Simple metaecoepidemic models

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Abstract

We consider a simple predator-prey system with two possible habitats and where an epidemic spreads by contact among the prey, but it cannot affect the predators. Only the prey population can freely move from one environment to another. Several models are studied, for different assumptions on the structure of the demographic interactions and on the predators' feeding. Some counterintuitive results are derived. The role the safety niche may in some cases entail negative consequences for the whole ecosystem. Also, depending on the system formulation, coexistence of all the populations may not always be supported.

Keywords: Eco-epidemiology; Local Stability; Global Stability; Holling Type-II; Hopf-bifurcation; Metapopulation; Habitat.

1 Introduction

In recent years classical population theory has evolved from the study of interacting populations and food chains to more complex situations encompassing communities living in separate environments, joined by possible migrations. This because heterogeneous environments and landscape fragmentation threaten persistence of wild populations and their conservation in these habitats becomes a major concern of environmentalists [27]. A tool for the understanding of population dynamics in these circumstances is provided by metapopulation theory, [26]. Local population dynamics and inter-patch migrations are responsible for metapopulation dynamics, with the possible

result that the population persists globally, although in some cases the local populations become extinct [28, 10, 7, 5, 26] But gathering field data for migrations between patches is problematic, in general these activities are not undertaken [15, 7, 5]. From this the role of models becomes relevant to predict possible outcomes of specific situations [15]. For instance in the case of the spotted owl (*Strix occidentalis*), or of the mountain sheep (*Ovis canadensis*) metapopulation dynamics becomes quite complex [8], since only the most favorable habitats are populated and the remaining ground in between is used for inter-patch migrations. Furthermore human activity also causes loss of habitat, since it tends to break the territorial distribution via human artifacts as buildings, roads, or clearing wild areas for creating new fields for agricultural purposes. The original population living in the unperturbed environment becomes separated into subpopulations, which continue to live independently, but may become now more sensible to adverse conditions. This situation may ultimately cause species extinction.

Ecologists have been looking for ways of assessing population dynamics in patched environments [20] and metapopulations represent a current answer, [12]. In the classical Levins model [17], colonization depends on just the portion of the environment that is actually inhabited; but more recent models, not making this assumption bur rather using the concept of incidence function, have been used to study the butterfly *Melitaea cinxia* in Finland [11] and then also other species [18, 19]. In the case of the butterfly, however, it has been remarked that variations in local populations may depend on the interaction with a specialist braconid parasitoid, *Cotesia melitaearum* [16], suggesting the need for a metapopulation approach explicitly modelling a host-parasitoid metapopulation dynamics [13]. In the light of these remarks, the need for accounting for diseases, whose occurrence in populations is a fact, in the above type of models is evident.

Ecoepidemiology is a rather new branch of population theory, dealing with the study of systems in which diseases spread among interacting populations. Various situations more or less complicated have been considered to date in the literature, in a time span which is reaching the two decades, from the first papers on the subject, [9, 6, 2, 21, 22, 24]. From the first researches dealing mostly with the quadratic predator-prey case, more complex models have also been introduced, [3, 1]. But also other demographics have been considered, namely competition models and interactions of symbiotic nature, [23, 25].

We do not aim at an approach providing a general solution, but rather content ourselves with a first step in the direction, allowing a simple interacting populations model incorporating a diseased population, with two possible living environments, in which one of them might constitute a refuge.

In this paper we thus consider a predator-prey system where two possible

habitats are assumed to exist. Furthermore, an epidemic is propagating by contact among the prey, but it cannot affect the predators. The prey population can freely move from one environment to another. Several models are built on these basic assumptions, differing on the structure of the underlying demographic models, and on the type of predators' hunting.

In all models throughout the paper, the notation is consistent, namely S denote the sound prey, I the infected prey and P the predators. Indices serve to distinguish the populations in the two patches.

The paper is organized as follows. We consider four different situations distinguished by the populations living in the separate patches and by the way predators feed. At first, we consider Holling type II hunting: in Section 2, the predator-prey system occupies the first patch, and the epidemic model patch 2; Section 3 instead deals with an ecoepidemic system in patch 1, while patch 2 serves only as a possible safety niche for the sound prey. The following Section relates the numerical experiments. The following two Sections describe systems in which feeding is modeled via a quadratic mass action term. Section 5 contains again predator-prey and epidemics patches and Section 6 the ecoepidemic model in the first patch and the safety niche in patch 2. Some further numerical simulations are reported in the final Section.

2 Holling type II SP-SI model

Let the patch common to both species be denoted by the index 1 while the index 2 is reserved for the niche unreacheable by the predators. Only in this patch where prey thrive, the epidemics occurs. We take the disease to strongly affect the infected individuals, so that they cannot compete with the sound ones, i.e. the susceptible prey do not feel any intraspecific demographic pressure from the infected ones, nor do the latter reproduce. Migration occurs back and forth from this niche to the territory in which prey is hunted, but only for sound individuals. This assumption, common to this and all the subsequent models, is plausible, since the disease weakens the infected individuals and if some effort must be exerted to reach the other patch, the weaker animals may well not be able to make it.

Let S denote the sound prey, I the infected ones and P the predators. The model reads then

$$\frac{dS_1}{dt} = r_1 S_1 \left(1 - \frac{S_1}{K_1}\right) - a\frac{S_1 P}{H + S_1} - m_{21}S_1 + m_{12}S_2, \qquad (1)$$

$$\frac{dS_2}{dt} = r_2 S_2 \left(1 - \frac{S_2}{K_2}\right) - \gamma S_2 I + \nu I + m_{21}S_1 - m_{12}S_2,$$

$$\frac{dI}{dt} = I[\gamma S_2 - \mu - \nu],$$
$$\frac{dP}{dt} = P\left(\frac{eS_1}{H + S_1} - b\right).$$

The first equation describes the evolution of the prey population which is hunted. We assume that its net reproduction rate r_1 depends on this environment, as well as on the carrying capacity K_1. The predation rate is a, and migration toward patch 2 occurs at rate m_{21} and m_{12} is the one in the opposite direction. The second equation describes the prey in the safe niche, with migration rates having opposite signs, net reproduction rate r_2 and carrying capacity K_2 now related to this habitat. In view of the remarks on the stength of the disease, in the logistic correction term in the sound prey evolution equation, no contribution from the infected is present. Thus infectives do not contribute to intraspecific competition, so that sound individuals do not feel their presence. The new feature here is the fact that sound prey can contract the disease, at rate γ. This process is simply described by a mass-action law. We assume that the disease is recoverable. The third equation states that new infectives are generated via the contact rate term appearing as a loss in the former equation, and leave this class via either a natural plus disease-related mortality μ or a recovery rate ν. No reproduction of infectives is allowed, nor do they feel the interspecific population pressure. The last equation describes the predators dynamics, accounting for natural mortality b and a Michaelis-Menten or Holling type II term for the feeding behavior, with half saturation constant H.

2.1   Preliminaries

The system (1) is constructed by letting migration occur among two niches, in each of which a different type of dynamics is present. We investigate briefly the results of each of these classical models, in terms of our notation, for later reference and comparison purposes.

Assume first that there in no patch 2, i.e. no safety niche. The SI-SP model, in this case becomes a simple SP, predator-prey model, with equilibria

$$Z_0 = O, \quad Z_1 = (K_1, 0), \quad Z_2 = \left(\frac{bH}{e-b}, \frac{r_1}{aK_1}\left(H + \frac{bH}{e-b}\right)\left(K_1 - \frac{bH}{e-b}\right)\right),$$

the latter is feasible for

$$(e-b)K_1 > bH, \quad e > b. \tag{2}$$

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Then Z_0 is unstable, Z_1 is stable for

$$(e - b)K_1 < bH \tag{3}$$

but no Hopf bifurcation can arise here. The equilibrium Z_2 is stable for

$$H^2 r_1 > \left(1 - \frac{b}{e}\right)^2 a P K_1 \tag{4}$$

and imposing equality in the latter, a Hopf bifurcation occurs.

