PREDATOR – PREY/HOST – PARASITE: A FRAGILE ECOEPIDEMIC SYSTEM UNDER HOMOGENEOUS INFECTION INCIDENCE

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Abstract. To underpin the concern that environmental change can flip an ecosystem from stable persistence to sudden total collapse, we consider a class of so-called ecoepidemic models, predator – prey/host – parasite systems, in which a base species is prey to a predator species and host to a micro-parasite species. Our model uses generalized frequency-dependent incidence for the disease transmission and mass action kinetics for predation.

We show that a large variety of dynamics can arise, ranging from dynamic persistence of all three species to either total ecosystem collapse caused by high transmissibility of the parasite on the one hand or to parasite extinction and prey-predator survival due to low parasite transmissibility on the other hand. We identify a threshold parameter (tipping number) for the transition of the ecosystem from uniform prey/host persistence to total extinction under suitable initial conditions.

1. Introduction. The decline and even disappearance of amphibian populations [13, 14, 19, 28, 29, 30, 49, 67] caused by viral and fungal diseases raise the concern that emerging infectious diseases may imperil not only single species but whole ecosystems [72]. To underpin the concern that environmental change of whatever sort (climate, habitat encroachment or fragmentation) can flip an ecosystem from stable persistence to sudden total collapse, we consider a class of so-called ecoepidemic models. Some ecoepidemic models [47] consider several hosts and a parasite that mediates or otherwise influences competition [5, 37, 41] or cooperation [63] between them; others consider a predator-prey-parasite system where the parasite afflicts the prey or/and the predator and affects the predation process ([1, 2, 4, 8, 9, 11, 12, 16, 26, 27, 39, 40, 46, 48, 52, 51, 64, 65, 68, 69, 70, 71] and the references therein).

The model class we consider is a subclass of predator-prey-parasite models. To make the analysis easier, we consider a micro-parasite that afflicts the prey but not

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the predator such that the prey is the exclusive host of the parasite (predator – prey/host – parasite system). Predator-prey-parasite models that have disease in both prey and predator have been considered by [7, 15, 24, 34, 36] and models that have disease only in the predator species by [27]. To give the parasite the potential to drive its host into extinction, we choose a generalized frequency-dependent incidence function [20, 21, 25, 31, 33, 59]. To have the possibility of collapse of the whole system, we choose a specialist predator rather than a generalist predator to make the predator depend on the specific prey for survival.

Most predator-prey-parasite models consider density-dependent incidence or generalizations of it; so the parasite alone can only cause decline but not extinction of the host [20, 21, 22], at least unless the prey is subject to an Allee effect [23, 42, 62]). Models with frequency-dependent incidence and a specialist predator are also considered in several publications. The models in each of [6, 26, 39, 40, 65] are close to our model, and use ‘standard’ or frequency-dependent incidence and logistic growth, where [6, 26, 40] include infectives in the growth term, while the growth term in [39, 65] includes susceptibles only (as in our model). Like us, [39, 40, 65] use mass action to describe predation while [26] uses a Holling Type II predation function.

The models in [6, 40, 65] do not address host and predator extinction for solutions with positive initial conditions. In [40, 65], this is due to the lack of disease-related death. [26] includes disease death and states without proof that the extinction equilibrium is always locally asymptotically stable; this claim is challenged by findings for the extinction equilibrium in [39] which will be clarified and expanded in this paper. [39] is more focused on bifurcations, while we explore persistence not only of the whole ecosystem but also of its subsystems. [6] also includes disease death, but simply does not seem to be interested in the possibility of parasite-mediated prey and predator extinction. In [66, 65], the predator has an additional food source and can survive in the absence of the prey species. [38] considers frequency-dependent incidence and a generalist predator that avoids infected prey.

Our model differs from the other models with frequency-dependent incidence by using a much broader class of incidences with similar features. This is motivated by the experiments and statistical analysis in [32] that show that density-dependent and frequency-dependent incidence are poor fits to infection experiments involving tiger salamanders and ranavirus. Therefore, in [20, 21], a thorough classification of incidences (power form, density-dependent on susceptibles, homogeneous) is performed as to whether the parasite can make its host disappear or merely decline. In particular, a wide class of homogeneous incidences is identified that has the potential of driving the host into extinction and contains quite a few examples that fit the infection experiments in [32] better than frequency-dependent incidence.

As far as we have seen, our predator–prey/host–parasite model differs from all predator-prey-parasite models by using a general growth function for the prey (host) rather than the logistic growth function. While this is partly done for the sake of generality, it also avoids the implausible feature of many predator-prey-parasite models that, at high prey density, susceptible prey dies at a higher per capita rate than infected prey ([36, 38, 40] are laudable exceptions). See the appendix in Section 13 for details.

Other authors have analyzed similar models from the viewpoint of a food chain/web [43, 50]. Indeed, the infected prey could be seen as a first level predator and the actual predator as a second level predator.
We will see the following phenomena, depending on the choice of the parameters. A phenomenon is called predator-mediated if it did not occur in the absence of the predator and parasite-mediated if it did not occur in the absence of the parasite. If the listed scenarios appear too vague, the discussion repeats them in more precise but also somewhat more technical language.

(i) Predator-mediated extinction of the parasite and survival of the prey and predator.
(ii) Parasite-mediated extinction of the predator and survival of the prey and parasite.
(iii) Persistence of all three species, with the persistence of the predator being mediated by the parasite.
(iv) Unmediated persistence of all three species.
(v) Predator-mediated survival of all three species at relatively high initial predator values and parasite-mediated extinction of all three species at low initial predator values.
(vi) Predator-mediated extinction of the parasite and survival of the prey and predator at high initial predator values, and parasite-mediated extinction of all three species at low initial predator values.
(vii) Predator-mediated extinction of the parasite and survival of the prey and predator at high initial predator values, and survival of all three species in the neighborhood of a coexistence equilibrium.
(viii) Parasite-mediated extinction of the predator with survival of the host and parasite at low initial predator values and survival of all three species in the neighborhood of a coexistence equilibrium.
(ix) Predator-mediated extinction of the parasite with survival of prey and predator at low initial parasite values and parasite-mediated extinction of the predator with survival of hosts and parasites at low initial predator values.
(x) Parasite-mediated extinction of all three species for all initial predator values.

The scenarios (i), (ii), (iii), and (iv) have been observed in other models, with density- or frequency-dependent incidence. Scenarios (v), (vi), and (x) can be observed because we have chosen a homogeneous infection function. They occur when the parasite would drive its host (which is also the prey of the predator) and itself into extinction if there were no predator. Phenomena (i), (ii), (iii), and (iv) occur if the parasite cannot drive the host/prey species into extinction in the absence of the predator. They can also be observed in models with a density-dependent infection incidence. (i) and (ii) are cases of competitive exclusion between the predator and the parasite which compete for the same prey/host species.

Phenomenon (i) occurs if the predator can persist on susceptible prey alone, but will also eat infective prey and does so in sufficient quantities to prevent the disease from spreading. ([2, 4, 8, 11, 12, 40, 48, 51, 64, 65].)

Phenomenon (ii) can occur in two distinct ways. The first way is if infective prey is of less nutritional value than susceptible prey and if predators that have eaten infective prey are too tired or satiated to kill susceptible prey as well. This includes cases where infected prey have ‘negative nutritional value’, so consumption of infected individuals causes the predator to be incapacitated and unable to hunt effectively, resulting in a net loss of biomass for the predator. Second, the parasite can cause very low levels of prey to be available, so even if infected prey is of similar nutritional value, there will not be enough biomass available for the predator to persist ([4, 8, 9, 11, 12, 39, 40, 48, 64, 65, 68, 69, 70, 71]).
Phenomenon (iii) occurs if the predator cannot persist on susceptible prey alone. It requires that healthy prey become infected, and thus easier to catch, in order to provide the sustenance needed to survive ([9, 40, 68, 69, 70, 71]).

Phenomenon (iv) occurs when the parasite cannot drive the host to extinction in the absence of the predator, the predator can survive on healthy prey alone, the parasite can invade the predator-prey subsystem, and the predator can invade the host-parasite subsystem ([2, 11, 12, 48, 39, 40, 51, 65, 68, 70]).

In scenarios (v) — (ix), there is bistability, where the dynamic outcome depends on the initial conditions. In (v) and (vi), for one set of initial constellations, the predator is initially at a high enough level that it eats enough of infective prey to keep the parasite from driving the host/prey species into extinction, along with itself and the predator. In the other set of constellations, the predator level is too low at the beginning and thereafter to prevent total ecosystem collapse. The difference in (v) and (vi) is that in (v), the non-collapse scenario has solutions tending toward a state with all three species continuing to coexist, while in (vi) there are solutions tending toward a parasite-free state. The bistability in (vii) is between extinction of the parasite, caused by the predator when it is at sufficiently high levels, and survival of all three species at lower predator levels.

The bistability in (viii) is between extinction of the predator when its initial values are too low, and survival of all three species at higher predator initial levels.

The bistability in (ix) is between extinction of the predator or the parasite, when the respective initial values are too low, with survival of susceptible prey/host in both cases.

In (x), the parameters are such that the predator cannot rescue the ecosystem even if it is a high levels.

2. The model. Let $S$, $I$, and $P$ denote the biomasses of prey that are susceptible to the disease, prey that are infected by the disease, and predators, respectively. Predation is modeled by mass action kinetics. The disease dynamics between host and disease are as in [21], and we assume that the parasite is not transmitted to or between predators. These are the model equations,

$$
S' = Sg(S) - \sigma f(S, I) - \kappa_1 SP,
$$

$$
I' = \sigma f(S, I) - \kappa_2 IP - \mu I,
$$

$$
P' = \gamma_1 SP + \gamma_2 IP - \nu P.
$$

The functions and parameters have the following meaning:

$g(S)$ denotes the per capita growth rate of susceptible prey biomass if it equals $S$.

$\sigma f(S, I)$ denotes the disease incidence, i.e., the number of new infections per unit of time. $f$ is called the incidence function and $\sigma$ the incidence coefficient.

$\mu > 0$ per unit biomass capita mortality rate of infected prey.

$\nu > 0$ per unit biomass natural mortality rate of predators.

$\kappa_1 \geq 0$ rate at which one unit of susceptible prey is killed by one unit of predator.

$\kappa_2 > 0$ rate at which one unit of infected prey is killed by one unit of predator.

$\gamma_1 \geq 0$ rate of per unit predator biomass increase by killing (and eating) one unit of susceptible prey.
\[ \gamma_2 \in \mathbb{R} \] rate of per unit predator biomass change by killing (and eating) one unit of infected prey.

We assume that infected prey/host does not reproduce because they are too weak to compete for vital resources, so there is no birth term in the infectives’ differential equation. For the same reason, the number of infected hosts does not affect the per capita growth rate \( g(S) \).

**Assumption 2.1.** We make the following mathematical assumptions about the susceptible growth rate function, \( g \).

- \( g \) is locally Lipschitz continuous and decreasing.
- \( g(0) > 0 \) and there is a carrying capacity \( K \) such that \( g(K) = 0 \), \( g \) is strictly decreasing and differentiable on \([0, K]\), and \( g(S) < 0 \) for \( S > K \).

**Assumption 2.2.** For the disease incidence function, \( f \), make the following assumptions.

- \( f \) is locally Lipschitz continuous.
- \( f \) is strictly increasing in \( S \).
- \( f \) is strictly increasing in \( I \).
- \( f(0, I) = 0 \) for all \( I \geq 0 \), \( f(S, 0) = 0 \) for all \( S \geq 0 \), and \( f(1, 1) > 0 \).
- \( f \) is homogeneous, i.e. \( f(\alpha S, \alpha I) = \alpha f(S, I) \), \( \alpha, I, S \geq 0 \).
- \( f(\infty, I) = \lim_{S \to \infty} f(S, I) < \infty \) for all \( I \geq 0 \).
- \( f(S, \infty) = \lim_{I \to \infty} f(S, I) < \infty \) for all \( S \geq 0 \).

Since \( f \) is homogeneous, the *incidence coefficient*, \( \sigma \), has the units of day\(^{-1} \). Examples for \( f \) can be found in Section 4. The classic example is frequency-depending (or standard) incidence, \( f(S, I) = \frac{\sigma I}{S+I} \).

All constants are non-negative with the possible exception of \( \gamma_2 \) which is positive if eating infected prey has a positive effect on a predator and negative if eating infected prey has a negative effect. [4, 12, 64, 65] have studied ecoepidemic systems where eating infected prey negatively affects the predator.

**Assumption 2.3.** If nothing else is said, we assume \( \kappa_2 \geq \kappa_1 \geq 0 \), i.e., infective prey are not harder to catch than susceptible prey. Sometimes, we also add results for \( \kappa_2 < \kappa_1 \), when this can be easily done.

Additionally, we assume \( \kappa_1 = 0 \) if and only if \( \gamma_1 = 0 \), i.e. uninfected prey are caught if and only if they can provide some nutrition to the predator.

Finally, we assume if \( \gamma_1 = 0 \) then \( \gamma_2 > 0 \), and if \( \gamma_2 \leq 0 \) then \( \gamma_1 > 0 \); so the predator has food available that provides it sustenance.

2.1. Existence, uniqueness and nonnegativity of solutions.

**Theorem 2.4.** If \( S(0) \geq 0, I(0) \geq 0 \) and \( P(0) \geq 0 \), then there exists a unique solution to System (1), such that \( S(t) \geq 0, I(t) \geq 0 \) and \( P(t) \geq 0 \) for all \( t \geq 0 \).

If \( S(0) = 0 \), then \( S(t) = 0 \) for all \( t \geq 0 \). If \( S(0) > 0 \), then \( S(t) > 0 \) for all \( t \geq 0 \). Analogous statements hold for \( I \) and \( P \).

**Proof.** We will use Theorem A.4 from [60]. Define \( x(t) = (S(t), I(t), P(t)) \), and the vector field via system (1) such that \( x' = F(x) \). By Assumptions 2.1 and 2.2 all functions in the vector field are locally Lipschitz. Observe that \( F_j(x) \geq 0 \) when \( x \in \mathbb{R}^3_+ \) and \( x_j = 0 \). For \( F_1 \), we have \( F_1(x) = x_1g(x_1) - \sigma f(x_1, x_2) - \kappa_2 x_1 x_3 \), which is 0 when \( x_1 = 0 \).

One can easily see that this result will hold for each \( F_j \).
Further, for any given functions \( I, P : \mathbb{R}_+ \to \mathbb{R}_+ \), the constant function \( S \) with value 0 is a solution of \( S' = F_1(S, I, P) \) on \( \mathbb{R}_+ \). Since solutions of this scalar ODE are unique by the local Lipschitz continuity of \( F_1 \), any solution \( S \) with \( S(s) = 0 \) for some \( s \geq 0 \) satisfies \( S(t) = 0 \) for all \( t \geq 0 \). \( \square \)

### 2.2. A preview of selected results.

Using a general per capita growth function \( g \) has the advantage that the central role of the parameter \( g(0) \) for the persistence of the prey/host becomes evident as highlighted by this short preview of few of a multitude of results. The following dimensionless compound threshold parameter will play an important role,

\[
\mathcal{T} = \sigma f \left( \frac{1}{g(0)} \frac{1}{\mu} \right). \tag{2}
\]

For frequency-dependent incidence, \( \mathcal{T} = \frac{\sigma}{\mu} \). We make an additional assumption for the incidence function \( f \), namely that

\[
\xi(r) := f(1 + r^{-1}, 1 + r), \quad r > 0, \quad \text{is a decreasing function of } r > 0. \tag{3}
\]

See Section 4 for examples. For frequency-dependent incidence, \( \xi \) is a constant function.

**Theorem 2.5.** Assume that \( \sigma f(\infty, 1/\mu) \leq 1 \). Then the disease goes extinct, \( I(t) \to 0 \) as \( t \to \infty \), and \( S(t) \) converges to a positive limit for all solutions with \( S(0) > 0 \). More precisely:

- If \( S^0 = \nu/\gamma_1 \geq K \), then \( S(t) \to K \) and \( P(t) \to 0 \) as \( t \to \infty \) for all solutions with \( S(0) > 0 \) and \( P(0) \geq 0 \).
- If \( S^0 < K \), then \( S(t) \to S^0 \) and \( P(t) \to g(S^0)/\kappa_1 > 0 \) as \( t \to \infty \) for all solutions with \( S(0) > 0 \) and \( P(0) > 0 \).

See Theorem 7.1 for a proof.

**Theorem 2.6.** Assume that \( \mathcal{T} < 1 \).

Then there exists some \( \epsilon \in (0,1] \) such that, for all solutions with \( S(0) > 0 \),

\[
\liminf_{t \to \infty} S(t) \geq \epsilon \quad \text{and} \quad \limsup_{t \to \infty} I(t)/S(t) \leq 1/\epsilon.
\]

See Theorem 5.4. The condition in Theorem 2.6 is almost sharp as can be seen from the next result which establishes \( \mathcal{T} \) as a tipping number because its crossing 1 tips the ecosystem from uniform prey/host persistence to total collapse for suitable initial conditions.

**Theorem 2.7.** If \( \mathcal{T} > 1 \), there is locally asymptotically stable total ecosystem extinction; There exists a subset \( D \) of \((0, \infty)^3\) with nonempty interior such that, for all solutions with \( (S(0), I(0)/S(0), P(0)) \in D \), \( (S(t), I(t)/S(t), P(t)) \in D \) for all \( t \geq 0 \) and \( S(t) + I(t) + P(t) \to 0 \) as \( t \to \infty \).

See Theorem 8.6 for a proof and note Remark 4.1 (b). The assumptions in Theorem 2.7 do not rule out that there may be predator–prey/host–parasite coexistence at a locally asymptotically stable strictly positive equilibrium which goes along with a second strictly positive equilibrium, which is a saddle. See Theorem 10.7. However, if \( \sigma \) is very large, the ecosystem totally collapses due to the parasite independent of the initial data.

**Theorem 2.8.** There exists some \( \zeta > 0 \), which does not depend on \( \sigma \), such that, if \( \mathcal{T} > 1 + \zeta \), there is initial-value independent collapse of the total ecosystem, \( S(t) + I(t) + P(t) \to 0 \) as \( t \to \infty \) for all solutions with \( I(0) > 0 \).
See Section 11 for a proof.

These results imply that dynamic coexistence (survival of predator, prey/host, and parasite for all positive initial data) can only occur – and does occur under additional assumptions – if $T = \sigma f(1/g(0), 1/\mu) < 1 < \sigma f(\infty, 1/\mu)$. Depending on the additional assumptions, the coexistence may be parasite-mediated (the predator would die out in absence of the parasite, Section 9.4.2), or may not (Section 9.4.1).

These results also show that there are no parameter constellations in which the prey/host persists there is initial-value independent rescue of the prey/host by the predator from the parasite-induced extinction. In Theorems 2.5 and 2.6, the prey/host persists whether or not predators are present, while in Theorem 2.7 the total ecosystem can crash even if predators are present but their initial number is too low.

3. Uniform eventual boundedness of solutions. Notice that $\gamma_i/\kappa_i$, $i = 1, 2$, are the nutritional values of susceptible and infective prey, respectively. We define

$$\alpha := \max_{1 \leq i \leq 2} \gamma_i/\kappa_i$$

as the maximum nutritional value, where $\gamma_i/\kappa_i := 0$ if $\gamma_i = 0$ (even if $\kappa_i = 0$ as well). By Assumption 2.3, $\alpha > 0$.

