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Host coexistence in a model for two host–one parasitoid interactions

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Abstract Building from a continuous-time host–parasitoid model introduced by Murdoch et al. (Am Nat 129:263–282, 1987), we study the dynamics of a 2 host–parasitoid model assuming, for the sake of simplicity, that larval stages have a fixed duration. If each host is subjected to density-dependent mortality in its larval stage, we obtain explicit conditions for the existence of an equilibrium where the two host species coexist with the parasitoid. However, if host demography is density-independent, equilibrium coexistence is impossible. If at least one of the 1 host–parasitoid systems has an oscillatory dynamics (which happens under some parameter values), we found, through numerical bifurcation, that coexistence is favoured. Coexistence between the two hosts may occur along a periodic solution even without density-dependence. Models of this type may be relevant for the use of parasitoids as biocontrol agents of insect pests.

Keywords Host–parasitoid model · Species coexistence · Delay differential equations · Periodic solutions · Numerical bifurcation · Characteristic multipliers

Mathematics Subject Classification 92B05

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1 Introduction

Parasitoids are a widespread group of insects often employed as a tool for biological control, and thus have been subjected to many modelling efforts as in Getz and Mills (1996).

Many parasitoid species are generalist (Godfray 1994) that are capable of attacking different hosts species. Conversely, host species are often attacked by different parasitoids. Several modelling papers have addressed this latter phenomenon, which at first sight may appear in contrast with the competitive exclusion principle (Gause 1934; Chesson and Case 1986); indeed, Briggs et al. (1993) have been able to prove that two parasitoid species can coexist at equilibrium on a single host species, as long as they attack different host stages, and the length of each stage is sufficiently variable (see Pfab et al. 2017 for a more detailed analysis of their model).

On the other hand, very little attention has, to our knowledge, been paid to the interactions of one or more parasitoid species with multiple hosts species. Several models (Charnov 1976; Iwasa et al. 1984; Charnov and Stephens 1988; Janssen 1989) have indeed been devoted to the evolution of host choice by parasitoids; however, in this approach host densities are simply taken as given without considering the dynamics of species interactions. In this respect, the present analysis can therefore provide the background for coupling evolutionary and ecological dynamics.

The recent invasion from Eastern Asia of *Drosophila suzukii* Matsumura, spotted-wing fruit-fly, into Europe and North America (Calabria et al. 2012; Cini et al. 2014; Walsh et al. 2011) with the consequent economic losses (Goodhue et al. 2011) has revived the interest in understanding multi-hosts multi-parasitoids interactions and the evolution of host choice. In fact, its control through insecticides is problematic (Van Timmeren and Isaacs 2013) and the risk to leave significant residues of insecticides in the fruit is high.

While the introduction into Europe and North America of native parasitoids would require careful studies and a long protocol for authorizations, it has been found (Rossi Stacconi et al. 2015) that *D. suzukii* is attacked by several indigenous parasitoids of other *Drosophila* species. It is therefore important to understand the population dynamics of these parasitoids, as well as the potential evolution of host choice.

In order to simplify the problem, we limit ourselves to consider the case of a single parasitoid species attacking two host species. We develop a model based on the scheme proposed by Murdoch et al. (1987) (earlier by Nisbet and Gurney 1984 and generalised by Briggs 1993; Briggs et al. 1993) where time is continuous and delays (fixed or distributed) occur between host stages. To our knowledge, this model has never been extended to a two host species model.

In Sect. 2 we describe the model studied and discuss its assumptions. In Sect. 3 we compute the equilibria and their stability, and find the conditions for equilibrium coexistence of the two host species. In Sect. 4, we extend the analysis to the case where a one-host model exhibits attracting periodic solutions; the analysis of the stability with respect to the complete system of such periodic solutions requires the use of numerical methods recently developed to approximate the dominant multiplier(s) of linear delay differential equations (DDEs) with periodic coefficients (Breda et al. 2012); it is also necessary to approximate the periodic solutions (see, e.g., Engelborghs et al. 2001),

and to use a continuation algorithm to track them when varying model parameters. It turns out that the periodicity induced by host–parasitoid interactions makes it easier for more host species to coexist, up to the point that species can coexist even when no density-dependence exists and their densities are controlled only by the parasitoids. Finally, in Sect. 5 we discuss the implications and the limitations of the results obtained, while longer computations are left to appendices.

2 Model

We introduce a 2 host–parasitoid model based on those proposed by Murdoch et al. (1987) and by Briggs (1993). We assume that the life cycle of the hosts can be divided into three developmental stages: eggs E, larvae L and adults A. We assume that the two hosts considered do not compete and that intra-specific competition is present at the larval stage that, in absence of parasitoids, would lead the two host species to their carrying capacity.

We assume that adult parasitoids P can attack only the larval stage of the host (adult hosts and eggs are invulnerable to parasitism) and that they can lay a single egg inside the host. Juvenile parasitoids then develop inside the larvae using them as food and emerge from them after a fixed host-dependent time $T_{iP}, i = 1, 2$ (Briggs et al. 1993; Murdoch et al. 1987; Rossi Stacconi et al. 2015). For the sake of simplicity, we neglect many details (such as parasitoid encapsulation (Rossi Stacconi et al. 2015)) of host–parasitoid interactions, we assume that all stage durations are fixed (see Briggs et al. 1993; Pfab et al. 2017, for different assumptions) and we include the pupal stage within the larval one. Finally, we assume that density-dependence occurs only at the larval stage, through increased mortality due to intra-specific competition. An alternative assumption, namely density-dependence through reduced adult fecundity will be briefly discussed. Indeed, it is known that different dynamical patterns may arise depending on the stage at which population regulation occurs (De Roos et al. 2003).

Thus, the 2 host–parasitoid model is given by

$$\begin{aligned}
E_i'(t) &= R_{E_i}(t) - M_{E_i}(t) - d_{E_i} E_i(t) \\
L_i'(t) &= M_{E_i}(t) - M_{L_i}(t) - \alpha_i P(t) L_i(t) - d_{L_i}(L_i(t)) L_i(t) \\
A_i'(t) &= M_{L_i}(t) - d_{A_i} A_i(t) \\
P'(t) &= \sum_{i=1}^{2} \alpha_i P(t - T_{iP}) L_i(t - T_{iP}) s_{iP} - d_P P(t)
\end{aligned} \tag{1}$$

where

$$\begin{aligned}
R_{E_i}(t) &= \rho_i d_{A_i} A_i(t) \\
M_{E_i}(t) &= R_{E_i}(t - T_{E_i}) e^{-d_{E_i} T_{E_i}} \\
M_{L_i}(t) &= M_{E_i}(t - T_{L_i}) e^{-\int_{t-T_{L_i}}^{t} (\alpha_i P(y) + d_{L_i}(L_i(y)))dy}.
\end{aligned} \tag{2}$$

The host birth rate, $\beta_i = \rho_i d_{A_i}$ is written, following the parametrization by Murdoch et al. (1987), as the product between the mortality d_{A_i} and a parameter ρ_i that represents

Table 1 Parameters of model (1)

Symbol	Description
ρ_i	Average total fecundity of adults
d_{E_i}	Mortality of host eggs
$d_{L_i}(L_i)$	Mortality of host larvae $= \mu_{L_i} + \nu_{L_i} L_i$
μ_{L_i}	Constant background mortality of host larvae
ν_{L_i}	Density-dependent component of larvae mortality
d_{A_i}	Mortality of adult hosts
d_P	Mortality of adult parasitoids
α_i	Attack rate of adult parasitoids on host larvae
s_{iP}	Survival of juvenile parasitoids
T_{E_i}	Duration of egg host stage
T_{L_i}	Duration of larva host stage
T_{iP}	Duration of juvenile parasitoid stage

the mean number of eggs produced per adult lifetime. Host mortality $d_{A_i} = 1/T_{A_i}$ can then be seen as the turn-over speed of species i (T_{A_i} is the average duration of the adult host stage) while ρ_i is its reproductive potential.

