



# Multiple coexistence equilibria in a two parasitoid-one host model



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## HIGHLIGHTS

- A stage structured model for two parasitoids with a common host is reanalyzed.
- Maturation delays of the host are randomly distributed.
- Depending on these distributions multiple coexistence equilibria can arise.
- Multiple coexistence equilibria can be simultaneously stable.
- Stable coexistence does not necessarily require mutual invasibility.

## ARTICLE INFO

### Article history:

Received 4 July 2015

Available online 17 November 2016

### MSC:

92-02

### Keywords:

Population dynamics

Parasitoid–host interaction

Delay differential equations

Multiplicity of coexistence equilibria

## 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 analyze 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.

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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 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-analyze 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 3–5, we formulate the original results in our somewhat different notation and, in Section 6, we show that coexistence equilibria are not unique for many distributions of the maturation delays. Finally, in Section 7, we set our results in the

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<http://dx.doi.org/10.1016/j.tpb.2016.10.002>

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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 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  $\rho$  (so  $\rho d_A$  is the rate with which an adult produces offspring).

The population dynamics are 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

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

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 $t$

and

Parameter	Description
$\rho$	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 formulas 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

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

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

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

As shown in [Appendix A.2](#), the expected duration of the egg stage is

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

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

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

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

$$\Gamma_3 = \frac{1}{d_A}. \quad (6)$$

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

$$R_E = \rho d_A A. \quad (7)$$

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  $\frac{dE}{dt} = 0$ ),

$$E = R_E \Gamma_1(P). \quad (8)$$

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  $\frac{dL}{dt} = 0$ ),

$$L = R_E \Pi_1(P) \Gamma_2(Q). \quad (9)$$

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  $\frac{dA}{dt} = 0$ ),

$$A = R_E \Pi_1(P) \Pi_2(Q) \Gamma_3. \quad (10)$$

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  $\rho$  and the probability for an egg to mature to an adult,

$$R_0 = \rho \Pi_1(P) \Pi_2(Q). \quad (11)$$

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

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

## 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

$$\rho \Pi_1(P^*) \Pi_2(0) = 1. \quad (13)$$

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

$$E_p^* = \frac{d_p}{a_p c_p}. \quad (14)$$

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

$$L_p^* = E_p^* \frac{\Pi_1(P^*) \Gamma_2(0)}{\Gamma_1(P^*)}. \quad (15)$$

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

$$\rho \Pi_1(0) \Pi_2(Q^*) = 1 \quad (16)$$

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

$$L_Q^* = \frac{d_Q}{a_Q c_Q}, \quad (17)$$

and the equilibrium egg density is

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

### 4.3. When both parasitoids are present

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

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

where  $\Pi_2^{-1}$  is the inverse function of  $\Pi_2$ . Plugging (19) into (12) yields a condition for all host stages to be in equilibrium

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

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

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

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 following condition:

$$f(P^{**}) = \frac{L_Q^*}{E_p^*}. \quad (22)$$

The corresponding larva parasitoid density  $Q^{**}$  can be obtained by Eq. (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

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

with  $\Pi_1^{-1}$  being the inverse function of  $\Pi_1$ . 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 Eq. (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

$$E_p^* < E_Q^*. \quad (24)$$

To demonstrate this, we compute the Malthusian parameter  $\lambda = \lambda_p(E)$  for the egg parasitoid at constant egg density  $E$ . Namely, we linearize system (1) around the equilibrium, obtaining

$$\frac{dP(t)}{dt} = a_p c_p E P(t - T_{jp}) - d_p P(t) \quad (25)$$

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

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

and obtain

$$\begin{aligned} \lambda P(t) &= a_p c_p E P(t) e^{-\lambda T_{jp}} - d_p P(t) \\ \lambda &= E a_p c_p e^{-\lambda T_{jp}} - d_p. \end{aligned} \quad (27)$$

The egg parasitoid can invade a stable equilibrium community of the larva parasitoid and the host when this equation has a positive real root for  $E = E_Q^*$ , that is  $\lambda_p(E_Q^*) > 0$ . The claim that this requires  $E_p^* < E_Q^*$  follows because the unique real root  $\lambda_p(E)$  increases strictly monotonically with  $E$  and  $\lambda_p(E_p^*) = 0$ . (Note that we do not have to consider complex roots for  $\lambda$  since their real parts cannot exceed the real root.)

