

Two-Strain Ecoepidemic Systems: The Obligated Mutualism Case

Chiara Bosica, Alessandra De Rossi*, Noemi Lucia Fatibene, Matteo Sciarra and Ezio Venturino

Department of Mathematics “G. Peano”, University of Torino, via Carlo Alberto 10, I-10123 Torino, Italy

Received: 4 Oct. 2014, Revised: 4 Jan. 2015, Accepted: 5 Jan. 2015

Published online: 1 Jul. 2015

Abstract: We present a model for obligated mutualistic associations, in which two transmissible diseases are allowed to infect just one population. As the general model proves too hard to be fully analytically investigated, some special cases are analysed. Among our findings, the coexistence of the two strains does not appear possible, under the model assumptions. Furthermore, in particularly unfavorable circumstances the ecosystem may disappear. In this respect, an accurate computation of the basin of attraction of the origin is provided using novel techniques. For this obligated mutualistic system the presence of the diseases appears to be less relevant than in many other circumstances in ecoepidemiology, including also the case of facultative symbiotic associations.

Keywords: symbiosis, ecoepidemiology, two-strain.

1 Introduction

Symbiotic associations occur frequently in nature, although in population theory mathematical models focus generally more on competing situations or predator-prey interactions: the classical examples are the anemone-damselfish and the ant-plant interactions leading to pollination, [4]. In the latter context, for instance moths (of genus *Tegeticula*) pollinate yuccas, [3]. Other known associations involve mycorrhizal fungi, fungus-gardening ants, mixed feeding flocks of birds dispersing seeds of *Casearia corymbosa* in Costa Rica, [17]. Commensalism and symbiotic populations have been considered within food chains where some of the other populations are in competition with each other, [18, 19, 20, 32, 12, 14, 24]. A recent contribution along these lines is [6], considering symbiotic models at various trophic levels in food chains.

Ecoepidemiology is a rather recent field of study, investigating the effect that epidemics have on the underlying demographic populations interactions. Many papers by now have been devoted to the study of ecoepidemic systems based on predator-prey or competing demographics. For an account of some of the early developments in this field, see Chapter 7 of [21]. In fact, diseases cannot be ignored in ecosystems. A whole wealth of possible ailments affecting populations in

aquatic, terrestrial or avian environments is contained in [13].

Specific examples involving populations living in symbiosis can also be found, e.g. several mushrooms (*Cantharellus cibarius*, *Boletus* spp., *Amanita* spp.) with chestnut trees (*Castanea sativa*). The disease in this case is represented by chestnut cancer (*Endothia parasitica*). Symbiotic associations are common among bacteria alone, [33], bacteria together with other organisms [5, 26], plants [23] and plants and mushrooms [22] and these symbiotic systems may affect the whole ecosystem in which they thrive, [11]. Other instances are the soil nematode *Caenorhabditis elegans*, that transfers the rhizobium species *Sinorhizobium melotiti* to the roots of the legume *Medicago truncatula* [2, 16], the L-form bacteria in non-pathogenic symbiosis with several plants that allow the latter to resist other bacterial pathogens [31]. These considerations were the underlying motivations for studying a symbiotic situation encompassing diseases, [30]. The investigation has been extended in [15], assuming a Holling type II term for the possible mutual rewards of the symbiotic populations.

Other developments in epidemiology have dealt with the case of two pathogens affecting together a host. Ecoepidemic situations of this type that have been investigated previously consist of two diseases that are assumed to spread in a predator-prey community,

* Corresponding author e-mail: alessandra.derossi@unito.it

affecting the predators, [25], or the prey, [9,10]. In this paper, our aim is to further extend the work [15], by considering different strains that affect the symbiotic environment. Specifically, we consider a general symbiotic model and some particular cases. The fundamental assumption that relates the two diseases is that they do not interfere with each other. This means that they cannot both affect at the same time the same individual, i.e. there is no coinfection, nor superinfection, i.e. once an individual gets a disease, he is prevented from being affected also by the other one. The mutualistic association is obligated, i.e. without the other one, each population would not thrive alone. Possible extensions that are not discussed here are represented instead by facultative mutualism; also the assumption that diseased individuals do not receive benefits from interactions with the other population could be removed.

The paper is organized as follows. We briefly discuss the demographic model as a further reference, then introduce in Section 3 the general model. As a complete analysis is not possible, in Sections 4 and 5 we investigate two particular cases, restricting somewhat the infected from taking part in the association. A final discussion concludes the paper.

2 Preliminaries

Before introducing the ecoepidemic models, for comparison purposes, we briefly discuss their underlying demographic model, i.e. the model without the infected individuals,

$$\frac{dS}{dt} = -nS + aSP, \quad \frac{dP}{dt} = -mP + eSP. \quad (1)$$

All parameters here and in the next Sections are always assumed to be nonnegative. System (1) has only two equilibria, the origin $\hat{E}_0 = (0,0)$ and the coexistence point $\hat{E}_1 = (me^{-1}, na^{-1})$. It is very simple to write down its Jacobian J_d ,

$$J_d = \begin{bmatrix} -n + aP & aS \\ Pe & -m + eS \end{bmatrix}$$

and from its evaluation at \hat{E}_0 to find the eigenvalues $-n$ and $-m$, while the evaluation at \hat{E}_1 gives the eigenvalues $\pm\sqrt{mn}$. It follows that the coexistence equilibrium is unstable, namely a saddle, and the origin is always stable. Thus the phase plane is partitioned into two domains, one for which the origin is an attractor, and the other one in which the trajectories ultimately drift to infinity. Therefore to prevent the system's extinction, in practical situations it is important to assess the basin of attraction of the origin. To this end, based on the very recent algorithm presented in [1,7], we show in Figure 1 the separatrix of these domains, obtained for the following set of parameter values $m = 5.0, e = 1.0, n = 6.0, a = 1.0$.