The maturation rate from eggs to larvae, $M_{E_i}(t)$, represents all hosts recruited time T_{E_i} before and survived egg mortality. Similarly, the maturation rate from larvae to adults, $M_{L_i}(t)$, represents all eggs matured time T_{L_i} before that have survived both natural mortality and attack by parasitoids.
Finally, we suppose that

$$d_{L_i}(L_i(t)) = \mu_{L_i} + \nu_{L_i} L_i(t), \tag{3}$$

where μ_{L_i} is a constant background mortality and ν_{L_i} is the quantity for which the per capita mortality changes by adding a new individual.

All model parameters are described in Table 1.

As mentioned above, an alternative assumption is to have density dependence in adult fertility. In that case, d_{L_i} is assumed to be a constant, while the first equation in (2) is substituted by

$$R_{E_i}(t) = \rho_i d_{A_i} \psi_i(A_i(t)) A_i(t) \tag{4}$$

where $\psi_i(\cdot)$ are decreasing functions such that $\psi_i(0) = 1$ (this is just a normalization) and $\lim_{A\to\infty} \psi_i(A) = 0$.

3 Equilibria

We start by looking for equilibria with only one host species present together with the parasitoid: $\overline{Eq}1$, the equilibrium with only host 1, and $\overline{Eq}2$, with only host 2.

Let us find, for instance and without loss of generality, the equilibrium $\overline{Eq}1$. Setting $P' = 0$ in (1) and assuming P constant and different from zero, we obtain $\bar{L}_1 = \frac{d_P}{\alpha_1 s_{1P}}$. Once $\bar{L}_1$ is known, we set $A_1' = 0$ and arrive at

$$\rho_1 d_{A_1} A_1 e^{-d_{E_1} T_{E_1} - (\alpha_1 P + d_{L_1}(\bar{L}))T_{L_1}} - d_{A_1} A_1 = 0.$$

Assuming $A_1 \neq 0$, we can immediately find $\bar{P}_1$.
Similarly, setting first $L_1' = 0$, then $E_1' = 0$, we obtain $\bar{A}_1$ and $\bar{E}_1$.
Finally, the equilibrium when only host 1 is present, $\overline{Eq}1$, is given by

$$\begin{aligned}
\bar{E}_1 &= \frac{\rho_1 d_{A_1} \bar{A}_1 (1 - e^{-d_{E_1} T_{E_1}})}{d_{E_1}} \\
\bar{L}_1 &= \frac{d_P}{\alpha_1 s_{1P}} \\
\bar{A}_1 &= \frac{\left(\alpha_1 \bar{P}_1 + \mu_{L_1} + \nu_{L_1} \bar{L}_1\right) \bar{L}_1}{\rho_1 d_{A_1} e^{-d_{E_1} T_{E_1}} \left(1 - e^{-(\alpha_1 \bar{P}_1 + \mu_{L_1} + \nu_{L_1} \bar{L}_1) T_{L_1}}\right)} \\
\bar{P}_1 &= \frac{\ln(\rho_1) - d_{E_1} T_{E_1} - \left(\mu_{L_1} + \nu_{L_1} \bar{L}_1\right) T_{L_1}}{\alpha_1 T_{L_1}}.
\end{aligned} \tag{5}$$

In a similar way, we can find $\overline{Eq}2$, the equilibrium when only host 2 is present.

It is convenient to define $\hat{P}_i$ as the value of $\bar{P}_i$ when $\nu_{L_i} = 0$, i.e.,

$$\hat{P}_i = \frac{\ln(\rho_i) - d_{E_i} T_{E_i} - \mu_{L_i} T_{L_i}}{\alpha_i T_{L_i}}. \tag{6}$$

Note that $\bar{P}_i = \hat{P}_i - \frac{\nu_{L_i} \bar{L}_i}{\alpha_i}$, so that all the components of the equilibrium $\overline{Eq}i$ are positive if and only if

$$\hat{P}_i > \frac{\nu_{L_i} \bar{L}_i}{\alpha_i} \iff \rho_i \exp\left\{-\left(d_{E_i} T_{E_i} + \left(\mu_{L_i} + \frac{\nu_{L_i} d_P}{\alpha_i s_{iP}}\right) T_{L_i}\right)\right\} > 1. \tag{7}$$

In what follows, we will always assume that $\overline{Eq}i$ is positive for $i = 1, 2$.

Proposition 1 summarizes the outcome of the linearisation of the system at the equilibria when only one host is present.

Proposition 1 *Equilibria $\overline{Eq}1$ and $\overline{Eq}2$ are both unstable if and only if*

$$\begin{aligned}
\hat{P}_1 &< \hat{P}_2 + \frac{\nu_{L_1}}{\alpha_1} \bar{L}_1 \\
\hat{P}_2 &< \hat{P}_1 + \frac{\nu_{L_2}}{\alpha_2} \bar{L}_2.
\end{aligned} \tag{8}$$

Proof The outcome of the linearisation of (1) around equilibrium $\overline{Eq}1$ (5) can be reduced to the single equation

$$\begin{aligned} A_2'(t) &= \bar{M}_{L_2}(t) - d_{A_2}A_2(t) \\ &\approx M_{E_2}(t - T_{L_2})e^{-\int_{t-T_{L_2}}^{t}(\alpha_2\bar{P}_1+\mu_{L_2})dy} - d_{A_2}A_2(t) \\ &= \rho_2 d_{A_2}A_2(t - T_{E_2} - T_{L_2})e^{-d_{E_2}T_{E_2}}e^{-\mu_{L_2}T_{L_2}-\alpha_2 T_{L_2}\bar{P}_1} - d_{A_2}A_2(t). \end{aligned} \tag{9}$$

Thus (see, for instance, Smith 2011) A_2 grows exponentially if

$$\rho_2 e^{-d_{E_2}T_{E_2}-\mu_{L_2}T_{L_2}-\alpha_2 T_{L_2}\bar{P}_1} - 1 > 0,$$

i.e., if

$$\bar{P}_1 < \frac{\ln(\rho_2) - d_{E_2}T_{E_2} - \mu_{L_2}T_{L_2}}{\alpha_2 T_{L_2}} = \hat{P}_2 \tag{10}$$

while it decreases exponentially if the inequality is reversed.
In the same way, A_1 increases if

$$\bar{P}_2 < \hat{P}_1 \tag{11}$$

Using $\bar{P}_i = \hat{P}_i - \frac{\nu_{L_i}\bar{L}_i}{\alpha_i}$, the coexistence conditions (10) and (11) can be written as in (8). □

Condition (8) can be seen as a double invasibility condition that has often been considered to grant species coexistence (Chesson and Ellner 1989). Note, moreover, that it is independent of d_{A_i}.

Corollary 2 *If $\nu_{L_1} = \nu_{L_2} = 0$, it is impossible to have mutual invasibility of $\overline{Eq}1$ and $\overline{Eq}2$.*

Proof The two inequalities in (8) are incompatible if $\nu_{L_1} = \nu_{L_2} = 0$. □

Proposition 3 ensures the existence of an equilibrium where both the host species are present under density-dependence conditions when equilibria $\overline{Eq}1$ and $\overline{Eq}2$ are both unstable. Let us name this equilibrium $\overline{Eq}12$.