In the same way it can be seen that the larva parasitoid can invade a stable equilibrium population with only the egg parasitoid when

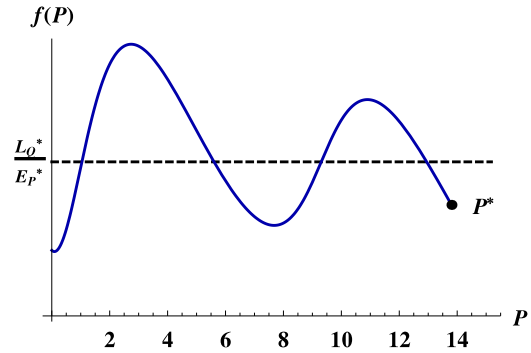
$$L_Q^* < L_p^*. \quad (28)$$

We speak of mutual invasibility of stable equilibria when

$$E_p^* < E_Q^* \quad \text{and} \quad L_Q^* < L_p^*. \quad (29)$$

The value of the function  $f$  defined in (21) at the boundary of its domain, relative to the right hand side of (22), turns out to be related to the invasibility conditions. Indeed,

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



**Fig. 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  $T_{E1} = 0.2$ ,  $T_{E2} = 1.35$ ,  $T_{L1} = 0.75$ ,  $T_{L2} = 5$ ,  $r_E = 0.5$ ,  $r_L = 0.3$ ,  $a_p = 2$ ,  $a_Q = 0.2$ ,  $d_E = 0$ ,  $d_L = 0$ ,  $\rho = 500$ ,  $d_p = 8$ ,  $d_Q = 0.175$ ,  $c_p = 0.5$  and  $c_Q = 0.5$ .

and

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

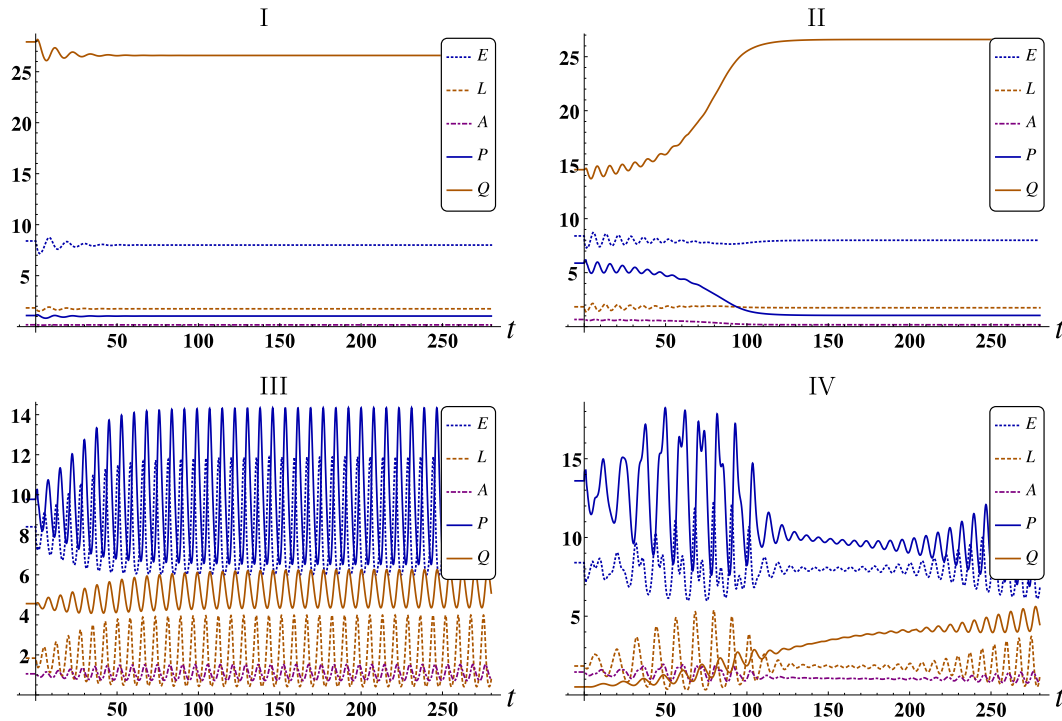
which implies that the egg parasitoid can invade a stable equilibrium with the larva parasitoid alone when  $f(0) < L_Q^*/E_p^*$  and the larva parasitoid can invade a stable equilibrium with the egg parasitoid alone when  $f(P^*) > L_Q^*/E_p^*$ .