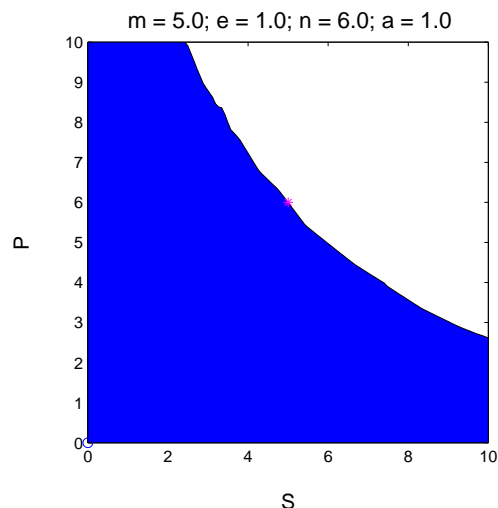


Fig. 1 The blue colored region represents the basin of attraction of the origin in the SP phase plane.

The result is partly unsatisfactory, since from the biological point of view the ecosystem is bound to disappear, if the population levels are low, or better said if they fall in the domain of attraction of the origin, otherwise they explode. From the ecological point of view this latter phenomenon is impossible, since finite resources cannot sustain an ever increasing population. However, it is imbedded in the assumptions of the model, which are kept at a minimal number, in order to better analyse the ecoepidemic models that follow and compare their results with those of the underlying purely demographic model. In this way the disease influence on the environment transpires more clearly.

3 The general model

As before, let S and P be the two symbiotic populations. We assume that two recoverable diseases spread by contact among the S population, giving rise to infected individuals of type H and Y . We assume that there is neither coinfection nor superinfection, i.e. whenever one individual is infected by one strain, it cannot catch the other disease and become infected with both, nor can he get the second disease and the latter replace the first one. The model, in which all parameters are assumed to be nonnegative, reads

$$\begin{aligned} \frac{dS}{dt} &= -nS - \lambda HS - \beta YS + aSP + \xi H + \varphi Y, \\ \frac{dH}{dt} &= \lambda HS - \mu H - \xi H + qHP, \\ \frac{dY}{dt} &= \beta YS - \nu Y - \varphi Y + rYP, \\ \frac{dP}{dt} &= -mP + eSP + fHP + gYP. \end{aligned} \quad (2)$$

The first equation models the dynamics of the S population. It dies out at an exponential rate n , and reproduces only in presence of the other mutualistic population P , at rate a . By causal encounters with infected individuals of type H and Y , a susceptible can then become infected, at rates λ and β respectively. Finally, individuals of the latter two classes that recover from the disease reenter the susceptible class.

The second equation considers the infected H ; they are recruited among the susceptibles at rate λ , as mentioned, they recover at rate ξ and are subject to natural plus disease-related mortality μ . The third equation contains a similar dynamics for the infected Y . Note that in this case the total mortality rate is named v and the recovery rate is expressed by the parameter φ .

Finally, the fourth equation shows the behavior of the mutualistic population P , which in absence of individuals of the mutualistic population dies out at an exponential rate m , and reproduces, when the symbiotic population is present, at rate e .

The system's equilibria are the following points. The origin $E_0 = (0, 0, 0, 0)$, and the coexistence equilibrium $E_4 = (S_4, H_4, Y_4, P_4)$ with population values

$$S_4 = \frac{vq + \varphi q - r\mu - r\xi}{\beta q - r\lambda}, \tag{3}$$

$$P_4 = \frac{\mu\beta + \xi\beta - \lambda v - \lambda\varphi}{\beta q - r\lambda},$$

$$H_4 = \frac{(ng + \beta m + \varphi e)S_4 - \beta e S_4^2 - agP_4 S_4 - \varphi m}{(\beta f - \lambda g)S_4 + \xi g - \varphi f},$$

$$Y_4 = \frac{e\lambda S_4^2 - (m\lambda + e\xi + fn)S_4 + afS_4 P_4 + m\xi}{(\beta f - \lambda g)S_4 + \xi g - \varphi f}.$$

and then $E_1 = (me^{-1}, 0, 0, na^{-1})$,

$$E_{2\pm} = \left(z_{2,\pm}, \frac{1}{f}(m - ez_{2,\pm}), 0, \frac{1}{q}(\mu + \xi - \lambda z_{2,\pm}) \right),$$

$$E_{3\pm} = \left(z_{3,\pm}, 0, \frac{1}{g}(m - ez_{3,\pm}), \frac{1}{r}(v + \varphi - \beta z_{3,\pm}) \right),$$

where $z_{2,\pm}$ are the roots of

$$R_2(Z) \equiv (a\lambda f - \lambda qe)Z^2 + (nqf + \lambda qm + \xi qe - a\mu f - a\xi f)Z - \xi qm = 0. \tag{4}$$

while $z_{3,\pm}$ solve

$$R_1(Z) \equiv (a\beta g - \beta re)Z^2 + (nrg + \beta rm + \varphi re - avg - a\varphi g)Z - \varphi rm = 0, \tag{5}$$

E_0 are E_1 always feasible.