Proposition 3 *Equilibrium $\overline{Eq}12$ exists if and only if (8) holds.*

Proof An equilibrium where both the host species are present is given by setting equal to zero the right hand sides of all equations in (1). Thus, we obtain

$$\begin{cases} \rho_1 e^{-d_{E_1}T_{E_1}-(\alpha_1 P^* + d_{L_1}(L_1^*))T_{L_1}} = 1 \\ \rho_2 e^{-d_{E_2}T_{E_2}-(\alpha_2 P^* + d_{L_2}(L_2^*))T_{L_2}} = 1 \\ \alpha_1 L_1^* s_{1P} + \alpha_2 L_2^* s_{2P} - d_P = 0. \end{cases} \tag{12}$$

By solving (12), using the definitions (6), we have

$$\begin{cases} P^* = \hat{P}_1 - \frac{\nu_{L_1}}{\alpha_1}L_1^* \\ P^* = \hat{P}_2 - \frac{\nu_{L_2}}{\alpha_2}L_2^* \\ L_1^* = \hat{L}_1 - \frac{\alpha_2 s_{2P}}{\alpha_1 s_{1P}}L_2^*. \end{cases} \tag{13}$$

Since the two expressions for P^* have to be equal, we have

$$\hat{P}_1 - \frac{\nu_{L_1}}{\alpha_1} L_1^* = \hat{P}_2 - \frac{\nu_{L_2}}{\alpha_2} L_2^*.$$

This equation, together with the last of (13) is a linear system in the unknowns L_1^* and L_2^* that can be easily solved by simple algebraic calculations, yielding

$$\begin{aligned} L_1^* &= \alpha_1 \hat{L}_1 \left(\frac{\alpha_2(\hat{P}_1 - \hat{P}_2) + \nu_{L_2} \hat{L}_2}{\alpha_2 \nu_{L_1} \hat{L}_1 + \alpha_1 \nu_{L_2} \hat{L}_2} \right) \\ L_2^* &= \alpha_2 \hat{L}_2 \left(\frac{\alpha_1(\hat{P}_2 - \hat{P}_1) + \nu_{L_1} \hat{L}_1}{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1} \right) \\ P^* &= \frac{\alpha_1 \nu_{L_2} \hat{L}_2 \hat{P}_1 - \nu_{L_1} \nu_{L_2} \hat{L}_2 \hat{L}_1 + \alpha_2 \nu_{L_1} \hat{L}_1 \hat{P}_2}{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1}. \end{aligned} \tag{14}$$

The values of L_1^* and L_2^* are both positive if and only if (8) holds. □

Remark 1 Using (8) in (14), we obtain

$$L_1^* < \hat{L}_1 \left(\frac{\alpha_2 \nu_{L_1} \hat{L}_1 + \alpha_1 \nu_{L_2} \hat{L}_2}{\alpha_2 \nu_{L_1} \hat{L}_1 + \alpha_1 \nu_{L_2} \hat{L}_2} \right) = \hat{L}_1.$$

Similarly

$$L_2^* < \hat{L}_2 \left(\frac{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1}{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1} \right) = \hat{L}_2.$$

In other words, the equilibrium value for each host species in presence of the other is always lower than in its absence. Hence, the presence of the common parasitoid always causes an indirect competition between the two species.

As for the parasitoid density at equilibrium, using the relation between $\hat{P}_i$ and $\bar{P}_i$, we can rewrite

$$P^* = \frac{\alpha_1 \nu_{L_2} \hat{L}_2 \bar{P}_1 + \alpha_2 \nu_{L_1} \hat{L}_1 \hat{P}_2}{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1}$$

showing that P^* is a weighted mean between $\bar{P}_1$ and $\hat{P}_2$. Symmetrically, one can also write

$$P^* = \frac{\alpha_1 \nu_{L_2} \hat{L}_2 \hat{P}_1 + \alpha_2 \nu_{L_1} \hat{L}_1 \bar{P}_2}{\alpha_1 \nu_{L_2} \hat{L}_2 + \alpha_2 \nu_{L_1} \hat{L}_1}$$

showing that P^* is a weighted mean between $\hat{P}_1$ and $\bar{P}_2$.

If, as often will be the case, $\min\{\hat{P}_1, \hat{P}_2\} \geq \max\{\bar{P}_1, \bar{P}_2\}$, it follows that equilibrium parasitoid density in presence of both hosts is higher than with either alone, but we cannot prove that this intuitive property always holds.

In any case, the above computation show that P^* is always positive, as required.

In Appendix 1 we analyse the 1-host 1–parasitoid equilibria under the assumption of density-dependent adult fecundity. It turns out that the model is more complex, since, depending on the function $\psi(A)$, backward bifurcations of the host-only equilibrium can occur, giving rise, for some parameter values, to two equilibria where the host coexists with the parasitoid. Moreover, there is no simple expression for the equilibria, so that the instability conditions (10) and (11) (that hold in case of density-dependent adult fecundity, too) cannot be transformed in simple conditions like (8).

Since the focus of this manuscript is on host coexistence, especially when intrinsic periodicity arises, we limit the analysis in the following Sections to the simplest situation, i.e., when density dependence acts through larval competition.

4 Invasibility under periodic conditions

Conditions for invasibility and host coexistence may change if periodic solutions are considered. Indeed, it has been shown by Murdoch et al. (1987) that (5) can be destabilized via Hopf bifurcation with the emergence of a stable periodic solution. In particular, Murdoch et al. (1987) show that this happens when the adult stage is infinitesimally short ($d_A \to \infty$). Thus, in order to see whether the double invasibility condition holds, it becomes necessary to study the stability of periodic solutions with only one host present (Metz et al. 1992).

The complexity of the proposed model hinders such a general achievement with analytical means. Resorting to linearisation leads to rather cumbersome characteristic equations whose analysis, in general, is unattainable. However, the recent literature on DDEs furnishes efficient numerical routines to tackle the several tasks required in this regard. In particular, in this section we make use of four reliable tools, namely:

- M1 the method in Breda et al. (2005) to approximate the rightmost eigenvalue(s) of the linearisation around given equilibria;
- M2 the method in Breda et al. (2012) to approximate the dominant multiplier(s) of the linearisation around given periodic orbits;
- M3 (an adaptation of) the method in Engelborghs et al. (2001) to compute periodic solutions of non-linear problems;
- M4 the Matlab built-in function `dde23` to integrate in time Cauchy problems for non-linear equations, see Shampine and Thompson (2001).

The four methods are often combined in a framework of parameter continuation, i.e., results for a certain parameter value are obtained starting from results previously computed for a different but close parameter value. Aside, note that an updated and complete presentation of M1 and M2 can be found in Breda et al. (2015), with user-friendly and freely available Matlab codes.

Table 2 Parameter values used in the computations. In these it is always assumed that the two hosts are identical except for the adult host mortality d_A and the fecundity ρ

Parameter	d_{E_i}	μ_{L_i}	ν_{L_i}	s_{iP}	α_i	T_{E_i}	T_{L_i}	T_{iP}	d_P
Value	0.2	0.1	0.1	1	1	1	1	1	1.1

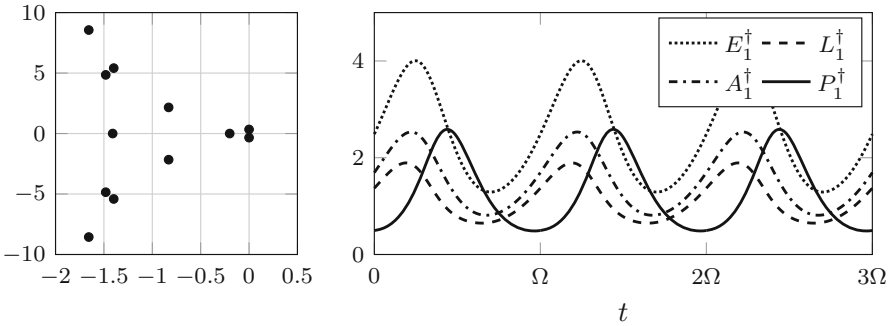

Fig. 1 Eigenvalues at Hopf bifurcation for $d_{A_1} = d_{HB_1} \approx 0.3089$ and $\rho_1 = 5$ (*left panel*); the periodic solution for $d_{A_1} = 0.35$ and $\rho_1 = 5$ (*right panel*) with host 1, $\Omega \approx 18.5938$. All other parameter values are as in Table 2

In order to have a model with a small number of parameters, we let only parameters related to fecundity and adult mortality of the two hosts vary, i.e., ρ_1, ρ_2, d_{A_1} and d_{A_2}. All the other parameters are kept fixed at the values listed in Table 2.