## 6. Applying distributions for the maturation delays

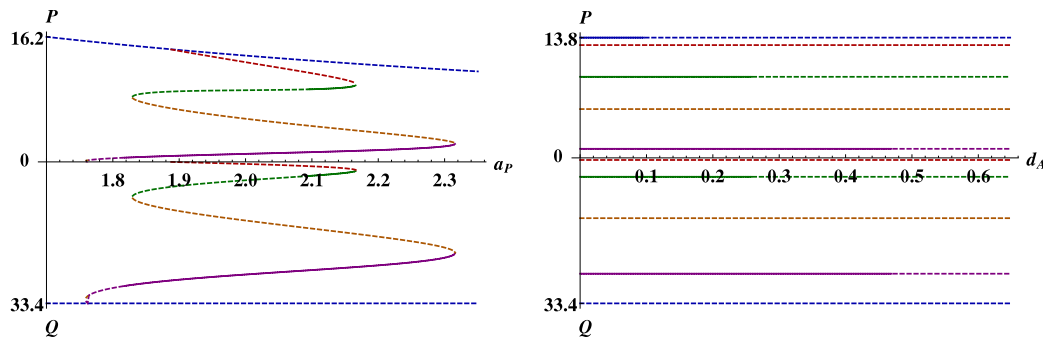
We apply several distributions for the maturation delays in order to analyze their influence on the multiplicity of coexistence equilibria. Among those are the constant-duration distribution, (shifted) exponential distribution and (shifted) gamma distribution, which have been introduced in the original 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).



**Fig. 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 fourth (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  $d_A = 0.3$ .



**Fig. 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 Figs. 1 and 2 (except axis parameters).

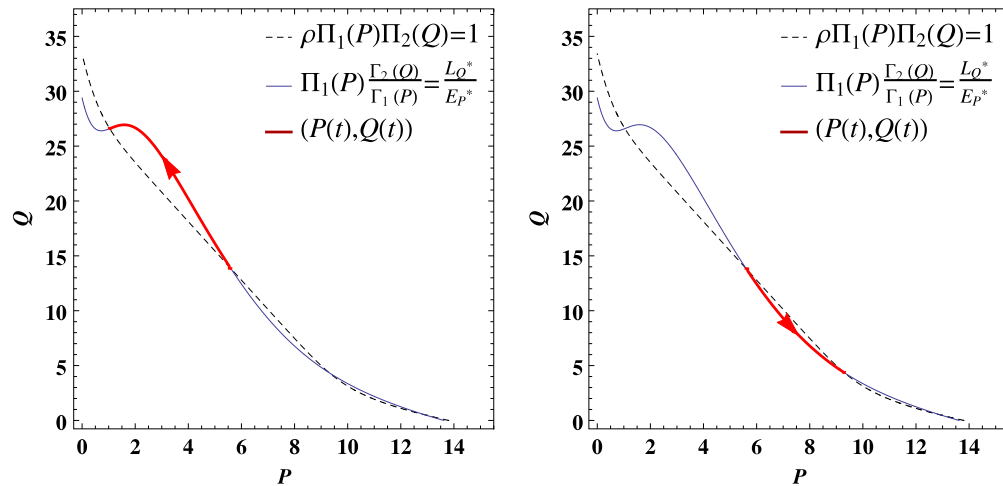
### 6.1. Simulations and stability

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.

