of a steady-state coexistence attractor can be facilitated by an invulnerable host stage. For modifications of this model, multiple non steady-state attractors have been found by Murdoch et al. (1992, 1997), Briggs (1993) and Briggs et al. (1999). Particularly Briggs (1993) shows that such non steady-state attractors can lead to parasitoid coexistence in situations where no stable coexistence equilibrium is predicted. Further Sieber and Hilker (2011) report multiple (non-)equilibrium attractors in a single host population that is exploited by microparasites and predators. Beyond that, there is a well-developed body of theory on coexistence in variable environments (deterministic and stochastic), see for example the works by Abrams (1984), Chesson (1994) and Li et al. (2016). Occurrence of oscillations in real parasitoid populations is documented by Godfray and Hassell (1989), who offer a review on oscillations of host parasitoid systems in the tropics and corresponding discrete and continuous models.

In our model we found that equilibria can have different properties. Single parasitoid equilibria are potentially stable and non-invadable only when the host stage of the other parasitoid is reduced more strongly than what would be needed by the competitor to sustain. Similarly we found that two-parasitoid coexistence equilibria are "potentially stable" only when increasing a parasitoid species reduces its own host stage relatively to its competitors host stage when the competing parasitoid species is chosen accordingly so that the host stays at equilibrium. Coexistence equilibria for which this is not the case turned out to be always unstable. This can be interpreted as a manifestation of the principle that coexistence of competitors can be possible only when intraspecific competition is stronger than interspecific competition, see for example the review by Chesson (2000). For the potentially stable equilibria we found that stability can be always altered with the parameter d_A of host adult mortality (which does not change the equilibrium values due to the way the model is parameterized). Especially, we found that low values for d_A generally stabilize potentially stable equilibria. In the other way around we found that high values for d_A are always destabilizing. This is similar to the observations of Murdoch et al. (1987), who found for a similar single-parasitoid model that stable equilibria can exist only when there is a

sufficiently long invulnerable adult stage of the host.

We made several observations concerning invasibility and single-parasitoid equilibria in the model. One point is that in the presence of multiple coexistence equilibria, stable coexistence can occur without mutual invasibility. We described a situation where the parasitoids can coexist although the larva parasitoid cannot invade a stable equilibrium of egg parasitoid and host ($L_P^* < L_Q^*$). This is similar to the findings of Buonomo and Cerasuolo (2014) in a model for plants and parasites. Our example also shows that host juvenile densities can increase when an additional parasitoid is introduced since the equilibrium larva density with the egg parasitoid alone L_P^* is lower than the equilibrium larva density L_Q^* when both parasitoids coexist. Analogous examples can be found for situations where introducing the egg parasitoid increases the equilibrium egg density. These findings differ from those of other authors including Briggs (1993) and Briggs et al. (1993), who assume that stable coexistence requires mutual invasibility, and conclude that (in the absence of other mechanisms such as hyperparasitism) introducing a second parasitoid cannot lead to higher equilibrium densities of host juveniles. This is interesting in the light of the discussion whether single or multiple parasitoids should be introduced for optimal biological pest control, see for example the contributions by Ehler (1990) and Pedersen and Mills (2004). Furthermore we found that the invasibility criterion suggested by Briggs et al. (1993) is not generally valid when there are multiple coexistence equilibria. The original criterion states that a parasitoid species can invade only if its growth rate is positive at the equilibrium host density set by the resident parasitoid. We found however that if there are multiple coexistence equilibria, and the residents single-parasitoid equilibrium is not stable, invasion of the other parasitoid can take place through oscillations eventually leading to coexistence of both parasitoids. This is related to the findings on invasion in oscillating conditions by Armstrong and McGehee (1980), Bacaër and Guernaoui (2006), Greenman and Norman (2007) and Bate and Hilker (2013). Since in our model such situations occurred only when there are multiple coexistence equilibria we conjecture that this is indeed a necessary condition.

The question remains of when coexistence equilibria can arise generally and what is the connection to the maturation delays of the hosts. A literature search reveals that the occurrence of multiple equilibria in population models is generally connected to some non-linearity or non-monotonicity in the interaction of different species. Evidence for that can be found in several models based on ordinary differential equations. Pimenov et al. (2015) find that in a
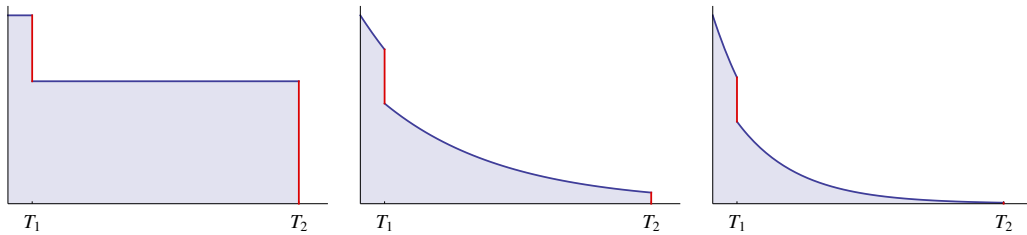
17

Figure 6: Age distribution of a host juvenile stage subjected to constant parasitism pressure $a_P P$ or $a_Q Q$ equal to 0, 0.2 or 0.4 (from left to right; note that there is no background death rate). The maturation delay for the stage is distributed by two discrete values T_1 and T_2 which occur with probabilities r and $1 - r$. The area under the curve represents the expectation value Γ_i for the time in this stage, while the sum of the lengths of the vertical bars at the times T_1 and T_2 represents the probability Π_i to reach the next stage. The ratio Γ_i / Π_i equals approximately 8.8, 9.5 and 7.9 from left to right, and thus first increases and then decreases with increasing parasitism. Parameter values are: $r = 0.35$, $T_1 = 1$, $T_2 = 12$

predator-prey model, multiple coexistence equilibria can arise when the prey changes its behavior in dependence of the predator density. Similarly Freeze et al. (2014) find multiple coexistence equilibria in a three species model where a super predator changes feeding behavior in dependence of its prey species densities. Buonomo and Cerasuolo (2014) find multiple coexistence equilibria in a model with host plants that react to parasitism in a non-linear way.