We use the notation

$$S^\infty := \limsup_{t \to \infty} S(t) \quad \text{and} \quad S_\infty := \liminf_{t \to \infty} S(t).$$

**Theorem 3.1.** For all non-negative solutions $S$, $I$, and $P$, $S(t) \leq \max \{ K, S(0) \}$ for all $t \geq 0$ and $S^\infty \leq K$. For a weighted total population size $N(t) = S(t) + I(t) + (1/\alpha)P(t)$,

$$N(t) \leq \max \{ K, S(0) \} \frac{g(0) + \beta}{\beta} + N(0)e^{-\mu t} =: N^\ominus + N(0)e^{-\mu t}, \quad \beta := \min \{ \mu, \nu \}$$

and

$$N^\infty \leq \sup \{ S(g(S) + \beta)/\beta; S \in [S_\infty, S^\infty] \} \leq \sup \{ S(g(S) + \beta)/\beta; S \in [0, K] \}$$

$$\leq S^\infty \frac{g(0) + \beta}{\beta} \leq K \frac{g(0) + \beta}{\beta}.$$

In particular, $P(t) \leq \alpha N(t)$, $I(t) \leq N(t)$, and

$$P^\infty \leq \sup \left\{ \frac{\alpha S(g(S) + \beta)}{\beta}; S \in [0, K] \right\} =: P^\ominus \leq \alpha K \frac{g(0) + \beta}{\beta}$$

and $I^\infty \leq K \frac{g(0) + \beta}{\beta} =: I^\ominus$, independent of initial conditions.

**Proof.** The choice of $\alpha$ gives us $(\gamma_i/\alpha) - \kappa_i \leq 0$. Set $N = S + I + \alpha^{-1}P$.

$$N' = Sg(S) - \mu I - (\nu/\alpha)P + ((\gamma_1/\alpha) - \kappa_1)SP + ((\gamma_2/\alpha) - \kappa_2)IP$$

$$\leq Sg(S) - \mu I - (\nu/\alpha)P \leq S(g(S) + \beta) - \beta(S + I + \alpha^{-1}P)$$

$$\leq \sup \{ S(g(S) + \beta); S \in [S_\infty, S^\infty] \} \leq \beta N.$$  

From here we follow the same steps as Theorem 4.1 in [21] to give the result. \( \square \)

**Corollary 3.2.** If $S(t) \to 0$, as $t \to \infty$, then $N(t) \to 0$.  

3.1. Can the population size under the disease exceed the disease-free carrying capacity? Since, in our model, infected hosts do not compete for resources, the disease could possibly bring population size above the disease-free carrying capacity. We give a condition for the per capita growth rate $g$ under which this cannot occur and present an example where this does occur.

**Corollary 3.3.** For all non-negative solutions $S$ and $I$, let $H(t) = S(t) + I(t)$ be the size of the host/prey population at time $t$.

(a) Then $H^\infty \leq \sup_{0 \leq S \leq g(S) + \mu} \frac{S(g(S) + \mu)}{\mu} \leq \sup_{0 \leq S \leq K} \frac{S(g(S) + \mu)}{\mu} =: H^\infty$.

(b) If the function $S(g(S) + \mu)$ is an increasing function of $S \in (0, K]$, then $H^\infty \leq K$.

(c) If the function $S(g(S) + \mu)$ is a strictly increasing function of $S \in (0, K]$ and if $I_\infty > 0$ or $\kappa_1 P_\infty > 0$, then $H^\infty < K$.

**Proof.** (a) The first inequality follows from the differential inequality $H' \leq S(g(S) + \mu) - \mu H$ with a slight modification to the calculation in Theorem 3.1.

(b) Using the hypothesis $S(g(S) + \mu)$ is an increasing function of $S$ for all $S \in (0, K)$, yields

$$\sup \{S(g(S) + \mu)/\mu; S \in [0, K]\} = K \frac{g(K) + \mu}{\mu} = K \frac{0 + \mu}{\mu} = K.$$ 

Applying part (a) of this Theorem will prove the claim.

(c) Assume $I_\infty > 0$ or $\kappa_1 P_\infty > 0$. Suppose $S^\infty = K$. By [60, Prop.A.22], there exists a sequence $(t_n)$ such that $t_n \to \infty$, $S(t_n) \to S^\infty$, and $S'(t_n) \to 0$ as $n \to \infty$. By (1),

$$0 = \lim_{n \to \infty} (S(t_n)g(S(t_n)) - \sigma f(S(t_n), I(t_n)) - \kappa_1 S(t_n)P(t_n))$$

$$= S^\infty g(S^\infty) - \lim_{n \to \infty} (\sigma f(S(t_n), I(t_n)) - \kappa_1 S(t_n)P(t_n))$$

$$\leq Kg(K) - \sigma f(S^\infty, I_\infty) - \kappa_1 S^\infty P_\infty < 0,$$

a contradiction. This implies $S^\infty < K$. Since $S(g(S) + \mu)$ is a strictly increasing function of $S \in [0, K]$, $\sup_{0 \leq S \leq S^\infty} \frac{S(g(S) + \mu)}{\mu} < \sup_{0 \leq S \leq K} \frac{S(g(S) + \mu)}{\mu} = K$. Applying part (a) yields the result. \qed

This corollary implies that if $S(g(S) + \mu)$ is increasing on $(0, K)$ then the total number of hosts (susceptible and infectives) will be less than the carrying capacity of the species, which we might expect from a biological perspective.

**Example 3.4.** In this example, the increase of $S(g(S) + \mu)$ as a function of $S \in [0, K]$ will be equivalent to $(S + I)^\infty \leq K$ for all solutions $S, I$ of (1).

We consider the system (1) with asymmetric frequency-dependent incidence

$$f(S, I) = \frac{SI}{pS + qI}, \quad S, I \geq 0,$$

where $p + q = 1$, $0 < p < 1$.

An endemic equilibrium $(S^*, I^*, 0)$, of (1) with no predator, $S^* > 0$ and $I^* > 0$, satisfies

$$S^* g(S^*) = \mu I^*, \quad \sigma \frac{S^*}{pS^* + qI^*} = \mu.$$

(6)
We solve the second equation for $I^*$,

$$I^* = \frac{(\sigma - p\mu)S^*}{q\mu},$$

(7)

assuming that $\sigma > p\mu$, and substitute it into the first equation

$$g(S^*) = \frac{(\sigma - p\mu)}{q}.$$

(8)

This has a unique solution $S^* \in (0, K)$ if we assume that

$$0 < \frac{(\sigma - p\mu)}{q} < g(0).$$

(9)

Notice from (7) that

$$S^* + I^* = \frac{(\sigma + [q - p]\mu)S^*}{q\mu}.$$

(10)

Can one choose the parameters in such a way that $S^* + I^* > K$? No more progress seems possible unless we choose a concrete $g$. The easiest choice seems to be a corrected logistic growth function (see the discussion in the appendix in Section 13),

$$g(S) = b[1 - (S/\tilde{S})]_+ - \theta, \quad S \geq 0.$$

Here $\theta > 0$ is the per capita death rate of susceptible prey, $b > \theta$ is the per capita birth rate without competition, and $\tilde{S}$ is the threshold density at which competition makes the per capita birth rate 0. $[s]_+ = \max\{0, s\}$ is the positive part of the real number $r$.

After scaling $S$, i.e. replacing $S$ by $S/\tilde{S}$ and $I$ by $I/\tilde{S}$, we can assume $\tilde{S} = 1,

$$g(S) = b[1 - S]_+ - \theta, \quad S \geq 0.$$ 

(11)

Since the incidence function is homogeneous, it is not affected by the scaling and $\sigma$ is not affected either. $\kappa_1$ and $\kappa_2$ remain the same, but $\gamma_1$ and $\gamma_2$ need to be absorbed into $\tilde{S}$.

The carrying capacity $K$ with $g(K) = 0$ is

$$K = (1 - (\theta/b)) < 1,$$

(12)

and $g$ is strictly decreasing on $[0, K]$.

The following can be shown:

(a) If $b > \theta + \mu$, then there exists an endemic equilibrium $(S^*, I^*, 0)$ of (1) with $S^*, I^* > 0$ and $K < S^* + I^* = H^\circ$ for $\sigma = (q/2)[b - (\mu + \theta)] + p\mu$.

(b) Let $b \leq \theta + \mu$. Then $S(g(S) + \mu)$ is a strictly increasing function of $S \in [0, K]$.

By Corollary 3.3, $(S + I)^\infty \leq K = H^\circ$ for all solutions $S, I, P$ of (1) with the inequality being strict if $I^\infty > 0$ or $\kappa_1 P^\infty > 0$. All equilibria $(S^\circ, I^\circ, P^\circ)$ with $S^\circ > 0$ and $I^\circ + \kappa_1 P^\circ > 0$ satisfy $S^\circ + I^\circ < K$.

3.2. Some preliminary persistence considerations.

**Theorem 3.5.** If there is an $\varepsilon > 0$ such that $\limsup_{t \to \infty} S(t) =: S^\infty > \varepsilon$ for all solutions with $S(0) > 0$, then there is some $\delta > 0$ such that $\liminf_{t \to \infty} S(t) =: S_\infty > \delta$ for all solutions with $S(0) > 0$. 
Proof. Let $\rho(S, I, P) = S$ be the persistence function. Note that once $\rho$ is zero, it will stay zero. Via Theorem 3.1 we define $B = [0, K] \times [0, F^\infty] \times [0, P^\infty]$, with $I^\infty$ and $P^\infty$ independent of initial conditions. Now we apply Theorem 4.5 from [57], using $B$, which tell us that uniform weak persistence implies uniform strong persistence. 

4. The ratio formulation of the model. Because we are using a homogeneous incidence function, standard stability analysis of the origin, i.e. collapse of the ecosystem, is impossible. Thus, we consider the ratio of infectives to susceptibles, $r = \frac{I}{S}$, replacing $I$ in our system with $r$. In the context of ecoepidemic models, ratios (or fractions) have been used in [38, 40, 66] (see also [65] and the references therein), though in the form $I/(S + I)$. For short, we call $r$ the infection ratio.

We define $h(r) := f(1, r)$, and $\xi(r) := \frac{1 + r}{r} h(r) = f(1 + r^{-1}, 1 + r)$. (13) We call $\sigma \xi$ the per unit infection ratio growth rate [21].

Remark 4.1. The Assumptions 2.2 on $f$ have quite a few consequences:

(a) $h$ is strictly increasing and $h(0) = 0$. The last equation in (13) follows from the homogeneity of $f$.

(b) $\xi(r) - h(r) = h(r)/r = f(1/r, 1)$ is a strictly decreasing function of $r > 0$,

\[
\xi(\infty) = \lim_{r \to \infty} \xi(r) = f(1, \infty) = h(\infty) \in (h(1), \infty),
\]

\[
\xi(0) = \lim_{r \to 0} \xi(r) = f(\infty, 1) = h'(0) \in (h(1), \infty),
\]

\[
\frac{\xi(g(0)/\mu)}{g(0)/\mu} = \frac{h(g(0)/\mu)}{g(0)} = f\left(\frac{1}{g(0)}, \frac{1}{\mu}\right) = \frac{T}{\sigma}.
\]

(c) In particular, $h$ is differentiable at 0 and $\xi$ has been continuously extended to $\mathbb{R}_+$.

(d) If $f(S, 1)$ is a differentiable function of $S > 0$ and $\partial_S f(S, 1) > 0$, then $h$ and $\xi$ are differentiable on $(0, \infty)$ and $\xi'(r) - h'(r) < 0$ for all $r > 0$.

With the new dependent variable $r$ and these definitions, System (1) can be equivalently rewritten as

\[
S' = S(g(S) - \sigma h(r) - \kappa_1 P),
\]

\[
r' = r(\sigma \xi(r) + (\kappa_1 - \kappa_2)P - \mu - g(S)),
\]

\[
P' = P(\gamma_1 S + \gamma_2 r S - \nu).
\]

In addition, it may be worthwhile to keep the equation for $I = r S$,

\[
I' = I\left(\sigma \frac{h(r)}{r} - \kappa_2 P - \mu\right).
\]

We make a crucial assumption on $\xi$ for our analysis which holds throughout the rest of the paper.

Assumption 4.2. $\xi : (0, \infty) \to \mathbb{R}_+$ is decreasing.

The combination of this assumption with Remark 4.1 has some important consequences [21, Lemma 7.37].
Remark 4.3. Assumption 4.2 implies the following inequalities
\[
\frac{\mu}{h'(0)} < \frac{\mu + g(0)}{h'(0)} \leq \frac{g(0)}{h(g(0)/\mu)} \leq \frac{\mu + g(0)}{h(\infty)}.
\] (16)

There are many homogeneous incidence functions, \(f\), that satisfy Assumption 2.2 and allow \(\xi\) to fit Assumption 4.2. Notably, when using the frequency-dependent incidence, \(f(S, I) = \frac{SI}{S + I}\), the resulting \(\xi\) is constant: \(\xi(r) \equiv 1\). A more general function, asymmetric frequency-dependent incidence, with \(f(S, I) = \frac{SI}{pS + qI}\), produces a strictly decreasing \(\xi\) when \(p < q\) and reproduces (a constant multiple of the) ‘symmetric’ frequency dependence when \(p = q\). In general, a decreasing \(\xi\) function can be crafted using an incidence function of the form
\[
f(S, I) = S\tilde{h}\left(\frac{I}{pS + qI}\right)
\]
where \(0 < p < q < 1\), \(p + q = 1\), \(\tilde{h}\) is increasing, and \(\tilde{h}(r)/r\) is decreasing. See [21, Sec. 7.3] for further details. In fact, in [21] the following functions, which meet Assumptions 4.2, were fit to data (from experiments in [32]):
\[
S \ln \left(1 + \frac{I}{S + I}\right), \quad \frac{SI}{S + I}, \quad S \ln \left(1 + \frac{I}{pS + qI}\right), \quad \text{and} \quad S \ln \left(1 + \frac{I}{pS + qI}\right) \quad \text{(with } p \leq q\text{)}.
\]
Among these, \(S \ln \left(1 + \frac{I}{S + I}\right)\) provided the best fit. Unfortunately, these conditions do exclude two homogeneous infection functions that were explicitly considered in [21], the constant risk \((f(S, I) = S)\) and homogeneous power law \((f(S, I) = SI^{p}, p \in (0, 1))\)

Two incidences that were not included in the fitting can be derived from the literature, from the arctangent [3, 53] response, \(h(t) = \zeta \arctan(\varphi t) = \zeta \tan^{-1}(\varphi t)\), and the hyperbolic tangent [45, 54] response \(h(t) = \zeta \tanh(\varphi t)\) where \(\tanh(s) = \frac{e^{s} - e^{-s}}{e^{s} + e^{-s}}\).

Remark 4.4. Frequency-dependent incidence is the only homogeneous incidence, that leads to constant \(\xi\).

Proof. If \(\xi\) is constant, then
\[
c = h(r)(1 + r^{-1}), \quad r > 0.
\]
With \(r = I/S\),
\[
f(S, I) = Sh(r) = S \frac{c}{1 + (S/I)} = \frac{cSI}{S + I}.
\]

The other examples of homogeneous incidence functions with decreasing \(\xi\) that we mention above all lead to strictly decreasing \(\xi\) (though one certainly could cook up an artificial example where \(\xi\) is decreasing but not strictly decreasing).

Note that the boundedness result in Theorem 3.1 will still hold for \(S\) and \(P\), but since \(r = \frac{I}{S}\), we will need to derive conditions for its boundedness.

Corollary 4.5. Suppose that there is some \(\varepsilon > 0\) such that \(S^\infty > \varepsilon\) for all solutions with \(S(0) > 0\). Then there is some \(c\) such that \(\limsup_{t \to \infty} r(t) =: r^\infty < c\) for all solutions with \(r(t) \geq 0\).
Proof. Theorem 3.5 will imply that there is some \( \delta > 0 \) such that \( S_\infty > \delta \). Using definition of \( r \) and Theorem 3.1 we see \( r = I/S \leq N/S \), which implies \( r^\infty \leq N^\infty/S_\infty \).

**Theorem 4.6.** If \( r(t) \to \infty \) as \( t \to \infty \), then \( S(t) \to 0, I(t) \to 0 \), and \( P(t) \to 0 \) as \( t \to \infty \).

Proof. \( r(t) = \frac{I(t)}{S(t)} \) implies \( r(t)S(t) = I(t) \), and Theorem 3.1 provides a bound on \( I, I^\circ \), which is independent of initial conditions. Thus, \( r(t)S(t) = I(t) \leq I^\circ \), and \( r(t) \to \infty \) as \( t \to \infty \). Therefore, it must be the case that \( S(t) \to 0 \) which, by Corollary 3.2, implies the result.

**Proposition 4.7.** Suppose that there is some \( c \in (0, \infty) \) such that for all solutions of System (14) with \( r(0) \geq 0 \) there is some \( c > 0 \) such that \( \liminf_{t \to \infty} r(t) =: r_\infty < c \). Then there is some \( d > 0 \) such that \( \limsup_{t \to \infty} r(t) =: r^\infty < d \) for all solutions with \( r(0) \geq 0 \).

Proof. Corollary A.33 in [60] states that if a semiflow has the property \( \liminf_{t \to \infty} \| \Phi_t(x) \| < C \) for some \( C \) independent of \( x \), then there exists some \( C \) such that \( \limsup_{t \to \infty} \| \Phi_t(x) \| < C \). Note that the standard Euclidean norm of the semiflow induced by system (14) is unbounded if and only if \( r \) is unbounded (Theorem 3.1 implies that \( S \) and \( P \) are bounded). Equivalently, the norm of the semiflow is bounded if and only if \( r \) is bounded.

**Proposition 4.8.** If \( S(t) \to K \) as \( t \to \infty \), then \( r(t) \to 0 \) and \( P(t) \to 0 \) as \( t \to \infty \).

Proof. Let \( S(t) \to K \) as \( t \to \infty \). Then \( \liminf_{t \to \infty} S(t) =: S_\infty = K \). Using Theorem 3.1, the following inequalities hold:

\[
K = S_\infty \leq S^\infty \leq N^\infty \leq \sup\{S(g(S) + \beta)/\beta; S \in [S_\infty, S^\infty]\} = \sup\{S(g(S) + \beta)/\beta; S \in [K, K]\} = K,
\]

so \( K = N^\infty \). Since \( S(t) \leq N(t) \) for all \( t \geq 0 \), \( N(t) \to K \) and \( S(t) \to K \), we find that \( I(t) + \alpha^{-1}P(t) = N(t) - S(t) \to 0 \) as \( t \to \infty \).

**Corollary 4.9.** If \( S(t) \geq K \) for all \( t \geq 0 \), then \( r(t) \to 0 \) and \( P(t) \to 0 \) as \( t \to \infty \).

Proof. Note that for all \( S(t) > K, S'(t) < 0 \), and if \( S(t) = K \), then \( S'(t) \leq 0 \). So, if \( S(t) \geq K \) for all \( t \geq 0 \), then \( S(t) \to K \) as \( t \to \infty \). Proposition 4.8 yields the result.

5. Uniform persistence of susceptible hosts. We aim at a preliminary persistence result for the prey/host which is prepared for by the next result.

**Proposition 5.1.** For any \( S^0 > 0 \), there exists some \( S^2 \in (0, S^0) \) such that

\[
\limsup_{t \to \infty} \left( [\sigma h(r(t)) - g(S^3)]_+ + S(t) \right) \geq S^2
\]

for all solutions to (14) with \( S(0) > 0 \).