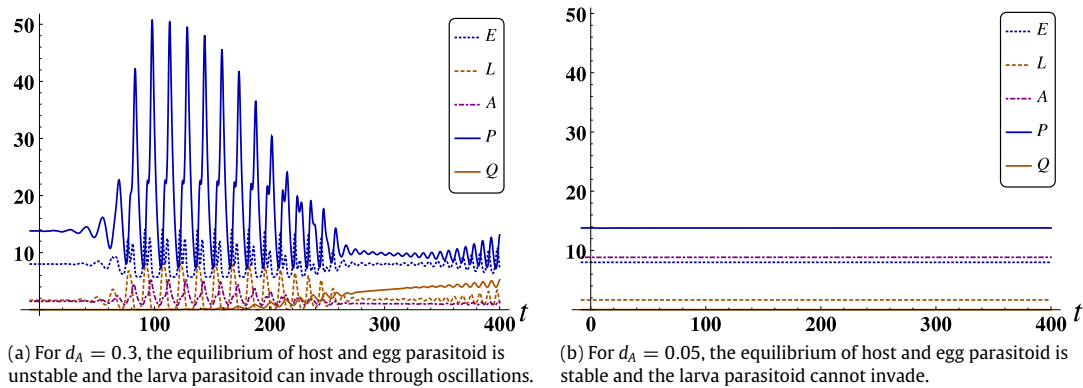
We further analyzed the dynamics for low values of the host adult death rate  $d_A$ . We show some simulations for that case in the

$(P, Q)$ -plane in Fig. 4. There we see that the population densities lie on the curve of equation  $\Pi_1(P) \frac{\Gamma_2(Q)}{\Gamma_1(P)} = \frac{I_Q^*}{E_P^*}$  and move in a direction depending on the relative position 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 Eq. (7). Numerical evidence suggests that this reduced system always quickly converges to its (quasi)-equilibrium, where  $E = E_P^*$ ,  $L = L_Q^*$  and Eqs. (8) and (9) hold, corresponding to the solid curve in the  $(P, Q)$ -plane in Fig. 4. Thus, on the slow time-scale,  $A(t)$  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 Eq. (11) is greater or smaller than 1, thus according to





**Fig. 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 Figs. 1 and 2.



**Fig. 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 low density  $Q = 0.01$  of the larva parasitoid. Distributions and parameter values are the same as in Figs. 1 and 2 with the exception of a lower value for  $d_A$  in the right panel.

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  $d_A \rightarrow 0$ , 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  $f'(P^{**}) > 0$ , 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 combining Fig. 5(b) 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.

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 and Chesson \(2016\)](#). 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.

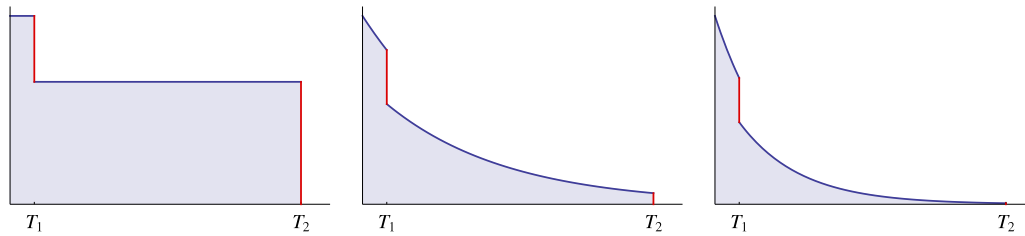
In our model, we found that equilibria can have different properties. Single parasitoid equilibria are potentially stable and non-invadable only when the host stage of the other parasitoid is reduced more strongly than what would be needed by the competitor to sustain. Similarly, we found that two-parasitoid 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 ( $L_p^* < L_0^*$ ). 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  $L_0^*$  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 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 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  $\Gamma_i$  of a juvenile stage and the probability  $\Pi_i$  to reach the next stage, both for different densities of the corresponding parasitoid. We see that increasing the parasitoid density first decreases  $\Pi_i$  heavily because only a small part of the hosts with long maturation delay reaches maturation, while further increasing the parasitoid density decreases  $\Gamma_i$  more strongly because parasitism still mainly affects



**Fig. 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  $I_i$  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  $\Pi_i$  to reach the next stage. The ratio  $I_i/\Pi_i$  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  $r = 0.35$ ,  $T_1 = 1$ , and  $T_2 = 12$ .

hosts with a long maturation delay whose contribution to  $\Pi_i$  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  $I_i/\Pi_i$  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.

## Acknowledgments

This research was funded by the Autonomous Province of Trento (Italy), Research funds for Grandi Progetti, Project LExEM (Laboratory of excellence for epidemiology and modeling, <http://www.lexem.eu>). We thank the editor and four anonymous reviewers for their comments which helped to improve the manuscript substantially.

## 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  $\Gamma_3$ , respectively. The calculations are valid for constant parasitoid densities  $P$  and  $Q$ . We use the following notations for the various random variables.