We found in our model too that multiple coexistence equilibria can occur only when the host larva-egg proportion depends in a non-monotonic way on the density of one parasitoid while the other parasitoid density is kept so that the host stays at equilibrium. We have seen that this can never happen for two important special cases: constant and exponentially distributed maturation delays. For constant maturation delays, increasing one parasitoid (and decreasing the other parasitoid accordingly) increases its own host stage relatively to the host stage of the competitor, which additionally implies that if there is a coexistence equilibrium, it is unstable and neither parasitoid can invade a stable population with the other parasitoid. Conversely for exponentially distributed maturation delays, increasing a parasitoid (and again decreasing the other parasitoid accordingly) reduces its host stage relatively to the host stage of the competitor, which additionally implies pairwise invasibility when there is a coexistence equilibrium. For all other distributions we investigated, the parasitoid densities can affect the hosts larva-egg proportion

18

in a non-monotonic fashion giving rise to multiple coexistence equilibria. An illustration of how this can happen with the two-value distributions we used in our numerical examples is shown in Fig. 6. There we show the expected duration Γ_i of a juvenile stage and the probability Π_i to reach the next stage, both for different densities of the corresponding parasitoid. We see that increasing the parasitoid density first decreases Π_i heavily because only a small part of the hosts with long maturation delay reaches maturation, while further increasing the parasitoid density decreases Γ_i more strongly because parasitism still mainly affects hosts with a long maturation delay whose contribution to Π_i was already low. Such mechanisms can lead to a non-monotonic relation between the parasitoid densities and the hosts larva-egg proportion, what potentially gives rise to multiple coexistence equilibria. Note however that the ratio of a parasitoids host stage and the other parasitoids host stage is according to (21) and (23) not only proportional to Γ_i/Π_i but depends also on $\Gamma_j(\Pi_j^{-1}(\frac{1}{\rho\Pi_i}))$ (where j refers to the other parasitoids host stage); thus this graphical illustration is incomplete, but still, in our view, sheds some light on the mechanisms through which the distribution of maturation delays affects coexistence equilibria.

Appendix A. Transition probabilities and expected duration of the stages

Here we derive formulas for the transition probabilities from egg to larva $\Pi_1(P)$ and from larva to adult $\Pi_2(Q)$, and for the expected duration of the egg, larva and adult stage, $\Gamma_1(P)$, $\Gamma_2(Q)$ and Γ_3 respectively. The calculations are valid for constant parasitoid densities P and Q. We use the following notations for the various random variables

19

random variable	density	description
X_E	$w_E(\tau)$	time needed for egg maturation
X_L	$w_L(\tau)$	time needed for larva maturation
K_E	$(a_P P + d_E)e^{-\tau(a_P P + d_E)}$	time until an egg dies or is infected (when it does not mature before), distributed exponentially
K_L	$(a_Q Q + d_L)e^{-\tau(a_Q Q + d_L)}$	time until a larva dies or is infected (when it does not mature before), distributed exponentially
K_A	$d_A e^{-\tau d_A}$	time until an adult dies, distributed exponentially

Appendix A.1. Transition probabilities $\Pi_1(P)$ and $\Pi_2(Q)$

When the parasitoid densities are constant, the probability for a freshly laid egg to mature to a larva is

$$
\begin{aligned}
\Pi_1(P) &= \mathbb{P}[X_E < K_E] \\
&= \int_0^\infty \int_\tau^\infty w_E(\tau)\,(a_P P + d_E)e^{-(a_P P + d_E)\sigma}\,d\sigma\,d\tau \\
&= \int_0^\infty w_E(\tau)\,e^{-(a_P P + d_E)\tau}\,d\tau,
\end{aligned}
\tag{A.1}
$$

where we use the independence of X_E and K_E. Likewise the probability for a freshly hatched larva to mature to an adult is given by

$$
\Pi_2(Q) = \mathbb{P}[X_L < K_L] = \int_0^\infty w_L(\tau)\,e^{-(a_Q Q + d_L)\tau}\,d\tau.
\tag{A.2}
$$

Obviously Π_1 and Π_2 decrease strictly monotonically to 0.

Appendix A.2. Expectation values for the durations of different stages

When the parasitoid densities are constant, the expected duration of the egg stage (which is either terminated by death of the egg or maturation to a larva) is for $a_P P + d_E \neq 0$

20

$$\begin{aligned}
\Gamma_1(P) &= \mathbb{E}[\min\{K_E, X_E\}] \\
&= \mathbb{E}[K_E | K_E \le X_E]\mathbb{P}[K_E \le X_E] + \mathbb{E}[X_E | X_E < K_E]\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E | K_E \le X_E]\mathbb{P}[K_E \le X_E] \\
&\quad + (\mathbb{E}[K_E | X_E < K_E] - \mathbb{E}[K_E - X_E | X_E < K_E])\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E | K_E \le X_E]\mathbb{P}[K_E \le X_E] \\
&\quad + (\mathbb{E}[K_E | X_E < K_E] - \mathbb{E}[K_E])\mathbb{P}[X_E < K_E] \\
&= \mathbb{E}[K_E] - \mathbb{E}[K_E]\mathbb{P}[X_E < K_E] \\
&= \frac{1}{a_P P + d_E}(1 - \Pi_1(P))
\end{aligned}$$
(A.3)

424   where we used that K_E is exponentially distributed.