The first goal is to see when 1-host periodic solutions are possible, with say host 1 without loss of generality. To this aim, we fix, e.g., $\rho_1 = 5$, and consider the non-trivial equilibrium $\overline{Eq}1$ of (1) varying d_{A_1}. Based on the use of M1, we found that the equilibrium is asymptotically stable as far as $d_{A_1} < d_{HB_1}$ with $d_{HB_1} \approx 0.3089$. At this value the associated rightmost complex-conjugate pair of eigenvalues crosses the imaginary axis left-to-right in a Hopf bifurcation, Fig. 1 left. The equilibrium loses stability and a periodic solution arises. The latter is computed as follows. M3 is applied for d_{A_1} slightly above d_{HB_1}, with initial guess the equilibrium itself. Indeed, the method converges to a periodic solution, with rather small amplitude. To obtain a more pronounced periodic behaviour, we increase d_{A_1} incrementally, each step starting the solution from the previously computed one. This way we are able to compute a distinct periodic solution for $d_{A_1} = 0.35$ with period $\Omega \approx 18.5938$, Fig. 1 right.

Such solution, call it $(E_1^\dagger, L_1^\dagger, A_1^\dagger, P_1^\dagger)$, is confirmed by using M4: integration forward in time leaves it unchanged.

The next step is to see whether host 2 can invade under the above determined periodic conditions. So we keep $\rho_1 = 5$ and $d_{A_1} = 0.35$ fixed and linearise (1) around $(E_1^\dagger, L_1^\dagger, A_1^\dagger, 0, 0, 0, P_1^\dagger)$. It is not difficult to realise that the stability of this periodic solution with only host 1 can be inferred by analysing only the linearised equation for host 2 adults, i.e.,

$$A_2'(t) = \rho_2 d_{A_2} A_2(t - T_{E_2} - T_{L_2}) e^{-d_{E_2} T_{E_2}} e^{-\mu_{L_2} T_{L_2} - \alpha_2 \int_{t-T_{L_2}}^{t} P^\dagger(y)dy} - d_{A_2} A_2(t). \tag{15}$$

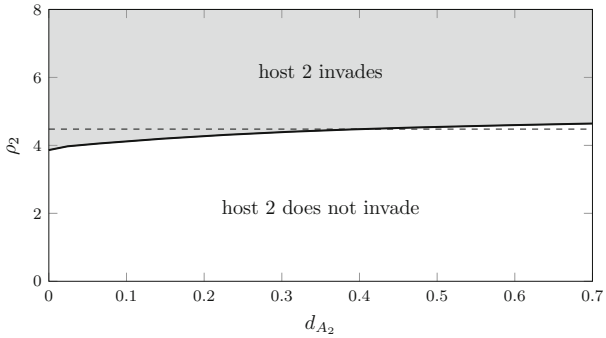

Fig. 2 Values of (d_{A_2}, ρ_2) for which the periodic solution $(E_1^\dagger, L_1^\dagger, A_1^\dagger, 0, 0, 0, P_1^\dagger)$ is stable or unstable for system (1). Above the *thick line*, it is unstable and host 2 can invade; below it is stable. The *straight dashed line* represents instead the value $\rho_1 e^{-\frac{v_L d_P T_L}{\alpha s_P}}$ that is obtained from (8) for $d_{A_1} < d_{HB_1}$. Parameter values are $\rho_1 = 5$, $d_{A_1} = 0.35$, while all others are from Table 2

This is a linear non autonomous DDE with periodic coefficients, periodicity essentially due to the behaviour of the parasitoid. According to Floquet theory (see, e.g., Hale and Verduyn Lunel 1993), the stability of its null solution depends on whether the dominant multiplier lies inside or outside the unit circle in the complex plane. Thus we compute the modulus of this quantity by using M2 for varying ρ_2 and d_{A_2}. In this way we construct a surface $\mathbb{R}^2 \to \mathbb{R}$, whose curve of level 1 divides the (d_{A_2}, ρ_2)-plane into stable and unstable regions.

Figure 2 shows this boundary (thick line), obtained with Matlab `contour`.

A simple verification lets us conclude that host 2 can invade when (d_{A_2}, ρ_2) is above this curve, otherwise coexistence is not possible. For comparison, we add in the same figure a straight (dashed) line that represents the first invasibility condition in (8) in the case when $\overline{Eq}1$ is stable, i.e., with the value of d_{A_1} below d_{HB_1}. If the equilibrium $\overline{Eq}1$ is stable, invasion of host 2 would be possible for ρ_2 above the line and would not depend on the value of d_{A_2}. We then see that the invasibility of the equilibrium $\overline{Eq}1$ and the presence of the periodic solution $(E_1^\dagger, L_1^\dagger, A_1^\dagger, 0, 0, 0, P_1^\dagger)$ make the invasion of host 2 easier if d_{A_2} is small and harder if d_{A_2} is large.

The effect of fluctuations on host coexistence can be illustrated more specifically in Fig. 3.

In it we study both invasibility conditions in the (d_A, ρ_2)-plane having assumed $d_{A_1} = d_{A_2} =: d_A$ while keeping $\rho_1 = 5$ fixed. The shaded region of mutual invasibility is obtained as follows. The straight lines for lower values of d_A account for (8), i.e.,

$$\rho_1 e^{-\frac{v_L d_P T_L}{\alpha s_P}} < \rho_2 < \rho_1 e^{\frac{v_L d_P T_L}{\alpha s_P}}.$$

The lower straight line ends at the Hopf bifurcation value d_{HB_1} as previously determined. For greater values of d_A we repeat the same arguments as above: we compute the periodic solution in absence of host 2 and we study its local stability by searching for the value of ρ_2 giving the dominant multiplier on the unit circle for (15). By repeating the procedure over all values of $d_A > d_{HB_1}$, we obtain the lower curve of

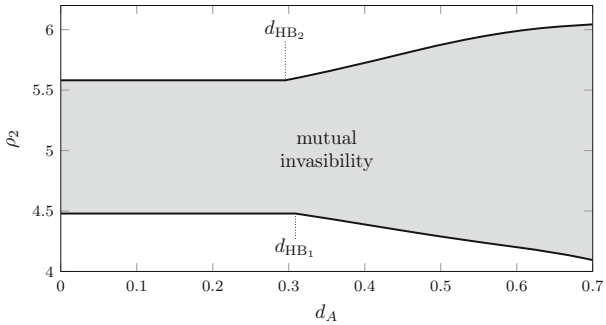

Fig. 3 Invasibility regions in the parameters $(d_A = d_{A_1} = d_{A_2}, \rho_2)$, while $\rho_1 = 5$ and all other parameters are as in Table 2. Host 2 can invade the attractor where host 1 coexists with the parasitoid when ρ_2 is above the *lower curve*; host 1 can invade the attractor where host 2 coexists with the parasitoid when ρ_2 is below the *upper curve*. For $d_A > d_{HB}$, the *lower curve* is a decreasing function of d_A, while the *upper curve* is an increasing function of d_A

Fig. 3. As before, host 2 can invade when introduced in a system where host 1 coexists with the parasitoid, if the parameter values are above the curve so computed; it will be excluded if they are below.