The model without patch 1 is an SIS model, with equilibria

$$W_0 = O, \quad W_1 = (K_2, 0), \quad W_2 = \left(\frac{\mu + \nu}{\gamma}, \frac{r_2}{\mu} \frac{\mu + \nu}{\gamma}\left(1 - \frac{\mu + \nu}{\gamma K_2}\right)\right).$$

W_2 is feasible for

$$\mu + \nu \leq \gamma K_2. \tag{5}$$

The origin is unstable, W_1 is stable for

$$\gamma K_2 < \mu + \nu, \tag{6}$$

and W_2 is if

$$\mu^2 + \gamma \nu K_2 > \nu^2. \tag{7}$$

Thus stability of W_1 occurs if and only if W_2 is infeasible. Note that instability of W_2 means that $\mu \nu^{(-1)}(\mu + \nu) + \gamma K_2 < \mu + \nu$, which violates (5), and thus entails infeasibility of W_2 and therefore feasibility of W_1, see (5). Thus this system can only have either the disease-free or the endemic equilibrium. No other dynamics is possible. The final outcome of the system is determined only by the basic reproductive ratio $\gamma K_2 (\mu + \nu)^{-1}$. Note that for the SI model, $\nu = 0$, (7) is always true.

2.2 Equilibria

We consider now (1). Its boundedness can easily be established by introducing the total environment population $\Pi = S_1 + S_2 + I + P$. On summing the equations (1), for an arbitrary $0 < \eta < \min\{b, \mu\}$, we have

$$\frac{d\Pi}{dt} + \eta \Pi \leq (r_1 + \eta)S_1 - \frac{r_1 S_1^2}{K_1} + (r_2 + \eta)S_2 - \frac{r_2 S_2^2}{K_2} \leq (r_1 + \eta)^2 \frac{K_1}{4 r_1} + (r_2 + \eta)^2 \frac{K_2}{4 r_2} \equiv M$$

so that $\dot{\Pi} \leq -\eta \Pi + M$ and the solutions are ultimately bounded, $\Pi(t) \leq M \eta^{-1} \equiv M^*$ for every $t \geq 0$.

The only possible equilibria of (1) are also easily found, to be the origin $E_0 \equiv O$ together with the boundary points $E_1 \equiv (S_1^{(1)}, S_2^{(1)}, 0, 0)$, $E_2 \equiv (S_1^{(2)}, S_2^{(2)}, 0, P^{(2)})$, $E_3 \equiv (S_1^{(3)}, S_2^{(3)}, I^{(3)}, 0)$, and the coexistence one $E_4 \equiv (S_1^{(4)}, S_2^{(4)}, I^{(4)}, P^{(4)})$.

Note that equilibrium E_1 is obtained by intersecting the two parabolae one gets from the first two equations of (1), namely

$$S_2 = \varphi(S_1) \equiv \frac{S_1}{m_{12}} \left[m_{21} - r_1 \left(1 - \frac{S_1}{K_1} \right) \right],$$

$$S_1 = \psi(S_2) \equiv \frac{S_2}{m_{21}} \left[m_{12} - r_2 \left(1 - \frac{S_2}{K_2} \right) \right].$$

They meet at the origin, and have another intersection in the first quadrant if their other roots are positive and a suitable condition on their slopes at the origin is satisfied; these in turn yield the feasibility conditions of E_1

$$m_{21} < r_1, \quad m_{12} < r_2, \quad r_1 r_2 \geq r_1 m_{12} + r_2 m_{21}. \tag{8}$$

For the other equilibria, we have

$$S_1^{(2)} = \frac{bH}{e-b}, \quad P^{(2)} = \frac{eH}{(e-b)a} \left[m_{12} S_2^{(2)} \frac{e-b}{bH} + r_1 - m_{21} - \frac{r_1 bH}{(e-b)K_1} \right],$$

$$S_2^{(2)} = \frac{K_2}{2r_2} \left[r_2 - m_{12} + \sqrt{(r_2 - m_{12})^2 + 4r_2 m_{21} \frac{bH}{(e-b)K_2}} \right]$$

so that feasibility for E_2 is given by

$$e > b, \quad S_2^{(2)} > \left[\frac{m_{21} - r_1}{m_{12}} + \frac{r_1 bH}{m_{12} K_1 (e-b)} \right] \frac{bH}{e-b}. \tag{9}$$

Then

$$S_2^{(3)} = \frac{\mu + \nu}{\gamma}, \quad S_1^{(3)} = \frac{K_1}{2r_1} \left[r_1 - m_{21} + \sqrt{(r_1 - m_{21})^2 + 4\frac{\mu + \nu}{K_1 \gamma} r_1 m_{12}} \right],$$

$$I^{(3)} = \frac{1}{\mu} \left[r_2 \frac{\mu + \nu}{\gamma} \left(1 - \frac{\mu + \nu}{\gamma K_2} \right) + m_{21} S_1^{(3)} - m_{12} \frac{\mu + \nu}{\gamma} \right],$$

so that E_3 is feasible for

$$S_1^{(3)} \geq \frac{\mu + \nu}{\gamma m_{21}} \left[m_{12} - r_2 + r_2 \frac{\mu + \nu}{\gamma K_2} \right]. \tag{10}$$

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E_4 has the following components

$$S_1^{(4)} = \frac{bH}{e-b}, \quad P^{(4)} = \frac{eH}{a(e-b)} \left[r_1 - m_{21} - \frac{r_1 bH}{(e-b)K_1} + m_{12} \frac{(e-b)(\mu+\nu)}{bH\gamma} \right],$$

$$S_2^{(4)} = \frac{\mu+\nu}{\gamma}, \quad I^{(4)} = \frac{\mu+\nu}{\gamma\mu} \left[r_2 - m_{12} - \frac{r_2(\mu+\nu)}{\gamma K_2} + m_{21} \frac{bH\gamma}{(e-b)(\mu+\nu)} \right]$$

and it is feasible first of all if $e \geq b$ and furthermore if

$$\frac{m_{21}\gamma K_2}{(m_{12} - r_2)\gamma K_2 + r_2(\mu+\nu)} \geq \frac{(e-b)(\mu+\nu)}{bH\gamma} \geq \frac{m_{21} - r_1}{m_{12}} + \frac{r_1 bH}{m_{12}(e-b)K_1}. \tag{11}$$

2.3 Stability

The Jacobian of the system (1) is

$$J = \begin{pmatrix} J_{11} & m_{12} & 0 & -\frac{aS_1}{H+S_1} \\ m_{21} & J_{22} & \nu - \gamma S_2 & 0 \\ 0 & \gamma I & \gamma S_2 - \mu - \nu & 0 \\ \frac{ePH}{(H+S_1)^2} & 0 & 0 & \frac{eS_1}{H+S_1} - b \end{pmatrix} \tag{12}$$

with

$$J_{11} = r_1 - 2\frac{r_1}{K_1}S_1 - m_{21} - \frac{aPH}{(H+S_1)^2}, \quad J_{22} = r_2 - 2\frac{r_2}{K_2}S_2 - m_{12} - \gamma I.$$

The eigenvalues of J at the origin are $-\nu - \mu$ and $-b$ and the roots of the quadratic $\lambda^2 + \lambda(m_{21} + m_{12} - r_1 - r_2) + r_1 r_2 - r_1 m_{12} - r_2 m_{21} = 0$. The Routh-Hurwitz conditions ensure stability for

$$r_1 r_2 > r_1 m_{12} + r_2 m_{21}, \quad r_1 + r_2 < m_{12} + m_{21}. \tag{13}$$

At E_1 we find the eigenvalues

$$\gamma S_2^{(1)} - \mu - \nu, \quad \frac{eS_1^{(1)} - bH - bS_1^{(1)}}{H + S_1^{(1)}} \tag{14}$$

and those of the reduced matrix $J_{[1,2;1,2]}$, where the notation emphasizes the rows and columns of the original matrix J that are taken, thus

$$J_{[1,2;1,2]} = \begin{pmatrix} r_1 - 2\frac{r_1}{K_1}S_1^{(1)} - m_{21} & m_{12} \\ m_{21} & r_2 - 2\frac{r_2}{K_2}S_2^{(1)} - m_{12} \end{pmatrix}. \tag{15}$$