425   For $a_P P + d_E = 0$ obviously

$$\Gamma_1(0) = \mathbb{E}[X_E].$$
(A.4)

426   In the same way the expected duration of the larva stage (given that it is
427   reached) can be calculated for constant parasitoid densities and $a_Q Q + d_L \neq 0$,

$$\Gamma_2(Q) = \mathbb{E}[\min\{K_L, X_L\}] = \frac{1}{a_Q Q + d_L}(1 - \Pi_2(Q))$$
(A.5)

428   and for $a_Q Q + d_L = 0$

$$\Gamma_2(0) = \mathbb{E}[X_L].$$
(A.6)

429   Note that the expectation values of K_E and K_L and thus Γ_1 and Γ_2 decrease
430   strictly monotonically with the corresponding parasitoid densities.

431   The expected duration of the adult stage of a freshly emerged adult is

$$\Gamma_3 = \mathbb{E}[K_A] = \frac{1}{d_A}.$$
(A.7)

Appendix B. Computing f for some distributions

433   Elementary representations for the function f from equation (21) can be
434   found for some distribution families for the maturation delays. To facilitate
435   the computations, we rearrange f by using the formulas for Γ_1 and Γ_2 derived

in Appendix A.2 (assuming that $a_P P + d_E$ and $a_Q \Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right) + d_L$ are non-zero),

$$
\begin{aligned}
f(P) &= \frac{\Pi_1(P)}{\Gamma_1(P)} \Gamma_2\left(\Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right)\right) \\
&= \frac{\Pi_1(P)}{\frac{1-\Pi_1(P)}{a_P P + d_E}} \frac{1 - \Pi_2\left(\Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right)\right)}{a_Q \Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right) + d_L} \\
&= (a_P P + d_E)\frac{\Pi_1(P)}{1 - \Pi_1(P)} \frac{1 - \frac{1}{\rho \, \Pi_1(P)}}{a_Q \Pi_2^{-1}\left(\frac{1}{\rho \, \Pi_1(P)}\right) + d_L}.
\end{aligned}
\tag{B.1}
$$

Now the following formulas for f in the special cases can be easily verified.

Appendix B.1. Constant durations

The maturation from egg to larva and from larva to adult takes a constant time T_E and T_L respectively. For this distribution

$$
\begin{aligned}
\Pi_1(P) &= e^{-(a_P P + d_E)T_E} \\
\Pi_2(Q) &= e^{-(a_Q Q + d_L)T_L}
\end{aligned}
\tag{B.2}
$$

and (for $d_E > 0$ and $d_L > 0$)

$$
f(P) = \frac{T_L(a_P P + d_E)\left(\rho e^{-(a_P P + d_E)T_E} - 1\right)}{\rho\left(\log(\rho) - (a_P P + d_E)T_E\right)\left(1 - e^{-(a_P P + d_E)T_E}\right)}.
\tag{B.3}
$$

The function $f(P)$ decreases strictly monotonically in its domain $P \in [0, P^*]$ with $P^* = (\log(\rho) - d_L T_L - d_E T_E)/(T_E a_P)$ obtained by solving (13).[1] Therefore the arguments of Section 4.3 show that a coexistence equilibrium is necessarily unique and arises only when none of the parasitoids can invade an equilibrium population of the other parasitoid and the host. To prove the monotonicity of $f(P)$ we define $\gamma = (a_P P + d_E)T_E$ and $q = \log(\rho)$. The

---

[1]Note that for $d_E = 0$ or $d_L = 0$, the stated representation of $f(P)$ is undefined at the boundary of its domain but our result on monotonicity stays generally valid for the original function defined in (21). This can be verified by a simple limit argument.

₄₄₉ domain for P implies that $0 < \gamma < q$. Obviously $f(P)$ is decreasing if the
₄₅₀ following function $g(\gamma)$ is decreasing,

$$g(\gamma) = e^q \frac{T_E}{T_L} f(P) = \frac{\gamma(e^\gamma - e^q)}{(\gamma - q)(e^\gamma - 1)}. \tag{B.4}$$

₄₅₁ To prove the desired monotonicity of $g(\gamma)$, we take the derivative by γ and
₄₅₂ show that $g_\gamma(\gamma) < 0$ for $0 < \gamma < q$. Differentiation yields

$$g_\gamma(\gamma) = \frac{e^\gamma \left(q + q\gamma - \gamma^2\right) + e^{q+\gamma}\left(q - q\gamma + \gamma^2\right) - qe^{2\gamma} - e^q q}{(\gamma - q)^2 \left(e^\gamma - 1\right)^2} \tag{B.5}$$

₄₅₃ and the numerator (now interpreted as a function of q for any $\gamma > 0$)

$$k(q) = e^\gamma \left(q + q\gamma - \gamma^2\right) + e^{q+\gamma}\left(q - q\gamma + \gamma^2\right) - qe^{2\gamma} - e^q q \tag{B.6}$$

₄₅₄ determines the sign of $g_\gamma(\gamma)$. The first two derivatives of $k(q)$ by q are

$$\begin{aligned}
k_q(q) &= e^{q+\gamma}\left(q - q\gamma + \gamma^2 + 1 - \gamma\right) - e^q(1+q) - e^{2\gamma} + e^\gamma(\gamma + 1) \\
k_{qq}(q) &= e^q \left(e^\gamma\left(q - q\gamma + \gamma^2 - 2\gamma + 2\right) - q - 2\right).
\end{aligned} \tag{B.7}$$

₄₅₅ It can be easily seen that the equation $k_{qq}(q) = 0$ has only one solution for
₄₅₆ q. Therefore $k_q(q) = 0$ has at most two solutions and $k(q)$ has at most two
₄₅₇ (local) extrema.
₄₅₈ Moreover, we see that $k(0) = k(\gamma) = 0$, that $k(q) \xrightarrow[q \to -\infty]{} \infty$ (the dominant
₄₅₉ term being qe^γ with coefficient $1 + \gamma - e^\gamma$), and that $k(q) \xrightarrow[q \to \infty]{} -\infty$ (the
₄₆₀ dominant term being qe^q with coefficient $e^\gamma(1-\gamma)-1$). Since $k_q(\gamma) = 0$, this
₄₆₁ implies $k(q) < 0$ for $q > \gamma$ (and actually $k(q) \leq 0$ for $q \geq 0$). This completes
₄₆₂ the proof that $f(P)$ decreases strictly monotonically.