For the increasing part of the upper bound of the shaded region, we repeat the reasoning by exchanging the roles of the two hosts. More precisely, for a fine mesh of points in that region of the (d_A, ρ_2)-plane we compute a periodic solution of (1) in absence of host 1.

For each point, we linearise the equation of host 1 around the computed periodic solution and determine the dominant multiplier. The curve is then obtained by selecting those points with dominant multiplier on the unit circle. Notice that this curve joins the upper straight line at a value $d_A = d_{HB_2} < d_{HB_1}$. Indeed, this is correct since $\rho_2 > 5$ and hence the Hopf bifurcation for host 2 (in absence of host 1) occurs at a lower value of d_A than that of host 1 (in absence of host 2), which was found for $\rho_1 = 5$.

Figure 3 shows clearly that, with larger values of d_A that cause each host alone to fluctuate with the parasitoid, the region in (ρ_1, ρ_2) where double invasibility conditions are satisfied, presumably leading to coexistence, becomes wider.

More surprisingly, use of this procedure shows that, when periodic solutions arise, double invasibility (and thus presumably coexistence) is possible even without density-dependence, a case where it has been seen (Corollary 2) that double invasibility of equilibria is impossible.

In this case, it is easy to show that, if $d_{A_1} = d_{A_2}$, host 2 will invade a periodic solution with only host 1 if $\rho_1 > \rho_2$ and vice versa; double invasibility is then impossible when $d_{A_2} = d_{A_1}$. In order to explore possible coexistence, we fix therefore the values of ρ_1 and d_{A_1} and let ρ_2 and d_{A_2} vary. Precisely, we set $\rho_1 = 5, d_{A_1} = 0.3$ and $\nu_{L_1} = \nu_{L_2} = 0$, and repeat the procedure used for Fig. 2 to construct the solid thick curve in Figure 4, below which host 1 excludes host 2 and coexistence is not possible.

The dashed thick curve represents the condition for invasibility of the host 2 periodic solution (or equilibrium). For larger values of d_{A_2}, this second curve is computed by

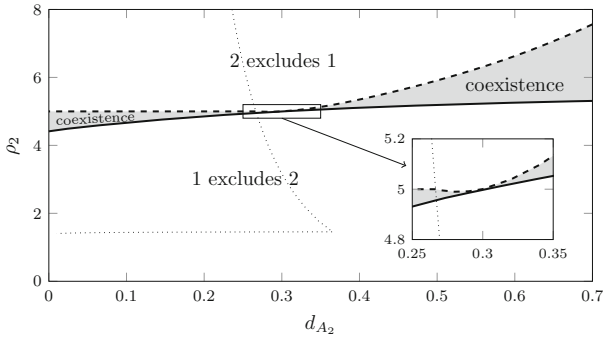

Fig. 4 Invasibility regions in the parameters (d_{A_2}, ρ_2), while $\rho_1 = 5$, $d_{A_1} = 0.3$, $\nu_{L_1} = \nu_{L_2} = 0$ and all other parameters, except ν_{L_i} are as in Table 2. Above the *solid thick curve* host 2 can invade the attractor where host 1 coexists with the parasitoid; below the *dashed thick curve* host 1 can invade the attractor where host 2 coexists with the parasitoid. The *dotted thin curve* is the bifurcation curve of the equilibrium $\overline{Eq}2$: the *right curve part* is the locus of the Hopf bifurcations leading to periodic solutions; the *bottom segment* is the locus of transcritical bifurcation with the trivial equilibrium

exchanging the roles of the two hosts, i.e., by following the same procedure used to obtain the upper bound of the dashed region of Fig. 3. For lower values of d_{A_2}, instead, there cannot be periodic solutions of (1) without host 1, since d_{A_2} is below the Hopf bifurcation point. To the left of this value, the dashed thick curve corresponds to the straight line obtained from (8). Indeed, the dotted thin curve is the bifurcation curve of the equilibrium $\overline{Eq}2$: the right curve part is the locus of the Hopf bifurcations leading to periodic solutions; the bottom segment is the locus of transcritical bifurcation with the trivial equilibrium. Both segments are obtained by using M1: the former searching for the rightmost eigenvalue in zero, the second for the rightmost conjugate pair on the imaginary axis.

Double invasibility conditions hold when (ρ_2, d_{A_2}) belongs to the shaded region enclosed between the two curves. We then see that, thanks to the periodicity induced by instability of the single-species equilibria, coexistence becomes possible even when both host populations are regulated by the parasitoid, in absence of density-dependence.

In Appendices 2 and 3 we give a heuristic explanation of host coexistence without density-dependence, using an approximation of the threshold coefficient for scalar linear periodic delay-differential equations (Chen and Wu 2012).

5 Discussion

In this work we have provided the first, as far as we know, analysis of a continuous-time model for a system consisting of a parasitoid species attacking two different host species.

The model is built on the framework proposed by Murdoch et al. (1987) assuming that developmental time in all stages is fixed, while other authors (e.g., Briggs et al. 1993) have allowed for distributed lengths of developmental stages, and have shown

that such an assumption is crucial for the possibility of equilibrium coexistence of several parasitoid species on a single host species.

The other assumption used is that the two host species do not compete directly but are regulated by independent resources, acting through a density-dependent mortality in the larval stage. Under this assumption, it is possible to find an explicit condition for the existence of an equilibrium where both host species coexist with the parasitoid. This condition is equivalent, as it often occurs in population models, to the double invasibility condition, e.g., that both equilibria with a single host species are unstable relatively to the invasion of the other host species. Although the two host species do not compete directly, they are subject to apparent competition (see e.g. Holt 1977; Holt and Lawton 1993) through the shared parasitoid.

In the special case without density-dependence in the hosts, the condition for coexistence is never satisfied; thus, it would appear that necessarily one host species will exclude the other. When host regulation occurs only because of the parasitoid, the species more strongly regulated by the parasitoid will get extinct, because the parasitoid will be able to reach even higher densities at which the host species with a weaker regulation gets under control.

However, it is well known that host–parasitoid systems can exhibit cycles, as usual in systems of predator-prey type, but more easily so, because of the delays built in the stage structure. The previous analysis holds if each system with a single host tends to an equilibrium, but becomes irrelevant when a single host–parasitoid system converges to a periodic solution. In this case, in order to assess the double invasibility condition, it is necessary to analyse the stability of the periodic solution in the complete system (Metz et al. 1992).

While finding explicit conditions for the stability of periodic solutions in systems of delay-differential equations is probably hopeless (it is generally impossible already in systems of two ordinary differential equations), recent advancements in the methods for the approximation of multipliers of the monodromy operator of linear delay-differential equations with periodic coefficients provide a fundamental tool for being able to numerically study the stability of a periodic solution. These methods have been coupled with a method to approximate periodic solutions of such systems, and to a continuation algorithm that allows for efficiently tracking the periodic solutions as a parameter is varied, and applied to the 2 host–parasitoid system in some cases that appear biologically significant.

A discussion of the results that have been obtained is that conditions for invasibility and host coexistence can be favoured by considering periodic solutions, where periodicity is due to the behaviour of the parasitoid and is not forced from the outside. In fact, periodicity favours host coexistence, up to the extreme case without density-dependence: even then, if at least one of the single host–parasitoid systems converges to a periodic solution, coexistence of the two hosts is possible, albeit under rather stringent conditions on the parameters. Li and Smith (2003) found that coexistence of multiple host species and multiple parasitoid species needs existence of a periodic solution, while Murdoch et al. (1987) discussed instead this possibility for an infinitesimally short invulnerable adult stage and constant fecundity.