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Using the Routh-Hurwitz conditions, combining with the earlier eigenvalues, stability occurs if and only if

$$S_1^{(1)} < \frac{bH}{e-b}, \quad S_2^{(1)} < \frac{\mu+\nu}{\gamma} \tag{16}$$

and

$$r_1 + r_2 < 2\left(r_1\frac{S_1^{(1)}}{K_1} + r_2\frac{S_2^{(1)}}{K_2}\right) + m_{12} + m_{21}, \tag{17}$$

$$r_1 r_2 \left(1 - 2\frac{S_1^{(1)}}{K_1}\right)\left(1 - 2\frac{S_2^{(1)}}{K_2}\right) > r_1 m_{12}\left(1 - 2\frac{S_1^{(1)}}{K_1}\right) + r_2 m_{21}\left(1 - 2\frac{S_2^{(1)}}{K_2}\right).$$

For E_2 one eigenvalue is $\gamma S_2^{(2)} - \mu - \nu$. The other ones are roots of the following cubic, where by $J_{ik}^{(2)}$ we denote the ik element of the Jacobian J evaluated at E_2,

$$\sum_{i=0}^{3} a_i \lambda^i = 0, \tag{18}$$

with

$$a_2 = -(J_{11}^{(2)}+J_{22}^{(2)}), \quad a_1 = J_{11}^{(2)} J_{22}^{(2)} - m_{12}m_{21} - \frac{abPH}{(H + S_1^{(2)})^2}, \quad a_0 = \frac{abPH J_{22}^{(2)}}{(H + S_1^{(2)})^2}. \tag{19}$$

Now the Routh-Hurwitz criterion for stability requires that $a_0 > 0$, $a_2 > 0$, $a_1 a_2 > a_0 a_3 = a_0$. From the definition of a_0 it follows then that we must have $J_{22}^{(2)} > 0$, and from the one of a_2, also $J_{11}^{(2)} < -J_{22}^{(2)} < 0$. Hence $J_{11}^{(2)} J_{22}^{(2)} < 0$ implying $a_1 < 0$, so that the remaining condition $a_1 a_2 > a_0$ is impossible to verify. Thus E_2 is inconditionally unstable.

At E_3, one eigenvalue is $(H + S_1^{(3)})^{-1}[(e-b)S_1^{(3)} - bH]$ and the others are the roots of the characteristic equation (18) which has coefficients

$$a_0 = -\mu\gamma I J_{11}^{(3)}, \quad a_1 = J_{11}^{(3)} + J_{22}^{(3)} + \mu\gamma I - m_{12}m_{21}, \quad a_2 = -(J_{11}^{(3)} + J_{22}^{(3)}),$$

and to satisfy the Routh-Hurwitz conditions, we need to require

$$J_{11}^{(3)} < 0, \quad J_{22}^{(3)} < -J_{11}^{(3)}$$

for $a_0 > 0$ and $a_2 > 0$ respectively, while the remaining condition becomes

$$J_{11}^{(3)}[J_{11}^{(3)} J_{22}^{(3)} - m_{12}m_{21}] + J_{22}^{(3)}[J_{11}^{(3)} J_{22}^{(3)} + \mu\gamma I - m_{12}m_{21}] < 0, \tag{20}$$

i.e.

$$J_{22}^{(3)}\mu\gamma I < (J_{11}^{(3)} + J_{22}^{(3)})[J_{11}^{(3)} J_{22}^{(3)} - m_{12}m_{21}]. \tag{21}$$

It is easily seen that (21) is impossible if $J_{22}^{(3)} > 0$, hence letting $J_{11}^{(3)} = A - m_{21}$, $J_{22}^{(3)} = B - m_{12}$, the conditions (20) and (21) are further implied by

$$AB - Am_{12} - Bm_{21} > 0$$

which is ensured if we take $A, B < 0$ i.e.

$$S_1^{(3)} > \frac{1}{2}K_1, \quad S_2^{(3)} > \frac{1}{2}K_2. \tag{22}$$

At E_4 the characteristic equation is a quartic,

$$\sum_{i=0}^{4} b_i \lambda^i = 0, \tag{23}$$

with

$$b_0 = \gamma\mu I^{(4)} \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3}, \quad b_1 = -\left[J_{22}^{(4)} \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3} + \gamma\mu I^{(4)} J_{11}^{(4)}\right],$$

$$b_2 = J_{11}^{(4)} J_{22}^{(4)} - m_{12}m_{21} + \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3} + \gamma\mu I^{(4)}, \quad b_3 = -\left(J_{11}^{(4)} + J_{22}^{(4)}\right).$$

The Routh-Hurwitz conditions ensure stability if

$$b_3 > 0, \quad b_0 > 0, \quad b_2 b_3 > b_1, \quad b_1(b_2 b_3 - b_1) > b_0 b_3^2.$$

Thus the first condition holds always and last condition requires $J_{11}^{(4)} + J_{22}^{(4)} < 0$. The remaining ones give

$$\left(J_{11}^{(4)} + J_{22}^{(4)}\right)\left[J_{11}^{(4)} J_{22}^{(4)} - m_{12}m_{21}\right] + J_{11}^{(4)} \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3} + J_{22}^{(4)}\gamma\mu I^{(4)} < 0, \tag{24}$$

$$J_{22}^{(4)} \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3} + \gamma\mu I^{(4)} J_{11}^{(4)} + \gamma\mu I^{(4)} \frac{\left(J_{11}^{(4)} + J_{22}^{(4)}\right)^2}{(b_2 b_3 - b_0)} \frac{aeHP^{(4)}S_1^{(4)}}{(H + S_1^{(4)})^3} < 0.$$

2.4 Hopf bifurcations

At the origin if we impose the quadratic to have purely imaginary roots, via

$$r_1 + r_2 = m_{12} + m_{21}, \quad r_1 r_2 < r_1 m_{12} + r_2 m_{21}, \tag{25}$$

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we see that limit cycles can be obtained, as in the $m_{12} - m_{21}$ parameter plane the conditions (25) are seen to have solutions.

At E_1 again we can obtain a Hopf bifurcation by acting on the quadratic characteristic equation, while requiring the remaining eigenvalues, one of which differs in the two cases, to be negative. We are led to

$$r_1 + r_2 = m_{12} + m_{21} + 2\left(\frac{r_1}{K_1}S_1^{(1)} + \frac{r_2}{K_2}S_2^{(1)}\right), \quad (26)$$

$$r_1\left[1 - \frac{2S_1^{(1)}}{K_1}\right]r_2\left[1 - \frac{2S_2^{(1)}}{K_2}\right] < r_1\left[1 - \frac{2S_1^{(1)}}{K_1}\right]m_{12} + r_2\left[1 - \frac{2S_2^{(1)}}{K_2}m_{21}\right], (27)$$

which again are seen to have a solution in the $m_{12} - m_{21}$ parameter plane, taking into account that (26) requires

$$r_1 - 2\frac{r_1}{K_1}S_1^{(1)} + r_2 - 2\frac{r_2}{K_2}S_2^{(1)} > 0$$

and thus the case of both terms on the left of (27) being simultaneously negative cannot occur.

At E_3 the cubic needs to be split as follows

$$\sum_{i=0}^{3} a_i\lambda^i = (\lambda^2 + \widehat{B}^2)(\lambda^2 + \widehat{C}) = 0$$

so that by expanding and equating coefficients of like powers, we find the relation

$$a_0 = a_1 a_2 \qquad (28)$$

that must be satisfied, and $\widehat{B} = \sqrt{b_1}$, $\widehat{C} = a_2$. Writing then $J_{11} = A - m_{12}$, $J_{22} = B - m_{21}$ one can observe that $S_1^{(3)}$ and A are both independent of the paramters r_2 and K_2. Choosing as bifurcation parameter the former, (28) can be expressed as a quadratic equation in r_2,

$$\sum_{k=0}^{2} r_2^k \eta_k = 0, \quad R = -\frac{\gamma}{\mu}\left(m_{21}S_1^{(3)} - m_{12}\frac{\mu + \nu}{\mu}\right) \qquad (29)$$

$$\eta_2 = (A - m_{21})\left(\frac{\nu^2 - \mu^2 - \nu\gamma K_2}{\gamma\mu K_2}\right)^2 +$$

$$\left(1 - \frac{\nu + \mu}{\gamma K_2}\right)(\nu + \mu)\left[\left(1 - 2\frac{S_1^{(3)}}{K_1}\right) - \frac{\nu + \mu}{\mu}\left(1 - \frac{\nu + \mu}{\gamma K_2}\right)\right],$$

$$\eta_1 = \left[2(A - m_{21})R - (A - m_{21})^2 - m_{12}m_{21}\right]\frac{\nu^2 - \mu^2 - \nu\gamma K_2}{\gamma\mu K_2}$$