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

### 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

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

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

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

Obviously,  $\Pi_1$  and  $\Pi_2$  decrease strictly monotonically to 0.

### 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  $a_P P + d_E \neq 0$

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

where we used that  $K_E$  is exponentially distributed.

For  $a_P P + d_E = 0$  obviously

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

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

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

and for  $a_Q Q + d_L = 0$

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



Note that the expectation values of  $K_E$  and  $K_L$  and thus  $\Gamma_1$  and  $\Gamma_2$  decrease strictly monotonically with the corresponding parasitoid densities.

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

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

## Appendix B. Computing $f$ for some distributions

Elementary representations for the function  $f$  from Eq. (21) can be found for some distribution families for the maturation delays. To facilitate the computations, we rearrange  $f$  by using the formulas for  $\Gamma_1$  and  $\Gamma_2$  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),

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

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

### 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,

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

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

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

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).<sup>1</sup> Therefore, the arguments of Sections 4.3 and 5 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 domain for  $P$  implies that  $0 < \gamma < q$ . Obviously  $f(P)$  is decreasing if the following function  $g(\gamma)$  is decreasing,

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

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

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

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

$$k(q) = e^\gamma (q + q\gamma - \gamma^2) + e^{q+\gamma} (q - q\gamma + \gamma^2) - qe^{2\gamma} - e^q q \quad (\text{B.6})$$

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

$$k_q(q) = e^{q+\gamma} (q - q\gamma + \gamma^2 + 1 - \gamma) - e^q (1 + q) - e^{2\gamma} + e^\gamma (\gamma + 1) \quad (\text{B.7})$$

$$k_{qq}(q) = e^q (e^\gamma (q - q\gamma + \gamma^2 - 2\gamma + 2) - q - 2).$$

It can be easily seen that the equation  $k_{qq}(q) = 0$  has only one solution for  $q$ . Therefore,  $k_q(q) = 0$  has at most two solutions and  $k(q)$  has at most two (local) extrema.

Moreover, we see that  $k(0) = k(\gamma) = 0$ , that  $k(q) \xrightarrow{q \rightarrow -\infty} \infty$  (the dominant term being  $qe^\gamma$  with coefficient  $1 + \gamma - e^\gamma$ ), and that  $k(q) \xrightarrow{q \rightarrow \infty} -\infty$  (the dominant term being  $qe^q$  with coefficient  $e^\gamma (1 - \gamma) - 1$ ). Since  $k_q(\gamma) = 0$ , this implies  $k(q) < 0$  for  $q > \gamma$  (and actually  $k(q) \leq 0$  for  $q \geq 0$ ). This completes the proof that  $f(P)$  decreases strictly monotonically.

### B.2. Two-value distribution

The maturation delay from egg to larva and from larva to adult are each distributed with two distinct values that occur with certain probabilities. The transformation from egg to larva has length  $T_{E1}$  with probability  $r_E$  and length  $T_{E2}$  with probability  $1 - r_E$ . The transformation from larva to adult has length  $T_{L1}$  with probability  $r_L$  and length  $T_{L2}$  with probability  $1 - r_L$ . For this distribution,

$$\begin{aligned} \Pi_E(P) &= r_E e^{(a_P P + d_E) T_{E1}} + (1 - r_E) e^{(a_P P + d_E) T_{E2}} \\ \Pi_L(Q) &= r_L e^{(a_Q Q + d_L) T_{L1}} + (1 - r_L) e^{(a_Q Q + d_L) T_{L2}}. \end{aligned} \quad (\text{B.8})$$

$\Pi_L^{-1}$  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.

### 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,

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

and

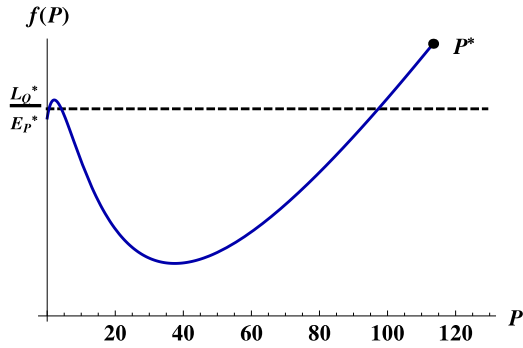
$$f(P) = \frac{a_P P + d_E + \lambda_E}{\rho \lambda_L}. \quad (\text{B.10})$$

Obviously,  $f(P)$  increases strictly monotonically in this case. Therefore, the arguments of Sections 4.3 and 5 state that a coexistence equilibrium is necessarily unique and arises only in the case of mutual invasibility.