Here \( [s]_+ = \max\{s, 0\} \) denotes the positive part of \( s \in \mathbb{R} \).
Proof. Let $S^* > 0$. Choose some $S^\dagger \in (0, S^\flat)$ such that
\[ g(S^\dagger) - 2S^\dagger > g(S^0). \] (18)
Such an $S^\dagger$ exists because $g(0) > g(S^0)$ and $g$ is continuous at 0. Let $\gamma = \max\{\gamma_1, \gamma_2\} > 0$.

Recall the definition of $N(t)$ and $\beta$ from Theorem 3.5. We perform a time shift such that $N(t) \leq N^\infty + \frac{\nu}{3\gamma}$ for all $t \geq 0$. Note that this implies $S(t) + I(t) \leq N^\infty + \frac{\nu}{3\gamma}$ for all $t \geq 0$. Set
\[ S^\sharp = \min \left\{ \frac{\beta \nu}{3\gamma(g(0) + \beta)}, S^\dagger \right\}. \]
We will suppose toward contradiction that (17) does not hold. Then $S^\infty < S^\sharp$ and, after another shift of time,
\[ \sigma h(r(t)) - g(S^\flat) \leq S^\sharp \leq S^\dagger, \quad t \geq 0. \] (19)

If $P(0) > 0$, then $P(t) > 0$ for all $t \geq 0$ by Theorem 2.4 and we see from the $P''$ equation in (1) that
\[ \frac{P''}{P} = \gamma_1 S + \gamma_2 I - \nu \leq \gamma(S(t) + I(t)) - \nu \leq \gamma N^\infty + \frac{\nu}{3} - \nu \leq \gamma S^\infty g(0) + \frac{\beta}{\beta} - \frac{2\nu}{3} < -\frac{\nu}{3}, \]
which implies that $P$ declines exponentially.

If $P(0) = 0$, $P(t) = 0$ for all $t \geq 0$ by Theorem 2.4. After another time shift, $\kappa_1 P(t) < S^\dagger$ and $S(t) \leq S^\dagger$ for all $t \geq 0$. Since $g$ is decreasing, by (18) and (19),
\[ \frac{S^\dagger}{S} = g(S) - \sigma h(r) - \kappa_1 P > g(S^\dagger) - \sigma h(r) - S^\dagger \geq g(S^\dagger) - g(S^0) - 2S^\dagger > 0, \]
which implies that $S$ increases exponentially, a contradiction to $S^\infty \leq S^\dagger$. \hfill \Box

Proposition 5.2. If $\sigma h(\infty) < g(0)$, then there exists some $\delta > 0$ such that $S^\infty > \delta$ for all solutions to System (14) with $S(0) > 0$.

Proof. Let $\sigma h(\infty) < g(0)$. Since $h$ is increasing and $g$ is continuous at 0, one can choose some $S^* > 0$ such that $\sigma h(r) \leq g(S^*)$ for all $r \geq 0$. Consider a solution to (14) with $S(0) > 0$. Then $[\sigma h(r(t)) - g(S^\flat)]_+ = 0$ for all $t \geq 0$ and $S^\infty \geq S^\sharp > 0$ by Proposition 5.1. Theorem 3.5 now yields the result. \hfill \Box

5.1. Eventual uniform boundedness of the infection ratio.

Theorem 5.3. If $\sigma h(\infty) < \mu + g(0)$, then there exists some $c$ such that $r^\infty < c$ for all solutions to System (14) with $r(0) \geq 0$.

Proof. Proposition 5.2 combined with Corollary 4.5 yield this result when $\sigma h(\infty) < g(0)$. Thus, we only need to consider when $\sigma h(\infty) \geq g(0)$. We can assume that $r(0) > 0$ and $S(0) > 0$. Via Proposition 4.7 it is sufficient to prove $r^\infty < d$ for some $d$ that is independent of initial data.

We can absorb $\sigma$ into $h$, i.e. assume that $\sigma = 1$. Choose some $S^\flat > 0$ such that
\[ \xi(\infty) = h(\infty) < g(S) + \mu, \quad S \leq S^\flat. \]
Since $g(S^p) < g(0) \leq h(\infty)$ and $\xi$ is decreasing, we can choose some $r^b > 0$ and $\delta > 0$
\[
\xi(r) < g(S^p) + \mu - \delta, \quad g(S^p) < h(r) - \delta, \quad r \geq r^b.
\]
Suppose that for a solution of System (14) has $r_\infty > r^b$. After a shift in time, $r(t) > r^b$ for all $t \geq 0$. Then
\[
g(S^p) - h(r(t)) - \kappa_1 P(t) \leq g(S^p) - h(r(t)) < -\delta, \quad t \geq 0.
\]
Since $S' = S(g(S) - h(r) - \kappa_1 P)$ and $g$ is strictly decreasing, this implies that $S^\infty < S'$. After another shift in time, $S(t) < S^p$ for all $t \geq 0$. Then
\[
r' = (1 + r)h(r) - r(g(S) + \mu) + r(\kappa_1 - \kappa_2) P < r(\xi(r) - (g(S^p) + \mu)) < r(-\delta).
\]
So $r$ decreases exponentially. This contradiction shows that $r_\infty < r^b$, a contradiction to the initial assumption. $\square$

5.2. An almost sharp result for uniform prey/host persistence. Armed with the boundedness result for the infection ratio, we are able to extend the preliminary persistence result in Proposition 5.2.

**Theorem 5.4.** Let $\sigma < \frac{g(0)}{h(g(0)/\mu)}$. Then there exists some $\epsilon > 0$ such that $S_\infty > \epsilon$
and $r^\infty \leq 1/\epsilon$ for all solutions with $S(0) > 0$. In particular, the host persists uniformly.

The condition for host persistence is almost sharp because host extinction can occur for $\sigma > \frac{g(0)}{h(g(0)/\mu)}$ and certain positive initial conditions (Theorem 2.7).

**Proof.** The system (14) induces a continuous semiflow on $\mathbb{R}_+^3$. By Remark 4.3 and Theorem 5.3, the statement concerning the uniform eventual boundedness of $r$ follows, and, by Theorem 3.1, the semiflow has a compact attractor.

To prove the persistence result for $S$, we will use the techniques in Sec.8.3 from [57] and choose the persistence function $\rho(S,r,P) = S$.

Let $\Omega$ be the union of all $\omega$-limit sets of solutions starting with $S(0) = 0$. Let $\hat{A}_0$ be the compact attractor of bounded sets for the semiflow induced by the differential system of equation
\[
r' = \sigma(1 + r)h(r) - r(g(0) + \mu) + (\kappa_1 - \kappa_2) Pr
\]
\[
P' = -\nu P.
\]
Then $\hat{A}_0$ is invariant and connected via Proposition 2.24 in [57], and $\hat{A}_0 = \{r_1\} \times \{0\}$, with $0 \leq r_1 < \infty$, is a point, and thus $A_0$ compact. Further $A := \{0\} \times A_0$ is isolated in $X_0$ [57, Def.5.14], is acyclic, and $\Omega \subseteq A_0$. Since $A_0$ is invariant, there exist a total solution $r$ of the equation with range in $\hat{A}_0$, $P(0) = 0$, and $r(0) = r_1$. This implies that $r'(0) = 0$, i.e., $r_1 = 0$ or $\sigma \xi(r_1) = g(0) + \mu$.

We show that, in either case, $A_0$ is uniformly weakly $\rho$-repelling.

Case 1: $r_1 = 0$.

Then $A_0 = \{(0,0,0)\}$. Choose some $\epsilon > 0$ such that $g(\epsilon) - \sigma h(\epsilon) - \kappa_1 \epsilon > \epsilon$. This is possible because $g$ and $h$ are continuous and $g(0) > 0 = \sigma h(0)$. Since $g$ is decreasing and $h$ is increasing, $g(S) - \sigma h(r) - \kappa_1 P > \epsilon$ for all $S, r, P \in [0, \epsilon]$. Suppose there is a solution with $S(0) > 0$ and
\[
\limsup_{t \to \infty} d(\{(S(t), r(t), P(t)), (0,0,0)\}) < \epsilon.
\]
Table 1. Summary of the dynamics of the host-parasite subsystem when $\xi$ is decreasing.

| Parameter Values | Dynamics |
|------------------|----------|
| $\sigma \leq \frac{\mu}{h(0)}$ | $S(0) > 0 \implies r(t) \to 0, S(t) \to K$ |
| $\frac{\mu}{h(0)} < \sigma \leq \frac{\mu + g(0)}{h(0)}$ | no $(0, r^\circ), (S^*, r^*)$ GAS$^\dagger$ for $(0, \infty)^2$ |
| $\frac{\mu + g(0)}{h(0)} < \sigma < \frac{\mu + g(0)}{h(\infty)}$ | $\exists (0, r^\circ), (S^*, r^*)$ GAS for $(0, \infty)^2$ |
| $\frac{\mu + g(0)}{h(\infty)} \leq \sigma < \frac{\mu + g(0)}{h(\infty)}$ | $r(0) > 0 \implies S(t) \to 0$ |
| $\frac{\mu + g(0)}{h(\infty)} \leq \sigma$ | $r(0) > 0 \implies S(t) \to 0, (r(t) \to \infty)^\dagger$ |

After a shift in time, $0 < S(t) < \epsilon, r(t) < \epsilon$, and $P(t) < \epsilon$ for all $t \geq 0$. By choice of $\epsilon$, $S'(t) \geq \epsilon S(t)$ and $S$ increases exponentially to $\infty$, a contradiction.

Case 2: $r_1 > 0$ and $\sigma \xi(r_1) = g(0) + \mu$.

The assumption of the theorem is equivalent to $\sigma \xi(g(0)/\mu) < g(0) + \mu$. See Remark 4.1 (b). Since $\xi$ is decreasing, $r_1 < g(0)/\mu$. Since $h$ is increasing, $\sigma h(r_1) < h(g(0)/\mu) < g(0)$, with the last inequality again following from the assumption of the theorem.

To show that $A_0$ is uniformly weakly $\rho$-repelling, choose some $\epsilon > 0$ such that $g(S) > \sigma h(r_1 + \epsilon) = \sigma h(0) + \epsilon + \kappa_1 \epsilon$ for all $S \in [0, \epsilon)$. Since $h$ is increasing, $g(S) > \sigma h(r) = \sigma h(0) + \epsilon + \kappa_1 P$ for all $S, P \in [0, \epsilon]$ and $r \in [0, r_1 + \epsilon]$. Assume that there exists a solution such that $S(0) > 0$ and $\lim_{t \to \infty} d((S(t), r(t), P(t)), A_0) < \epsilon$. Then, after a shift in time, $S(t), P(t) \in [0, \epsilon]$ and $r(t) \in [0, r_1 + \epsilon]$ for all $t \geq 0$. So $g(S(t)) \geq h(r(t)) + \epsilon + \kappa_1 \epsilon$ for all $t \geq 0$ and $S$ grows to infinity, a contradiction.

By Theorem 8.20 in [57], the induced semiflow is uniformly weakly $\rho$-persistent and thus uniformly persistent by Theorem 4.13 in [57].

This finishes the proof of the uniform persistence of susceptible prey/hosts. □

6. Two-dimensional subsystems.

6.1. Host-parasite subsystem. This is fully considered in [21], so we merely show a summary of the results (Table 1). Consulting Remark 4.3 will help to understand the order of cases.

Concerning the equilibria of the subsystem, there is always a parasite-free equilibrium $(K, 0)$. An endemic equilibrium $(S^*, r^*)$, with $S^*, r^* > 0$, exists when $\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}$, and satisfy the equations $g(S^*) = \sigma h(r^*) = \mu r^*$. When $\xi$ is constant and $\frac{g(0)}{h(g(0)/\mu)} = \frac{\mu + g(0)}{h(\infty)} = \frac{\mu + g(0)}{h'(0)} = \sigma$, then the $S = 0$ axis is a line of equilibria. When $\xi$ is strictly decreasing, a unique extinction equilibrium $(0, r^\circ)$ exists when $\frac{\mu + g(0)}{h'(0)} < \sigma < \frac{\mu + g(0)}{h(\infty)}$ and $r^\circ$ is the solution of $\sigma \xi(r^\circ) = g(0) + \mu$. 

† means that this event only occurs if the corresponding parameter inequality is strict or $\xi$ is strictly decreasing; GAS stands for “globally asymptotically stable.”
We see there are three possible fixed points, (0, 0), and (g, h). By Theorem 6.4, if \[ \frac{\mu + g(0)}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \], then both \( r^* \) and \( r^0 \) exist, \( r^* > r^0 \), and \( g(0) > \sigma h(r^0) \).

**Proof.** Both equilibria exist in this parameter range, as seen above, and
\[ \xi(r^*) = g(S^*) + \mu < g(0) + \mu = \xi(r^0). \]
Recall that \( g \) is strictly decreasing as long as it is positive. Since \( \xi \) is decreasing and \( h \) is strictly increasing, \( r^* > r^0 \) and then \( g(0) > g(S^*) = \sigma h(r^*) > \sigma h(r^0) \). \( \square \)

**Remark 6.2.** If \( r^* \) exists, \( r^* < g(0)/\mu \).

The proof of this statement can be found in [21, Cor. 7.10]

### 6.2. Prey-predator subsystem

\[
S' = S(g(S) - \kappa_1 P), \quad P' = P(\gamma_1 S - \nu). \tag{20}
\]

**Corollary 6.3.** There exists some \( c > 0 \) such that \( S_\infty > c \) for all solutions to System (20) with \( S(0) > 0 \).

**Proof.** This is the special case of Proposition 5.1 with \( r(0) = 0 = r(t) \) for all \( t \geq 0 \).

**Theorem 6.4.** (a) Let \( \gamma_1 K \leq \nu \) (i.e. \( g(\nu/\gamma_1) \leq 0 \)). Then \( (S(t), P(t)) \to (K, 0) \) as \( t \to \infty \) if \( S(0) > 0 \).

(b) Let \( \gamma_1 K > \nu \) (i.e. \( g(\nu/\gamma_1) > 0 \)). Then, if \( S(0) > 0 \) and \( P(0) > 0 \),

\[
S(t) \to \frac{\nu}{\gamma_1} =: S^0, \quad \text{and} \quad P(t) \to \frac{g(\nu/\gamma_1)}{\kappa_1} =: P^0.
\]

**Proof.** We see there are three possible fixed points, (0, 0), (K, 0), (recalling that \( g(K) = 0 \)) and \( \left( \frac{\nu}{\gamma_1}, \frac{g(\nu/\gamma_1)}{\kappa_1} \right) \). The condition for existence and positivity of the third equilibrium is \( \frac{g(\nu/\gamma_1)}{\kappa_1} > 0 \implies \frac{\nu}{\gamma_1} > 0 \implies \nu < K \). By Theorem 3.1 and Corollary 6.3, the \( \omega \)-limit set of this system is contained within \([c, K] \times [0, P^0]\), therefore no solutions converge to (0,0). We can apply the Bendixson-Dulac theorem, using \( \phi = \frac{1}{SP} \), to get

\[
\rho f_1(S, P) = \frac{g(S)}{P} - \kappa_1, \quad \text{and} \quad \rho f_2(S, P) = \gamma_1 - \frac{\nu}{S}.
\]

Thus \( \nabla \rho f = \frac{g'(S)}{P} < 0 \), so there are no periodic orbits in \((0, \infty)^2\).

**Part (a):** The only equilibria are (0,0) and (K,0). Since there are no periodic orbits, the Poincaré-Bendixson trichotomy implies that all solutions must converge to (K,0).

**Part (b):** Now all three equilibria exist. Choose \( \varepsilon > 0 \) such that \( \gamma_1 (K - \varepsilon) > \nu \), which is possible because \( \nu < K \gamma_1 \). Suppose toward contradiction that \( S(t) \to K \) as \( t \to \infty \). Then, after a time shift, \( S(t) > K - \varepsilon \) for all \( t \geq 0 \). Then \( \frac{P'}{P} = \gamma_1 S - \nu > 0 \),
implying that $P(t)$ grows exponentially, a contradiction. Thus, $S$ cannot converge to $K$, and so the $\omega$-limit is contained within $[c, K) \times [0, P^\circ]$, which only contains one equilibrium. Therefore, by the Pointcaré-Bendixson Theorem, this fixed point is globally stable for $S(0) > 0, P(0) > 0$.

Here we see that comparing the incoming predator biomass to the outgoing predator biomass will determine if the predator can invade. If incoming predator biomass exceeds outgoing predator biomass, i.e. \( \gamma_1 K > \nu \), then the predator can invade and persist. If not, i.e. \( \gamma_1 K \leq \nu \), then the predator eventually will die, and the equilibrium \((K, 0)\) is globally stable.

Remark 6.5. It may be interesting to compare $P^\circ = \frac{g(S^\circ)}{\kappa_1}$ to the large-time estimate $P^\circ$ that was obtained in Theorem 3.1. Since the existence of $P^\circ$ requires \( \gamma_1 > 0 \) and $S^\circ = \nu/\gamma_1 < K$, we have \( \alpha \geq \gamma_1/\kappa_1 \) and \( \beta \leq \nu \) and

\[
P^\circ \geq \alpha S^\circ (g(S^\circ) + \beta) \geq \frac{\alpha(\nu/\gamma_1)(g(S^\circ) + \nu)}{\nu} \geq \frac{1}{\kappa_1}(g(S^\circ) + \nu) = P^\circ + \frac{\nu}{\kappa_1}.
\]

7. Disease extinction. Recall the overall Assumption 2.3, \( \kappa_2 \geq \kappa_1 \), that the predator prefers infected over susceptible prey.

Theorem 7.1. Let \( \sigma h'(0) \leq \mu \). Then the disease goes extinct for all solutions \( r(t) \) with \( r \geq 0 \). Additionally, if \( \nu < \gamma_1 K \) solutions with \( S(0) > 0 \) and \( P(0) > 0 \) will converge to \((S^\circ, 0, P^\circ)\), and if \( \nu \geq \gamma_1 K \), solutions with \( S(0) > 0 \) will converge to \((K, 0, 0)\).

Proof. Since \( \xi(0) = h'(0) \) and \( \xi \) is decreasing, \( \sigma \xi(r) \leq \mu \) for all \( r \geq 0 \). By Corollary 4.9, and a time shift as needed, we only need to consider when \( S(t) \leq K \). By (14),

\[
r' = \sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2)P \leq -g(S) + (\kappa_1 - \kappa_2)P \leq 0.
\]

Thus, \( r \) is decreasing, bounded above by \( r(0) \), and bounded below by 0. We can reuse the portion of the proof of Proposition 4.8 to show that the boundedness of \( r \) implies uniform continuity of \( S', r' \), and \( P' \).

Suppose, toward contradiction, that \( \lim_{t \to \infty} r(t) = c > 0 \). By Barbalat’s Lemma [56, Lemma 4.2], \( r'(t) \to 0 \) as \( t \to \infty \). This is only a possibility if \( P(t) \to 0 \) and \( S(t) \to K \) as \( t \to \infty \). Now we apply Proposition 4.8, which implies \( r(t) \to 0 \) as \( t \to \infty \), a contradiction to \( r(t) \) having a strictly positive limit. Thus it is the case that \( r(t) \to 0 \) as \( t \to \infty \).