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$$+ R \left[\left(1 - \frac{\nu + \mu}{\gamma K_2} \right) (\nu + \mu) - \left(1 - 2 \frac{S_1^{(3)}}{K_1} \right) + \frac{\nu + \mu}{\mu} \left(1 - \frac{\nu + \mu}{\gamma K_2} \right) \right],$$

$$\eta_0 = (A - m_{21}) R^2 - (A - m_{12} - m_{21}) A m_{12} - R^2 + \left[(A - m_{21})^2 - m_{12} m_{21} \right] R.$$

Thus a sufficient condition to ensure the existence of one positive root, i.e. one feasible value for the bifurcation parameter $r_2^\dagger$, is to impose

$$\eta_2 \eta_0 < 0. \tag{30}$$

At E_4 we can proceed in a similar fashion, expanding (23)

$$\sum_{i=0}^{4} b_i \lambda^i = (\lambda^2 + \omega^2)(\lambda + \rho)(\lambda + \sigma) = 0$$

and equating coefficients to get the condition

$$b_1^2 + b_3^2 b_0 = b_1 b_2 b_3. \tag{31}$$

An appropriate bifurcation parameter can once more be found to be again r_2. Expansion of the condition in terms of the system parameters leads this time to a cubic equation,

$$\sum_{k=0}^{3} r_2^k \phi_k = 0. \tag{32}$$

The parameter expressions are very involved and therefore omitted. Once again a feasible value for the Hopf bifurcation to occur r_2^* is obtained by imposing

$$\phi_3 \phi_0 < 0. \tag{33}$$

2.5 Results interpretations

The origin E_0 can be stabilized, i.e. the whole ecosystem may be wiped out, under suitably unfavorable conditions, (13), in contrast to what happens to the two separate models corresponding to each single patch, namely equilibria Z_0 and W_0. Thus, surprisingly, the "refuge" niche could be an endangerement for the whole environment, threatening its long term sustainability. In addition the only other possible stable equilibria are the predator-free one E_3, the predator- and disease-free point E_1 and the coexistence of the whole ecosystem E_4. Thus if the origin is unstable, the prey can never be wiped

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out of the system. In this sense the existence of the niche protects them, but note that this happens also for the SP submodel, since the equilibria Z_1 and Z_2 contain the prey. The instability of E_2 coupled with the one of the origin and of E_1 renders impossible the disease eradication, thus in this case the niche establishes the disease in the ecosystem. When E_3 is stable, the predators are wiped out.

Note that for the SP subsystem for

$$\sigma \equiv \frac{(e-b)K_1}{bH} > 1 \tag{34}$$

the predators invade the environment, since Z_1 the predator-free equilibrium, becomes unstable. Also in the SI subsystem for the basic reproduction number, [14]

$$\rho \equiv \frac{\mu + \nu}{\gamma} < 1 \tag{35}$$

the disease gets eradicated, while it remains endemic conversely.

In the combined model, the disease together with the predators can be wiped out for low enough prey levels, see (16). A similar condition for the prey in patch 1 must be ensured for stability of E_3, still given by the first condition (16), but here stability is instead ensured if the prey in both patches are also above certain levels, see (22).

3 Holling type II SIP-S model

In this second model the ecoepidemics occurs in the first patch, the second one is a safe niche only for the sound prey, which are the only ones able to migrate there. Once again, the diseased individuals are assumed not to be able to make the effort to reach the safe environment. Predators do not feed on infected prey, though.

$$
\begin{aligned}
\frac{dS_1}{dt} &= r_1 S_1 \left(1 - \frac{S_1}{K_1}\right) - a\frac{S_1 P}{H + S_1} - m_{21}S_1 + m_{12}S_2 - \gamma S_1 I + \nu I, \\
\frac{dS_2}{dt} &= r_2 S_2 \left(1 - \frac{S_2}{K_2}\right) + m_{21}S_1 - m_{12}S_2, \tag{36} \\
\frac{dI}{dt} &= I[\gamma S_1 - \mu - \nu], \\
\frac{dP}{dt} &= P\left(\frac{eS_1}{H + S_1} - b\right).
\end{aligned}
$$

Boundedness for (36) is established as for the model (1).

The equilibria are $Q_0 = E_0 = O$, $Q_1 = E_1$, with the same feasibility conditions (8), $Q_2 = E_2$, again with same feasibility conditions (9) and $Q_3 = (S_1^{(3)}, \widetilde{S_2^{(3)}}, \widetilde{I^{(3)}}, 0)$, with components given by

$$S_1^{(3)} = \frac{\mu + \nu}{\gamma}, \quad \widetilde{S_2^{(3)}} = \frac{K_2}{2r_2}\left[r_2 - m_{12} + \sqrt{(r_2 - m_{12})^2 + 4m_{21}\frac{r_2}{K_2}\frac{\mu + \nu}{\gamma}}\right],$$

$$\widetilde{I^{(3)}} = \frac{1}{\mu}\left[r_1\frac{\mu + \nu}{\gamma}\left(1 - \frac{\mu + \nu}{K_1\gamma}\right) - m_{21}\frac{\mu + \nu}{\gamma} + m_{12}\widetilde{S_2^{(3)}}\right].$$

Note that in this case the interior equilibrium does not exist, i.e. coexistence in this metaecoepidemic environment is not possible.

3.1 Stability

The Jacobian of the system differs slightly in the structure from (12),

$$J = \begin{pmatrix} J_{11} & m_{12} & \nu - \gamma S_1 & -\frac{aS_1}{H+S_1} \\ m_{21} & J_{22} & 0 & 0 \\ \gamma I & 0 & \gamma S_1 - \mu - \nu & 0 \\ \frac{ePH}{(H+S_1)^2} & 0 & 0 & \frac{eS_1}{H+S_1} - b \end{pmatrix} \tag{37}$$

with

$$J_{11} = r_1 - 2\frac{r_1}{K_1}S_1 - m_{21} - \frac{aPH}{(H+S_1)^2} - \gamma I, \quad J_{22} = r_2 - 2\frac{r_2}{K_2}S_2 - m_{12}.$$

The eigenvalues of J at the origin are exactly the same as for E_0 in (1), thus the stability conditions coincide with (13).

At Q_1 we find the eigenvalues

$$\gamma S_1^{(1)} - \mu - \nu, \quad \frac{(e-b)S_1^{(1)} - bH}{H + S_1^{(1)}}$$

the second of which coincides with the second eigenvalue of E_1 (14), and those remaining are also the other ones of E_1 coming from the quadratic of the same reduced matrix (15). Thus using the Routh-Hurwitz conditions, combining with the earlier eigenvalues, stability occurs if and only if conditions (17) hold, together with

$$S_1^{(1)} < \min\left\{\frac{\mu + \nu}{\gamma}, \frac{bH}{e - b}\right\}. \tag{38}$$

For Q_2 one eigenvalue differs from the corresponding one of E_2, namely it is $\gamma S_1^{(2)} - \mu - \nu$. The other ones are the roots of the cubic (18), with the

same coefficients (19) as for the equilibrium E_2 of (1). Hence inconditional instability follows.

At Q_3 one eigenvalue is $(H + S_1^{(3)})^{-1}[(e - b)S_1^{(3)} - bH]$, which of course needs to be negative for stability, the others are the roots of a cubic (18) with coefficients

$$\widetilde{a_0} = -\gamma\mu\widetilde{I^{(3)}}\,\widetilde{J_{22}^{(3)}}, \quad \widetilde{a_1} = \widetilde{J_{11}^{(3)}}\,\widetilde{J_{22}^{(3)}} + \gamma\mu\widetilde{I^{(3)}} - m_{12}m_{21}, \quad \widetilde{a_2} = -(\widetilde{J_{11}^{(3)}} + \widetilde{J_{22}^{(3)}}).$$

Considering the equilibrium definition it follows that

$$\widetilde{J_{11}^{(3)}} = -\frac{\nu\widetilde{I^{(3)}} + m_{12}\widetilde{S_2^{(3)}}}{S_1^{(3)}} - \frac{r_1 S_1^{(3)}}{K_1} < 0, \quad \widetilde{J_{22}^{(3)}} = -\frac{m_{21}S_1^{(3)}}{\widetilde{S_2^{(3)}}} - \frac{r_2\widetilde{S_2^{(3)}}}{K_2} < 0.$$

Thus $\widetilde{a_0} > 0$, $\widetilde{a_2} > 0$ and the remaining condition for stability becomes

$$-(\widetilde{J_{11}^{(3)}} + \widetilde{J_{22}^{(3)}})(\widetilde{J_{11}^{(3)}}\,\widetilde{J_{22}^{(3)}} - m_{12}m_{21}) - \gamma\mu\widetilde{I^{(3)}}\,\widetilde{J_{11}^{(3)}} > 0 \tag{39}$$

and the latter is implied by (22) evaluated at $S_1^{(3)}$ and $\widetilde{S_2^{(3)}}$.