To investigate feasibility of E_{2+} , let Δ_2 be the discriminant of (4). Imposing $z_{2,+} > 0$ we have $nqf + \lambda qm - a\mu f - \sqrt{\Delta_2} < \xi(af - eq)$, which together with the nonnegativity conditions for the remaining populations, that give $e < mz_{2,+}^{-1}$ and $\lambda z_{2,+} - \xi < \mu$, provides bounds for ξ . Namely, for

$$f > \max \left\{ \frac{\mu eq - \lambda mq + \sqrt{\Delta_2}}{nq}, \frac{\mu e^2 q + e\sqrt{\Delta_2}}{m\lambda a + nqe} \right\} \tag{6}$$

we find

$$\frac{nqf + \lambda qm - a\mu f - \sqrt{\Delta_2}}{af - eq} < \xi < \frac{nqf - m\lambda q - a\mu f - \sqrt{\Delta_2}}{af - eq} + \frac{2m\lambda af}{e(af - eq)}, \tag{7}$$

which to be consistent, requires $af > eq$.

In case instead that

$$\frac{\mu e^2 q + e\sqrt{\Delta_2}}{m\lambda a + nqe} < f \leq \frac{\mu eq - \lambda mq + \sqrt{\Delta_2}}{nq}, \tag{8}$$

we find the interval

$$\frac{2\mu eq - a\mu f - nqf - \lambda qm + \sqrt{\Delta_2}}{af - eq} < \xi < \frac{nqf - m\lambda q - a\mu f - \sqrt{\Delta_2}}{af - eq} + \frac{2m\lambda af}{e(af - eq)}, \tag{9}$$

which implies

$$f > \frac{\mu e^2 q + e\sqrt{\Delta_2}}{m\lambda a + nqe},$$

if we take $af > eq$, or a contradiction with (8) in the opposite case. In summary E_{2+} is feasible if

$$af > eq \tag{10}$$

together with either (6) and (7), or together with (9) and (8). The inequality (8) to be true implies $\mu eaq - m\lambda aq - nq^2 e + a\sqrt{\Delta_2} > 0$.

For E_{2-} we have similar results. We need again (10) together with the same two alternative sets of conditions (6) and (7), or respectively (9) and (8), in which however the plus sign in front of the square root is replaced by a minus.

Note that when these two points, $E_{2\pm}$ coalesce, the same feasibility conditions still hold, in a simplified form: it is enough to set $\Delta_2 = 0$ in all the previous formulae.

For the pair of equilibria $E_{3\pm}$ similar steps lead to the following feasibility conclusions. If we denote by Δ_3 the discriminant of (5), for E_{3-} we need

$$ag > er \tag{11}$$

and

$$g > \max \left\{ \frac{ver - \beta mr - \sqrt{\Delta_3}}{rn}, \frac{ve^2 r - e\sqrt{\Delta_3}}{m\beta a + nre} \right\} \tag{12}$$

together with

$$\frac{nrg + \beta rm - avg + \sqrt{\Delta_3}}{ag - er} < \varphi < \frac{2m\beta ag - m\beta er + enrg - eavg + e\sqrt{\Delta_3}}{e(ag - er)} \tag{13}$$

or (11) together with

$$\frac{ve^2 r - e\sqrt{\Delta_3}}{m\beta a + nre} < g \leq \frac{ver - \beta mr - \sqrt{\Delta_3}}{nr}, \tag{14}$$

which requires

$$vera - m\beta ar - nr^2e - a\sqrt{\Delta_3} > 0,$$

and

$$\frac{v(2er - ag) - r(ng + \beta m) - \sqrt{\Delta_3}}{ag - er} < \varphi \tag{15}$$

$$< \frac{m\beta(2ag - er) + eg(nr - av) + e\sqrt{\Delta_3}}{e(ag - er)}.$$

For E_{3+} again to obtain feasibility conditions it is enough to change the signs of the square root terms, or to set it to zero in case the two points coalesce.

To assess stability analytically is too complex. From our simulations, it seems that all these points are unstable, the system tending either to the origin, or eventually the trajectories becoming unbounded.

To better analyse the system, we now turn to the analysis of some simplified cases.

4 No intermingling with infected allowed

We make here the simplifying assumption that the second population P does not interact with the infected both strains of the population S , because they can be recognized and therefore avoided, for instance. This corresponds to setting $f = q = g = r = 0$ in (2). Explicitly, we thus have

$$\frac{dS}{dt} = -nS - \lambda HS - \beta YS + aSP + \xi H + \varphi Y, \tag{16}$$

$$\frac{dH}{dt} = \lambda HS - \mu H - \xi H,$$

$$\frac{dY}{dt} = \beta YS - \nu Y - \varphi Y,$$

$$\frac{dP}{dt} = -mP + eSP.$$

In this case, however, there are only the two feasible equilibria $Q_0 \equiv E_0 = (0,0,0,0)$ and $Q_1 \equiv E_1 = (me^{-1}, 0, 0, na^{-1})$, that are always feasible. They clearly coincide with those of (1), except that have two dimensions, i.e. two populations, more, the infected, although the latter are at zero level. We note thus that either one of nor both the two diseases cannot survive in this system, they are eradicated. From the epidemiological point of view this is a very important result, subject of course to the rather peculiar assumptions of the underlying demographic model, i.e. Malthusian growth, or in terms of ecosystem, of the fact that that this is an obligated mutualism. The mathematical reason for which equilibria with diseases at positive level are not sustainable, is that the points Q_2^* with only nonzero populations $S_2^* = (v + \varphi)\beta^{-1}$, $Y_2 = -\nu v^{-1}S_2^*$ and Q_3^* with the nonzero population levels $S_3^* = (\mu + \xi)\lambda^{-1}$, $H_3^* = -n\mu^{-1}S_3^*$ have both a negative component.