### 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

<sup>1</sup> 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.



**Fig. 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  $c_Q = 1$ .

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,

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

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

#### 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  $\lambda_E$  and  $\lambda_L$ , respectively. For this distribution,

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

$\Pi_L^{-1}$  and therefore  $f$  have elementary representations,

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

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

#### 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 shape parameter  $p_E$  and  $p_L$ , respectively, and inverse scale parameter  $\lambda_E$  and  $\lambda_L$ , respectively. For this distribution,

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

$\Pi_L^{-1}$  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  $(\bar{E}, \bar{L}, \bar{A}, \bar{P}, \bar{Q})$ ,

$$\begin{aligned} E(t) &= \bar{E} + e(t), & L(t) &= \bar{L} + l(t), \\ A(t) &= \bar{A} + a(t) \end{aligned} \quad (\text{C.1})$$

$$P(t) = \bar{P} + p(t), \quad Q(t) = \bar{Q} + q(t)$$

and assume that

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

The aim of the characteristic equation is to investigate stability of an equilibrium by the complex roots for  $\lambda$ . 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

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

$$\bar{M}_L := \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} w_L(x_L) dx_L$$

and

$$\begin{aligned} r_E(t) &:= R_E(t) - \bar{R}_E \\ &= \rho d_A A(t) - \bar{R}_E \\ &= \rho d_A (\bar{A} + a(t)) - \bar{R}_E \\ &= \rho d_A a(t) \end{aligned} \quad (\text{C.4})$$

and

$$\begin{aligned} m_E(t) &:= M_E(t) - \bar{M}_E \\ &= \int_0^\infty R_E(t - x_E) S_E(x_E, t) w_E(x_E) dx_E - \bar{M}_E \\ &= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} \\ &\quad \times e^{-a_P \int_{t-x_E}^t p(y) dy} w_E(x_E) dx_E - \bar{M}_E \\ &= \int_0^\infty (\bar{R}_E + r_E(t - x_E)) e^{-x_E \gamma_E} \\ &\quad \times \left( 1 - a_P \int_{t-x_E}^t p(y) dy \right) w_E(x_E) dx_E - \bar{M}_E \\ &= \int_0^\infty r_E(t - x_E) e^{-x_E \gamma_E} w_E(x_E) dx_E \\ &\quad - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E}^t p(y) dy w_E(x_E) dx_E \end{aligned} \quad (\text{C.5})$$

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

$$\begin{aligned} m_L(t) &:= M_L(t) - \bar{M}_L \\ &= \int_0^\infty m_E(t - x_L) e^{-x_L \gamma_L} w_L(x_L) dx_L \end{aligned}$$

$$\begin{aligned}
& - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L \\
& = \int_0^\infty \left( \int_0^\infty r_E(t-x_E-x_L) e^{-x_E \gamma_E} w_E(x_E) dx_E \right. \\
& \quad - \int_0^\infty \bar{R}_E e^{-x_E \gamma_E} a_P \int_{t-x_E-x_L}^{t-x_L} p(y) dy w_E(x_E) dx_E \\
& \quad \cdot e^{-x_L \gamma_L} w_L(x_L) dx_L \\
& \quad \left. - \int_0^\infty \bar{M}_E e^{-x_L \gamma_L} a_Q \int_{t-x_L}^t q(y) dy w_L(x_L) dx_L \right). \quad (C.6)
\end{aligned}$$

Now we can state the derivatives

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

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

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

We introduce the notation

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

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

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

where we divide on both sides by  $e^{\lambda t}$  and use that  $\bar{M}_E = \rho d_A \bar{A} \bar{\Pi}_1$ . 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

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

Using the solutions from (C.11) and the first two equations in (C.10), we can express  $h_E$  and  $h_L$  in the form of Eq. (C.12), which is given in Box I. 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  $G(\lambda) = 1$ ,

$$\begin{aligned}
G(\lambda) &= \frac{\rho d_A}{\lambda + d_A} \left( \bar{\Pi}_1(\lambda) \bar{\Pi}_2(\lambda) \right. \\
&\quad \left. - \bar{A} a_P \bar{\Pi}_2(\lambda) \Phi_P(\lambda) \Phi_E(\lambda) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right. \\
&\quad \left. - \bar{A} a_Q \bar{\Pi}_1 \Phi_Q(\lambda) \Phi_L(\lambda) \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right). \quad (C.13)
\end{aligned}$$