3.2 Hopf bifurcations

The analysis for the points Q_0 and Q_1 is exactly the same as for E_0 and E_1.

At Q_3 we proceed once again as for E_3 remarking that (28) in this case leads also to a quadratic equation, this time in the bifurcation parameter r_1,

$$\sum_{i=0}^{2} \theta_i r_1^i = 0.$$

In this case, we find

$$\theta_2 = -J_{22}\left[\left(1 - 2\frac{\widetilde{S_2^{(3)}}}{K_2}\right) - \frac{\gamma}{\mu}\left(1 - \frac{\widetilde{S_1^{(3)}}}{K_1}\right)\right]^2$$

$$-\gamma\left(1 - 2\frac{\widetilde{S_2^{(3)}}}{K_2}\right)\left(1 - \frac{\widetilde{S_1^{(3)}}}{K_1}\right)\widetilde{S_1^{(3)}} + \frac{\gamma^2}{\mu}\left(1 - \frac{\widetilde{S_1^{(3)}}}{K_1}\right)^2\left(\widetilde{S_1^{(3)}}\right)^2$$

and in view of (22) and the fact that $J_{22} < 0$, requiring then

$$\frac{1}{2}K_1 < \widetilde{S_1^{(3)}} < K_1 \tag{40}$$

ensures that $\theta_2 > 0$, so that to have a feasible value for the Hopf bifurcation parameter $r_1^\dagger$ it is enough to require

$$\theta_0 < 0. \tag{41}$$

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3.3 Discussion

Note that for the alternative model, we can delete only patch 2, to make a reasonable comparison. We get an ecoepidemic model in patch 1 which has been analyzed and is known to produce bifurcations, [4] for the case of no external removal.

Again in the metaecosystem the origin can become stable, indicating the possibility of extinction, caused by the existence of the survival niche. Also here as well as for (1), the instability of E_2 means that the disease alone cannot be eradicated. Equilibrium Q_1 has a more stringent condition on the prey size in patch 1, compare (38) and (16) and a more relaxed one for the prey in the safety niche, since the latter have only to obey conditions (17) as in (1). In this model it is also not possible to eradicate the disease while preserving all the remaining populations, since Q_2 is always unstable. A situation common for this case and to (1) is that the parameter a plays no role whatsoever in the bifurcations. But the main result in this context is that the metaecoepidemic model does not sustain all the populations. Therefore the existence of a safety niche for the prey surprisingly becomes a negative factor from the biodiversity point of view.

4 Simulations

To further investigate the metaecoepidemic model with Holling type II dynamics, we have performed numerical experiments on (1). Some of the results are here reported. In all the figures the left column contains the graphs of the populations in two patches as separate entities, without any communication between them. With the same parameters, this time including nonzero migration rates, we run the simulations again and report their results on the right column.

Figure 1 shows that the limit cycles present in the underlying demographic model in patch 1 get transferred via the migration also to the second patch. In this particular case we observe also that the disease is eradicated in patch 2, but the oscillations amplitudes become larger and larger and ultimately the system collapses. The Figure is obtained from the following hypothetical parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 1.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 2$, $r_2 = 1$, $K_2 = 150$, $\gamma = 0.5$, $\nu = 0.3$, $\mu = 0.3$, $e = 1.3$, $b = 0.1$. In Figure 2 we show instead that stable coexistence equilibria in the two patches can be reached in spite of the fact that in the purely demographic model oscillations are present. The parameters in this case are $r_1 = 1.4$, $K_1 = 100$, $a = 1.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 2$, $r_2 = 1$, $K_2 = 150$, $\gamma = 0.75$, $\nu = 0.03$, $\mu = 0.03$,
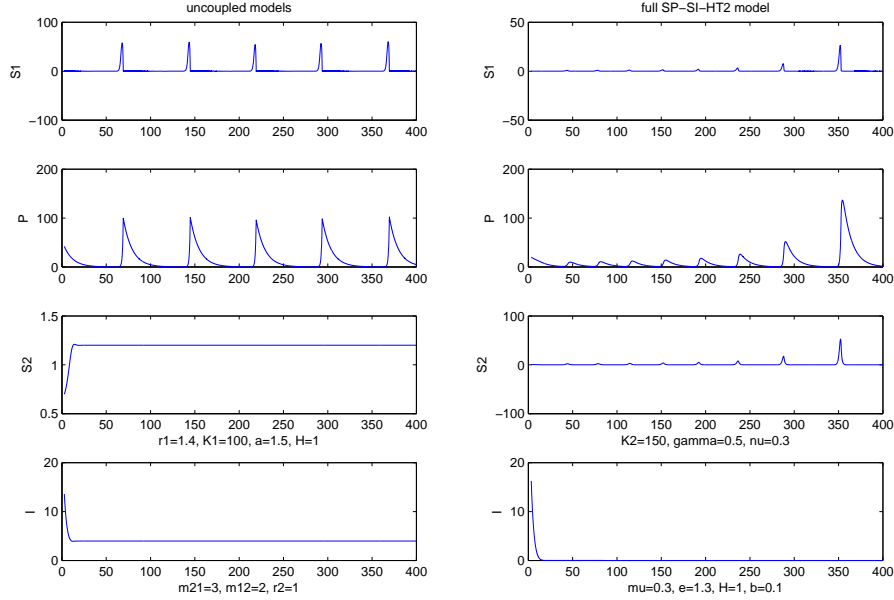
Figure 1: Demographic oscillations are carried through to the epidemics patch.

$e = 1.3$, $b = 0.1$. Figure 3 instead shows that the limit cycles inherited by the underlying demographic model are present in both patches, but in this case the disease, endemic in the isolated patch 2, is wiped out in the model with migrations, for the parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 1.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 2$, $r_2 = 1$, $K_2 = 150$, $\gamma = 0.75$, $\nu = 0.3$, $\mu = 0.03$, $e = 1.3$, $b = 0.1$ Figure 4, obtained for the parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 1.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 2$, $r_2 = 1$, $K_2 = 150$, $\gamma = .5$, $\nu = 0.3$, $\mu = .3$, $e = 0.8$, $b = .9$, instead shows that the same behavior of the two separate patches can be shown also by the combined metaecoepidemic model, which settles to the predator-free equilibrium E_3.

5   Holling type I SI-SP case

We turn now to the setting up and the analysis of metaecoepidemic models with mass action predation terms. At first we formulate the analogous model of system (1), namely