The Jacobian of (16) is

$$J = \begin{bmatrix} -n - \lambda H - \beta Y + aP & -\lambda S + \xi & & \\ \lambda H & \lambda S - \mu - \xi & & \\ \beta Y & & 0 & \\ Pe & & & 0 \end{bmatrix}$$

$$\begin{bmatrix} -\beta S + \varphi & aS \\ 0 & 0 \\ \beta S - \nu - \varphi & 0 \\ 0 & -m + eS \end{bmatrix}.$$

Its evaluation at Q_0 gives the eigenvalues $-v - \varphi$, $-n$, $-\mu - \xi$, $-m$, which are all negative. Thus the origin is once again unconditionally stable. Evaluation at Q_1 leads instead to the eigenvalues $\pm\sqrt{mn}$, $(\beta m - \nu e - \varphi e)^{-1}$, $(\lambda m - \mu e - e\xi)^{-1}$. Since the first two are those inherited from the corresponding equilibrium \hat{E}_1 , and one of them is positive, we conclude that also Q_1 is unstable. Thus the disease in this context does not really change the system's behavior.

Due to the threat of a vanishing ecosystem, a small region of attraction of the origin is desirable. Reliable procedures for its determination have been devised, by computation of the separatrix surface, [8]. In Figure 2 we show the picture of the basin of attraction of the origin, which lies below the surface, for the hypothetical parameter values $\lambda = 3$, $\mu = 2.5$, $\xi = 2.4$, $m = 6.$, $\nu = 0.$, $\beta = 0.$, $a = 1$, $\phi = 0.$, $e = 1.5$, $n = 3$.

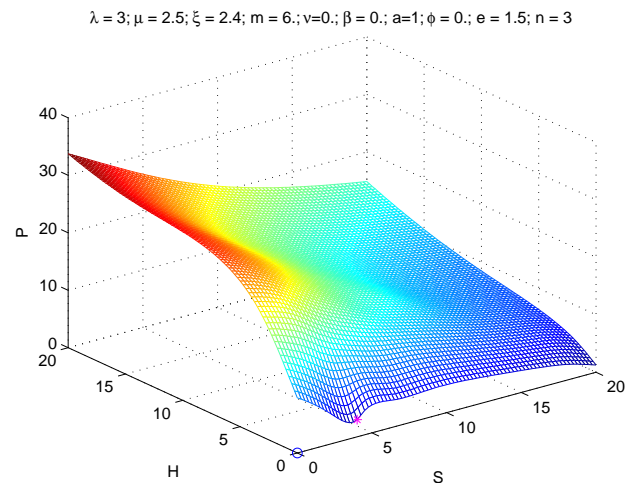


Fig. 2 The region below the surface represents the basin of attraction in the SHP phase subspace $Y = 0$. The star represents the projection of the $Q_1 \equiv E_1 = (4, 0, 0, 3)$ saddle point.

5 Infected do not get reward from symbiosis

In this case the P population gains from the interactions also with the infected individuals of the first one, but the latter do not feel the benefit of the mutualism. In other words, we set only $r = q = 0$ in (2). Thus, explicitly,

$$\begin{aligned} \frac{dS}{dt} &= -nS - \lambda HS - \beta YS + aSP + \xi H + \varphi Y, & (17) \\ \frac{dH}{dt} &= \lambda HS - \mu H - \xi H, \\ \frac{dY}{dt} &= \beta YS - \nu Y - \varphi Y, \\ \frac{dP}{dt} &= -mP + eSP + fHP + gYP. \end{aligned}$$

The equilibria are now

$$\begin{aligned} \tilde{E}_0 &= (0, 0, 0, 0), \quad \tilde{E}_1 = \left(\frac{m}{e}, 0, 0, \frac{n}{a}\right), & (18) \\ \tilde{E}_2 &= \left(\frac{\mu + \xi}{\lambda}, \frac{m\lambda - e\mu - e\xi}{f\lambda}, 0, \frac{m\lambda\mu - e\mu^2 - e\xi\mu + fn\mu + fn\xi}{fa(\mu + \xi)}\right), \\ \tilde{E}_3 &= \left(\frac{\nu + \varphi}{\beta}, 0, \frac{m\beta - e\nu - e\varphi}{g\beta}, \frac{m\beta\nu - e\nu^2 - e\varphi\nu + g\nu\nu + gn\varphi}{ga(\nu + \varphi)}\right). \end{aligned}$$

Again, note that two more disease-unaffected-population-free equilibria with endemic disease are not feasible, and coincide with those of the former model (16), $E_2^* \equiv Q_2^*$ and $E_3^* \equiv Q_3^*$.

While the origin and \tilde{E}_1 are always feasible, the remaining points are only if some conditions hold. Specifically, feasibility conditions can now be explicitly stated as follows: for \tilde{E}_2 we have

$$e \leq \frac{m\lambda}{\mu + \xi}, \quad n \geq \frac{\mu(e\mu - m\lambda + e\xi)}{f(\mu + \xi)}, \quad (19)$$

while for \tilde{E}_3 we find

$$e \leq \frac{m\beta}{\nu + \varphi}, \quad n \geq \frac{\nu(e\nu - m\beta + e\varphi)}{g(\nu + \varphi)}. \quad (20)$$

The system's (17) Jacobian is

$$J = \begin{bmatrix} J_{11} & -\lambda S + \xi & -\beta S + \varphi & aS \\ \lambda H & \lambda S - \mu - \xi & 0 & 0 \\ \beta Y & 0 & \beta S - \nu - \varphi & 0 \\ Pe & Pf & Pg & J_{44} \end{bmatrix},$$

with $J_{11} = -n - \lambda H - \beta Y + aP$, $J_{44} = -m + eS + fH + gY$.