₄₆₃ *Appendix B.2. Two-value distribution*
₄₆₄ The maturation delay from egg to larva and from larva to adult are each
₄₆₅ distributed with two distinct values that occur with certain probabilities.
₄₆₆ The transformation from egg to larva has length T_{E_1} with probability r_E and
₄₆₇ length T_{E_2} with probability $1 - r_E$. The transformation from larva to adult
₄₆₈ has length T_{L_1} with probability r_L and length T_{L_2} with probability $1 - r_L$.
₄₆₉ For this distribution

$$\begin{aligned}
\Pi_E(P) &= r_E e^{(a_P P + d_E)T_{E_1}} + (1 - r_E)e^{(a_P P + d_E)T_{E_2}} \\
\Pi_L(Q) &= r_L e^{(a_Q Q + d_L)T_{L_1}} + (1 - r_L)e^{(a_Q Q + d_L)T_{L_2}}.
\end{aligned} \tag{B.8}$$

Π_L^{-1} and therefore f have no elementary representations. The numerical example presented in Fig. 1 shows however that f can be non-monotonic and that therefore multiple coexistence equilibria can occur.

Appendix B.3. Exponential distribution

The maturation delays from egg to larva and from larva to adult are exponentially distributed with expectation $1/\lambda_E$ and $1/\lambda_L$ respectively. For this distribution

$$\begin{aligned}
\Pi_1(P) &= \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\
\Pi_2(Q) &= \frac{\lambda_L}{a_Q Q + d_L + \lambda_L}
\end{aligned} \tag{B.9}$$

and

$$f(P) = \frac{a_P P + d_E + \lambda_E}{\rho \lambda_L}. \tag{B.10}$$

Obviously $f(P)$ increases strictly monotonically in this case. Therefore the arguments of Section 4.3 state that a coexistence equilibrium is necessarily unique and arises only in the case of mutual invasibility.

Appendix B.4. Shifted exponential distribution

The maturation delay from egg to larva and from larva to adult have shifted exponential distributions. They have a minimum duration of m_E and m_L respectively, followed by an additional time which is distributed exponentially with expectation $1/\lambda_E$ and $1/\lambda_L$ respectively. For this distribution

$$\begin{aligned}
\Pi_E(P) &= e^{-(a_P P + d_E)m_E} \frac{\lambda_E}{a_P P + d_E + \lambda_E} \\
\Pi_L(Q) &= e^{-(a_Q Q + d_L)m_L} \frac{\lambda_l}{a_Q Q + d_L + \lambda_L}.
\end{aligned} \tag{B.11}$$

Π_L^{-1} and therefore f have no elementary representations. Numerical calculations show that f can become non-monotonous and therefore multiple equilibria can arise.
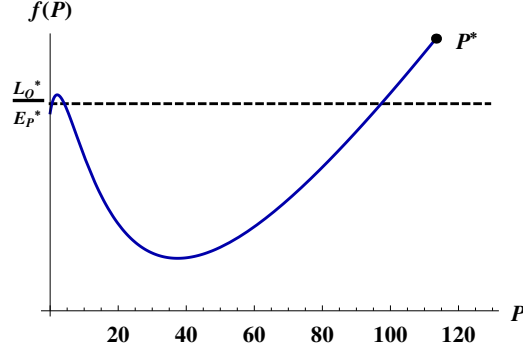
24

Figure B.7: The graph of the function f with gamma distributed maturation delays. Parameter values are $p_E = 2$, $p_L = 5$, $\lambda_E = 1$, $\lambda_L = 1$, $a_P = 0.198$, $a_Q = 1$, $d_E = 0$, $d_L = 0$, $\rho = 550$, $d_P = 1$, $d_Q = 1$, $c_P = 1$ and $c_Q = 1$

Appendix B.5. Gamma distribution

The maturation delay from egg to larva and from larva to adult have gamma distributions with shape parameter p_E and p_L respectively and inverse scale parameter λ_E and λ_L respectively. For this distribution

$$
\begin{aligned}
\Pi_E(P) &= \left(\frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\
\Pi_L(Q) &= \left(\frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L}.
\end{aligned}
\tag{B.12}
$$

Π_L^{-1} and therefore f have elementary representations,

$$
f(P) = \frac{(a_P P + d_E)((a_P P + d_E + \lambda_E)^{p_E} - \rho \lambda_E^{p_E}) \left(\frac{\lambda_E^{-p_E}(a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L}}{\lambda_L \rho ((a_P P + d_E + \lambda_E)^{p_E} - \lambda_E^{p_E}) \left(\left(\frac{\lambda_E^{-p_E}(a_P P + d_E + \lambda_E)^{p_E}}{\rho} \right)^{1/p_L} - 1 \right)}.
\tag{B.13}
$$

Numerical calculations show that f can become non-monotonous and therefore multiple equilibria can arise, see Fig. B.7.

Appendix B.6. Shifted gamma distribution

The maturation delay from egg to larva and from larva to adult have shifted gamma distributions. They have a minimum duration of m_E and m_L respectively, followed by an additional time which is gamma distributed with

25

shape parameter p_E and p_L respectively and inverse scale parameter λ_E and λ_L respectively. For this distribution

$$
\begin{aligned}
\Pi_E(P) &= e^{-(a_P P + d_E) m_E} \left(\frac{\lambda_E}{a_P P + d_E + \lambda_E} \right)^{p_E} \\
\Pi_L(Q) &= e^{-(a_Q Q + d_L) m_L} \left(\frac{\lambda_L}{a_Q Q + d_L + \lambda_L} \right)^{p_L}.
\end{aligned}
\tag{B.14}
$$

Π_L^{-1} and therefore f have no elementary representations. As with the non-shifted gamma distribution, f can become non-monotonous and therefore multiple equilibria can arise.