$$\frac{dS_1}{dt} = r_1 S_1 \left(1 - \frac{S_1}{K_1} \right) - a S_1 P - m_{21} S_1 + m_{12} S_2, \qquad (42)$$
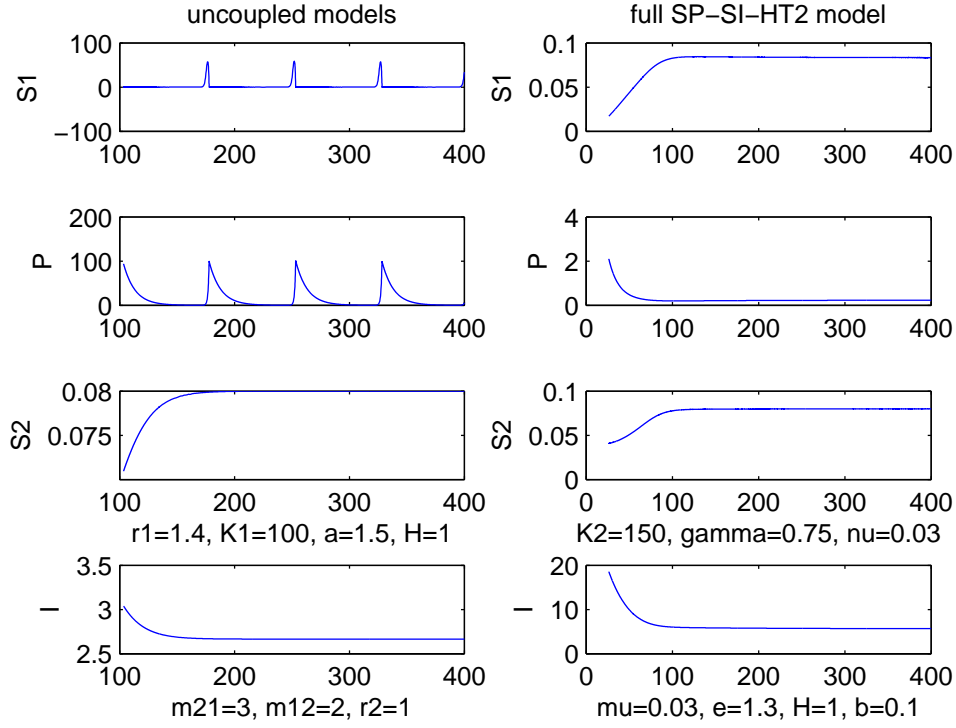
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Figure 2: Demographic oscillations are damped in the metaecoepidemic model.

$$\frac{dS_2}{dt} = r_2 S_2 \left(1 - \frac{S_2}{K_2}\right) - \gamma S_2 I + \nu I + m_{21} S_1 - m_{12} S_2,$$

$$\frac{dI}{dt} = I[\gamma S_2 - \mu - \nu],$$

$$\frac{dP}{dt} = P(eS_1 - b).$$

For this model, equilibria are the points $U_0 = O$, $U_1 = E_1$, $U_2 = (\frac{b}{e}, \widehat{S_2^{(2)}}, 0, \widehat{P^{(2)}})$ here given by

$$\widehat{S_2^{(2)}} = \left[r_2 - m_{12} + \sqrt{(r_2 - m_{12})^2 + 4m_{21}\frac{br_2}{eK_2}}\right] \frac{K_2}{2r_2}, \tag{43}$$

$$\widehat{P^{(2)}} = \left[r_1 \frac{b}{e}\left(1 - \frac{b}{eK_1}\right) + m_{12}\widehat{S_2^{(2)}} - m_{21}\frac{b}{e}\right] \frac{e}{ab} \tag{44}$$
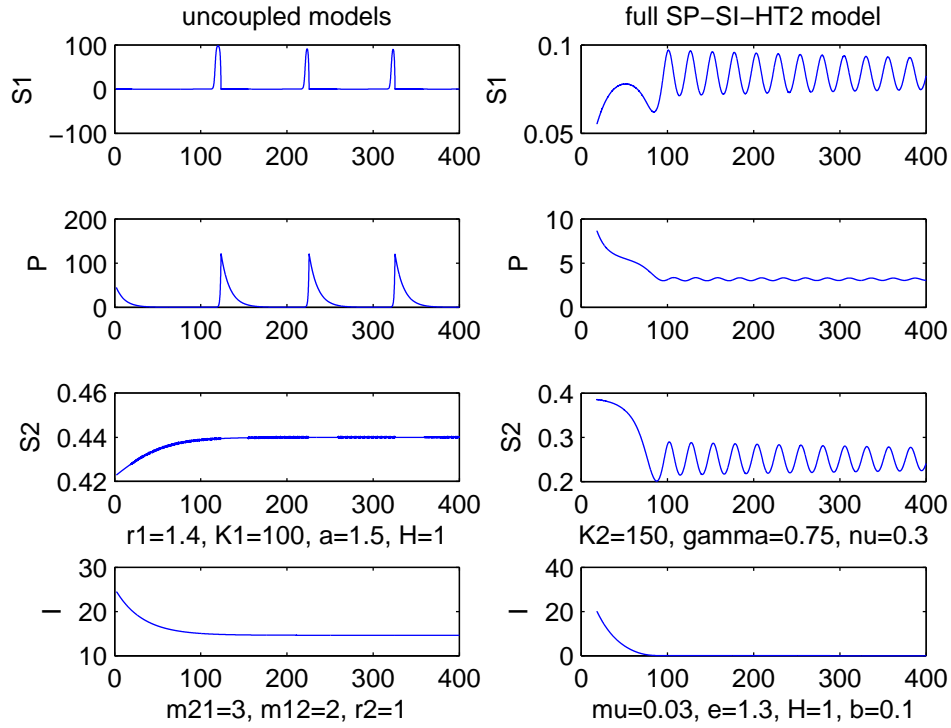
Figure 3: The disease is wiped out in the metaecoepidemic model.

feasible for

$$r_1 \frac{b}{e} \left(1 - \frac{b}{eK_1} \right) + m_{12} \widehat{S_2^{(2)}} \geq m_{21} \frac{b}{e}. \tag{45}$$

Also, $U_3 \equiv E_3$ with the very same feasibility conditions (10). For U_4 the coexistence equilibrium

$$\widehat{S_1^{(4)}} = \frac{b}{e}, \quad \widehat{I^{(4)}} = \frac{1}{\mu} \left[r_2 \frac{\mu + \nu}{\gamma} \left(1 - \frac{\mu + \nu}{\gamma K_2} \right) + m_{21} \frac{b}{e} - m_{12} \frac{\mu + \nu}{\gamma} \right] \tag{46}$$

$$\widehat{S_2^{(4)}} = \frac{\mu + \nu}{\gamma}, \quad \widehat{P^{(4)}} = \left[r_1 \frac{b}{e} \left(1 - \frac{b}{eK_1} \right) + m_{12} \frac{\mu + \nu}{\gamma} - m_{21} \frac{b}{e} \right] \frac{e}{ab}, \tag{47}$$

with feasibility conditions

$$r_2 \frac{\mu + \nu}{\gamma} \left(1 - \frac{\mu + \nu}{\gamma K_2} \right) \geq m_{12} \frac{\mu + \nu}{\gamma} - m_{21} \frac{b}{e} \geq r_1 \frac{b}{e} \left(\frac{b}{eK_1} - 1 \right). \tag{48}$$

The boundedness of the solution trajectories is established with the same steps as for (1), recalling that $e < a$.
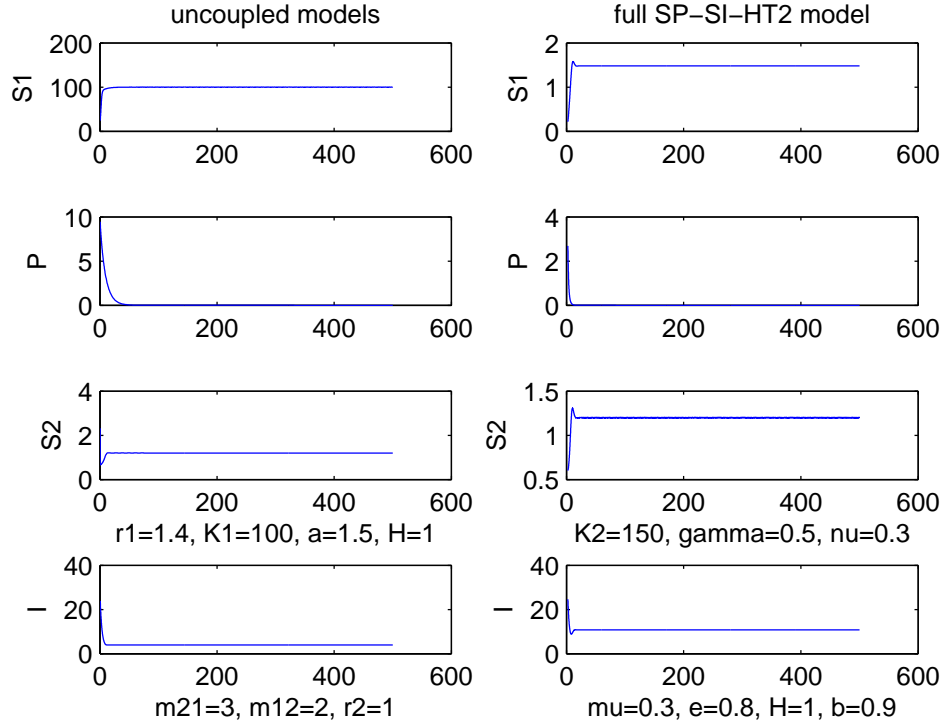
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Figure 4: The metaecoepidemic model shows the same behavior of the two separate models, settling to equilibrium E_3.