It is easy to verify that E_0 and E_1 retain the stability properties respectively of Q_0 and \tilde{E}_0 , as well as Q_1 and \tilde{E}_1 . The eigenvalues of the Jacobian evaluated at \tilde{E}_2 are

$$\frac{\beta\mu + \beta\xi - \nu\lambda - \varphi\lambda}{\lambda}$$

and the roots of the cubic monic polynomial ($c_3 = 1$), $p(t) = \sum_{i=0}^3 c_i t^i$, with

$$\begin{aligned} c_0 &= \frac{1}{f\lambda} (e\mu^2 fn - e^2\mu^3 - 2e^2\mu^2\xi + & (21) \\ & 2m\lambda e\mu^2 + 2e\mu fn\xi - m^2\lambda^2\mu - m\lambda fn\mu \\ & 2m\lambda e\xi\mu - e^2\xi^2\mu + e\xi^2 fn + m\lambda fn\xi), \\ c_1 &= \frac{\mu^2 e^2 - \lambda e\mu^2 + \mu m\lambda^2 - \lambda e\xi\mu}{f\lambda} + \\ & \frac{-\mu m\lambda e - \mu e fn + \mu e^2\xi - e fn\xi}{f\lambda}, \\ c_2 &= \frac{\xi(m\lambda - e\mu - e\xi)}{f(\mu + \xi)}. \end{aligned}$$

The Routh-Hurwitz stability criterion requires strict positivity for the following quantities:

$$D_{2,1} = |c_2|, \quad D_{2,2} = \begin{vmatrix} c_2 & c_0 \\ c_3 & c_1 \end{vmatrix}, \quad D_{2,3} = \begin{vmatrix} c_2 & c_0 & 0 \\ c_3 & c_1 & 0 \\ 0 & c_2 & c_0 \end{vmatrix}.$$

Now $D_{2,1} > 0$ is a consequence of the strict feasibility condition (19).

For $D_{2,2} > 0$, we have

$$\begin{aligned} D_{2,2} &= \frac{1}{\lambda(\mu + \xi)f^2} (m\lambda - e\mu - e\xi) \times & (22) \\ & (e^2\mu^2\xi + e^2\xi^2\mu - f\mu^3e - \lambda e\mu^2\xi + \\ & -2ef\mu^2\xi - fe\mu\xi^2 - fne\mu\xi - e\lambda\mu\xi^2 + \\ & -me\lambda\mu\xi - fen\xi^2 + nf^2\mu^2 + mf\lambda\mu^2 + \\ & + m\lambda^2\mu\xi + mf\lambda\mu\xi + 2nf^2\mu\xi + f^2n\xi^2). \end{aligned}$$

The denominator is positive as well as the first factor, when the first (19) is satisfied as a strict inequality. The second factor is a quadratic in the parameter e , whose roots we indicate by e_1 and e_2 . The second factor is positive for the values: $e < e_2$ or $e > e_1$ in the case of real roots, ($e_2 < e_1$); for every $e \neq e_1$ in case of a double real root; for every value of e when the roots are complex.

Finally, to have $D_{2,3} > 0$ we need

$$\begin{aligned} D_{2,3} &= \frac{1}{\lambda^2(\mu + \xi)f^3} \times & (23) \\ & (m\lambda - e\mu - e\xi)^2 (e^2\mu^2\xi + e^2\xi^2\mu - f\mu^3e + \\ & -\lambda e\mu^2\xi - 2ef\mu^2\xi - fe\mu\xi^2 - fne\mu\xi + \\ & -e\lambda\mu\xi^2 - me\lambda\mu\xi - fen\xi^2 + nf^2\mu^2 + \\ & + mf\lambda\mu^2 + m\lambda^2\mu\xi + mf\lambda\mu\xi + \\ & + 2nf^2\mu\xi + f^2n\xi^2) \times \\ & (e\mu^2 - m\lambda\mu + e\xi\mu - fn\mu - fn\xi) > 0. \end{aligned}$$

Here too the denominator is positive, the first factor is when

$$e \neq \frac{m\lambda}{\mu + \xi},$$

the second one coincides with the second one of $D_{2,2}$, the third one is positive for

$$e > \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)}.$$

By combining all these cases we find $D_{2,3} > 0$ for the following different cases

1. for different real roots of the second factor, we need one of the following two alternative situations

$$e > \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)}, \quad e \neq \frac{m\lambda}{\mu + \xi}, \quad e < e_2;$$

$$e > e_1, \quad e > \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)}, \quad e \neq \frac{m\lambda}{\mu + \xi},$$

or all the following conditions

$$e \neq \frac{m\lambda}{\mu + \xi}, \quad e_2 < e < e_1, \quad e < \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)};$$

2. when there are two double roots, we need all the following conditions

$$e \neq \frac{m\lambda}{\mu + \xi}, \quad e \neq e_1 \equiv e_2, \quad e > \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)};$$

3. for complex roots instead the required conditions are

$$e \neq \frac{m\lambda}{\mu + \xi}, \quad e > \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)}.$$

But none of these conditions can hold, namely:

-the conditions $e_2 < e < e_1$ cannot hold in view of the request $D_{2,2} > 0$;

-the remaining three cases require

$$\begin{aligned} e &> \frac{m\lambda\mu + fn\mu + fn\xi}{\mu(\mu + \xi)} \\ &= \frac{m\lambda\mu}{\mu(\mu + \xi)} + \frac{fn(\mu + \xi)}{\mu(\mu + \xi)} \\ &= \frac{m\lambda}{\mu + \xi} + \frac{fn}{\mu} > \frac{m\lambda}{\mu + \xi}, \end{aligned} \tag{24}$$

which contradicts the feasibility condition (19).