Using this, we can reduce the asymptotically autonomous 2 dimensional system

\[
S' = S(g(S) - \sigma h(r(t)) - \kappa_1 P),
P' = P(\gamma_1 S + \gamma_2 S r(t) - \nu),
\]

to the following limit system (previously seen in Section 6.2),

\[
S' = S(g(S) - \kappa_1 P), \quad P' = P(\gamma_1 S - \nu).
\]

We seek to use [61, Corollary 4.3], which tells us that if the \( \omega \)-limit set of solutions to System 21 intersects with the basin of attraction of a locally asymptotically stable fixed point in System (20), then solutions of System 14 will converge to that fixed point. By Theorem 5.4 and Equation (16), we know that there is some \( c > 0 \) such that \( S(t) > c \) for all \( t \geq t_0 \). Thus the \( \omega \)-limit set of solutions from System (21) is a subset of \([\delta, \infty) \times [0, P^\circ]\).
Theorem 6.4 implies that if $\nu \geq \gamma_1 K$, then, in System (20), the equilibrium $(K,0)$ attracts all solutions in $(0,\infty) \times (0,\infty)$. Thus, the $\omega$-limit set of System (21) intersects with the basin of attraction for $(K,0)$, so solutions to System (21) converge to $(K,0)$. This is equivalent to the global stability of $(K,0,0)$ for solutions of System (14) when $\nu \geq \gamma_1 K$ and $S(0) > 0$.

Now we consider when $\nu < \gamma_1 K$. Theorem 6.4 implies that if $\nu < \gamma_1 K$, then, in System (20), the equilibrium $(S^\circ, P^\circ)$ attracts all solutions in $(0,\infty) \times (0,\infty)$. Recall that by Theorem 5.4, $S_\infty > c > 0$. By the fluctuation method, there is a sequence $t_k$, such that $t_k \to \infty$ as $k \to \infty$ with the property $S'(t_k) \to 0$ and $S(t_k) \to S_\infty$. This shows us

$$0 = \lim_{k \to \infty} S'(t_k) = \lim_{k \to \infty} [S(t_k)(g(S(t_k)) - \sigma h(r(t_k)) - \kappa_1 P(t_k))]$$

which implies $P^\infty \geq \lim_{k \to \infty} P(t_k) = \frac{g(S_\infty)}{\kappa_1} > 0$. This implies that the $\omega$-limit set of solutions to System 21 contains points $(S, P)$ with $S, P > 0$ and has nonempty intersection with the domain of attraction of $(S^\circ, P^\circ)$.

Therefore, when $\nu < \gamma_1 K$, $(S^\circ, 0, P^\circ)$ is globally stable for solutions to System (14) with $S(0), P(0) > 0$. \[\square\]

8. Existence and local stability of boundary equilibria. We record the Jacobian matrix here for future use,

$$\begin{pmatrix}
\frac{d}{dS}[g(S)] - \sigma h(r) - \kappa_1 P & -S\sigma h'(r) & -\kappa_1 S \\
-r g'(S) & \sigma \frac{d}{dS}[r \xi(r)] + (\kappa_1 - \kappa_2) P & r(\kappa_1 - \kappa_2) \\
\gamma_1 P + \gamma_2 r P & P\gamma_2 S & \gamma_1 S + S r \gamma_2 - \nu
\end{pmatrix}.$$ (22)

8.1. The total extinction equilibrium $(0,0,0)$ with zero infection ratio. This equilibrium exists for all parameter values and has eigenvalues $\lambda_1 = g(0) > 0$, $\lambda_2 = \sigma h'(0) - \mu - g(0)$ and $\lambda_3 = -\nu < 0$. Thus the origin is a saddle so long as $\sigma h'(0) - \mu - g(0) \neq 0$.

8.2. The prey/host boundary equilibrium $(K,0,0)$. This equilibrium exists for all parameter values. The Jacobian matrix (22) evaluated at this equilibrium takes the form

$$\begin{pmatrix}
K g'(K) & -K \sigma h'(0) & -\kappa_1 K \\
0 & \sigma h'(0) - \mu & 0 \\
0 & 0 & \gamma_1 K - \nu
\end{pmatrix},$$

The eigenvalues are

$$\lambda_1 = K g'(K) < 0, \quad \lambda_2 = \sigma h'(0) - \mu, \quad \lambda_3 = \gamma_1 K - \nu.$$ The conditions for local stability in the 3-D system are the same as being stable in both of the 2 dimensional subsystems, as can be seen via the eigenvalues. Thus this point is either a sink if both $\sigma h'(0) - \mu < 0$ and $\gamma_1 K - \nu < 0$, or a saddle otherwise so long as $\sigma h'(0) - \mu \neq 0$ and $\gamma_1 K - \nu \neq 0$. 
8.3. The total extinction equilibrium \((0, r^0, 0)\) with positive infection ratio.
When \(\xi\) is constant, such an equilibrium only exists if \(\mu + g(0) = \sigma \xi(0) = \sigma h'(0)\), in which case there is a whole line of equilibria \(\{(0, r^0, 0) \mid r^0 \in [0, \infty]\}\).

When \(\xi\) is strictly decreasing, an ‘equilibrium’ of the form \((0, r^0, 0)\) exists if and only if \(\frac{\mu + g(0)}{h'(0)} < \sigma\) and is uniquely determined. We say ‘equilibrium’ because the infinite extinction state \((0, \infty, 0)\) is not a proper equilibrium.

8.3.1. \(0 < r^0 < \infty\).

**Theorem 8.1.** Assume that \(f(1, \cdot)\) is differentiable and \(\xi'(r) < 0\) for all \(r > 0\).
Then an equilibrium \((0, r^0, 0)\) with \(r^0 \in (0, \infty)\) only exists if \(\frac{\mu + g(0)}{\xi(0)} < \sigma < \frac{\mu + g(0)}{\xi(\infty)}\) (recall \(\xi(0) = h'(0)\) and \(\xi(\infty) = h(\infty)\)).

- If \(\frac{\mu + g(0)}{\xi(0)/\mu} < \sigma < \frac{\mu + g(0)}{\xi(\infty)/\mu}\) (equivalently if \(\frac{g(0)}{h'(0)/\mu} < \sigma < \frac{\mu + g(0)}{h(\infty)/\mu}\)), the boundary equilibrium \((0, r^0, 0)\) with \(r^0 \in (g(0)/\mu, \infty)\) exists and is locally stable.
- If \(\frac{\mu + g(0)}{\xi(0)/\mu} < \sigma < \frac{\mu + g(0)}{\xi(\infty)/\mu}\) (equivalently if \(\frac{g(0)}{h'(0)/\mu} < \sigma < \frac{\mu + g(0)}{h(\infty)/\mu}\)), the boundary equilibrium \((0, r^0, 0)\) with \(r^0 \in (0, g(0)/\mu)\) exists and is a saddle.
- If \(\sigma = \frac{\mu + g(0)}{\xi(0)/\mu}\) (equivalently if \(\sigma = \frac{g(0)}{h'(0)/\mu}\)), the boundary equilibrium \((0, r^0, 0)\) with \(r^0 \in (0, \infty)\) exists but nothing can be said about its stability from a linearized stability analysis, and \(r^0 = \frac{g(0)}{\mu}\).

**Proof.** As seen in Section 6.1, the equation \(\xi(r^0) = \frac{g(0) + \mu}{\sigma}\) has a unique solution if and only if \(\frac{\mu + g(0)}{h'(0)} < \sigma < \frac{\mu + g(0)}{h(\infty)}\). The Jacobian matrix (22) at this point is
\[
\begin{pmatrix}
g(0) - \sigma h(r^0) & 0 & 0 \\
-r^0 g'(0) & \sigma r^0 \xi'(r^0) & r^0 (\kappa_1 - \kappa_2) \\
0 & 0 & -\nu
\end{pmatrix},
\]
which has eigenvalues \(\lambda_1 = g(0) - \sigma h(r^0), \lambda_2 = \sigma r^0 \xi'(r^0) < 0\), and \(\lambda_3 = -\nu < 0\). Since \(\xi'(r^0) < 0\), the sign of \(g(0) - \sigma h(r^0)\) determines the local stability.

Note that \(r^0\) is an increasing function of \(\sigma\) and if \(r^0 = \frac{g(0)}{\mu}\) then \(\sigma = \frac{g(0)}{h(g(0)/\mu)}\).

Thus, \(r^0 > \frac{g(0)}{\mu}\) if and only if \(\sigma > \frac{g(0)}{h(g(0)/\mu)}\). The second inequality is equivalent to \(\lambda_1 < 0\). Therefore, if \((0, r^0, 0)\) exists, it is locally asymptotic stable if and only if \(\frac{g(0)}{h(g(0)/\mu)} < \sigma\). When equality holds, \(\lambda_1 = 0\).

The next result does not assume that the decrease of \(\xi\) is strict or that \(\xi\) (and thus \(f(\cdot, 1)\)) is differentiable. Its proof uses Lyapunov’s direct method instead of a linearized stability analysis, with the local Lyapunov function
\[
V(S, r, P) = S + r - r^0 \ln r + P, \quad S \geq 0, r > 0, P \geq 0.
\]
Theorem 8.2. Let $\xi$ be decreasing, $\sigma h(g(0)/\mu) > g(0)$ and $\sigma \xi(r) \leq \mu + g(0)$ for some $r > 0$. Then there exists an equilibrium $(0, r^\circ, 0)$ with $r^\circ \in (g(0)/\mu, \infty)$ and no equilibrium $(0, r^\circ, 0)$ with $r^\circ \in (0, g(0)/\mu]$. All equilibria $(0, r^\circ, 0)$ satisfy $\sigma h(r^\circ) > g(0)$ and are locally stable. Further, there is some $\epsilon \in (0, r^\circ)$ such that, for all solutions with $\sigma h(0) > \epsilon$ and $r(0) \in (r^\circ - \epsilon, r^\circ + \epsilon)$, the $\omega$-limit sets are of the form $\{0\} \times J \times \{0\}$ with an interval $J$, $\xi(J) = \{\xi(r^\circ)\}$, and $S(t) + I(t) + P(t) \to 0$ as $t \to \infty$.

Proof. By Remark 4.1 (b), $\sigma h(g(0)/\mu) > g(0)$ is equivalent to $\mu + g(0) < \sigma \xi(g(0)/\mu)$. By the intermediate value theorem, there exists some $r^\circ \in (g(0)/\mu, \infty)$ with $\sigma \xi(r^\circ) = \mu + g(0)$. Since $\xi$ is decreasing, there is no $r^\circ \in (0, g(0)/\mu]$ with $\xi(r^\circ) = \mu + g(0)$. Since $h$ is increasing, $\sigma h(r^\circ) \geq \sigma h(g(0)/\mu) > g(0)$.

We define a local Lyapunov function in Equation (23). Notice that $V(S, r, P) > V(0, r^\circ, 0)$, $(S, r, P) \not= (0, r^\circ, 0)$. The orbital derivative of $V$ [35, p.313] is

$$
\dot{V}(S, r, P) = S(g(S) - \sigma h(r) - \kappa_1 P) + (r - r^\circ)(\sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2) P) + P(\gamma_1 S + \gamma_2 r S - \nu).
$$

Notice that

$$
\frac{d}{dt} V(t) = \dot{V}(t), t \geq 0.
$$

Since $\xi$ is decreasing and $\mu = \sigma \xi(r^\circ) - g(0)$

$$
\dot{V}(S, r, P) \leq S(g(S) - \sigma h(r) - \kappa_1 P) + (r - r^\circ)(g(0) - g(S) + (\kappa_1 - \kappa_2) P) + P(\gamma_1 S + \gamma_2 r S - \nu).
$$

Notice that $\dot{V}(S, r, P) \leq 0$ if $S = 0$. If $S \in [0, K]$, with $\Lambda = \sup_{S \in [0, K]} |g'(S)|$

$$
\dot{V}(S, r, P) \leq S\alpha(S, r, P) + P\beta(S, r, P)
$$

with continuous functions $a, b : \mathbb{R}^+_\infty \to \mathbb{R}$,

$$
a(S, r, P) = g(S) - \sigma h(r) - \kappa_1 P + \Lambda [r^\circ - r]_+
$$

$$
b(S, r, P) = \gamma_1 S + \gamma_2 r S + (\kappa_1 - \kappa_2)(r - r^\circ) - \nu.
$$

Notice that

$$
a(0, r^\circ, 0) = g(0) - \sigma h(r^\circ) < 0 \quad \text{and} \quad b(0, r^\circ, 0) = -\nu < 0.
$$

Set

$$
U_\epsilon = \{(S, r, P); S, P \geq 0, r > 0, V(S, r, P) < V(0, r^\circ, 0) + \epsilon\}.
$$

Notice that $U_\epsilon$ is an open neighborhood of $(0, r^\circ, 0)$ in the metric space $\mathbb{R}^+_\infty$. If $\epsilon > 0$ is small enough and $(S, r, P) \in U_\epsilon$, $r$ is close enough to $r^\circ$ and $S$ and $P$ are close enough 0 such that $\dot{V}(S, r, P) \leq 0$.

So $U_\epsilon$ is forward invariant for sufficiently small $\epsilon > 0$ and $\dot{V}(S, r, P) = 0$ for $(S, r, P) \in U_\epsilon$ only if $S = 0$, $P = 0$, and $\xi(r) = \xi(r^\circ)$. By the Lyapunov-LaSalle principle [35, X.1.1], the $\omega$-limit set of a solution starting in $U_\epsilon$ is of the form described in the statement of the theorem. In particular, $S(t) + P(t) \to 0$ as $t \to \infty$. $I(t) \to 0$ as $t \to \infty$ follows from Corollary 3.2. \qed
Theorem 8.3. Let \( \xi \) be constant, i.e., the incidence function is proportional to the frequency-dependent one.

(a) If \( \sigma \xi \neq \mu + g(0) \), there exists no equilibrium of the form \((0, r^0, 0)\) with \( r^0 \in (0, \infty) \).

Let \( \sigma \xi = \mu + g(0) \).

(b) Then every point \((0, r^0, 0)\) with \( r^0 > 0 \) is a non-zero equilibrium.

(c) All equilibria \((0, r^0, 0)\), \( r^0 \in (g(0)/\mu, \infty) \), satisfy \( \sigma h(r^0) > g(0) \) and are locally stable. Further, there is some \( \epsilon \in (0, r^0) \) such that \( S(t) + I(t) + P(t) \to 0 \) as \( t \to \infty \) for all solutions with \( S(0), P(0) \in [0, \epsilon] \) and \( r(0) \in (r^0 - \epsilon, r^0 + \epsilon) \).

Proof. Let \( \sigma \xi = \mu + g(0) \). By Remark 4.1 (b), \( \sigma h(g(0)/\mu) = g(0) \) and \( \sigma h(r^0) > g(0) \) for any \( r^0 > g(0)/\mu \).

Define \( V \) by (23). The proof now proceeds as for Theorem 8.2.

8.3.2. \( r^0 = \infty \). Here we consider the formal state \((0, \infty, 0)\) in which there are no susceptible prey, or predators, and the ratio of infectives to susceptibles is infinite.

Theorem 8.4. Assume \( \sigma \xi(r) > g(0) + \mu \) for all \( r \in [0, \infty) \). Then the state \((0, \infty, 0)\) is locally asymptotically stable. More precisely, there exist \( r^\sharp \in (g(0)/\mu, \infty) \), \( P^\sharp > 0 \), \( S^\sharp > 0 \) such that all solutions starting in the set

\[
Q := \{(S, r, P) ; \quad 0 < S \leq S^\sharp, \quad r > r^\sharp, \quad 0 < Sr \leq S^\sharp r^\sharp, \quad 0 < P < P^\sharp \}
\]

stay in the set for \( t > 0 \) and satisfy \( S(t) \to 0, \quad r(t) \to \infty, \quad P(t) \to 0, \quad I(t) = r(t)S(t) \to 0 \) as \( t \to \infty \).

Remark 8.5. \( r^\sharp \in (g(0)/\mu, \infty) \), \( P^\sharp > 0 \), \( S^\sharp > 0 \) can be chosen successively as follows:

\[
\sigma \frac{h(r^\sharp)}{r^\sharp} = \mu, \quad P^\sharp = \frac{\sigma \xi(r^\sharp) - g(0) - \mu}{\kappa_2 - \kappa_1}, \quad S^\sharp = \frac{\nu}{\gamma_1 + \gamma_2 r^\sharp}.
\] (28)

The stability statement can be formulated completely in terms of \( S, I, P \).

The total extinction equilibrium \( S = 0, I = 0, P = 0 \) of (1) is locally asymptotically stable in the following sense:

There exist \( r^\sharp \in (g(0)/\mu, \infty) \), \( P^\sharp > 0 \), \( S^\sharp > 0 \) such that if \( t_0 \geq 0 \) and the inequalities

\[
0 < S(t) \leq I(t)/r^\sharp \leq S^\sharp, \quad P(t) \leq P^\sharp
\]

hold for \( t = t_0 \), then they hold for all \( t > t_0 \) and \( S(t) \to 0, P(t) \to 0, I(t) \to 0 \) and \( I(t)/S(t) \to \infty \) as \( t \to \infty \).

Proof. We first choose \( r^\sharp > 0 \) such that

\[
\sigma \frac{h(r^\sharp)}{r^\sharp} = \mu.
\] (29)

Recall that \( h'(0) = \xi(0) \geq g(0) + \mu \). Since \( g(0) > 0 \), \( h(r)/r > \mu \) for \( r > 0 \) sufficiently small to 0. Further \( h(r)/r \to 0 \) as \( r \to \infty \) because \( h \) is bounded by assumption. By the intermediate value theorem, \( r^\sharp > 0 \) can be chosen to satisfy Equation (29).