### C.1. A sufficient condition for instability

The following observation can be helpful for proving instability of an equilibrium. It is easily verified that  $G(\lambda) \xrightarrow{\lambda \rightarrow \infty} 0$ . 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

$$\begin{aligned}
\lim_{\lambda \rightarrow 0} \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} &= -\frac{d\bar{\Pi}_1/d\bar{P}}{\lambda} \\
\lim_{\lambda \rightarrow 0} \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} &= -\frac{d\bar{\Pi}_2/d\bar{Q}}{a_Q}. \quad (C.14)
\end{aligned}$$

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

$$\begin{aligned}
&\Phi_P(\lambda) \Phi_E(\lambda) \\
&= \Phi_P(\lambda) \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\lambda + d_E + a_P \bar{P} + \Phi_P(\lambda) (a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda})} \\
&= \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\frac{\lambda + d_E + a_P \bar{P}}{\Phi_P(\lambda)} + (a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda})}. \quad (C.15)
\end{aligned}$$

Since  $1/\Phi_P(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$ ,

$$\lim_{\lambda \rightarrow 0} \Phi_P(\lambda) \Phi_E(\lambda) = \frac{\rho d_A (1 - \bar{\Pi}_1)}{a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1}. \quad (C.16)$$

In the same way Eq. (C.17) is given in Box II. Since  $1/\Phi_Q(\lambda) \xrightarrow{\lambda \rightarrow 0} 0$ ,

$$\begin{aligned}
&\lim_{\lambda \rightarrow 0} \Phi_Q(\lambda) \Phi_L(\lambda) \\
&= \frac{\rho d_A (1 - \bar{\Pi}_2) (a_P \bar{E} \bar{\Pi}'_1 + \rho d_A \bar{A} \bar{\Pi}'_1)}{(a_Q \bar{L} + \rho d_A \bar{A} \bar{\Pi}'_1 \bar{\Pi}'_2) (a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1)}. \quad (C.18)
\end{aligned}$$

Now,  $G(0)$  can be simplified as

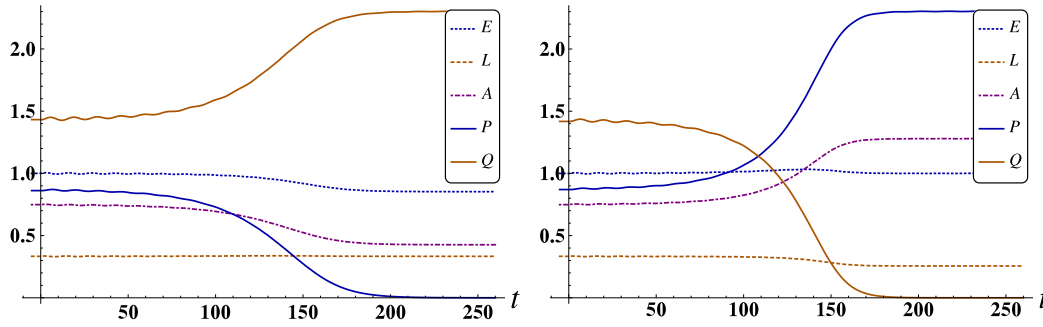
$$\begin{aligned}
G(0) &= \rho \left( \bar{\Pi}_1 \bar{\Pi}_2 + \bar{A} \bar{\Pi}_2 \bar{\Pi}'_1 \frac{\rho d_A (1 - \bar{\Pi}_1)}{a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1} \right. \\
&\quad \left. + \bar{A} \bar{\Pi}_1 \bar{\Pi}'_2 \frac{\rho d_A (1 - \bar{\Pi}_2) (a_P \bar{E} \bar{\Pi}'_1 + \rho d_A \bar{A} \bar{\Pi}'_1)}{(a_Q \bar{L} + \rho d_A \bar{A} \bar{\Pi}'_1 \bar{\Pi}'_2) (a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1)} \right) \\
&= \rho \left( \frac{\bar{\Pi}_2 (a_P \bar{E} \bar{\Pi}'_1 + \rho d_A \bar{A} \bar{\Pi}'_1)}{a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1} \right. \\
&\quad \left. + \bar{A} \bar{\Pi}_1 \bar{\Pi}'_2 \frac{\rho d_A (1 - \bar{\Pi}_2) (a_P \bar{E} \bar{\Pi}'_1 + \rho d_A \bar{A} \bar{\Pi}'_1)}{(a_Q \bar{L} + \rho d_A \bar{A} \bar{\Pi}'_1 \bar{\Pi}'_2) (a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1)} \right) \\
&= \rho \frac{(a_P \bar{E} \bar{\Pi}'_1 + \rho d_A \bar{A} \bar{\Pi}'_1) (a_Q \bar{L} \bar{\Pi}_2 + \rho d_A \bar{A} \bar{\Pi}'_1 \bar{\Pi}'_2)}{(a_P \bar{E} + \rho d_A \bar{A} \bar{\Pi}'_1) (a_Q \bar{L} + \rho d_A \bar{A} \bar{\Pi}'_1 \bar{\Pi}'_2)}. \quad (C.19)
\end{aligned}$$