In conclusion, $D_{2,3}$ cannot be positive, so that \tilde{E}_2 is unconditionally unstable for all parameter choices.

Note that Hopf bifurcations also cannot arise. We would need $c_1c_2 - c_0 = 0$, but solving it in terms of the parameter n , the value it must have so that purely imaginary eigenvalues arise is

$$n = \frac{(m\lambda - e\mu - e\xi)(e\xi - f\mu - \lambda\xi - f\xi)\mu}{(\mu + \xi)(f\mu + f\xi - e\xi)f}.$$

However, the feasibility condition (19) for \tilde{E}_2 in terms of n requires

$$n \geq \frac{\mu(e\mu - m\lambda + e\xi)}{f(\mu + \xi)}.$$

Combining the two above conditions, we find

$$\frac{e\xi - f\mu - \lambda\xi - f\xi}{e\xi - f\mu - f\xi} \geq 1,$$

which implies $e\xi - f\mu - \lambda\xi - f\xi \geq e\xi - f\mu - f\xi$ and finally $-\lambda\xi \geq 0$, which is impossible.

For \tilde{E}_3 the situation is similar, we have one eigenvalue as follows

$$\frac{\varphi\lambda - \beta\mu - \beta\xi + v\lambda}{\beta}$$

and the roots of the cubic $q(t) = \sum_{i=0}^3 h_i t^i$ with coefficients $h_3 = 1$ and

$$h_0 = \frac{1}{g\beta}(2m\beta ev^2 - e^2 v^3 - 2e^2 v^2 \varphi + \tag{25}$$

$$ev^2 gn + 2evgn\varphi - e^2 \varphi^2 v - m^2 \beta^2 v + 2m\beta e\varphi v - m\beta gn v - m\beta gn\varphi + e\varphi^2 gn),$$

$$h_1 = \frac{1}{g\beta}(v^2 e^2 - \beta ev^2 + vm\beta^2 - \beta e\varphi v$$

$$+ ve^2 \varphi - vm\beta e - v egn - egn\varphi),$$

$$h_2 = \frac{\varphi(m\beta - ev - e\varphi)}{g(v + \varphi)}.$$

Once again, $D_{3,1} = c_2 > 0$ follows from the strict first feasibility condition (20). We then need the positivity of

$$D_{3,2} = \begin{vmatrix} c_2 & c_0 \\ c_3 & c_1 \end{vmatrix}$$

which gives

$$D_{3,2} = \frac{1}{g^2(v + \varphi)\beta}(m\beta - ev - e\varphi) \times \tag{26}$$

$$\begin{aligned} &(e^2 v^2 \varphi + e^2 \varphi^2 v - ev^3 g - 2ev^2 g\varphi + \\ &- ev^2 \beta \varphi - evg\varphi^2 - e\varphi^2 v\beta + \\ &- m\beta e\varphi v - evgn\varphi - e\varphi^2 gn + m\beta gv^2 \\ &+ v^2 g^2 n + \varphi m\beta v g + m\beta^2 v\varphi + 2vg^2 n\varphi \\ &+ g^2 n\varphi^2) > 0. \end{aligned}$$

The denominator is positive, the first factor is also when the first feasibility condition (20) is strictly satisfied. The second factor is a quadratic in e , whose roots are denoted e_3 and e_4 . It is positive for $e < e_4$ or $e > e_3$ when $e_3 > e_4$ are the two real roots. When they coincide, we need $e \neq e_3 \equiv e_4$; finally, for complex roots, $D_{3,2} > 0$ unconditionally.

The third Routh-Hurwitz condition requires

$$D_{3,3} = \frac{1}{g^3(v + \varphi)\beta^2}(m\beta - ev - e\varphi)^2 \times \tag{27}$$

$$\begin{aligned} &(ev^2 - m\beta v + e\varphi v - gn v - gn\varphi) \times \\ &(e^2 v^2 \varphi + e^2 \varphi^2 v - ev^3 g - 2ev^2 g\varphi + \\ &- ev^2 \beta \varphi - evg\varphi^2 - e\varphi^2 v\beta + \\ &- m\beta e\varphi v - evgn\varphi - e\varphi^2 gn + \\ &m\beta gv^2 + v^2 g^2 n + \varphi m\beta v g \\ &+ m\beta^2 v\varphi + 2vg^2 n\varphi + g^2 n\varphi^2) > 0. \end{aligned}$$

If we take

$$e \neq \frac{m\beta}{v + \varphi}$$

the sign of $D_{3,3}$ depends only on the last two factors, and the last one is the second factor of $D_{3,2}$ so that we find once again the roots e_3 and e_4 . The third factor is positive whenever

$$e > \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)}.$$

In summary, $D_{3,3} > 0$ in the following situations

1. for two real distinct roots e_3 and e_4 we either need both the following conditions

$$e > \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)}, \quad e \neq \frac{m\beta}{v + \varphi}, \quad e < e_2;$$

$$e > e_1, \quad e > \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)}, \quad e \neq \frac{m\beta}{v + \varphi},$$

or, alternatively, we can also have

$$e \neq \frac{m\beta}{v + \varphi}, \quad e_2 < e < e_1 \quad e < \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)};$$

2. for real identical roots, $e_3 \equiv e_4$ we need

$$e \neq \frac{m\beta}{v + \varphi}, \quad e \neq e_1 \equiv e_2, \quad e > \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)};$$

3. for complex roots, instead the requirement is

$$e \neq \frac{m\beta}{v + \varphi}, \quad e > \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)}.$$

Again, none of the above conditions can hold. In fact,

–whenever $e_2 < e < e_1$, we contradict the statement that $D_{3,2} > 0$;

–in the remaining cases we want

$$\begin{aligned} e &> \frac{m\beta v + gnv + gn\varphi}{v(v + \varphi)} \\ &= \frac{m\beta v}{v(v + \varphi)} + \frac{gn(v + \varphi)}{v(v + \varphi)} \\ &= \frac{m\beta}{(v + \varphi)} + \frac{gn}{v} > \frac{m\beta}{(v + \varphi)} \end{aligned} \tag{28}$$

which clashes with the first feasibility condition (20) for \tilde{E}_3 .