Appendix C. Characteristic equation

Here we derive a characteristic equation by considering a small perturbation from an equilibrium $(\overline{E}, \overline{L}, \overline{A}, \overline{P}, \overline{Q})$,

$$
\begin{aligned}
E(t) &= \overline{E} + e(t), \ L(t) = \overline{L} + l(t), \ A(t) = \overline{A} + a(t) \\
P(t) &= \overline{P} + p(t), \ Q(t) = \overline{Q} + q(t)
\end{aligned}
\tag{C.1}
$$

and assume that

$$
\begin{aligned}
e(t) &= h_E e^{\lambda t}, \ l(t) = h_L e^{\lambda t}, \ a(t) = h_A e^{\lambda t} \\
p(t) &= h_P e^{\lambda t}, \ q(t) = h_Q e^{\lambda t}.
\end{aligned}
\tag{C.2}
$$

The aim of the characteristic equation is to investigate stability of an equilibrium by the complex roots for λ. An equilibrium is stable when all roots have negative real parts while it is unstable when there are roots with positive real part, see (Diekmann et al., 1995). In order to derive the characteristic equation, we define

$$
\begin{aligned}
\overline{R}_E &:= \rho d_A \overline{A} \\
\gamma_E &:= a_P \overline{P} + d_E \\
\gamma_L &:= a_Q \overline{Q} + d_L \\
\overline{M}_E &:= \int_0^\infty \overline{R}_E e^{-x_E \gamma_E} w_E(x_E) dx_E \\
\overline{M}_L &:= \int_0^\infty \overline{M}_E e^{-x_L \gamma_L} w_L(x_L) dx_L
\end{aligned}
\tag{C.3}
$$

26

and

$$r_E(t) := R_E(t) - \overline{R}_E$$
$$= \rho d_A A(t) - \overline{R}_E$$
$$= \rho d_A(\overline{A} + a(t)) - \overline{R}_E \qquad \text{(C.4)}$$
$$= \rho d_A a(t)$$

515 and

$$m_E(t) := M_E(t) - \overline{M}_E$$
$$= \int_0^\infty R_E(t - x_E)S_E(x_E, t)w_E(x_E)dx_E - \overline{M}_E$$
$$= \int_0^\infty (\overline{R}_E + r_E(t - x_E))e^{-x_E\gamma_E}e^{-a_P \int_{t-x_E}^t p(y)dy}w_E(x_E)dx_E - \overline{M}_E$$
$$= \int_0^\infty (\overline{R}_E + r_E(t - x_E))e^{-x_E\gamma_E}\left(1 - a_P \int_{t-x_E}^t p(y)dy\right)w_E(x_E)dx_E - \overline{M}_E$$
$$= \int_0^\infty r_E(t - x_E)e^{-x_E\gamma_E}w_E(x_E)dx_E$$
$$- \int_0^\infty \overline{R}_E e^{-x_E\gamma_E}a_P \int_{t-x_E}^t p(y)dy w_E(x_E)dx_E$$

(C.5)

516 where we use that $e^x \approx 1 + x$ for small x and that $r_E(t - x_E)p(y) \approx 0$. In
517 the same way

$$m_L(t) := M_L(t) - \overline{M}_L$$
$$= \int_0^\infty m_E(t - x_L)e^{-x_L\gamma_L}w_L(x_L)dx_L$$
$$- \int_0^\infty \overline{M}_E e^{-x_L\gamma_L}a_Q \int_{t-x_L}^t q(y)dy w_L(x_L)dx_L$$
$$= \int_0^\infty \left(\int_0^\infty r_E(t - x_E - x_L)e^{-x_E\gamma_E}w_E(x_E)dx_E\right.$$
$$\left. - \int_0^\infty \overline{R}_E e^{-x_E\gamma_E}a_P \int_{t-x_E-x_L}^{t-x_L} p(y)dy w_E(x_E)dx_E\right) \cdot e^{-x_L\gamma_L}w_L(x_L)dx_L$$
$$- \int_0^\infty \overline{M}_E e^{-x_L\gamma_L}a_Q \int_{t-x_L}^t q(y)dy w_L(x_L)dx_L.$$

(C.6)

518 Now we can state the derivatives

$$
\begin{aligned}
\dot{e}(t) = \dot{E}(t) &= R_E(t) - M_E(t) - a_P E(t) P(t) - d_E E(t) \\
&= \overline{R}_E + r_E(t) - (\overline{M}_E + m_E(t)) - a_P(\overline{E} + e(t))(\overline{P} + p(t)) - d_E(\overline{E} + e(t)) \\
&= r_E(t) - m_E(t) - a_P(\overline{E}p(t) + e(t)\overline{P}) - d_E e(t)
\end{aligned}
$$
(C.7)

519 where we use that $\overline{R}_E - \overline{M}_E - a_P \overline{E}\overline{P} - d_E \overline{E} = 0$ and $e(t)p(t) \approx 0$. In the
520 same way

$$
\begin{aligned}
\dot{l}(t) &= m_E(t) - m_L(t) - a_Q(\overline{L}q(t) + l(t)\overline{Q}) - d_L l(t) \\
\dot{a}(t) &= m_L(t) - d_A a(t) \\
\dot{p}(t) &= c_P a_P(\overline{E}p(t - T_{JP}) + e(t - T_{JP})\overline{P}) - d_P p(t) \\
\dot{q}(t) &= c_Q a_Q(\overline{L}q(t - T_{JQ}) + l(t - T_{JQ})\overline{Q}) - d_Q q(t).
\end{aligned}
$$
(C.8)