Suppose that \( r^\sharp \leq g(0)/\mu \). Since \( h(r)/r \) is decreasing,

\[
h(g(0)/\mu)g(0)/\mu \leq h(r^\sharp)/r^\sharp = \mu
\] (30)

which implies \( h(g(0)/\mu) \leq g(0) \) and

\[
\sigma \xi(g(0)/\mu) \leq (1 + (\mu/g(0)))h(g(0)/\mu) \leq g(0) + \mu,
\]
a contradiction to the assumptions for \( \xi \).
This implies that
\[ r^* > g(0)/\mu. \]  
Thus, we obtain the reverse of the inequality seen in Equation (30), which implies
\[ g(0) < \sigma h(g(0)/\mu) \leq h(r^*). \]
By the assumptions on \( \xi \), we can and do choose \( P^* > 0 \) and \( S^* > 0 \) such that
\[ 0 = \sigma \xi(r^*) - g(0) - \mu + (\kappa_1 - \kappa_2)P^*, \quad 0 = \gamma_1 S^* + \gamma_2 S^* r^* - \nu. \]  
For any solution in the set \( Q \), the following holds (recall that \( I = Sr \)
\[ \frac{S'}{S} = g(S) - \sigma h(r) - \kappa_1 P < g(0) - \sigma h(r^*) < 0, \]
\[ \frac{I'}{I} = \frac{h(r)}{r} - \kappa_2 P - \mu \leq \frac{h(r^*)}{r^*} - \mu = 0, \]
\[ \frac{P'}{P} = \gamma_1 S + \gamma_2 I - \nu \leq \gamma_1 S^* + \gamma_2 S^* r^* - \nu = 0, \]
\[ r' = \sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2)P. \]
These inequalities imply that the \( S, I, P \) components of any solution in \( Q \) are decreasing and that the solution does not leave \( Q \) as far as these components are concerned. The only way in which a solution starting in \( Q \) can leave \( Q \) is that its \( r \) component crosses \( r^* \) in an decreasing way. But when \( r \) takes the value \( r^* \),
\[ r' = r^* (\sigma \xi(r^*) - \mu - g(S) + (\kappa_1 - \kappa_2)P) > r^* (\sigma \xi(r^*) - \mu - g(0) + (\kappa_1 - \kappa_2)P) = 0, \]
a contradiction. So any solution starting in \( Q \) remains in \( Q \) in forward time.
Further, it follows from the inequality for \( S' \) that \( S(t) \to 0 \) as \( t \to \infty \). Then \( I(t) \to 0 \) and \( P(t) \to 0 \) as \( t \to \infty \) by Corollary 3.2.
Suppose that \( r \) is bounded. Then there exists some \( \tilde{r} > r^* \) such that \( r(t) \in [r^*, \tilde{r}] \) for all \( t \geq 0 \). By the differential equation for \( r \), since \( \xi \) is decreasing and \( S(t), P(t) \to 0 \) as \( t \to \infty \),
\[ \liminf_{t \to \infty} \frac{r'}{r} \geq \sigma \xi(\tilde{r}) - \mu - g(0) > 0, \]
which implies that \( r \) increases exponentially to infinity.
This contradiction implies that \( r \) is unbounded. Suppose that \( r(t) \) does not converge to infinity as \( t \to \infty \). Then there exists some \( \tilde{r} > r^* \) and a sequence \( t_n \to \infty \) as \( n \to \infty \) such that \( r \) takes a local minimum at all \( t_n \) and \( r(t_n) \leq \tilde{r} \). By the differential equation for \( r \), since \( \xi \) is decreasing,
\[ 0 = \frac{r'(t_n)}{r(t_n)} = \sigma \xi(r(t_n)) - \mu - g(S(t_n)) + (\kappa_1 - \kappa_2)P(t_n) \geq \sigma \xi(\tilde{r}) - \mu - g(S(t_n)) + (\kappa_1 - \kappa_2)P(t_n) \to_{n \to \infty} \sigma \xi(\tilde{r}) - \mu - g(0) > 0. \]
This contradiction implies that \( r(t) \to \infty \) as \( t \to \infty \). \( \square \)
When \( \xi \) is strictly decreasing, the condition of Theorem 8.4 is equivalent to \( \sigma h(\infty) \geq g(0) + \mu \). Thus, the ‘stability’ condition presented above is sharp when \( \xi \) is strictly decreasing and almost sharp when \( \xi \) is constant, which we see via Theorem 5.3.
Although \( (0, \infty, 0) \) is not an equilibrium in the strict sense, we can define its domain of attraction (sometimes also called stable set), \( W \). By definition, a point
(S₀, r₀, P₀) ∈ ℝ³ is in W if the solution S, r, P of (14) with initial values S(0) = S₀,
\ r(0) = r₀, and P(0) = P₀ satisfies S(t) → 0, r(t) → ∞, and P(t) → 0 as t → ∞.

W contains [0, ∞) × (0, ∞) × {0} and {0} × (0, ∞) × [0, ∞) and the set described
in Theorem 8.4. It follows from the definition of W that W and ℝ⁺ \ W are forward
invariant, i.e., solutions with initial values in these sets have their values in them for
all positive times. ℝ⁺ \ W contains ℝ⁺ × {0} × ℝ⁺. Since the solutions continuously
depend on their initial data, W is a relatively open subset of ℝ⁺ and its closure W
is also forward invariant and so is the boundary ∂W = W \ W, ∂W is nonempty
because ℝ⁺ is connected. Any locally stable interior equilibrium would be in the
interior of ℝ⁺ \ W. Any interior equilibrium that is a saddle is in ∂W provided its
unstable manifold intersects with W.

8.3.3. 0 < r² ≤ ∞. The following summary will be helpful which combines Theo-rem 8.2 and 8.4.

Theorem 8.6. Let σh(g(0)/µ) > g(0). Then there is locally asymptotically stable
total ecosystem extinction in the following sense: Then there exists a subset D of
(0, ∞)³ with nonempty interior such that (S(t), r(t), P(t)) ∈ D for all t ≥ 0 and
S(t) + I(t) + P(t) → 0 as t → ∞ if (S(0), r(0), P(0)) ∈ D.

8.4. The predator-prey boundary equilibrium (S°, 0, P°).

Theorem 8.7. If γ₁K > ν, the equilibrium (S°, 0, P°) exists. Recall

\[ S° = \frac{\nu}{\gamma₁} \quad \text{and} \quad P° = \frac{g(\nu/\gamma₁)}{\kappa₁} = \frac{g(S°)}{\kappa₁}. \]

If σh’(0) < κ₂P° + µ in addition, the equilibrium (S°, 0, P°) is locally asymptotically
stable.

If instead σh’(0) > κ₂P° + µ, the equilibrium is a saddle point.

Proof. From the calculations in Section 6.2, γ₁K > ν implies the existence of
(S°, 0, P°). We consider the Jacobian matrix (22) evaluated at (S°, 0, P°) and
use ξ(0) = h’(0), which yields

\[
\begin{pmatrix}
S°g'(S°) & -S°σh'(0) & -κ₁S° \\
0 & δ & 0 \\
κ₁P° & P°γ₂S° & 0
\end{pmatrix},
\]

where δ = σh’(0) − κ₂P° − µ.

The characteristic polynomial is

\[ (δ - λ)[λ² - S°g'(S°)λ + γ₁P°κ₁S°]. \]

This form gives us an obvious eigenvalue of λ₁ = δ. The remaining, bracketed,
portion is the characteristic equation for the point (S°, P°) in Section 6.2. Thus,
by Theorem 6.4, the remaining two eigenvalues have negative real parts, therefore
the point is locally asymptotically stable if δ < 0.

By a similar argument, this point is a saddle point if δ > 0. In this case, the
S − P plane is the stable manifold and the unstable manifold is one dimensional
and points into (0, ∞)³.

Note that in [39], a Hopf bifurcation of this equilibrium is proposed, while our
analysis indicates that this cannot occur even if κ₂ ≥ κ₁ is not assumed. We guess
that the periodic solutions shown in [39, Fig.3] are due to a Hopf bifurcation of
the coexistence equilibrium rather than the prey-predator boundary equilibrium. See
the comment after Theorem 10.1.
8.5. The host-parasite boundary equilibrium \((S^*, r^*, 0)\). In this section, we assume that \(f(\cdot, 1)\) is differentiable on \((0, \infty)\) with strictly positive derivative. By Remark 4.1 (d), \(h\) and \(\xi\) are differentiable on \((0, \infty)\) and \(h' - \xi'\) is strictly positive on \((0, \infty)\).

**Theorem 8.8.** If

\[
\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)},
\]

\((S^*, r^*, 0)\) exists. Recall that \(S^*\) and \(r^*\) satisfy \(r^* \in (0, g(0)/\mu)\) and

\[g(S^*) = r^* \mu = \sigma h(r^*).\]

Two of the eigenvalues of the Jacobian matrix at this point are the eigenvalues of the Jacobian matrix of the locally asymptotically point \((S^*, r^*)\) in the two-dimensional \(P = 0\) plane.

Further, if \(\nu > S^*(\gamma_1 + \gamma_2 r^*)\), the equilibrium \((S^*, r^*, 0)\) is locally asymptotically stable.

If instead \(\nu < S^*(\gamma_1 + \gamma_2 r^*)\), the equilibrium is a saddle.

**Proof.** The existence of \((S^*, r^*)\) in the two dimensional case (see [21] and Table 1) implies the existence of \((S^*, r^*, 0)\) in three dimensions.

Evaluating the Jacobian matrix (22) at \((S^*, r^*, P^*)\) yields

\[
J = \begin{pmatrix}
S^* g'(S^*) & -S^* \sigma h'(r^*) & -\kappa_1 S^* \\
-r^* g'(S^*) & r^* \sigma \xi'(r^*) & r^* (\kappa_1 - \kappa_2) \\
0 & 0 & \psi
\end{pmatrix},
\]

where \(\psi = \gamma_1 S^* + \gamma_2 S^* r^* - \nu\).

The characteristic polynomial is

\[
(\psi - \lambda)[\lambda^2 - (S^* g'(S^*) + r^* \sigma \xi'(r^*))\lambda + S^* g'(S^*) r^* \sigma \xi'(r^*) - S^* \sigma h'(r^*) r^* g'(S^*)] = 0.
\]

This form gives us an obvious eigenvalue of \(\lambda_3 = \psi\). The other two eigenvalues are those of the upper left 2 \times 2 submatrix, which has a strictly negative trace while the determinant has the sign of \(h'(r^*) - \xi'(r^*)\) which is strictly positive. Thus the other two eigenvalues have strictly negative real part. So the equilibrium \((S^*, r^*, 0)\) is locally asymptotically stable if \(\nu > S^*(\gamma_1 + \gamma_2 r^*)\), and unstable (a saddle) if \(\nu < S^*(\gamma_1 + \gamma_2 r^*)\).

9. **Uniform persistence of the whole ecosystem and its parts.** Conditions for persistence of susceptible hosts have been found in Theorem 5.4.

Note that for a given parameter set, Corollary 3.2 implies that \(P\) and \(I\) cannot persist uniformly for all positive initial conditions if there is one solution with positive initial conditions and \(S\) component such that \(S(t) \to 0\) as \(t \to \infty\). This restriction, however, does not extend to \(r\), the ratio of infectives to susceptibles, which is not the parasite itself.

Throughout this section, we assume that \(f(\cdot, 1)\) is differentiable on \((0, \infty)\) with strictly positive derivative. By Remark 4.1 (d), \(h\) and \(\xi\) are then differentiable on \((0, \infty)\) and \(h' - \xi'\) is strictly positive on \((0, \infty)\).

This makes the equilibrium \((S^*, r^*, 0)\) locally asymptotically stable in the \(P = 0\) plane (Theorem 8.8) whenever it exists.

For improved readability, we have moved the more technical proofs in this section (Section 9) to the appendix in Section 14. To avoid repetition, we do not explicitly state at each theorem that the proof has been moved.
9.1. Persistence of the prey/host and the predator.

Theorem 9.1. Let \( \nu < \gamma_1 K \), and either

- \( \sigma \leq \frac{\mu}{h'(0)} \)

or

- \( \frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \), and \( \nu < \gamma_1 S^* + \gamma_2 S^* r^* \).

Then the prey/host and the predator persist uniformly, i.e. there exists some \( \epsilon > 0 \) such that \( S_\infty > \epsilon \) and \( P_\infty > \epsilon \) for all solutions with \( S(0) > 0 \) and \( P(0) > 0 \).

Recall that \( S^* \) and \( r^* \) satisfy \( \sigma h(r^*) = \mu r^* = g(S^*) \).

Remark 9.2. Under the first assumption, the uniform persistence of the prey/host and predator goes along with global parasite extinction.

Under the second assumption, the uniform persistence of the prey/host and predator can go along with predator-mediated parasite extinction. In the absence of the predator, the solutions of host-parasite subsystem converge to \((S^*,0,r^*)\) if \( P(0) = 0 \), \( r(0) > 0 \), \( S(0) > 0 \), while the predator-prey boundary equilibrium \((S^*,0,P^o)\) exists and is locally asymptotically stable if \( \sigma h'(0) < \kappa g(S^*) + \mu \), \( S^o = \nu/\gamma_1 \), \( \kappa = \kappa_1/\kappa_2 \).

The change in conditions between bullet points may seem strange at first; however, we see that for \( \sigma \leq \frac{\mu}{h'(0)} \), the equilibrium \((S^*,r^*,0)\) does not exist, and if \( \sigma \to \frac{\mu}{h'(0)} \) from above, then \((S^*,r^*) \to (K,0)\). This implies \( \gamma_1 S^* + \gamma_2 S^* r^* \to \gamma_1 K \) as \( \sigma \to \frac{\mu}{h'(0)} \) from above. With this observation, we can see the first bullet is the natural extension of the second as \( \sigma \) crosses \( \frac{\mu}{h'(0)} \).

9.2. Persistence of host and parasite. We start with the following observation.

Proposition 9.3. Both \( S \) and \( r \) persist uniformly for all solutions with \( S(0) > 0 \) and \( r(0) > 0 \) if and only if \( I \) persists uniformly for all solutions with \( S(0) > 0 \) and \( r(0) > 0 \).

Theorem 9.4. Let \( \frac{\mu}{K'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \).

If \( \gamma_1 K > \nu \), such that the prey-predator boundary equilibrium \((S^o,0,P^o)\) exists, then we add the condition of \( \sigma h'(0) > \mu + \kappa_2 P^o \).

Then the host and the parasite persist uniformly: There exists some \( \epsilon > 0 \) such that \( S_\infty \geq \epsilon \), \( I_\infty \geq \epsilon \) and \( r_\infty \geq \epsilon \) for all solutions with \( S(0) > 0 \) and \( I(0) > 0 \).

9.3. Persistence of the ratio of infective to susceptible prey.

Theorem 9.5. Assume that \( \sigma h'(0) > g(0) + \mu \).

If \( \gamma_1 K > \nu \) such that the prey-predator boundary equilibrium \((S^o,0,P^o)\) exists, then we add the condition of \( \sigma h'(0) > \mu + \kappa_2 P^o \).

Then the ratio of infective to susceptible prey is uniformly persistent: There is some \( \epsilon > 0 \) such that \( r_\infty \geq \epsilon \) for all solutions with \( r(0) > 0 \).

Recall \( \kappa_1 P^o = g(S^o) = g(\nu/\gamma_1) \).

Remark 9.6. Theorem 9.5 does not hold if \( \sigma h'(0) \leq g(0) + \mu \).
Because of Remark 9.6, we make the following assumption.

Assumption 9.7. Either \( \xi \) is strictly decreasing, or \( \xi \) is constant and \( \mu + g(0) \neq \sigma h'(0) = \sigma \xi \).

Corollary 9.8. Let Assumption 9.7 hold and \( \sigma h'(0) > \mu \). If \( \gamma_1 K > \nu \), then we suppose the stronger condition of \( \sigma h'(0) > \mu + \kappa_2 P^0 \).

Then the ratio persists uniformly: There exists some \( \varepsilon > 0 \) such that \( r_\infty > \varepsilon \) for all solutions with \( S(0) > 0 \) and \( r(0) > 0 \).

Theorem 7.1 shows that this result is sharp as for the condition \( \nu \geq \gamma_1 K \).

9.4. Uniform persistence of all three species. We speak about dynamic coexistence if all three species, predator, prey/host and parasite, persist uniformly: There exists some \( \varepsilon > 0 \) such that \( \liminf_{t \to \infty} S(t) \geq \varepsilon \), \( \liminf_{t \to \infty} I(t) \geq \varepsilon \), and \( \liminf_{t \to \infty} P(t) \geq \varepsilon \) for all solutions with \( S(0), I(0), P(0) > 0 \).

9.4.1. Unmediated dynamic coexistence. We assume that the prey-predator boundary equilibrium \((S^0, 0, P^0)\) exists,

\[
\gamma_1 S^0 = \nu, \quad \kappa_1 P^0 = g(S^0) > 0 \quad \text{(i.e. } \nu < \gamma_1 K)\tag{33}
\]

We further assume that the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists,

\[
g(S^*) = \mu r^* = \sigma h(r^*),
\]

which is the case if and only if

\[
\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}. \tag{34}
\]

Finally we assume that the parasite can invade the predator-prey boundary equilibrium,

\[
\sigma h'(0) > \mu + \kappa_2 P^0 \tag{35}
\]

and the predator can invade the host-parasite boundary equilibrium,

\[
\nu < S^* (\gamma_1 + \gamma_2 r^*). \tag{36}
\]

Theorem 9.9. Let (33), (34), (35), and (36). Then there is dynamic predator–prey/host–parasite coexistence: There exists some \( \varepsilon > 0 \) such that

\[
\liminf_{t \to \infty} S(t) \geq \varepsilon, \quad \liminf_{t \to \infty} I(t) \geq \varepsilon, \quad \liminf_{t \to \infty} P(t) \geq \varepsilon
\]

whenever \( S(0) > 0, I(0) > 0, P(0) > 0 \).

The coexistence of all three species is called unmediated because, under these assumptions, host/prey and predator dynamically coexist in the absence of the parasite (Theorem 6.4), and prey/host and parasite dynamically coexist in the absence of the predator (Table 1).

Proof. Under these hypotheses, the assumptions of Theorems 9.1 and 9.4 are satisfied, which imply the uniform persistence of \( S \) and \( P \) and of \( S \) and \( I \), respectively. If \( I_\infty \geq \varepsilon_1, P_\infty \geq \varepsilon_2, \) and \( S_\infty \geq \max\{\varepsilon_1, \varepsilon_2\} \), then setting \( \varepsilon := \min\{\varepsilon_1, \varepsilon_2\} \) yields the result.

Looking ahead to existence of the interior equilibrium, we note that the assumptions (33), (34), (35), (36), imply the existence of an interior equilibrium that is locally asymptotically stable for almost all \( \mu > 0 \) for which it exists (Theorem 10.5).
9.4.2. Parasite-mediated dynamic coexistence. This is a scenario where the predator could not survive on healthy prey alone but needs the infected prey because it is easier to catch.

So the prey-predator boundary equilibrium does not exist,

$$\gamma_1 = \kappa_1 = 0, \quad \kappa_1 > 0, \gamma_1 > 0, \quad g(\nu / \gamma_1) \leq 0,$$

i.e. $$\nu / \gamma_1 \geq K.$$

(37)

However, the host-parasite equilibrium exists,

$$\mu_{h}'(0) < \sigma < g(0) h(r^*) \quad (34 \text{ revisited})$$

and the predator can invade it,

$$\nu < S^*(\gamma_1 + \gamma_2 r^*).$$

(36 revisited)

Recall that $$S^*$$ and $$r^*$$ satisfy $$g(S^*) = r^* \mu = h(r^*)$$. We also recall that $$(S^*, r^*, 0)$$ is always stable in the $$S-r$$ plane when it exists, as seen in Proposition 7.14. Equation (37) implies that $$(S^*, 0, P^0)$$ does not exist, so Equation (33) does not need to be satisfied. Note that Equation (34) and the equations for $$S^*$$ and $$r^*$$ are independent of $$\nu$$, $$\gamma_1$$ and $$\gamma_2$$, so changing any of these parameters will not effect the existence or values of $$(S^*, r^*, 0)$$. So, for Equation (37), we can choose $$\nu$$ and $$\gamma_1$$ for this relationship to hold. Then, for Equation (36) we can choose $$\gamma_2$$ large enough for this relationship to hold. Thus we see that it is possible to fulfill Equations (34), (36), and (37).

**Theorem 9.10.** Assume (34), (36), and (37). Then there is dynamic predator–prey/host–parasite coexistence: There exists some $$\epsilon > 0$$ such that

$$\lim \inf_{t \to \infty} S(t) \geq \epsilon, \quad \lim \inf_{t \to \infty} I(t) \geq \epsilon, \quad \lim \inf_{t \to \infty} P(t) \geq \epsilon$$

whenever $$S(0) > 0, I(0) > 0, P(0) > 0$$.

By [57, Thm.6.2], there is an interior equilibrium under the assumptions required for Theorem 9.10. Theorem 10.5 will show the existence of an interior equilibrium that is locally asymptotically stable for almost all $$\mu > 0$$ for which it exists.