In summary, \tilde{E}_3 is always unstable. Here too, Hopf bifurcations are impossible, since $h_1 h_2 - h_0 = 0$ in term of n gives

$$n = \frac{(ev - m\beta + e\varphi)(e\varphi - gv - g\varphi - \beta\varphi)v}{(e\varphi - gv - g\varphi)g(v + \varphi)},$$

while feasibility (20) yields

$$n \geq \frac{v(ev - m\beta + e\varphi)}{(v + \varphi)g},$$

which together with the former one implies

$$\frac{e\varphi - gv - g\varphi - \beta\varphi}{e\varphi - gv - g\varphi} \geq 1$$

from which $e\varphi - gv - g\varphi - \beta\varphi \geq e\varphi - gv - g\varphi$ and ultimately $-\beta\varphi \geq 0$, once again an impossible condition. The system therefore does not allow limit cycles.

6 Conclusions

We have proposed a two-strain model for an obligated mutualistic ecoepidemic system. Although in its generality we were unable to analyse all the equilibria stability, except by means of numerical simulations, in the two particular cases examined we have shown that no stable equilibria other than the origin exist. This at first sight appears not to be a good result from the ecological point of view, since it states that in fact the ecosystem can vanish. One must keep in mind though that as for the underlying demographic model, a saddle in the phase space is present, given by E_1 or its equivalent points. Therefore the system trajectories, as also shown by the simulations, may instead very well grow unbounded. When the initial conditions do not fall into its basin of attractions, trajectories are repelled away from the saddle point E_1 in case of model (16) as well as from the remaining equilibria \tilde{E}_2 and \tilde{E}_3 , when we consider model (17) and in both cases tend to grow without bounds. This is to be ascribed to the intrinsic limitations of the demographic assumptions of the model, which underlie the construction of the ecoepidemic model, or, in other more biological words, to the quadratic type (Holling type I) mutualistic interactions in the ecosystem. These results should be compared with [30], where logistic growth is assumed instead of an exponential mortality, i.e. the symbiosis is not obligated. In such case the disease does affect the system's behavior, in some cases even favoring the increment of the coexisting populations levels, at the expense of having part of them infected.

We have also shown that the two strains cannot coexist together, and this result parallels what has been found in [25,9,10]. Further, the diseases do not alter the behavior of the underlying demographic model. Therefore the disease influence on the obligated mutualistic ecoepidemic systems is clearly less relevant than in ecoepidemic models with other types of population interactions, in which instead the introduction of the epidemic changes the stability of some of the equilibria, [27,28,29]. For facultative associations, it is instead known that the results are in line with other ecoepidemic systems of predatory interaction or competing nature, [15]. Thus, our future research in two-strained symbiotic systems will aim at removing the obligated mutualism assumption and investigate its consequences.

Acknowledgements

This research was partially supported by the project “Metodi numerici in teoria delle popolazioni” of the Dipartimento di Matematica “Giuseppe Peano”.