521 We introduce the notation

$$
\begin{aligned}
\overline{\Pi}_1 &:= \Pi_1(\overline{P}) = \int_0^\infty e^{-x_E \gamma_E} w_E(x_E) dx_E \\
\overline{\Pi}_2 &:= \Pi_2(\overline{Q}) = \int_0^\infty e^{-x_L \gamma_L} w_L(x_L) dx_L \\
\overline{\Pi}_1(\lambda) &:= \Pi_1(\overline{P} + \frac{\lambda}{a_P}) = \int_0^\infty e^{-x_E(\gamma_E + \lambda)} w_E(x_E) dx_E \\
\overline{\Pi}_2(\lambda) &:= \Pi_2(\overline{Q} + \frac{\lambda}{a_Q}) = \int_0^\infty e^{-x_L(\gamma_L + \lambda)} w_L(x_L) dx_L
\end{aligned}
$$
(C.9)

522 and obtain the following by plugging (C.2) into (C.7) and (C.8)

$$
\begin{aligned}
\lambda h_E &= \rho d_A \left(h_A - h_A \overline{\Pi}_1(\lambda) + \overline{A} a_P h_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} \right) - a_P(\overline{E}h_P + h_E \overline{P}) - d_E h_E \\
\lambda h_L &= \rho d_A \left(h_A \overline{\Pi}_1(\lambda) - \overline{A} a_P h_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} - h_A \overline{\Pi}_1(\lambda)\overline{\Pi}_2(\lambda) + \overline{A} a_P h_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda}\overline{\Pi}_2(\lambda) \right. \\
&\quad \left. + \overline{A} a_Q h_Q \overline{\Pi}_1 \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda} \right) - a_Q(\overline{L}h_Q + h_L \overline{Q}) - d_L h_L \\
\lambda h_A &= \rho d_A \left(h_A \overline{\Pi}_1(\lambda)\overline{\Pi}_2(\lambda) - \overline{A} a_P h_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda}\overline{\Pi}_2(\lambda) - \overline{A} a_Q h_Q \overline{\Pi}_1 \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda} \right) - d_A h_A \\
\lambda h_P &= a_P c_P e^{-\lambda T_{JP}}(\overline{E}h_P + h_E \overline{P}) - d_P h_P \\
\lambda h_Q &= a_Q c_Q e^{-\lambda T_{JQ}}(\overline{L}h_Q + h_L \overline{Q}) - d_Q h_Q
\end{aligned}
$$
(C.10)

28

where we divide on both sides by $e^{\lambda t}$ and use that $\overline{M}_E = \rho d_A \overline{A}\overline{\Pi}_1$. From the last two equations of (C.10) we can express h_p and h_q explicitly in terms of h_e and h_l as

$$
\begin{aligned}
h_P = h_E \Phi_P(\lambda) \quad &\text{where} \quad \Phi_P(\lambda) = \frac{\overline{P}a_P c_P e^{-\lambda T_{JP}}}{\lambda + d_P - a_P c_P \overline{E} e^{-\lambda T_{JP}}} \\
h_Q = h_L \Phi_Q(\lambda) \quad &\text{where} \quad \Phi_Q(\lambda) = \frac{\overline{Q}a_Q c_Q e^{-\lambda T_{JQ}}}{\lambda + d_Q - a_Q c_Q \overline{L} e^{-\lambda T_{JQ}}}.
\end{aligned} \tag{C.11}
$$

Using the solutions from (C.11) and the first two equations in (C.10) we can express h_E and h_L in the following form,

$$h_E = h_A \Phi_E(\lambda)$$

$$\text{where} \qquad \Phi_E(\lambda) = \frac{\rho d_A (1 - \overline{\Pi}_1(\lambda))}{\lambda + d_E + a_P \overline{P} + \Phi_P(\lambda)\left(a_P \overline{E} - \rho d_A \overline{A} a_P \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda}\right)}$$

$$h_L = h_A \Phi_L(\lambda)$$

$$\text{where} \qquad \Phi_L(\lambda) = \frac{\rho d_A \left(\overline{\Pi}_1(\lambda)(1 - \overline{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\overline{A} a_P (1 - \overline{\Pi}_2(\lambda))\frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda}\right)}{\lambda + d_L + a_Q \overline{Q} + \Phi_Q(\lambda)\left(a_Q \overline{L} - \rho d_A \overline{A} a_Q \overline{\Pi}_1 \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda}\right)}. \tag{C.12}$$

Plugging h_P, h_Q, h_E and h_L in the third equation of (C.10) we have the characteristic equation in the form $G(\lambda) = 1$,

$$G(\lambda) =$$

$$\frac{\rho d_A}{\lambda + d_A}\left(\overline{\Pi}_1(\lambda)\overline{\Pi}_2(\lambda) - \overline{A} a_P \overline{\Pi}_2(\lambda)\Phi_P(\lambda)\Phi_E(\lambda)\frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} - \overline{A} a_Q \overline{\Pi}_1 \Phi_Q(\lambda)\Phi_L(\lambda)\frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda}\right). \tag{C.13}$$

Appendix C.1. A sufficient condition for instability

The following observation can be helpful for proving instability of an equilibrium. It is easily verified that $G(\lambda) \xrightarrow[\lambda \to \infty]{} 0$. Hence if $G(0) > 1$ then there is a positive real root for the characteristic equation and the coexistence equilibrium is unstable. Therefore we investigate the structure of $G(0)$. First we see that

$$
\begin{aligned}
\lim_{\lambda \to 0} \frac{\overline{\Pi}_1 - \overline{\Pi}_1(\lambda)}{\lambda} &= -\frac{d\overline{\Pi}_1/d\overline{P}}{a_P} \\
\lim_{\lambda \to 0} \frac{\overline{\Pi}_2 - \overline{\Pi}_2(\lambda)}{\lambda} &= -\frac{d\overline{\Pi}_2/d\overline{Q}}{a_Q}.
\end{aligned} \tag{C.14}
$$