The Jacobian differs slightly from (12), namely some of its entries are different,

$$J_{11} = r_1 - 2\frac{r_1}{K_1}S_1 - m_{21} - aP, \quad J_{14} = -aS_1, \quad J_{41} = eP.$$

The origin has the same stability properties as for (1) namely it is stable when (13) hold. The point U_1 coincides in part with E_1 also for stability purposes, i.e. it has two different eigenvalues, $\gamma S_2^{(1)} - \mu - \nu$, $eS_1^{(1)} - b$, while the remaining originate from the same quadratic as for E_1, so that its stability is ensured by (17) and

$$S_2^{(1)} < \frac{\mu + \nu}{\gamma}, \quad S_1^{(1)} < \frac{b}{e}. \tag{49}$$

For U_2 the analysis follows the same steps as for E_2 and it is again inconditionally unstable. At U_3 one eigenvalue is $eS_1 - b$ which is negative if

$$e(\mu + \nu) < \gamma b \tag{50}$$

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and once again the remaining stability analysis coincides with the one of E_3, thus stability is ensured by (22).

At U_4 we get a quartic, with coefficients

$$\widehat{a_0} = ae\gamma \widehat{P^{(4)}} \widehat{S_1^{(4)}} \widehat{I^{(4)}} > 0, \quad \widehat{a_1} = -(\gamma\mu \widehat{I^{(4)}} \widehat{J_{11}^{(4)}} + ae \widehat{P^{(4)}} \widehat{S_1^{(4)}} \widehat{J_{22}^{(4)}}),$$

$$\widehat{a_2} = \widehat{J_{11}^{(4)}} + \widehat{J_{22}^{(4)}} + \gamma\mu \widehat{I^{(4)}} + m_{12}m_{21} + ae \widehat{P^{(4)}} \widehat{S_1^{(4)}}, \quad \widehat{a_3} = -(\widehat{J_{11}^{(4)}} + \widehat{J_{22}^{(4)}}).$$

For stability we need

$$-(J_{11} + J_{22}) > 0, \quad \widehat{a_2}\widehat{a_3} > \widehat{a_1}, \quad \widehat{a_1}(\widehat{a_2}\widehat{a_3} - \widehat{a_1}) > \widehat{a_0}\widehat{a_3}^2. \tag{51}$$

If $J_{11}, J_{22} < 0$ the first two conditions (51) are satisfied.

In this case the search for Hopf bifurcations for Q_3 coincides with the one for E_3, while in the case of Q_4, we are led once again to a cubic

$$\sum_{k=0}^{3} \pi_k r_2^k = 0$$

in the bifurcation parameter r_2. A sufficient condition then for having a feasible value for the parameter would again be

$$\pi_3 \pi_0 < 0. \tag{52}$$

6 Holling type I SIP-S case

The final model we consider is the counterpart of (36). Again, no "satiation effect", modeled by a Michaelis Menten term is here assumed:

$$\frac{dS_1}{dt} = r_1 S_1 \left(1 - \frac{S_1}{K_1}\right) - aS_1 P - m_{21}S_1 + m_{12}S_2 - \gamma S_1 I + \nu I, \tag{53}$$

$$\frac{dS_2}{dt} = r_2 S_2 \left(1 - \frac{S_2}{K_2}\right) + m_{21}S_1 - m_{12}S_2,$$

$$\frac{dI}{dt} = I[\gamma S_1 - \mu - \nu],$$

$$\frac{dP}{dt} = P(eS_1 - b).$$

The equilibria are found as follows: $R_0 = O$, $R_1 \equiv E_1$, $R_2 \equiv U_2$, $R_3 \equiv Q_3$, but the interior equilibrium does not exist in general, unless $b\gamma = e(\mu + \nu)$ in which case it is not unique, it becomes a line of equilibria and will not by analyzed any further.

The Jacobian in this case differs from (37) in the elements

$$J_{11} = r_1 - 2r_1 \frac{S_1}{K_1} - aP - \gamma I - m_{21}, \quad J_{14} = -aS_1, \quad J_{41} = eP, \quad J_{44} = eS_1 - b.$$

At R_0 the stability analisis is the same as for E_0, at R_1 two eigenvalues are $\gamma S_1^{(1)} - \mu - \nu$, $eS_1^{(1)} - b$, and the remaining quadratic coincides with the one of E_1. Thus stability is implied by (17) and

$$S_1^{(1)} < \max\left\{\frac{\mu + \nu}{\gamma}, \frac{b}{e}\right\}. \tag{54}$$

For R_2 only the first eigenvalue differs, namely $\gamma \frac{b}{e} - \mu - \nu$, the others are those of U_2 and therefore it is again inconditionally unstable. At R_3 the first eigenvalue is $eS_1^{(3)} - b$, the others are those of Q_3, so that stability is achieved for (50), i.e. implied by (22), and (39).

The particular case SI-SP model with no patch 2, gives the equilibria $L_0 \equiv O$, $L_1 = (\frac{b}{e}, \frac{r_1}{a}[1 - \frac{b}{3K_1}])$. The former is unstable, the latter always stable. When patch 1 is absent, we get the same equilibria W_0, W_1, W_2 found earlier. For the SIP-S model we get only the standard quadratic ecoepidemic model, [22].

7 Simulations

To support the theoretical analysis, more experiments have been carried out. We report here some of the results obtained for those related to model (53). Figure 5 shows that the predator-free equilibrium in the uncoupled model contains the endemic disease with a moderate prevalence. In presence of the refuge, while the susceptible levels in both patches are essentially unaltered, for S_1, or for S_2 moderately decreased, of about 5%, the infected experience a 45-fold increase! Evidently, if the goal is the disease fight, the safety niche in this case is to be avoided. On the contrary, in a two-patch ecosystem as described here, the removal of the safety niche contributes to significantly decreasing the disease prevalence. Also, for migration rates that are 10 times higher, $m_{21} = 0.3$, $m_{12} = 0.6$, the decrease of the sound population in patch 2 is more that 50%, while the infected in patch one increase almost 200 times! Also, in these conditions a decrease of the disease incidence to $\gamma = 0.5$ does not seem to affect the final equilibrium values, remaining at about 1600. In decreasing the incidence value we found essentially little change in the endemic value of the disease equilibrium, until about $\gamma = 0.105$ where the latter drops to low values. In figure 6 we show instead that the disease-free
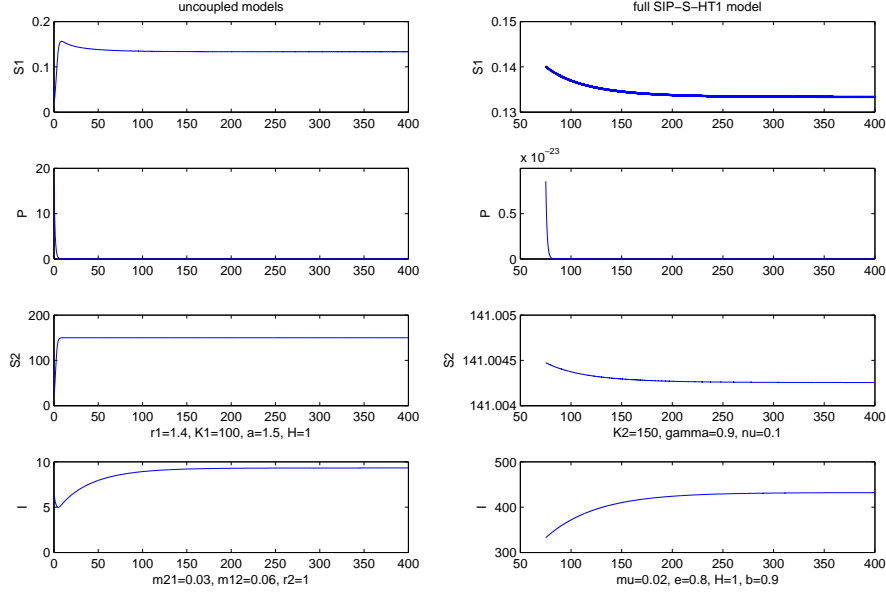
Figure 5: Equilibrium R_3, for the parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 1.5$, $H = 1$, $m_{21} = 0.03$, $m_{12} = 0.06$, $r_2 = 1$, $K_2 = 150$, $\gamma = .9$, $\nu = 0.1$, $\mu = .02$, $e = 0.8$, $b = .9$.