References

- [1] G. Allasia, R. Besenghi, R. Cavoretto and A. De Rossi, *Appl. Math. Comput.* **217** (2011), 5949-5966.
- [2] B. J. Adams, A. Fodor, H. S. Koppenhöfer, E. Stackebrandt, S. P. Stock and M. G., Klein, *Biological Control* **37** (2006), 32-49.
- [3] J. F. Addicott, In: D.H. Boucher (Ed.), *The Biology of Mutualism: Ecology and Evolution*, Croom Helm, London, 1985, pp. 217-247.
- [4] D. H. Boucher, *The Biology of Mutualism: Ecology and Evolution*, Croom Helm, London, 1985.
- [5] C. Boursaux-Eude and R. Gross, *Res. Microbiol.* **151** (2000), 513-519.
- [6] E. Caccherano, S. Chatterjee, L. Costa Giani, L. Il Grande, T. Romano, G. Visconti and E. Venturino, In: *Symbiosis: Evolution, Biology and Ecological Effects*, Alejandro F. Camisão and Celio C. Pedroso (Eds.), Nova Science Publishers, Hauppauge, NY, 2012, pp. 189-234.
- [7] R. Cavoretto, S. Chaudhuri, A. De Rossi, E. Menduni, F. Moretti, M. C. Rodi and E. Venturino, In: T. Simos et al. (Eds.), *AIP Conf. Proc.* **1389** (2011), 1220-1223.
- [8] R. Cavoretto, A. De Rossi, E. Perracchione and E. Venturino, to appear in *Int. J. Comp. Math.* 2014, DOI: 10.1080/00207160.2013.867955.
- [9] E. Elena, M. Grammauro and E. Venturino, In: T. Simos et al. (Eds.), *AIP Conf. Proc.* **1389** (2011), 1228-1231.
- [10] E. Elena, M. Grammauro and E. Venturino, *Network Biology* **3(1)** (2013), 29-44.
- [11] L. K. Finkes, A. B. Cady, J. C. Mulroy, K. Clay and J. A. Rudgers, *Ecology Letters* **9** (2006), 347-356.
- [12] W. Gan and Z. Lin, *J. Math. Anal. Appl.* **337** (2008), 1089-1099.
- [13] F. M. D. Gulland, In: B.T. Grenfell and A.P. Dobson (Eds.) *Ecology of infectious diseases in natural populations*, Cambridge Univ. Press., 1995, pp. 20-51.
- [14] M. Gyllenberg, P. Yan and Y. Wang, *Phys. D* **221** (2006), 135-145.
- [15] M. Haque and E. Venturino, In: J.D. Harris and P.L. Brown (Editors), *Wildlife: Destruction, Conservation and Biodiversity*, NOVA Science Publ., New York, 2009, pp. 135-179.
- [16] J. I. Horiuchi, B. Prithiviraj, H. P. Bais, B. A. Kimball and J. M. Vivanco, *Planta* **222** (2005), 848-857.
- [17] D. H. Jantzen, P. De Vries, D. E. Gladstone, M. L. Higgins and T. M. Levinsohn, *Biotropica* **12** (1980), 1398-1406.
- [18] B. W. Kooi, L. D. J. Kuijper and S. A. L. M. Kooijman, *J. Math. Biol.* **49** (2004), 227-271.
- [19] R. Kumar and H. I. Freedman, *Nonlinear Dyn. Syst. Theory* **2** (2002), 25-44.
- [20] R. Kumar and H. I. Freedman, *Math. Biosci.* **97** (1989) 235-261.
- [21] H. Malchow, S. Petrovskii and E. Venturino, *Spatiotemporal patterns in Ecology and Epidemiology*, CRC, 2008.
- [22] C. B. Muller and J. Krauss, *Current Opinion in Plant Biology* **8** (2005), 450-456.
- [23] U. Paszkowski, *Current in Plant Biology* **9** (2006), 364-370.
- [24] B. Rai, H. I. Freedman and J. F. Addicott, *Math. Biosci.* **65** (1983), 13-50.
- [25] F. Roman, F. Rossotto and E. Venturino, *WSEAS Transactions on Biology and Biomedicine* **8** (2011), 73-85.
- [26] F. J. Stewart and C. M. Cavanaugh, *Bacterial endosymbioses in Solemya (Mollusca: Bivalvia)—Model system for studies of symbiont-host adaptation*, *Antonie van Leeuwenhoek* **90** (2006), 343-360.
- [27] E. Venturino, In: O. Arino, D. Axelrod, M. Kimmel and M. Langlais: *Mathematical Population Dynamics: Analysis of Heterogeneity*, Vol. one: *Theory of Epidemics*, Wuerz Publishing Ltd, Winnipeg, Canada, 1995, pp. 381-393.
- [28] E. Venturino, *Math. Biosci.* **174** (2001), 111-131.
- [29] E. Venturino, *IMA Journal of Mathematics Applied in Medicine and Biology* **19** (2002), 185-205.
- [30] E. Venturino, *Math. Biosci.* **206** (2007), 11-30.
- [31] R. Walker, C. M. J. Ferguson, N. A. Booth and E. J. Allan, *Letters in Applied Microbiology* **34** (2002), 42-45.
- [32] A. A. S. Zaghrou, *Appl. Math. Comput.* **45** (1991), 1-15.
- [33] B. G. Zhao and F. Lin, *For. Path.* **35** (2005), 339-345.



Chiara Bosica has obtained a Master in Mathematics at the University of Torino in 2013. In her thesis she analyzed preservation of topology of radial basis functions transformations in image registration. Her research activities are mainly focused on topics of applied mathematics, biomathematics and scattered data approximation with applications to image registration.



Alessandra De Rossi is Assistant Professor of Numerical Analysis at the University of Torino. She received the PhD degree in “Computational Mathematics” at the University of Milano (Italy) in 1997. She has published more of fifteen research articles in international journals and conference proceedings. She is referee of several international journals in the frame of numerical analysis and applied mathematics. Her main research interests are: meshfree approximation, fast algorithms for scattered data interpolation, image registration, biomathematics.

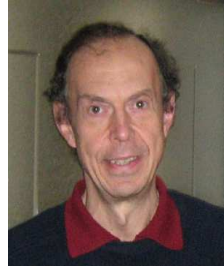


Noemi Lucia Fatibene has obtained a Master in Mathematics at the University of Torino in 2013. In her thesis she calibrated the parameters in a fish-plankton interaction model, assessing the larvae growth rates of *Perca fluviatilis*. Her main current research interests are population theory and

mathematical modeling.



Matteo Sciarra got a Master in Mathematics at the University of Torino in 2013. In his thesis a new scheme using splines for numerical integration was presented and related theoretical results were analyzed. His research activities are mainly focused on topics of biomathematics and numerical analysis.



Ezio Venturino is Professor of Mathematics at the University of Torino. He got the Ph. D. in Applied Mathematics at SUNY at Stony Brook. His fields of research are numerical analysis and mathematical modeling in biology. The main current research interests are

population theory, epidemiology, ecoepidemiology. He has coauthored a book for CRC and coedited another for Birkhäuser, authored about forty research papers in numerical analysis and more than hundred in mathematical modeling. He regularly takes active part in international conferences, with plenary invited talks, contributed papers and organizing special sessions. He referees regularly for international Journals. He is associate Editor of SIMPAT (Elsevier), MMAS (Wiley), member of the Editorial Board of J. Biological Systems (World Scientific) and a few other open access Journals.