10. The interior equilibrium. Recall the full system

$$\begin{align*}
\frac{S'}{S} &= g(S) - \sigma h(r) - \kappa_1 P, \\
\frac{r'}{r} &= \sigma \xi(r) + (\kappa_1 - \kappa_2) P - \mu - g(S), \\
\frac{P'}{P} &= \gamma_1 S + \gamma_2 r S - \nu.
\end{align*}$$

For an interior equilibrium (a strictly positive time-independent solution), the left hand sides of these equations are zero.

Immediately we notice from the $$P'$$ equation that at an interior equilibrium,

$$S^\dagger = \frac{\nu}{\gamma_1 + \gamma_2 r^\dagger},$$

thus $$\gamma_1 + \gamma_2 r^\dagger > 0$$ for an interior equilibrium to exist. Further, if $$\gamma_1 > 0$$ then

$$\begin{align*}
S^\dagger &= \begin{cases} 
\frac{\nu}{\gamma_1} & \text{if } \gamma_2 > 0 \\
S^0 & \text{if } \gamma_2 = 0 \\
\nu & \text{if } \gamma_2 < 0
\end{cases}
\end{align*}$$

(38)
We use $\nu \gamma_1$ in the first case, as $S^\circ$ may not exist in this case, however the condition $\nu \gamma_1 < K$ must be fulfilled in order for $S^\dagger < K$ in the other two cases. Thus, if an interior equilibrium exists, $\gamma_2 \leq 0$ implies the predator-prey equilibrium exists as well.

Throughout this section, we assume that $f(\cdot, 1)$ is differentiable on $(0, \infty)$ with strictly positive derivative. By Remark 4.1 (d), $h$ and $\xi$ are differentiable on $(0, \infty)$ and $h' - \xi'$ is strictly positive on $(0, \infty)$. For better readability, we move the more technical proofs in this section to the appendix in Section 15. In some theorems, it is not clear that the assumptions are feasible and feasibility is established shortly after the proof. To avoid repetition, we do not explicitly state at each theorem that the proof or the verification that its conditions can be met have been moved.

10.1. Local stability of interior equilibrium.

**Theorem 10.1.** Suppose that a coexistence equilibrium $(S^\dagger, r^\dagger, P^\dagger)$ exists, and define

$$\Delta(r, S) := \kappa_1 \nu \sigma(\xi'(r) - h'(r)) + \kappa_2 (S^2 g'(S) \gamma_2 + \nu \sigma h'(r)).$$

(39)

If $\Delta(r^\dagger, S^\dagger) < 0$, then the coexistence equilibrium is locally asymptotically stable. If $\Delta(r^\dagger, S^\dagger) > 0$, then that the coexistence equilibrium is a saddle, with its unstable manifold being one dimensional.

We emphasize that this result relies on assuming $\kappa_2 \geq \kappa_1$, that the predator does not prefer susceptible over infected prey. [39] find a Hopf bifurcation at the coexistence equilibrium for $\kappa_2 < \kappa_1$.

**Corollary 10.2.** Suppose a coexistence equilibrium $(S^\dagger, r^\dagger, P^\dagger)$ exists and $\kappa_1 = \gamma_1 = 0$.

If $S^\dagger g'(S^\dagger) + r^\dagger \sigma h'(r^\dagger) < 0$, then $(S^\dagger, r^\dagger, P^\dagger)$ is locally asymptotically stable. If $S^\dagger g'(S^\dagger) + r^\dagger \sigma h'(r^\dagger) > 0$, then $(S^\dagger, r^\dagger, P^\dagger)$ is a saddle.

**Proof.** By Assumption 2.3, $\gamma_1 = 0$ implies $\gamma_2 > 0$. The local stability then follows from Theorem 10.1 and, when $\gamma_1 = 0, \nu = \gamma_2 S^\dagger r^\dagger$.

10.2. Towards existence and multiplicity of interior equilibria. So far we have not excluded that the predator only eats infected prey because it did not make much difference for the analysis. For the discussion of interior equilibria, however, this case requires a separate treatment [20].

While for a specialist predator as we consider in this paper one could dream up a quirky evolutionary path that would lead to its eating only the infectives of the one prey species it relies on, this may rarely happen and we are not aware of any real world example.

Therefore, we now assume that the predator eats both susceptible and infected prey,

$$\kappa_1 > 0, \text{ and } \gamma_1 > 0.$$  

(40)

In the coming context, it is suggestive to introduce the notation

$$S^\circ = \frac{\nu}{\gamma_1}, \quad \gamma = \frac{\gamma_2}{\gamma_1}$$

(41)

to eliminate the parameter $\nu$. Recall that $S^\circ$ is the susceptible prey coordinate of the predator-prey equilibrium $(S^\circ, 0, P^\circ)$ provided that $P^\circ = \frac{g(S^\circ)}{\kappa_1} > 0$. Here, we use this notation also if $g(S^\circ) < 0$. 

Recall that \( r(t) \to 0 \) as \( t \to \infty \) if \( \sigma h'(0) \leq \mu \) (Theorem 7.1). So a coexistence (or interior) equilibrium only exists if
\[
\sigma h'(0) > \mu,
\]
which we assume throughout this section.

10.3. **Existence of at least one interior equilibrium.**

**Theorem 10.3.** Assume \( \kappa_1 > 0, \quad \gamma_1 > 0, \) and
\[
\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}, \quad g(\nu/\gamma_1) > 0.
\]

Then the host-parasite boundary equilibrium \((S^*, r^*, 0)\) and the predator-prey boundary equilibrium \((S^\circ, 0, P^\circ)\) exist,
\[
g(S^*) = r^* \mu = \sigma h(r^*), \quad S^\circ = \frac{\nu}{\gamma_1}, \quad P^\circ = \frac{g(S^\circ)}{\kappa_1} = \frac{g(\nu/\gamma_1)}{\kappa_1}.
\]

Further the susceptible hosts persist uniformly. Assume
\[
\sigma h'(0) < \mu + \kappa g(S^\circ), \quad 0 < S^* + \gamma S^* r^* < S^\circ
\]
such that both boundary equilibria are locally asymptotically stable.

Then an interior equilibrium exists. Further, for almost all \( \mu \) such that the above inequalities hold, there is an interior equilibrium that is a saddle.

**Remark 10.4.** If the interior equilibrium is unique and a saddle, we believe that its stable manifold acts as a separatrix between the basins of attraction of the two locally asymptotically stable boundary equilibria, giving bistability.

**Theorem 10.5.** Assume \( \kappa_1 > 0, \quad \gamma_1 > 0 \) and
\[
\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}.
\]

Then the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists, \( g(S^*) = r^* \mu = \sigma h(r^*) \).

Assume that \( 0 < S^\circ < S^*[1 + \gamma r^*] \) such that the host-parasite boundary equilibrium is a saddle which can be invaded by the predator.

Assume one of the following for \( S^\circ = \nu/\gamma_1 \):

(i) \( g(S^\circ) \leq 0 \), the predator-prey boundary equilibrium \((S^\circ, 0, P^\circ)\) does not exist.
(ii) \( g(S^\circ) > 0 \) and \( \sigma h'(0) > \mu + \kappa g(S^\circ) \); so the predator-prey boundary equilibrium \((S^\circ, 0, P^\circ)\) with \( P = (1/\kappa_1) g(S^\circ) \) exists and is unstable.

Then the predator and the prey/host and the parasite persist uniformly, and an interior equilibrium exists. For almost all \( \mu \) for which all these assumptions are satisfied, there exists an interior equilibrium that is locally asymptotically stable.

We conjecture that if the interior equilibrium is unique, then for almost all \( \mu \) the interior equilibrium is stable and attracts all solutions starting in \((0, \infty)^3\). The feasibility of the assumptions of Theorem 10.5 has been established in Section 9.4.1 and Section 9.4.2.

**Theorem 10.6.** Assume \( \kappa_1 > 0, \quad \gamma_1 > 0, \quad g(S^\circ) > 0, \quad 0 < 1 + \gamma \frac{g(0)}{\mu} \). Then the predator-prey boundary equilibrium \((S^\circ, 0, P^\circ)\) exists,
\[
P^\circ = \frac{g(S^\circ)}{\kappa_1}.
\]
Further, we assume
\[
\frac{g(0)}{h(g(0)/\mu)} \leq \sigma < \frac{\kappa g(S^\circ) + \mu}{h'(0)}.
\] (44)

So, the host-parasite boundary equilibrium \((S^*, r^*, 0)\) does not exist, but \((S^\circ, 0, P^\circ)\) is locally asymptotically stable.

Then an interior equilibrium exists. Further, for almost all \(\mu\) such that the above inequalities hold, there is an interior equilibrium that is a saddle.

This theorem extends Theorem 10.3 to the case where \((S^*, r^*, 0)\) no longer exists. However, (assuming \(\xi\) is strictly decreasing or \(g(0) < \sigma h(g(0)/\mu)\)) there exists an extinction ‘equilibrium’ of the form \((0, r^\circ, 0)\), where \(r^\circ\) could be infinity, which is locally asymptotically stable by Theorem 8.6. This again suggests a bistable situation, where solutions are attracted either to \((S^\circ, 0, P^\circ)\), or \((0, r^\circ, 0)\), where \(r^\circ\) could be infinity, and the stable manifold of the interior saddle acts as a separatrix.

The assumptions of Theorem 10.6 are feasible. First, choose \(\sigma\) large enough to make the left inequality of (44) hold, then increase \(\kappa_2\) (which increases \(\kappa\), Equation (58)) until the right inequality holds.

10.4. Existence of at least two interior equilibria.

Theorem 10.7. Let
\[
g(S^\circ) \leq 0, \quad g(0) < \sigma h(g(0)/\mu).
\] (45)

Then neither the predator-prey nor the host-parasite boundary equilibrium exist, but the parasite persists uniformly in form of the ratio of infected to susceptible hosts.

Further, let
\[
g(0)/\mu > 1, \quad 1 + \gamma \frac{g(0)}{\mu} > 0,
\] (46)
\[
\sigma h(1)(1 + \kappa) - \kappa g\left(\frac{S^\circ}{1 + \gamma}\right) < \mu.
\]

Then there exist two interior equilibria associated with \(0 < r^1 < 1 < r^2 \leq g(0)/\mu\).

For almost all \(\mu\) for which the inequalities (46) are satisfied, the interior equilibrium associated with \(r^1\) is locally asymptotically stable and the interior equilibrium associated with \(r^2\) is a saddle.

Remark 10.8. Since \(\sigma > \frac{g(0)}{h(g(0)/\mu)} = \frac{g(0) + \mu}{\xi(g(0)/\mu)}\), there is a locally asymptotically stable extinction state: either the boundary equilibrium \((0, r^\circ, 0)\) (Theorem 8.2) or the formal boundary state \((0, \infty, 0)\), in the sense of Theorem 8.4. So there is a bistable situation between the locally asymptotically interior equilibrium associated with \(r^1\) and a locally asymptotically stable extinction state with the stable manifold of the interior saddle associated with \(r^2\) possibly forming a separatrix. The ratio of infected to susceptible hosts persists uniformly nevertheless. Notice that \((0, r^\circ, 0)\) attracts all solutions with \(P(0) = 0\) and \(r(0) > 0\); so the survival of all three species in a neighborhood of the coexistence equilibrium is predator-mediated by the predator’s preference for infected over susceptible prey.

Theorem 10.9. Suppose the following:
\[
\nu < \gamma_1 K, \quad \sigma h'(0) < \kappa g(S^\circ) + \mu, \quad \sigma h(g(0)/\mu) < g(0)
\]
Then the predator-prey boundary equilibrium \((S^*, 0, P^*)\) exists and is locally asymptotically stable and the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists and is a saddle, with \(r^* > 1\). Further, there exist at least two interior equilibria that are associated with \(0 < r^*_1 < 1 < r^*_2 < r^*\). For almost all \(\mu\) such that the conditions above are satisfied, the interior equilibrium associated with \(r^*_1\) is a saddle and the interior equilibrium associated with \(r^*_2\) is locally asymptotically stable.

**Remark 10.10.** Note that under these assumptions there is bistability between predator-mediated extinction of the parasite with survival of prey and predator at high initial predator levels (Theorem 8.7) and survival of all three species at low predator levels, and also uniform persistence of predators and susceptible prey (Theorem 9.1).

**Theorem 10.11.** Suppose the following:

\[
g(0) > \mu, \quad \frac{\mu}{h(1)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \quad \text{(equivalently) \quad \frac{2\mu}{\xi(1)} < \sigma < \frac{g(0) + \mu}{\xi(g(0)/\mu)}},
\]

\(S^* > S^*(1 + \gamma r^*), \quad \sigma h'(0) - \kappa g(S^*) > \mu, \quad \text{and} \quad \sigma h(1)[1 + \kappa] - \kappa g\left(\frac{S^*}{1 + \gamma}\right) < \mu.\)

Then the predator-prey/host boundary equilibrium \((S^*, 0, P^*)\) either does not exist or is unstable, while the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists and is locally asymptotically stable, with \(r^* > 1\). Further, there exist at least two interior equilibria associated with \(0 < r^*_1 < 1 < r^*_2 < r^*\).

For almost all \(\mu > 0\) for which all the assumed inequalities are satisfied, the interior equilibrium associated with \(r^*_1\) is locally asymptotically stable, and the interior equilibrium associated with \(r^*_2\) is a saddle.

**Remark 10.12.** Under these assumptions, host and parasite persist uniformly (Theorem 9.1). Further, there is bistability between the locally asymptotically stable host-parasite boundary equilibrium \((S^*, r^*, 0)\) (Section 8.5) and a locally asymptotically stable coexistence (interior) equilibrium \((S^*_1, r^*_1, P^*_1)\), in other words between locally asymptotically stable predator extinction and locally asymptotically stable survival of all three species. If the predator-prey boundary equilibrium exists but is a saddle (Section 8.4), the predator extinction is parasite-mediated. There also is an interior saddle, the stable manifold of which may act as a separatrix between the domains of attraction of the host-parasite boundary equilibrium and the stable coexistence equilibrium.

### 10.5. Two nonexistence results.

**Theorem 10.13.** Assume that

\[
\sigma h'(0) < \kappa g(S^*) + \mu, \quad S^* = \frac{\nu}{\gamma_1} \quad \text{and} \quad \gamma_2 \geq 0, \quad \kappa = \frac{\kappa_2}{\kappa_1}.
\]

(a) If \(\kappa_2 \leq \kappa_1\), there is no interior equilibrium.
(b) Assume that \(\kappa_2 \geq \kappa_1\) and that \(g\) is convex on \([0, S^*]\).

(i) If \(\gamma_2 \geq \gamma_1\), assume that \(\sigma h'(0)(\kappa - 1) + \kappa g'(S^*)S^* \leq 0\).

(ii) If \(\gamma_2 \leq \gamma_1\), assume that \(\sigma h'(0)(\kappa - 1) + \kappa \gamma g'(S^*)S^* \leq 0\).

Then there exists no interior equilibrium.
Remark 10.14. The assumptions of Theorem 10.13 for nonexistence of an interior equilibrium, are compatible with those of the existence and local asymptotic stability of the predator-prey boundary equilibrium that just additionally require that \( g(S^0) > 0 \) (Theorem 8.7). They are also compatible with the assumptions of Theorem 9.1 for uniform persistence of the predator and prey/host, 
\[ \sigma h'(0) \leq \mu \quad \text{or} \quad \frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \]
and \( S^0 < S^*(1 + \gamma r^* \) for the host-parasite boundary equilibrium \((S^*, r^*, 0)\) to be a saddle.

Theorem 10.15. Suppose the following 
\[ \frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} \quad \text{(equivalently)} \quad \frac{\mu}{\xi(0)} < \sigma < \frac{g(0) + \mu}{\xi(g(0)/\mu)} \]
and either 
\[ S^0 > S^*(1 + \gamma r^*) \quad \text{or} \quad S^0 = \nu/\gamma_1 \quad \text{and} \quad \gamma_2 > 0, \]
and either 
\[ g(S^0/(1 + \gamma r^*)) \leq 0 \]
or 
\[ 1 \leq \kappa \leq \frac{g(S^*)}{g(S^0/(1 + \gamma r^*))} \quad \text{and} \quad \kappa = \kappa_2/\kappa_1. \]

Then the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists and is locally asymptotically stable, and there are no interior equilibria.

Remark 10.16. Notice \( g(S^*)/(1 + \gamma r^*) \) exceeds one because \( g \) is strictly decreasing wherever it is positive. The assumptions of this nonexistence result also satisfy Theorem 8.8, which implies parasite-mediated locally asymptotically stable predator extinction, and (with the additional assumption \( \sigma h'(0) > \mu + \kappa g(S^0) \)) Theorem 9.4, which implies the uniform persistence of the host and the parasite.

10.6. A uniqueness result.

Theorem 10.17. Let \( \kappa_2 \leq \kappa_1 \) and \( \gamma_2 > 0 \). Then there is at most one interior equilibrium.

Proof. Since \( \xi \) is decreasing and \( g \) is strictly decreasing wherever it is positive, \( E \) is strictly decreasing. \( \square \)

11. Parasite-mediated collapse of the ecosystem. Here we show conditions for the disease to collapse the ecosystem no matter the initial condition of the predator.

Recall that initial-condition-dependent ecosystem collapse has been established in Theorem 8.6 and its bistability with the predator-prey boundary equilibrium in Theorem 10.6 and with an interior equilibrium in Remark 10.8.

Recall that we assume that the predator prefers infected over susceptible prey, \( \kappa_2 > \kappa_1 \). Also recall from Theorem 3.1 that \( P \) has an asymptotic time bound \( P^\circ \), which is independent of initial conditions and independent of \( \sigma \).

Proposition 11.1. For all solutions of (14), \( S(t) \to 0, I(t) \to 0 \) and \( P(t) \to 0 \) as \( t \to \infty \) if \( I(0) > 0 \) and 
\[ \sigma \xi(g(0)/\mu) > \mu + g(0) + (\kappa_2 - \kappa_1)P^\circ. \]
Proof. We can assume that $S(0) > 0$. Otherwise $S(t) = 0$ for all $t \geq 0$ and $I(t), P(t) \to 0$ as $t \to \infty$ by Corollary 3.2. Since $I(0) > 0$, $I(t) > 0$ for all $t \geq 0$ and $r(t) \in (0, \infty)$ for all $t \geq 0$. Since $\xi$ is decreasing and $P^\infty \leq P^\circ$, we can conclude that $r_\infty > g(0)/\mu$. The inequality (47) implies\

$$\sigma \left(1 + \frac{\mu}{g(0)}\right)h(g(0)/\mu) > \mu + g(0),$$

and $\sigma h(g(0)/\mu) > g(0)$.

Suppose that $S^\infty > 0$. By the fluctuation method, there exists a sequence $(t_n)$ with $t_n \to \infty$, $S(t_n) \to S^\infty$ and $S'(t_n) \to 0$ as $n \to \infty$. By Model (14), since $g(0) > g(S)$ for all $S > 0$ and $h$ is increasing

$$0 = g(S^\infty) - \lim_{n \to \infty} \left(\sigma h(r(t_n)) - \kappa_1 P(t_n)\right) < g(0) - \sigma h(r_\infty) \leq g(0) - \sigma h(g(0)/\mu) < 0,$$

a contradiction.