It has been known for several decades, since the seminal works by De Mottoni and Schiaffino (1981) and by Cushing (1976) that coexistence of competitors is easier if the

environment fluctuates periodically (see also Smith and Waltman 1995). This system is different, in that periodicity is not forced from outside but is generated intrinsically by host–parasitoid interactions. It is worthwhile noticing that the effect is the same; it can be said that fluctuations in one host–parasitoid system improve the chances of a second host species to coexist.

A similar phenomenon has been proved to occur in predator-prey systems (Hsu et al. 1978; Armstrong and McGehee 1980): two predator species cannot coexist on a single prey species at equilibrium, but can coexist along a periodic solution, that emerges because of the periodicity generated by one prey-predator system. The situation here is analogous except that the coexistence occurs between two host species (corresponding to prey) and one parasitoid (corresponding to predator). In simple predator-prey models, it is not possible to obtain coexistence of two prey species with a common predator, unless some type of density-dependence is assumed for the two species. Indeed, in the prototype predator-prey system without density-dependence (i.e., the classical Volterra system with neutral cycles) a simple computation shows that it is impossible to satisfy the double invasibility. All other models that we know of (for instance, those examined by Chesson and Kuang (2008) reviewing the interactions between competition and predation) assume that each basal species has a carrying capacity. In this sense, host–parasitoid systems based on delay-differential equations are more stable than predator-prey systems and may be more suitable for examining general ecological principles. Moreover, the present model is simple enough to allow for a quantification of the degree of density-dependence necessary for coexistence both at equilibrium and when periodicity arises.

A specific feature of this model (that makes easier its analysis) is that the stage attacked by parasitoids is exactly the same at which density-dependence occurs. It would be interesting studying how the results change under different assumptions, for instance if density-dependence acts through reduced adult fecundity. The preliminary analysis presented in Appendix 1 shows that the structure of equilibria is definitely more complex, and might give rise to different features.

In the present model, it is assumed that there is no dependence of attack rate on parasitoid density but it is well known (May and Hassell 1981; Kakehashi et al. 1984; Godfray and Waage 1991) that if attack rates are density-dependent, results on coexistence and the effect on host abundance can be altered. Moreover, consumer species adaptively adjust their consumption behaviour when they are in presence of more host species (Murdoch 1969; Murdoch and Oaten 1975; May 1977; Abrams 1987; Tregenza et al. 1996). Several authors (Charnov 1976; Iwasa et al. 1984; Janssen 1989) have studied optimal host choice by parasitoids, but, to our knowledge, only Abrams and Kawecki (1998) studied parasitoid trade-off in its ability to exploit two different hosts by coupling evolutionary and population dynamics. They found that adaptive behaviour and evolution frequently destabilize population dynamics and increase the difference between host densities. Their analysis was however based on a discrete-time host–parasitoid model. We believe that the present analysis yields a background to be able to apply adaptive dynamics methods to a continuous-time host–parasitoid model.

In order to be able to apply these results to a specific system, for instance the parasitoids of *Drosophila* spp., it would be necessary to add many details to the model.

There are several indigenous species of parasitoids (Rossi Stacconi et al. 2015) of *D. melanogaster* that attack also *D. suzukii*, some of which (e.g., *Leptopilina heterotoma*) are larval parasitoids, while others (especially *Pachycrepoideus vindemiae*) attack the pupal stage. Applying this model to the existing data necessarily requires extending the model to more parasitoid species, and adding more stages to hosts' life cycle. Moreover, it would be necessary to include seasonal (and perhaps stochastic) changes in climate (and thus in demographic rates), as well as in resource availability for hosts.

Despite these limitations, we believe that the analysis of models like the ones presented in this work will be relevant for modelling control strategies for *D. suzukii* based on native parasitoids of indigenous fruit flies.

Acknowledgements We thank Gianfranco Anfora and Valerio Rossi Stacconi for providing many useful information about parasitoids of *Drosophila* spp. and Stefano Maset for a useful discussion about numerically computing periodic solutions of DDEs. We thank two anonymous reviewers for useful suggestions.

Appendix 1: Equilibria for the 1 host–parasitoid model with density-dependent fecundity

We analyse here the model in which intra-specific host competition affects adult fecundity, perhaps because of competition for egg-lying sites. Precisely we consider the following modification of (1)–(2):

$$\begin{aligned} E'(t) &= R_E(t) - M_E(t) - d_E E(t) \\ L'(t) &= M_E(t) - M_L(t) - \alpha P(t)L(t) - d_L L(t) \\ A'(t) &= M_L(t) - d_A A(t) \\ P'(t) &= \alpha P(t-T_P)L(t-T_P)s_P - d_P P(t) \end{aligned} \tag{16}$$

where

$$\begin{aligned} R_E(t) &= \rho d_A \psi(A(t))A(t) \\ M_E(t) &= R_E(t-T_E)e^{-d_E T_E} \\ M_L(t) &= M_E(t-T_L)e^{-\int_{t-T_L}^{t}(\alpha P(y)+d_L)dy}. \end{aligned} \tag{17}$$

where $\psi(\cdot)$ is a decreasing function such that $\psi(0) = 1$ (this is just a normalization) and $\lim_{A\to\infty} \psi(A) = 0$.

Let us look for equilibria of (16)–(17). It is easy to see that there may be an equilibrium $E_0 = (E_K, L_K, A_K, 0)$ without parasitoids where

$$\rho\psi(A_K)e^{-(d_E T_E + d_L T_L)} = 1. \tag{18}$$

A necessary and sufficient condition for (18) to have a positive solution is

$$\rho e^{-(d_E T_E + d_L T_L)} > 1. \tag{19}$$

In what follows, we will always assume that (19) holds.

Then the other components are obtained setting $L' = 0$ and then $E' = 0$ and are

$$L_K = \frac{d_A}{d_L} A_K \left(e^{d_L T_L} - 1\right) \qquad E_K = \frac{d_A}{d_E} A_K \left(e^{d_E T_E} - 1\right) e^{d_L T_L}.$$

We now look for equilibria $(\bar{E}, \bar{L}, \bar{A}, \bar{P})$ with all positive components. Setting $P' = 0$, one immediately obtains

$$\bar{L} = \frac{d_P}{\alpha s_P} \tag{20}$$

as in (5). Equations (17) immediately yield

$$\begin{aligned} R_E &= s\rho d_A \bar{A}\psi(\bar{A}), \quad M_E = R_E e^{-d_E T_E}, \\ M_L &= M_E e^{-(\alpha\bar{P}+d_L)T_L} = R_E e^{-d_E T_E} e^{-(\alpha\bar{P}+d_L)T_L}. \end{aligned} \tag{21}$$

Setting $A' = 0$ yields $M_L = d_A \bar{A}$; hence using (21)

$$\rho d_A \bar{A}\psi(\bar{A}) e^{-d_E T_E} e^{-(\alpha\bar{P}+d_L)T_L} = d_A \bar{A} \iff \rho\psi(\bar{A}) e^{-d_E T_E} e^{-(\alpha\bar{P}+d_L)T_L} = 1. \tag{22}$$

As the expression on the left hand side of (22) is decreasing both in $\bar{A}$ and in $\bar{P}$ a necessary condition to find a solution of (22) is (19). From (22), we can solve for $\bar{P}$ in function of $\bar{A}$ as

$$\bar{P} = \frac{\log(\rho\psi(\bar{A})) - d_E T_E - d_L T_L}{\alpha T_L}. \tag{23}$$

Setting $L' = 0$ then yields

$$M_E \left(1 - e^{-(\alpha\bar{P}+d_L)T_L}\right) = (\alpha\bar{P} + d_L)\bar{L}.$$

Substituting (17) and remembering that $\bar{L}$ is known and $\bar{P}$ is given by (23), one arrives at

$$\rho d_A \bar{A}\psi(\bar{A}) e^{-d_E T_E} \left(1 - e^{-(\alpha\bar{P}+d_L)T_L}\right) = (\alpha\bar{P} + d_L)\bar{L}. \tag{24}$$