$$\begin{aligned}
h_E &= h_A \Phi_E(\lambda) \\
\text{where } \Phi_E(\lambda) &= \frac{\rho d_A (1 - \bar{\Pi}_1(\lambda))}{\lambda + d_E + a_P \bar{P} + \Phi_P(\lambda) \left( a_P \bar{E} - \rho d_A \bar{A} a_P \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)} \\
h_L &= h_A \Phi_L(\lambda) \\
\text{where } \Phi_L(\lambda) &= \frac{\rho d_A \left( \bar{\Pi}_1(\lambda) (1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda) \Phi_P(\lambda) \bar{A} a_P (1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\lambda + d_L + a_Q \bar{Q} + \Phi_Q(\lambda) \left( a_Q \bar{L} - \rho d_A \bar{A} a_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)}
\end{aligned} \tag{C.12}$$

Box I.

$$\begin{aligned}
\Phi_Q(\lambda) \Phi_L(\lambda) &= \Phi_Q(\lambda) \frac{\rho d_A \left( \bar{\Pi}_1(\lambda) (1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda) \Phi_P(\lambda) \bar{A} a_P (1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\lambda + d_L + a_Q \bar{Q} + \Phi_Q(\lambda) \left( a_Q \bar{L} - \rho d_A \bar{A} a_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)} \\
&= \frac{\rho d_A \left( \bar{\Pi}_1(\lambda) (1 - \bar{\Pi}_2(\lambda)) - \Phi_E(\lambda) \Phi_P(\lambda) \bar{A} a_P (1 - \bar{\Pi}_2(\lambda)) \frac{\bar{\Pi}_1 - \bar{\Pi}_1(\lambda)}{\lambda} \right)}{\frac{\lambda + d_L + a_Q \bar{Q}}{\Phi_Q(\lambda)} + \left( a_Q \bar{L} - \rho d_A \bar{A} a_Q \bar{\Pi}_1 \frac{\bar{\Pi}_2 - \bar{\Pi}_2(\lambda)}{\lambda} \right)}
\end{aligned} \tag{C.17}$$

Box II.



**Fig. 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  $T_{JQ} = 1$ .

## 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 Appendices B.1 and C.1, it is easily verified that with constant maturation delays  $\bar{\Pi}'_1 = -a_P T_E \bar{\Pi}_1$  and  $\bar{\Pi}'_2 = -a_Q T_L \bar{\Pi}_2$ . Plugging into (C.19) yields with the notation  $\bar{\Gamma}_1(\bar{P}) = \bar{\Gamma}_1$  and  $\bar{\Gamma}_2(\bar{Q}) = \bar{\Gamma}_2$ ,

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

where we use  $\bar{E} = \rho d_A \bar{A} \bar{\Gamma}_1$ ,  $\bar{L} = \rho d_A \bar{A} \bar{\Pi}_1 \bar{\Gamma}_2$  and  $\rho \bar{\Pi}_1 \bar{\Pi}_2 = 1$  according to Eqs. (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 Eq. (A.3) that

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

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

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

where  $\gamma = (a_P \bar{P} + d_E) T_E$ . 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.

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