stable equilibrium in the SIP phase space of the single patch model is also reached, but at a faster pace, in the metaecoepidemic model, R_2, for the parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 3.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 5$, $r_2 = 1$, $K_2 = 150$, $\gamma = .25$, $\nu = 0.1$, $\mu = .2$, $e = 0.8$, $b = .2$. Lower migration rates seem to decrease the amplitude of the oscillations and to increase instead their frequencies. Figure 7 shows that the stable disease-free coexistence equilibrium is reached by the single patch system, while in the second patch the susceptible population thrives at carrying capacity. By allowing migration rates among the patches, the latter drops to very low levels, while the equilibrium in patch 1 remains essentially unaltered. For a relevant difference between the migration rates, $m_{21} = 30$, $m_{12} = .05$ and a highly virulent disease, $\gamma = .95$, coupled with the remaining parameters $r_1 = 1.4$, $K_1 = 10$, $a = .5$, $H = 1$, $r_2 = 1$, $K_2 = 150$, $\nu = 0.7$, $\mu = .2$, $e = 0.2$, $b = .2$, one can observe that the predator-free endemic equilibrium of patch 1 is converted into a disease-free equilibrium in the metaecoepidemic model, Figure 8, but raising the emigration rate from patch 2 to $m_{12} = .5$ or higher values, the metaecoepidemic model does exhibit the same behavior as the single patch 1 system. Allowing instead a much larger m_{12} than m_{21}
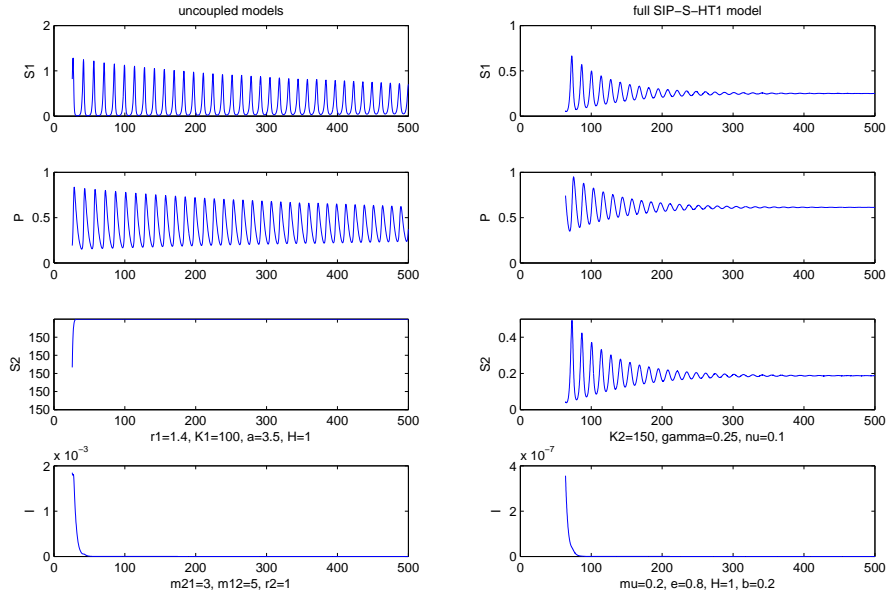
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Figure 6: Equilibrium R_2, for the parameter values $r_1 = 1.4$, $K_1 = 100$, $a = 3.5$, $H = 1$, $m_{21} = 3$, $m_{12} = 5$, $r_2 = 1$, $K_2 = 150$, $\gamma = .25$, $\nu = 0.1$, $\mu = .2$, $e = 0.8$, $b = .2$.

produces only much lower levels of susceptibles in patch 2, while leaving the disease endemic in patch 1.

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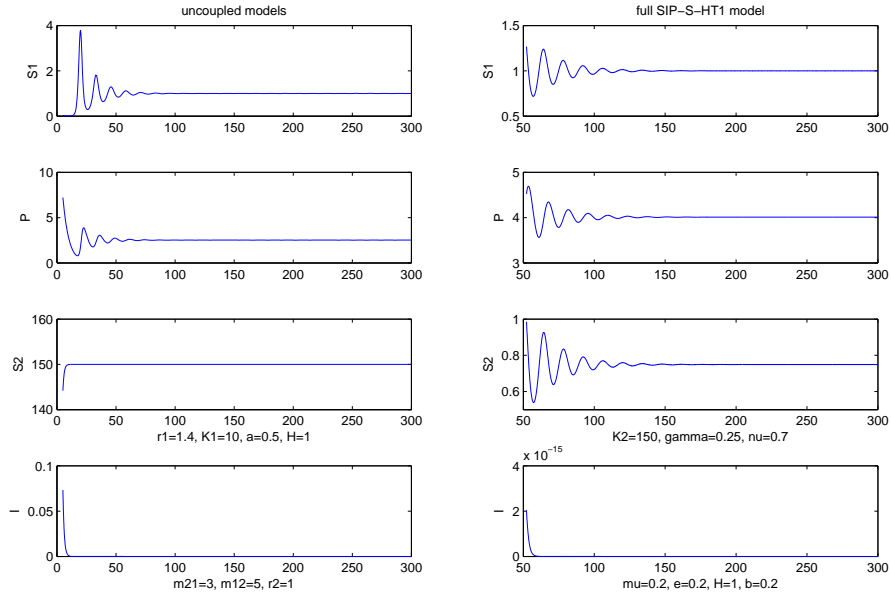
Figure 7: Equilibrium R_2, for the parameter values $r_1 = 1.4$, $K_1 = 10$, $a = .5$, $H = 1$, $m_{21} = 3$, $m_{12} = 5$, $r_2 = 1$, $K_2 = 150$, $\gamma = .25$, $\nu = 0.7$, $\mu = .2$, $e = 0.2$, $b = .2$.

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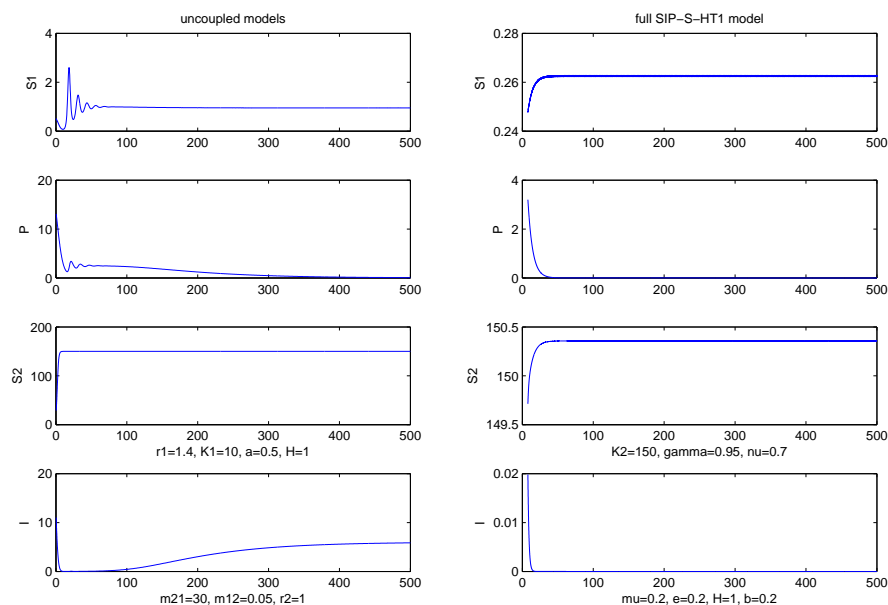
Figure 8: The predator-free equilibrium of patch 1 is converted into a disease-free equilibrium in the metaecoepidemic system, for the parameter values $r_1 = 1.4$, $K_1 = 10$, $a = .5$, $H = 1$, $m_{21=30}$, $m_{12} = .05$, $r_2 = 1$, $K_2 = 150$, $\gamma = .95$, $\nu = 0.7$, $\mu = .2$, $e = 0.2$, $b = .2$.

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