Now, using (22) in (24), we obtain

$$d_A \bar{A} \left(e^{(\alpha\bar{P}+d_L)T_L} - 1\right) = (\alpha\bar{P} + d_L)\bar{L}. \tag{25}$$

This can be written as

$$c\bar{A} = G(\bar{A}) \quad \text{with} \quad c = \frac{d_A T_L}{\bar{L}}, \quad G(A) = \frac{\log(m(A))}{m(A) - 1}, \quad m(A) = \rho\psi(A) e^{-d_E T_E}. \tag{26}$$

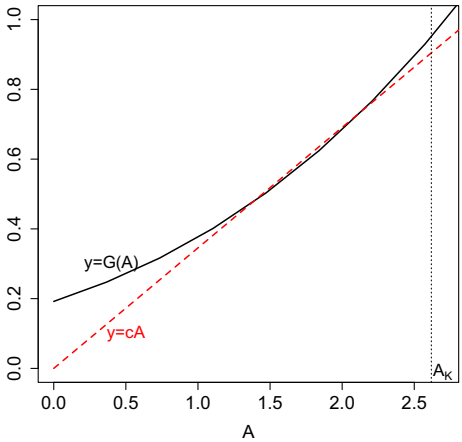

Fig. 5 The functions cA and $G(A)$ with $\psi(A) = e^{-A}$. Equilibria are found at the intersections $\bar{A}$ of the two curves as long as $\bar{A} < A_K$. Parameter values are $\rho = 2e^e$, $T_E = T_L = 1$, $s_P = 1/(e-1)$, $d_P = e-1$, $\alpha = 1$, $d_E = \log(2)$, $d_L = 0.1$, $d_A = 1.02$

From (23), we see that $\alpha T_L \bar{P} = \log(m(\bar{A})) - d_L T_L$. Since this quantity has to be positive we are interested in solutions of (26) such that $\log(m(\bar{A})) > d_L T_L$, i.e. $\rho\psi(\bar{A})e^{-(d_E T_E + d_L T_L)} > 1$, hence $\bar{A} < A_K$.

Thus we look for solutions of (26) in $(0, A_K)$. At $A = 0$, the left hand side is equal to 0, while $G(0) > 0$. On the other hand, $G(A_K) = \dfrac{\log(m(A_K))}{m(A_K) - 1} = \frac{d_L T_L}{e^{d_L T_L} - 1}$. If the left hand side at $A = A_K$ is larger than $G(A_K)$, then a positive equilibrium exists.

Performing the computations, we have thus obtained:
if $\frac{d_A T_L}{\bar{L}} A_K > \frac{d_L T_L}{e^{d_L T_L} - 1}$, i.e., $\frac{d_A}{d_L} A_K \left(e^{d_L T_L} - 1\right) > \bar{L}$, then there exists a positive equilibrium.

Note that, recalling the definition of L_K, this condition can be written as $L_K > \bar{L}$, i.e., the density of larvae at the equilibrium without parasitoids must be larger than the density at which parasitoid density remains constant.

We cannot say more than this without making specific assumptions on the function $\psi(\cdot)$. For instance, if $\psi(A) = (1 + \nu A)^{-1}$, then it is possible to show that $G(A)$ is a concave function, so that there is a unique solution in $(0, A_K)$ of (26) if $L_K > \bar{L}$ and no solutions if $L_K \leq \bar{L}$.

On the other hand, for $\psi(A) = e^{-A}$, $G(A)$ is a convex function. Thus, if $L_K > \bar{L}$, there is a unique solution in $(0, A_K)$ of (26); it is possible that solutions occur also when $L_K < \bar{L}$.

An example with two intersections among cA and $G(A)$ is shown in Fig. 5 . With the parameter values used $A_K = e - 0.1 \approx 2.62$, $L_K \approx 1.07$, $\bar{L} = (e-1)^2 \approx 2.95$. However, there exist two equilibria

$$(\bar{E}_1, \bar{L}, \bar{A}_1, \bar{P}_1) \approx (2.22, 2.95, 1.36, 3.97)$$
$$(\bar{E}_2, \bar{L}, \bar{A}_2, \bar{P}_2) \approx (3.50, 2.95, 2.15, 3.18).$$

Appendix 2: Approximation of dominant eigenvalue of monodromy operator for a delay-differential equation

Several authors have studied the linear delay equation with periodic coefficients (see e.g. Chen and Wu 2012)

$$x'(t) = \alpha\,(\beta f(t)x(t-\tau) - x(t)) \tag{27}$$

Assuming that α is a positive constant and f a positive 1-periodic function, Chen and Wu (2012) have shown that there exists a $\beta^* \in (0, \infty)$ such that the zero solution is stable if $\beta < \beta^*$ and unstable if $\beta > \beta^*$. At $\beta = \beta^*$ the dominant eigenvalue of the monodromy operator will be 1.

Here we show how to approximate β^* by assuming that f is a 1-periodic sinusoidal of small amplitude. In order to make explicit computations, assume

$$f(t) = 1 + \varepsilon\cos(2\pi t)$$

and expand in order of ε.
Hence, the problem is to find β such that

$$x'(t) = \alpha\,(\beta(1+\varepsilon\cos(2\pi t))x(t-\tau) - x(t)) \tag{28}$$

has 1-periodic non-trivial solutions.
Expand the periodic solution $x(t)$ and the value β as

$$\begin{aligned} x(t) &= x_0(t) + \varepsilon x_1(t) + \varepsilon^2 x_2(t) + \cdots \\ \beta &= \beta_0 + \varepsilon\beta_1 + \varepsilon^2\beta_2 + \cdots \end{aligned} \tag{29}$$

At zero order, the solution is $\beta_0 = 1$, $x_0(t) \equiv c$, that we set equal to 1.
At first order

$$x_1'(t) = \alpha\,(\beta_1 + \cos(2\pi t) + x_1(t-\tau) - x_1(t)) \tag{30}$$

Assuming that $x_1(t)$ is 1-periodic, we immediately have

$$0 = \int_0^1 x_1'(t)\,dt = \alpha\left(\beta_1 + \int_0^1 \cos(2\pi t)\,dt + \int_0^1 x_1(t-\tau)\,dt - \int_0^1 x_1(t)\,dt\right) \tag{31}$$

As the integral of cosine is zero and $\int_0^1 x_1(t-\tau)\,dt = \int_0^1 x_1(t)\,dt$, $\beta_1 = 0$.
Thus, Eq. (30) becomes

$$x_1'(t) = \alpha\,(\cos(2\pi t) + x_1(t-\tau) - x_1(t)) \tag{32}$$

for which we search for a periodic solution.