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We will denote $\overline{\Pi}'_1 = d\overline{\Pi}_1/d\overline{P}$ and $\overline{\Pi}'_2 = d\overline{\Pi}_2/d\overline{Q}$. Then we calculate

$$
\Phi_P(\lambda)\Phi_E(\lambda) = \Phi_P(\lambda)\frac{\rho d_A(1-\overline{\Pi}_1(\lambda))}{\lambda + d_E + a_P\overline{P} + \Phi_P(\lambda)\left(a_P\overline{E} - \rho d_A\overline{A}a_P\frac{\overline{\Pi}_1-\overline{\Pi}_1(\lambda)}{\lambda}\right)}
$$

$$
= \frac{\rho d_A(1-\overline{\Pi}_1(\lambda))}{\frac{\lambda+d_E+a_P\overline{P}}{\Phi_P(\lambda)} + \left(a_P\overline{E} - \rho d_A\overline{A}a_P\frac{\overline{\Pi}_1-\overline{\Pi}_1(\lambda)}{\lambda}\right)}.
$$

(C.15)

Since $1/\Phi_P(\lambda) \xrightarrow[\lambda\to 0]{} 0$,

$$
\lim_{\lambda\to 0}\Phi_P(\lambda)\Phi_E(\lambda) = \frac{\rho d_A(1-\overline{\Pi}_1)}{a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1}.
$$

(C.16)

In the same way

$$
\Phi_Q(\lambda)\Phi_L(\lambda) = \Phi_Q(\lambda)\frac{\rho d_A\left(\overline{\Pi}_1(\lambda)(1-\overline{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\overline{A}a_P(1-\overline{\Pi}_2(\lambda))\frac{\overline{\Pi}_1-\overline{\Pi}_1(\lambda)}{\lambda}\right)}{\lambda + d_L + a_Q\overline{Q} + \Phi_Q(\lambda)\left(a_Q\overline{L} - \rho d_A\overline{A}a_Q\overline{\Pi}_1\frac{\overline{\Pi}_2-\overline{\Pi}_2(\lambda)}{\lambda}\right)}
$$

$$
= \frac{\rho d_A\left(\overline{\Pi}_1(\lambda)(1-\overline{\Pi}_2(\lambda)) - \Phi_E(\lambda)\Phi_P(\lambda)\overline{A}a_P(1-\overline{\Pi}_2(\lambda))\frac{\overline{\Pi}_1-\overline{\Pi}_1(\lambda)}{\lambda}\right)}{\frac{\lambda+d_L+a_Q\overline{Q}}{\Phi_Q(\lambda)} + \left(a_Q\overline{L} - \rho d_A\overline{A}a_Q\overline{\Pi}_1\frac{\overline{\Pi}_2-\overline{\Pi}_2(\lambda)}{\lambda}\right)}.
$$

(C.17)

Since $1/\Phi_Q(\lambda) \xrightarrow[\lambda\to 0]{} 0$,

$$
\lim_{\lambda\to 0}\Phi_Q(\lambda)\Phi_L(\lambda) = \frac{\rho d_A(1-\overline{\Pi}_2)(a_P\overline{E}\overline{\Pi}_1 + \rho d_A\overline{A}\overline{\Pi}'_1)}{(a_Q\overline{L} + \rho d_A\overline{A}\overline{\Pi}_1\overline{\Pi}'_2)(a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1)}.
$$

(C.18)

Now $G(0)$ can be simplified,

$G(0)$

$$
= \rho\left(\overline{\Pi}_1\overline{\Pi}_2 + \overline{A}\overline{\Pi}_2\overline{\Pi}'_1\frac{\rho d_A(1-\overline{\Pi}_1)}{a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1} + \overline{A}\overline{\Pi}_1\overline{\Pi}'_2\frac{\rho d_A(1-\overline{\Pi}_2)(a_P\overline{E}\overline{\Pi}_1 + \rho d_A\overline{A}\overline{\Pi}'_1)}{(a_Q\overline{L} + \rho d_A\overline{A}\overline{\Pi}_1\overline{\Pi}'_2)(a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1)}\right)
$$

$$
= \rho\left(\frac{\overline{\Pi}_2(a_P\overline{E}\overline{\Pi}_1 + \rho d_A\overline{A}\overline{\Pi}'_1)}{a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1} + \overline{A}\overline{\Pi}_1\overline{\Pi}'_2\frac{\rho d_A(1-\overline{\Pi}_2)(a_P\overline{E}\overline{\Pi}_1 + \rho d_A\overline{A}\overline{\Pi}'_1)}{(a_Q\overline{L} + \rho d_A\overline{A}\overline{\Pi}_1\overline{\Pi}'_2)(a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1)}\right)
$$

$$
= \rho\frac{(a_P\overline{E}\overline{\Pi}_1 + \rho d_A\overline{A}\overline{\Pi}'_1)(a_Q\overline{L}\overline{\Pi}_2 + \rho d_A\overline{A}\overline{\Pi}_1\overline{\Pi}'_2)}{(a_P\overline{E} + \rho d_A\overline{A}\overline{\Pi}'_1)(a_Q\overline{L} + \rho d_A\overline{A}\overline{\Pi}_1\overline{\Pi}'_2)}.
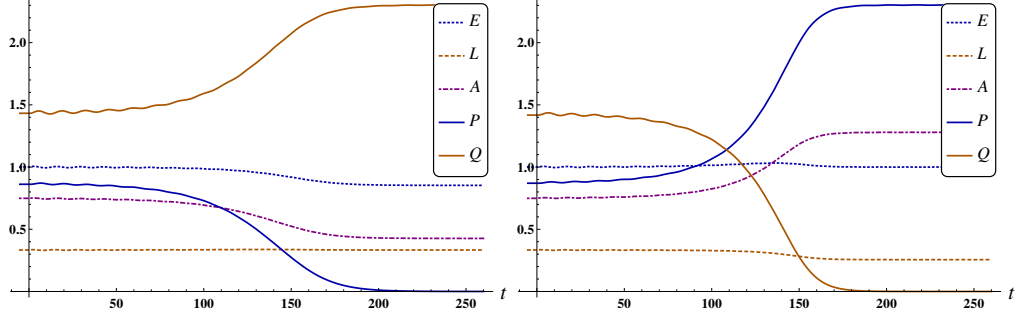$$