This implies $S(t) \to 0$ as $t \to \infty$ and so $S(t) + I(t) + (1/\alpha) P(t) \to 0$ as $t \to \infty$. \hfill \Box

Since $\xi(g(0)/\mu) = (1 + (\mu/g(0))h(g(0)/\mu)$, we can rewrite the condition in the previous proposition as follows.

**Theorem 11.2.** Let $\kappa_2 \geq \kappa_1$ and

$$\sigma > \left(1 + \frac{\kappa_2 - \kappa_1}{\mu + g(0)} P^\circ\right) \frac{g(0)}{h(g(0)/\mu)}.$$

Then there is extinction of all three species for all positive initial values: For all solutions of (14) with $I(0) > 0, S(t) \to 0, I(t) \to 0$ and $P(t) \to 0$ as $t \to \infty$.

We can achieve this result by increasing $\sigma$ as much as needed, since none of the parameters on the right hand side of the inequality depend on $\sigma$.

**Remark 11.3.** Recall that we assume $\kappa_2 > \kappa_1$. If the predator does not prefer infected over susceptible prey, $\kappa_2 \leq \kappa_1$, as assumed in [6, 38], then the assumption $\sigma > \frac{g(0)}{h(g(0)/\mu)}$ is sufficient for a parasite-mediated collapse of the ecosystem no matter the initial conditions.

12. Discussion. To demonstrate the risk that environmental change (climate change, habitat fragmentation, habitat encroachment) can cause a pathogen-mediated shift from persistence to collapse of a whole ecosystem, we have investigated an ecoepidemic model consisting of a base species that is prey to a specialist predator species and host to a microparasite species. While one may object to calling a system of three species an ecosystem, the state of art of ecoepidemic systems still seems to be mainly limited to the elementary counting “one, two, many” because of the technical difficulties of handling too many equations and the problem of loosing the message in a maze of too much detail. Still, this relatively simple model can mimic recent field observations: A snake community (predator) contained fewer species after the catastrophic loss of amphibians (prey/host) due to chytridiomycosis, a fungal disease (parasite), though no other systematic changes in the environment were observed [72].

As for disease transmission, we consider a homogeneous incidence that generalizes frequency-dependent incidence. Infected hosts have a per capita death rate that is different (presumably higher) than susceptible hosts and do not recover from the infection.
The predation process is modeled by a simple mass action term, while a general per capita growth rate is chosen for the prey/host species. We assume that the predator prefers infected over susceptible prey because it is easier to catch. Many plausible arguments and some experiments [44, 58] in the literature support this assumption, but also the case that a predator may not prefer or even avoid infected prey has been made [6, 38]. We make these assumptions to create a wide range of ecoepidemiologic scenarios under relative ease of mathematical analysis. Frequency-dependent incidence is known to empower the parasite to drive the host/prey (and itself) into extinction for appropriate parameter values while a predator that preferably eats infected prey is able to counteract the parasite though it also takes out healthy prey. For a specialist predator (which relies on this one prey), this ability can be necessary for its own survival.

Though there is a multitude of ecoepidemic models ([65] and the references therein), the assumptions of which are supported by all kind of plausible circumstantial evidence, there are few that address concrete real world systems. Some of these concern macroparasites (like worms) [34, 44] which need to be modeled differently from microparasites. In some cases [34], these parasites need to pass both through the prey and the predator in order to be able to complete their life cycle and have a negative effect on both species. Also microparasites may infect both the prey and the predator as tuberculosis bacteria in a lion-buffalo system [16] or rabies virus in a rabbit-fox system [66]. A system where the prey (small ruminants) does not pass on the parasite (a mycoplasma) to the predator (golden eagle, red fox) is considered in [1], but here density-dependent incidence is chosen, infected hosts can become susceptible again, and some susceptible hosts are vaccinated.

The real world system closest to our model that we could find in the literature [6] has phytoplankton as prey/host, zooplankton as predator and a virus as microparasite. The incidence is frequency-dependent and prey/host growth is of logistic type. While only susceptible hosts reproduce as in [39] and in our model, differently from our model and the one in [39] infected hosts contribute to the density-dependent per capita death rate as much as susceptible hosts. This makes some sense for phytoplankton because light is one of the limiting resources though a somewhat reduced contribution may be more appropriate to account for other limiting resources. Our model follows [39] in assuming that infected hosts are too weak to compete for resources at all, which simplifies the mathematical analysis. The virus only infects the phytoplankton which is plausible because the species barrier to zooplankton may be too high. The argument in favor of frequency-dependent incidence in [6] that algal concentrations are typically high does not seem very convincing, and some papers motivated by [6] have chosen density-dependent incidence instead [10, 55]. Our model follows [6, 39] rather than [10, 55] in assuming a generalized frequency-dependent incidence, which gives the parasite the potential to drive its host into extinction while density-dependent incidence (and its generalizations) does not [21].

[6] does not use biomass conversion factors when phytoplankton biomass is digested by zooplankton. Therefore, it is difficult to tell whether the choice of parameters in [6], in our notation $\gamma_1 = \kappa_1 > \gamma_2 = \kappa_2$, is an assumption about the predation preference for or the predation benefit of susceptible and infected prey. The assumption as made above goes along with the purpose of [6] to explain phytoplankton blooms because, if $\kappa_1 > \kappa_2$, there can be a Hopf bifurcation [39] of the coexistence equilibrium, which does not occur if $\kappa_1 \leq \kappa_2$ (Theorem 10.1) as it is assumed in this paper, in [55], and in much of the ecoepidemic literature. Indeed, it is
debatable whether zooplankton is able to recognize whether or not phytoplankton is infected. The assumption $\kappa_1 \leq \kappa_2$ (the predator does not prefer susceptible over infective prey) allows the predator to counteract the potential of the parasite to drive the host/prey into extinction and makes for a wider array of extinction/survival scenarios. $\kappa_1 \leq \kappa_2$ does not preclude $\gamma_1 > \gamma_2$ because the nutritional value of susceptible prey may be much larger than that of infected prey.

We have seen the following phenomena:

(i) Predator-mediated extinction of the parasite close to a locally asymptotically stable predator-prey equilibrium, uniform persistence of the prey/host and the predator; no coexistence equilibrium (Remark 10.14).

(ii) Parasite-mediated extinction of the predator close to a locally asymptotically stable host-parasite equilibrium, uniform persistence of the prey/host and the parasite; no coexistence equilibrium (Remark 10.16).

(iii) Coexistence of all three species (independent of initial data as long as they are positive) and existence of a locally asymptotically stable coexistence equilibrium: The persistence of the predator is mediated by the parasite because the predator, which catches infected prey more easily than susceptible prey, would die out without the parasite (Theorems 9.10 and 10.5).

(iv) Unmediated coexistence of all three species (independent of initial data as long as they are positive); existence of a locally asymptotically stable coexistence equilibrium (Theorems 9.9 and 10.5).

(v) Bistability between predator-mediated survival of all three species close to a locally asymptotically stable coexistence equilibrium and parasite-mediated extinction of all three species at low initial predator and prey levels; uniform persistence of the ratio of infected to susceptible hosts (Remark 10.8).

(vi) Bistability between predator-mediated extinction of the parasite close to a locally asymptotically stable predator-prey boundary equilibrium and parasite-mediated extinction of all three species at low initial predator and prey levels (Theorem 10.6 and subsequent remarks).

(vii) Bistability between predator-mediated extinction of the parasite close to a locally asymptotically stable predator-prey boundary equilibrium and survival of all three species close to a locally asymptotically stable coexistence equilibrium; uniform persistence of predator and susceptible prey/host (Remark 10.10).

(viii) Bistability between parasite-mediated extinction of the predator close to a locally asymptotically stable host-parasite boundary equilibrium and survival of all three species close to a locally asymptotically stable coexistence equilibrium; uniform persistence of host and parasite (Remark 10.12).

(ix) Bistability between predator-mediated extinction of the parasite close to a locally asymptotically stable predator-prey boundary equilibrium and parasite-mediated extinction of the predator close to locally asymptotically stable host-parasite boundary equilibrium; uniform persistence of the susceptible prey/host (Theorem 10.3 and Remark 10.4.)

(x) Parasite-mediated extinction of all three species for all positive initial values (Theorem 11.2).

The nonexistence of an interior equilibrium in (i) and (ii) may suggest that the respective locally asymptotically boundary equilibria are globally asymptotically stable. The bistable scenarios (vi) — (ix) may explain why we have not succeeded in finding Lyapunov functions to prove it; they all involve the existence of an interior
saddle (equilibrium) as does (v). At this point, the reader may like to revisit the comments made on each scenario in the introduction.

All these various scenarios are mathematically possible: Each one comes with many assumptions concerning the model parameters, and we check that these assumptions do not exclude each other. Environmental change can move the parameters around so that, theoretically, transitions between all these scenarios can occur if not directly then in steps. Whether all transitions are biologically possible is another question because the parameters may not change independently of each other. Any temperature change, for instance, that increases the transmissibility of the parasite may also increase its fatality and vice versa. However that may be, our analysis shows that transitions between ecosystem scenarios can be quite unpredictable.

13. Appendix: Modeling consistency issues for the per capita prey/host growth rate. Any per capita growth function \( g(S) \) for susceptible hosts has the form

\[
g(S) = \beta(S) - \theta(S)
\]

with the nonnegative per capita birth rate \( \beta \) and the positive per capita death rate \( \theta \) (\( \theta \) like Thanatos). If the per capita death rate \( \theta \) for susceptible hosts is density-dependent, so should be the per capita death rate \( \mu \) for infective hosts [36, 38, 40]. If susceptible hosts die from starvation, infected hosts even more so because the infection makes them more vulnerable. If we assume a constant per capita death rate for infected hosts, modeling consistency demands that we assume a constant per capita death rate for susceptible hosts as well, i.e., \( \theta > 0 \) is a constant and \( \theta \leq \mu \) because the per capita death rate of susceptible hosts should not exceed that of infected hosts. Since \( \beta \) is nonnegative, modeling consistency forbids logistic growth \( g(S) = c(1 - S/K) \), which is almost exclusively assumed in ecoepidemic models, because it cannot be written in the form \( g(S) = \beta(S) - \theta \) for all \( S \geq 0 \). Alternatives are the Ricker birth rate \( \beta(S) = be^{-aS} \) and the Beverton/Holt birth rate \( \beta(S) = \frac{b}{1 + aS} \). If one likes the carrying capacity to appear in the growth rate explicitly, for the Beverton-Holt per capita birth rate the function \( g \) can be rewritten in the F.E. Smith form

\[
g(S) = \frac{(b - \theta)(1 - (S/K)}}{1 + aS}, \quad K = \frac{(b - \theta)/a}{\theta},
\]

which formally makes it an extension of the logistic (Verhulst) per capita growth rate. See [60, Chap.5] for derivations, properties, and references. The logistic growth rate can be sort of salvaged by choosing

\[
\beta(S) = [b - (b - \theta)(S/K)]_+, \quad S \geq 0,
\]

where \( s_+ = \max\{s, 0\} \) is the positive part of \( s \in \mathbb{R} \), \( K > 0 \) is the desired carrying capacity and \( b > \theta \) is the per capita birth rate without competition. Then

\[
g(S) = \begin{cases} 
(b - \theta)(1 - (S/K)), & 0 \leq S \leq bK/(b-\theta) \\
-\theta, & S \geq bK/(b-\theta).
\end{cases}
\]

Our mathematical assumptions include \( g(S) = (b-\theta)(1 - (S/K)) \) for all \( S \geq 0 \), but modeling consistency asks for the alternative formulation. As for the mathematical results, this does not matter fortunately, because all relevant dynamics end up and then stay in the forward invariant set \( \{S \in [0, K]\} \). See Theorem 3.1 and Corollary 4.9.
14. Appendix: Proofs of results in Section 9. In the following sections, we use the singleton sets containing the possible boundary equilibria,
\[ M_1 = \{(0, 0, 0)\}, \quad M_2 = \{(K, 0, 0)\}, \]
\[ M_3 = \{(S^*, r^*, 0)\}, \quad M_4 = \{(0, r^0, 0)\}, \quad M_5 = \{(S^0, 0, P^0)\}. \tag{48} \]

We define \( \beta_\varepsilon^i \) to be the ball of radius \( \varepsilon \) surrounding the set \( M_i \). We denote the equilibrium in \( M_i \) as \( m_i \), thus \( \beta_\varepsilon^i \) is equivalently the \( \varepsilon \) ball surrounding the point \( m_i \).

As a reminder, we assumed that \( f(\cdot, 1) \) is differentiable on \((0, \infty)\) with strictly positive derivative throughout Section 9 and thus will do so here. By Remark 4.1 (d), \( h \) and \( \xi \) are then differentiable on \((0, \infty)\) and \( h' - \xi' \) is strictly positive on \((0, \infty)\). Further, \( M_3 \) is an isolated compact invariant set \([57, \text{Def.5.14}]\).

**Proof of Theorem 9.1.** The first bullet can be seen from Theorem 7.1.

Consider the second bullet. It implies \( \sigma < \frac{\mu + g(0)}{\xi + \zeta(\infty)} \leq \frac{\mu + g(0)}{\xi + \zeta(\infty)} \) and so there exists some \( c > 0 \) such that \( r^\infty < c \) for all solutions of (14) with \( r(0) \geq 0 \) by Theorem 5.3. It also implies uniform persistence of susceptible prey/host (Theorem 5.4).

We seek to apply the results in \([57, \text{Sec.8.3}]\) to give us uniform weak persistence, then use \([57, \text{Thm.4.5}]\) to upgrade to uniform persistence. We choose the state space \( X = (0, \infty) \times \mathbb{R}_+^2 \) and the persistence function \( \rho(S, r, P) = P \). Notice that Hypothesis (H) of \([57, \text{Sec.8.3}]\) and the assumptions ◆ in \([57, \text{Thm.4.5}]\) are satisfied by Theorems 2.4, 3.1 and 5.4.

For this choice of \( \rho \), \( X_0 = \{(S, r, 0) \in X; S > 0, r \geq 0\} \) in the notation of \([57, \text{Sec.8.3}]\), and any solutions with initial conditions in \( X_0 \) will converge to \( M_2 \) or \( M_3 \).

These sets are disjoint, compact and invariant. \( M_2 \) is isolated in \( X_0 \) because it is a saddle for this set and \( M_3 \) is isolated \( X_0 \) because it is locally asymptotically stable for \( X_0 \). For that reason, \( M_3 \) cannot be part of a cyclic chain that chains \( M_2 \) and \( M_3 \) in \( X_0 \) or of a cyclic chain that chains it to itself in \( X_0 \). \( M_2 \) cannot be chained to itself in \( X_0 \) because the stable manifold is the \( r = 0 \) axis which is invariant and the unstable manifold is the \( S = K \) axis which is also invariant.

We show that \( M_3 \) is uniformly weakly \( \rho \)-repelling by supposing toward contradiction that it is not. Thus, assume that for all \( \varepsilon > 0 \), there exists a solution such that \( \limsup_{t \to \infty} d((S(t), r(t), P(t)), M_3) < \varepsilon \) whenever \( \rho(S(0), r(0), P(0)) > 0 \).

Choose \( \varepsilon > 0 \) such that
\[
\gamma_1(S^* + \varepsilon) + \gamma_2(r^* + \varepsilon)(S^* + \varepsilon) = \gamma_1 S^* + \gamma_2 r^* S^* + \varepsilon \gamma_1 + \varepsilon^2 \gamma_2 > \nu.
\]

Then solutions in \( \beta_\varepsilon^3 \) satisfy \( \frac{P'}{P} = \gamma_1 S + \gamma_2 r S - \nu > 0 \), implying that \( P \) will grow exponentially. Thus, \( d((S(t), r(t), P(t)), M_3) > \varepsilon \) as \( t \) increases, and so \( M_3 \) is uniformly weakly \( \rho \)-repelling.

By a similar argument, \( M_2 \) is uniformly weakly \( \rho \)-repelling because \( \nu < \gamma_1 K \).

By \([57, \text{Sec.8.3}]\), the system is uniformly weakly \( \rho \)-persistent and uniformly \( \rho \)-persistent by \([57, \text{Thm.4.5}]\).

**Proof of Proposition 9.3.** (⇒) Recall that \( I = Sr \), and suppose that both \( S \) and \( r \) persist uniformly, with \( S_\infty > \varepsilon > 0 \) and \( r_\infty > \delta > 0 \). Then we see \( \varepsilon \delta < S_\infty r_\infty \leq I_\infty \).

(⇐) Suppose \( I \) persists uniformly, with \( I_\infty > 2 \varepsilon > 0 \). Then, after a time shift,
\[
\varepsilon < I(t) = S(t) r(t) < K r(t),
\]
so \( \frac{\varepsilon}{K} < r(t) \), which implies \( r \) persists uniformly.
For $S$, we see from Theorem 3.1 that $I(t) < N(t)$ and so

$$I_\infty \leq I^\infty \leq N^\infty \leq S^\infty \frac{g(0) + \beta}{\beta}.$$ 

Thus, for all solutions, $S^\infty > I_\infty \frac{\beta}{g(0) + \beta}$, which by Theorem 3.5 implies the result.

Proof of Theorem 9.4. Uniform persistence of the susceptible prey/host has already been established in Theorem 5.4. We choose the state space $X = (0, \infty) \times \mathbb{R}_+^2$, and the persistence function $\rho(S, r, P) = r$. For this choice of $\rho$, hypothesis (H) of [57, Sec.8.3] is satisfied with the attracting set $B = (\epsilon/2, K] \times \mathbb{R}_+ \times [0, P^\infty]$ with $P^\infty$ from Theorem 3.1 and $\epsilon > 0$ from Theorem 5.4. and $X_0 = \{(S,0,P) \in X\}$. All solutions in $X_0$ converge to $(K,0,0)$ or $(S^\infty,0,P^\infty)$ provided that the latter exists. So it is sufficient to consider $M_2$ and $M_5$. These sets are compact, invariant and isolated in $X_0$ and $\{M_2, M_5\}$ is acyclic.

Since $\mu < \lambda h'(0) = \sigma \xi(0)$, $M_2$ is uniformly weakly $\rho$-repelling. Indeed, we can choose $\epsilon > 0$ such that $\sigma \xi(\epsilon) - \mu - g(K - \epsilon) + (\kappa_1 - \kappa_2)\epsilon > \epsilon$, and so for any solution in $\beta_2^\infty$, $r' = \sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2)P > \epsilon$, leading to the exponential growth of $r$.

If $M_3$ exists, it is uniformly weakly $\rho$-repelling by $\sigma h'(0) > \mu + \kappa_2 P^\infty$. Indeed, $g(S^\infty) = \kappa_1 P^\infty$ implies $-\kappa_2 P^\infty = -g(S^\infty) + (\kappa_1 - \kappa_2)P^\infty$. Using $h'(0) = \xi(0)$, we find an $\epsilon > 0$ such that $\sigma \xi(\epsilon) - \mu - g(S^\infty - \epsilon) + (\kappa_1 - \kappa_2)(P^\infty + \epsilon) > \epsilon$, which implies that any solution in $\beta_3^\infty$, $r' = \sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2)P > \epsilon$, leading to the exponential growth of $r$.

Therefore, $r$ persists uniformly weakly by [57, Thm.8.20].

Recall $B = (\epsilon/2, K] \times [0, \infty) \times [0, P^\infty]$, where $P^\infty$ is defined in Theorem 3.1, is the chosen attracting set. Note that if $r(s) = 0$ for some $s$, then $r(t) = 0$ for all $s \geq t$, and so once $\rho(S, r, P) = 0$, it cannot become positive again.