If we assume that

$$x_1(t) = K\cos(2\pi t) + L\sin(2\pi t) \tag{33}$$

we can easily compute $x_1'(t)$ and $x_1(t-\tau)$. Substituting the expressions in (32), we obtain

$$\cos(2\pi t)(2\pi L - \alpha - \alpha AK + \alpha BL + \alpha K) = \sin(2\pi t)(2\pi K + \alpha BK + \alpha AL - \alpha L) \tag{34}$$

where

$$A = \cos(2\pi\tau) \quad \text{and} \quad B = \sin(2\pi\tau).$$

From (34) we get the system in K and L,

$$\begin{cases} K(2\pi + \alpha B) - L\alpha(1-A) = 0 \\ K\alpha(1-A) + L(2\pi + \alpha B) = \alpha \end{cases} \tag{35}$$

whose solution is

$$\begin{cases} K = \frac{\alpha^2(1-A)}{(2\pi+\alpha B)^2+\alpha^2(1-A)^2} \\ L = \frac{\alpha(2\pi+\alpha B)}{(2\pi+\alpha B)^2+\alpha^2(1-A)^2}. \end{cases} \tag{36}$$

Using (33) with (36) the required periodic solution of (32) is easily obtained.
By considering the second order of (28), we obtain, as $\beta_1 = 0$,

$$x_2'(t) = \alpha(\beta_2 + \cos(2\pi t)x_1(t-\tau) + x_2(t-\tau) - x_2(t)). \tag{37}$$

By assuming $x_2(t)$ is a 1-periodic solution, and using the fact that $\int_0^1 x_2(t-\tau)\,dt = \int_0^1 x_2(t)\,dt$, it is possible to obtain

$$0 = \int_0^1 x_2'(t)\,dt = \alpha\left(\beta_2 + \int_0^1 \cos(2\pi t)x_1(t-\tau)\,dt\right), \tag{38}$$

i.e.,

$$\begin{aligned} \beta_2 = -\int_0^1 \cos(2\pi t)x_1(t-\tau)\,dt = -K\int_0^1 \cos(2\pi t)\cos(2\pi(t-\tau))\,dt \\ -L\int_0^1 \cos(2\pi t)\sin(2\pi(t-\tau))\,dt \end{aligned} \tag{39}$$

Computing the integrals in (39) and using (36) one, remembering $A^2 + B^2 = 1$, arrives at

$$\begin{aligned}\beta_2 &= \frac{-\alpha^2(1-A)A + \alpha(2\pi+\alpha B)B}{2\left((2\pi+\alpha B)^2+\alpha^2(1-A)^2\right)} = \frac{\alpha^2(1-A)+2\pi\alpha B}{4\left(\alpha^2(1-A)+2\pi(\pi+\alpha B)\right)} \\ &= \frac{\alpha^2(1-\cos(2\pi\tau))+2\pi\alpha\sin(2\pi\tau)}{4\left(\alpha^2(1-\cos(2\pi\tau))+2\pi(\pi+\alpha\sin(2\pi\tau))\right)}.\end{aligned} \tag{40}$$

This shows that β_2 is always positive.

Consider now how β depends on α, letting $\beta_2 = G(\alpha)$. It is immediate to see that $G(0) = 0$ and $G(\infty) = \frac{1}{4}$. Moreover from

$$G'(\alpha) = \frac{(1-A)\pi^2\alpha + \pi^3 B}{\left(\alpha^2(1-A)+2\pi(\pi+\alpha B)\right)^2} \tag{41}$$

one sees that $G' > 0$ in $(0, \bar{\alpha})$ and $G' < 0$ on $(\bar{\alpha}, \infty)$ where $\bar{\alpha}$ is the root of a quadratic equation, whose complicated expression does not seem easy to interpret.

Appendix 3: Application to host–parasitoid model

Here we see how the results of the previous section can be used to provide a heuristic justification for the possibility of host coexistence even without density-dependence.

Take in fact $\nu_{L_1} = \nu_{L_2} = 0$ and, for the sake of simplicity as in Section 4, we assume that different hosts share the values of d_E, μ_L, T_E, T_L.

Assume that host 1 coexists with the parasitoid along an (attractive) T-periodic solution $(E_1^\dagger(t), L_1^\dagger(t), A_1^\dagger(t), P_1^\dagger(t))$. The equation for adult hosts is then

$$A_1^{\dagger\prime}(t) = d_{A_1}\left(\rho_1 e^{-d_E T_E - \mu_L T_L - \alpha_1 \int_{t-T_L}^{t} P_1^\dagger(y)\,dy} A_1(t-T_E-T_L) - A_1(t)\right). \tag{42}$$

By considering $P_1^\dagger(t)$ as a given function, the monodromy operator corresponding to Eq. (42) has dominant eigenvalue equal to 1.
By changing the time ($\bar{t} = t/T$), $P_1^\dagger$ becomes 1-periodic, and (42) is equal to

$$A_1^{\dagger\prime}(t) = d_{A_1} T\left(\rho_1 e^{-d_E T_E - \mu_L T_L - \alpha_1 T \int_{t-T_L/T}^{t} P_1^\dagger(y)\,dy} A_1(t-\tau) - A_1(t)\right) \tag{43}$$

where $\tau = (T_E + T_L)/T$ and the functions have been rescaled.
Set

$$\begin{aligned}\alpha_1 &= d_{A_1} T \\ \beta_1 &= \rho_1/K \\ f_1(t) &= K e^{-d_E T_E - \mu_L T_L - \alpha_1 T \int_{t-T_L/T}^{t} P_1^\dagger(y)\,dy}\end{aligned} \tag{44}$$

where

$$K = \frac{e^{d_E T_E + \mu_L T_L}}{\int_0^1 e^{-\alpha_1 T \int_{t-T_L/T}^{t} P_1^{\dagger}(y)\,dy}\,dt}.$$

so to have $\int_0^1 f_1(t)\,dt = 1$ and the equation written exactly as (27).
Suppose that $f_1(t) \approx 1 + \varepsilon cos(2\pi t)$; then, using the results of Appendix 2

$$\rho_1 \approx (1 + \varepsilon^2 G(\alpha_1))K.$$

The invasion by a second host sharing all parameter values as in Section 4 will succeed if and only if the linearised equation

$$A_2^{\dagger\prime}(t) = d_{A_2} T \left(\rho_2 e^{-d_E T_E - \mu_L T_L - \alpha T \int_{t-T_L/T}^{t} P_1^{\dagger}(y)\,dy} A_2(t-\tau) - A_2(t) \right) \quad (45)$$

has dominant monodromy eigenvalue greater than 1. The equation can be written as

$$A_2^{\dagger\prime}(t) = \alpha_2 \left(\beta_2 f_1(t) A_2(t-\tau) - A_2(t) \right) \quad (46)$$

with $\alpha_2 = d_{A_2} T$ and $\beta_2 = \rho_2 / K$.
The eigenvalue is larger than 1 if and only if

$$\rho_2 > (1 + \varepsilon^2 G(\alpha_2))K.$$

If α_1 is in the region where G is increasing, this will be possible for $\rho_2 < \rho_1$ if $\alpha_2 < \alpha_1$. Vice versa, in the region where G is decreasing.
This mechanism can presumably give rise to mutual invasibility. However, when the roles of host 1 and host 2 are switched, also the period will in principle change as well as f_i, so G does not remain the same.
It is easier to show mutual coexistence, if we take a value of $\alpha_2 < \alpha_1$ such that 2-host only solutions are attracted to a stable equilibrium (this is certainly true if α_2 is small enough).

Then as all other parameters are the same, and the value of d_{A_i} do not enter the invasibility conditions (8), host 1 invades the equilibrium with only host 2 if and only if $\rho_2 > \rho_1$.
Thus mutual invasibility occurs if we find a pair (d_{A_1}, ρ_1) and (d_{A_2}, ρ_2) such that the first gives rise to a periodic solution and the second to a stable equilibrium with

$$d_{A_2} < d_{A_1} \quad \text{and} \quad \frac{1 + \varepsilon^2 G(d_{A_2} T)}{1 + \varepsilon^2 G(d_{A_1} T)} < \frac{\rho_2}{\rho_1} < 1 \quad (47)$$

where G and T refer to 1-parameters. Clearly (47) is only possible if G is increasing between $d_{A_2} T$ and $d_{A_1} T$. This result can be compared with Fig. 4 and it can be noticed that it corresponds to what is seen in the left edge of the Figure.

Of course, this argument is purely heuristic as it is based on the unlikely assumption that $f_1(t)$ is exactly a sinusoidal function. However, the argument can possibly be extended to Fourier series, and anyway we believe it gives some intuition on why coexistence may occur even without density-dependence.

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