(C.19)

Figure C.8: Time plots of population dynamics after small perturbations from equilibrium densities. Both maturation delays, from egg to larva and from larva to adult, have constant lengths T_E and T_L respectively. The initial densities for $t \leq 0$ are constant and correspond to perturbations from the unique set of coexistence equilibrium densities. In the left panel, the egg parasitoid density P is decreased by 1% and the larva parasitoid wins the competition. In the right panel, the larva parasitoid density Q is decreased by 1% and the egg parasitoid wins the competition. Parameter values are $T_E = 1$, $T_L = 1$, $a_P = 1$, $a_Q = 1$, $d_E = 0$, $d_L = 0$, $d_A = 0.2$, $\rho = 10$, $d_P = 1$, $d_Q = 1$, $c_P = 1$, $c_Q = 3$, $T_{JP} = 1$ and $T_{JQ} = 1$

Appendix C.2. Instability of the coexistence equilibrium when maturation delays are constant

We have seen in Appendix B.1, that with constant maturation delays at most one coexistence equilibrium exists, and that if it exists, none of the parasitoids can invade an equilibrium population of the other parasitoid and the host. This observation and the simulations shown in Fig. C.8 suggest that the coexistence equilibrium is unstable. We will now prove this conjecture by using the criteria from Appendix C.1, which states that an equilibrium is unstable when the corresponding $G(0) > 1$. Using the formulations of Appendix B.1 and Appendix C.1, it is easily verified that with constant maturation delays $\overline{\Pi}'_1 = -a_P T_E \overline{\Pi}_1$ and $\overline{\Pi}'_2 = -a_Q T_L \overline{\Pi}_2$. Plugging into (C.19) yields with the notation $\Gamma_1(\overline{P}) = \overline{\Gamma}_1$ and $\Gamma_2(\overline{Q}) = \overline{\Gamma}_2$,

$$
\begin{aligned}
G(0) &= \rho \frac{(a_P \overline{E} \overline{\Pi}_1 - a_P T_E \rho d_A \overline{A} \overline{\Pi}_1)(a_Q \overline{L} \overline{\Pi}_2 - a_Q T_L \rho d_A \overline{A} \overline{\Pi}_1 \overline{\Pi}_2)}{(a_P \overline{E} - a_P T_E \rho d_A \overline{A} \overline{\Pi}_1)(a_Q \overline{L} - a_Q T_L \rho d_A \overline{A} \overline{\Pi}_1 \overline{\Pi}_2)} \\
&= \frac{\overline{\Gamma}_1 - T_E}{\overline{\Gamma}_1 - T_E \overline{\Pi}_1} \frac{\overline{\Gamma}_2 - T_L}{\overline{\Gamma}_2 - T_L \overline{\Pi}_2},
\end{aligned}
\tag{C.20}
$$

31

where we use $\overline{E} = \rho d_A \overline{A} \overline{\Gamma}_1$, $\overline{L} = \rho d_A \overline{A} \overline{\Pi}_1 \overline{\Gamma}_2$ and $\rho \overline{\Pi}_1 \overline{\Pi}_2 = 1$ according to equation (7), (8), (9) and (11). For both fractions in the last line of (C.20), the numerator is positive and the denominator is negative. To verify this, we deduce from equation (A.3) that

$$
\begin{aligned}
\overline{\Gamma}_1 &= \mathbb{E}[\min\{K_E, T_E\}] < T_E \text{ and} \\
\overline{\Gamma}_1 &= \overline{\Pi}_1 T_E + (1 - \overline{\Pi}_1)\mathbb{E}[K_E | K_E \leq T_E] > \overline{\Pi}_1 T_E,
\end{aligned}
\tag{C.21}
$$

where K_E is an exponentially distributed random variable. In the same way $\overline{\Gamma}_2 < T_L$ and $\overline{\Pi}_2 T_L < \overline{\Gamma}_2$. To prove $G(0) > 1$, it is therefore enough to show that $\overline{\Gamma}_1 - T_E \overline{\Pi}_1 < T_E - \overline{\Gamma}_1$ and $\overline{\Gamma}_2 - T_L \overline{\Pi}_2 < T_L - \overline{\Gamma}_2$. To verify the first –and in the same way the second– inequality, we use $\overline{\Gamma}_1 = (1 - \overline{\Pi}_1)/(a_P \overline{P} + d_E)$ from equation (A.3), and argue

$$
\begin{aligned}
\overline{\Gamma}_1 - T_E \overline{\Pi}_1 &< T_E - \overline{\Gamma}_1 \Leftrightarrow \\
\frac{1 - \overline{\Pi}_1}{a_P \overline{P} + d_E} - T_E \overline{\Pi}_1 &< T_E - \frac{1 - \overline{\Pi}_1}{a_P \overline{P} + d_E} \Leftrightarrow \\
1 - \overline{\Pi}_1 - \overline{\Pi}_1 (a_P \overline{P} + d_E) T_E &< (a_P \overline{P} + d_E) T_E - 1 + \overline{\Pi}_1 \Leftrightarrow \\
1 - e^{-\gamma} - \gamma e^{-\gamma} &< \gamma - 1 + e^{-\gamma} \Leftrightarrow \\
\int_0^\gamma (x e^{-x}) dx &< \int_0^\gamma (1 - e^{-x}) dx \Leftarrow \\
x e^{-x} &< 1 - e^{-x} \quad \forall x > 0 \Leftrightarrow \\
1 + x &< e^x \quad \forall x > 0,
\end{aligned}
\tag{C.22}
$$

where $\gamma = (a_P \overline{P} + d_E) T_E$. The last line of (C.22) is obviously true. This completes the proof that the coexistence equilibrium is unstable when the maturation delays are constant.

Acknowledgment

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