Applying [57, Thm.4.2] yields $\rho$-persistence. Uniform persistence of infected prey/host follows from Proposition 9.3.

Proof of Theorem 9.5. By assumption, $\sigma \xi(0) = \sigma h'(0) > g(0) + \mu$.

We will follow [57, Sec.8.3] and the proof of Theorem 9.1. We choose the state space $X = \mathbb{R}_+^3$, and the persistence function $\rho(S, r, P) = r$. For this choice of $\rho$, hypothesis (H) of [57, Sec.8.3] is satisfied and $X_0 = \{(S,0,P) \in X\}$. Note that, at most, $M_1, M_2$ and $M_5$ will be subsets of $X_0$. From the considerations in Theorem 9.1, it is clear (for whichever sets exist) that the $M_i$ are compact, invariant, isolated in $X_0$, and pairwise disjoint. Thus all that needs to be shown is (for whichever sets exist) that $\{M_1, M_2, M_5\}$ are acyclic, and $M_i$ is uniformly weakly $\rho$-repelling for $i = 1, 2, 5$.

The possible chains of equilibria are

- $(0,0,0) \rightarrow (K,0,0)$,
- $(0,0,0) \rightarrow (K,0,0) \rightarrow (S^\infty,0,P^\infty)$, if $(S^\infty,0,P^\infty)$ exists,

and thus there will be no cycles. As above, we will assume toward contradiction that $M_i$ for $i \in \{1,2,5\}$ are not uniformly weakly $\rho$-repelling.

For $M_2$ and $M_5$, this is the same argument as in the proof of Theorem 9.4.

We now only need to show that $M_1$ is uniformly weakly $\rho$-repelling.
Recall that \( \sigma \xi(0) > g(0) + \mu \). Thus, there is some \( \varepsilon > 0 \) such that \( \sigma \xi(\varepsilon) - \mu - g(\varepsilon) + (\kappa_1 - \kappa_2)\varepsilon > \varepsilon \), since \( \xi(0) = h'(0) \). This implies that for any solution in \( \beta_r, \quad r' = \sigma \xi(r) - \mu - g(S) + (\kappa_1 - \kappa_2)P > \varepsilon \). This inequality implies the exponential growth of \( r \), a contradiction. This proves \( M_1, M_2, \) and \( M_5 \) (if it exists) are uniformly weakly \( \rho \)-repelling, and thus there is uniform weak persistence of \( r \) in this case.

Therefore, \( r \) persists uniformly weakly. The attracting set required in \([57, \text{Sec.8.3}]\) is chosen as \( B = [0, K] \times [0, \infty) \times [0, P^c] \), where \( P^c \) is defined in Theorem 3.1. We can see in System (14) that if \( r(s) = 0 \) for some \( s \), then \( r(t) = 0 \) for all \( s \geq t \), and so once \( \rho(S, r, P) = 0 \), it cannot become positive again. Thus, by applying Theorem 4.2 from [57], we will have uniform \( \rho \)-persistence.

Proof of Remark 9.6. Let \( g(0) + \mu \geq \sigma h'(0) = \sigma \xi(0) \). Since \( \xi \) is decreasing \( g(0) + \mu \geq \sigma \xi(r) \) for all \( r \geq 0 \).

Consider a solution of (14) with \( S(0) = 0 = P(0) \). Then \( S(t) = 0 = P(t) \) for all \( t \geq 0 \) and \( r(t) \leq 0 \) for all \( t \geq 0 \). So \( r(t) \leq r(0) \) for all \( t \geq 0 \) and the uniform persistence statement in Theorem 9.5 does not hold.

Proof of Corollary 9.8. The assertion follows from Theorem 9.4, if \( \frac{\mu}{\xi(0)} < \sigma < \frac{g(0)}{\kappa_2(0) / \mu} \).

Let \( \sigma \geq \frac{g(0)}{\kappa_2(0) / \mu} = \frac{g(0) + \mu}{\xi(0)} \).

Let \( \xi \) be strictly decreasing. Then \( \sigma > \frac{g(0) + \mu}{\xi(0)} = \frac{g(0) + \mu}{\kappa_2(0)} \).

Now assume that \( \xi \) is constant. By Assumption 9.7, \( \sigma > \frac{\xi(0)}{\kappa_2(0) / \mu} = \frac{\xi(0)}{\kappa_2(0)} \).

In either case, the statement follows from Theorem 9.5.

Remark 14.1. Here we show the feasibility of the conditions in Theorem 9.9.

We make the extra assumption that susceptible and infective prey have the same nutritional value for the predator, \( \gamma_2 / \kappa_2 = \gamma_1 / \kappa_1 \), which can be rewritten as

\[
\frac{\gamma_2}{\gamma_1} = \frac{\kappa_2}{\kappa_1} =: \eta.
\]

Using (49) and (33), (35) and (36) can be equivalently expressed as

\[
\sigma h'(0) > \mu + \eta g(S^0), \quad S^0 < S^*(1 + \eta r^*).
\]

These two inequalities can be rewritten as two inequalities for \( \eta \),

\[
\left( \frac{S^0}{S^*} - 1 \right) \frac{1}{r^*} < \eta < \frac{\sigma h'(0) - \mu}{g(S^0)}.
\]

Since the boundary equilibria are unrelated to \( \gamma_2 \) and \( \kappa_2 \), \( \eta \) given by (49) can be chosen independently of them. So (51) can be satisfied provided the left term is smaller than the right term. If we choose \( \sigma \) such that (34) is fulfilled, then the term on the right of (51) is positive. Now \( S^0 \) can be determined independently of \( S^* \) from (33) with every small positive value being possible such that the term on the left of (51) can be made negative.

Proof of Theorem 9.10. The uniform persistence results concerning \( S \) and \( I \) as well as a uniform persistence result for \( r \) follow from Theorem 5.4 and Theorem 9.4.

As for \( P \), we seek to apply the results in [57, Sec.8.3] to give us uniform weak persistence, then use [57, Thm.4.5] to upgrade to uniform persistence. We choose the state space \( X = \{(S, r, P); S > 0, r > 0, P \geq 0 \} \) and the persistence function.
\[ \rho(S, r, P) = P. \] Notice that Hypothesis (H) of [57, Sec.8.3] and the assumptions ♦ of [57, Thm.4.5] are satisfied by Theorem 3.1, the uniform persistence results for \( S \) and \( r \), and the eventual boundedness result for \( r \) in Theorem 5.4.

For this choice of \( \rho \), \( X_0 = \{(S, r, 0) \in X; S > 0, r > 0\} \) in the notation of [57, Sec.8.3]. Solutions in \( X_0 \) converge to \( M_3 \).

\( M_3 \) is an isolated compact invariant set because it is locally asymptotically stable for \( X_0 \). For that reason, \( M_3 \) cannot be part of a cyclic chain that chains it to itself in \( X_0 \).

We show that \( M_3 \) is uniformly weakly \( \rho \)-repelling as in the proof of Theorem 9.1. By [57, Sec.8.3], the system is uniformly weakly \( \rho \)-persistent. Uniform strong \( \rho \)-persistence follows from [57, Thm.4.5].

15. Appendix: Proofs of results in Section 10. As a reminder, we assumed that \( f(\cdot, 1) \) is differentiable on \((0, \infty)\) with strictly positive derivative throughout Section 10. By Remark 4.1 (d), \( h \) and \( \xi \) are differentiable on \((0, \infty)\) and \( h' - \xi' \) is strictly positive on \((0, \infty)\). We first prove some auxiliary results to help in the proofs to come.

A coexistence equilibrium of System (14), which is denoted by \((S^\dagger, r^\dagger, P^\dagger)\) and lies in \((0, \infty)^3\), satisfies the following equations,

\[
\begin{align*}
0 &= g(S^\dagger) - \sigma h(r^\dagger) - \kappa_1 P^\dagger, \\
0 &= \sigma \xi(r^\dagger) + (\kappa_1 - \kappa_2) P^\dagger - \mu - g(S^\dagger), \\
S^\dagger &= \frac{S^0}{1 + \gamma r^\dagger} > 0,
\end{align*}
\]

with the side conditions \( g(S^\dagger) > 0 \). We add (52) and (53) and reorganize the result, which gives us a side condition,

\[
0 < \kappa_2 P^\dagger = \sigma \xi(r^\dagger) - \sigma h(r^\dagger) - \mu = \sigma \frac{h(r^\dagger)}{r^\dagger} - \mu =: D_2(r^\dagger).
\]

(52) and (54) give us the side condition

\[
0 < \kappa_1 P^\dagger = g\left(\frac{S^0}{1 + \gamma r^\dagger}\right) - \sigma h(r^\dagger) =: D_1(r^\dagger).
\]

Notice that this inequality implies that \( g(S^\dagger) > 0 \).

The combination of (55) and (56) yields

\[
\mu = \sigma \xi(r^\dagger) - \sigma h(r^\dagger) + \kappa \sigma h(r^\dagger) - \kappa g\left(\frac{S^0}{1 + \gamma r^\dagger}\right) =: E(r^\dagger),
\]

with

\[
\kappa = \frac{\kappa_2}{\kappa_1} \geq 1.
\]

Notice that for \( r^\dagger > 0 \) with \( E(r^\dagger) = \mu \), the side conditions \( D_1(r^\dagger) > 0 \) and \( D_2(r^\dagger) > 0 \) ((55) and (56)) are equivalent.

Proposition 15.1. There exists a coexistence equilibrium if and only if there is some \( r^\dagger > 0 \) with the following properties:

(a) \( 1 + \gamma r^\dagger > 0 \),

(b) \( E(r^\dagger) = \mu \).

(c) \( D_1(r^\dagger) > 0 \) or (equivalently) \( D_2(r^\dagger) > 0 \).
The coexistence equilibrium, if it exists, has the form \((S^\dagger, r^\dagger, P^\dagger)\) with \(S^\dagger\) being determined by (54) and \(P^\dagger\) by both (55) and (56).

The coexistence equilibrium is a saddle if \(E'(r^\dagger) > 0\), and locally asymptotically stable if \(E'(r^\dagger) < 0\).

**Proof.** Differentiating (57) gives \(E'(r^\dagger) = \kappa_1 \nu \Delta \left( r^\dagger, \frac{\nu}{1 + \gamma r^\dagger} \right)\), where \(\Delta\) is defined in Equation (39). The stability statement now follows from Theorem 10.1. \(\square\)

**Remark 15.2.** Let \((S^\dagger, r^\dagger, P^\dagger)\) be an interior equilibrium. Then any \(r \in (0, r^\dagger)\) with \(E(r) = \mu\) is associated with an interior equilibrium.

**Proof.** By Proposition 15.1, \(E(r^\dagger) = \mu, 1 + \gamma r^\dagger > 0, \text{ and } D_2(r^\dagger) > 0\).

Let \(r \in (0, r^\dagger)\) with \(E(r) = \mu\). Then \(1 + \gamma r > 0\). Since \(D_2\) is strictly decreasing, \(D_2(r) > D_2(r^\dagger) > 0\). By Proposition 15.1, \(r\) is associated with an interior equilibrium. \(\square\)

In the following, we need the following very special case of Sard’s lemma \([17, \text{Prop.1.4}].\)

**Lemma 15.3** (Sard). Let \(J\) be an open interval in \(\mathbb{R}\) and \(\varphi: J \to \mathbb{R}\) be continuously differentiable. Then the one-dimensional Lebesgue measure of \(\varphi\{r \in J; \varphi'(r) = 0\}\) is zero.

In other words: For almost all \(z \in \mathbb{R}\), \(\varphi'(r) \neq 0\) for all \(r \in J\) with \(\varphi(r) = z\).

**Remark 15.4.** Proposition 15.1 in combination with Sard’s Lemma 15.3 allows the following conclusions for almost all \(\mu > 0\).

\[ E'(r^\dagger) \neq 0 \] for any \(r^\dagger > 0\) that is associated with an interior equilibrium. This implies that, for almost all \(\mu > 0\), all interior equilibria are isolated. Since \(D_2(r^\dagger) > 0\) and \(D_2(r)\) is decreasing and eventually strictly negative, there at most finitely many interior equilibria.

If there are any, we can enumerate them if the following way: \(0 < r_1^\dagger < \cdots < r_m^\dagger < \infty\) with some \(m \in \mathbb{N}\). If \(m \geq 2\), for each \(j = 1, \ldots, m - 1\) the following alternative holds by the intermediate value theorem and Remark 15.2:

- \(E(r) < \mu\) for all \(r \in (r_j^\dagger, r_{j+1}^\dagger)\) and \(E'(r_j^\dagger) < 0\) and the associated interior equilibrium is locally asymptotically stable and \(E'(r_{j+1}^\dagger) > 0\) and the associated interior equilibrium is a saddle; or

- \(E(r) > \mu\) for all \(r \in (r_j^\dagger, r_{j+1}^\dagger)\) and \(E'(r_j^\dagger) > 0\) and the associated interior equilibrium is a saddle and \(E'(r_{j+1}^\dagger) < 0\) and the associated interior equilibrium is locally asymptotically stable.

Further we have the following alternative.

- (a) If \(E(0) > \mu\), all odd-numbered interior equilibria have negative \(E'\) and are locally asymptotically stable, and all even-numbered interior equilibria have positive \(E'\) and are saddles.
- (b) If \(E(0) < \mu\), all odd-numbered interior equilibria are saddles and all even-numbered equilibria are locally asymptotically stable.

**Lemma 15.5.** It seems practical to calculate \(E(r)\) for \(r = 0\) and some other particular values of \(r \geq 0\). Recall this section’s master assumption \(\sigma h'(0) > \mu\).

(a) By (57),

\[ E(0) = \sigma h'(0) - \kappa g(S^\circ). \] (59)
The sign of $E(0) - \mu$ is tied to the existence and stability of the predator-prey boundary equilibrium $(S^0, 0, P^0)$ with $P^0 = g(S^0)/\kappa_1$, if this expression is positive (Section 8.4).

(a1) If this boundary equilibrium does not exist, $g(S^0) \leq 0$, or if it exists and is a saddle, more precisely, $\sigma h'(0) > \kappa g(S^0) + \mu$, then $E(0) > \mu$.

(a2) If the predator-prey boundary equilibrium exists and is locally asymptotically stable, more precisely $\sigma h'(0) < \kappa g(S^0) + \mu$, then $E(0) < \mu$.

(b) Another interesting value for the ratio of infectives to susceptibles is

$$r = g(0)/\mu.$$  \hfill (60)

By (57),

$$E(g(0)/\mu) = \sigma \frac{h(g(0)/\mu)}{g(0)/\mu} + \kappa \sigma h(g(0)/\mu) - \kappa g\left(\frac{\nu}{\gamma_1 + \gamma_2(g(0)/\mu)}\right).$$  \hfill (61)

Under the master assumption $\sigma h'(0) > \mu$, the host-parasite boundary equilibrium $(S^0, r^*, 0)$ does not exist if and only $\sigma h(g(0)/\mu) \geq g(0)$. So, if the host-parasite boundary equilibrium does not exist,

$$E(g(0)/\mu) \geq \mu + \kappa \left(g(0) - g\left(\frac{S^0}{1 + \gamma(g(0)/\mu)}\right)\right) > \mu$$  \hfill (62)

for all $\gamma \in \mathbb{R}$ with

$$1 + \gamma(g(0)/\mu) > 0$$  \hfill (63)

because $g(0) > g(S)$ for all $S > 0$. Further

$$D_2(g(0)/\mu) = \sigma \frac{h(g(0)/\mu)}{g(0)/\mu} - \mu > 0.$$

(c) Moreover, we consider $r = 1$,

$$E(1) = \sigma h(1)(1 + \kappa) - \kappa g\left(\frac{S^0}{1 + \gamma}\right).$$  \hfill (64)

assuming that $1 + \gamma > 0$,

$$D_1(1) = g\left(\frac{S^0}{1 + \gamma}\right) - \sigma h(1), \quad D_2(1) = \sigma h(1) - \mu.$$  \hfill (65)

(d) Let $\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}$. By Theorem 8.8, the host-parasite boundary equilibrium $(S^*, r^*, 0)$ exists and satisfies $0 < r^* < g(0)/\mu$ and $g(S^*) = r^* \mu = \sigma h(r^*)$ and $D_2(r^*) = 0$. Assume that $1 + \gamma r^* > 0$. By (57),

$$E(r^*) = \mu + \kappa g(S^*) - \kappa g\left(\frac{S^0}{1 + \gamma r^*}\right).$$

The sign of $E(r^*) - \mu$ depends on the stability of this boundary equilibrium. See Theorem 8.8 and recall that $g$ is strictly decreasing as long as it is positive.

If $S^0 > S^*(1 + \gamma r^*)$ such that $(S^*, r^*, 0)$ is locally asymptotically stable, then $E(r^*) > \mu$. If $S^0 < S^*(1 + \gamma r^*)$ such that $(S^*, r^*, 0)$ is a saddle, then $E(r^*) < \mu$.

Remark 15.6. If the host-parasite boundary equilibrium $(S^*, r^*, 0)$ exists, then $r^\dagger < r^* < g(0)/\mu$ for any interior equilibrium $(S^\dagger, r^\dagger, P^\dagger)$. Recall $r^*$ is the solution to $r^* \mu = \sigma h(r^*)$.

If $\gamma > 0$ and $g(S^0/(1 + \gamma r^*)) < 0$, then there exists no interior equilibrium.
Proof. Recall that \( D_2 \) (Equation (55)) is strictly decreasing. Also recall the master assumption \( \sigma h'(0) > \mu \). The host-parasite boundary equilibrium exists if and only if \( \sigma < \frac{g(0)}{h(g(0)/\mu)} \). Then \( r^* \) exists, and \( D_2(r^*) = 0 \). By Proposition 15.1, for any interior equilibrium \( D_2(r^1) > 0 \) and so \( r^1 < r^* \). Recall that by Remark 6.2, \( r^* < g(0)/\mu \).

It \( (S^\dagger, r^1, P^\dagger) \) is an interior equilibrium and \( \gamma \geq 0 \), then \( S^\dagger = \frac{S^0}{1+\gamma r^\dagger} > \frac{S^0}{1+\gamma r^*} \). Since \( g \) is decreasing, \( g \left( \frac{S^0}{1+\gamma r^*} \right) < g \left( \frac{S^0}{1+\gamma r^\dagger} \right) < 0 \). This implies \( D_1(r^1) < 0 \), which by Proposition 15.1 implies there is no interior equilibrium. \qed

After these preparations, we prove the theorems in Section 10.

Proof of Theorem 10.1. The Jacobian matrix (22) evaluated at \( (S^\dagger, r^1, P^\dagger) \) is

\[
\begin{pmatrix}
S^\dagger g'(S^\dagger) & -S^\dagger \sigma h'(r^1) & -\kappa_1 S^\dagger \\
-r^1 g'(S^\dagger) & \sigma r^1 \xi'(r^1) & r^1 (\kappa_1 - \kappa_2) \\
\gamma_1 P^\dagger + \gamma_2 r^1 P^\dagger & P^\dagger \gamma_2 S^\dagger & 0
\end{pmatrix}.
\]

Observe that the trace is \( S^\dagger g'(S^\dagger) + \sigma r^1 \xi'(r^1) < 0 \).

The characteristic polynomial is

\[
\text{Det}(J) = -S^\dagger \kappa_1 \left[ -r^1 g'(S^\dagger) P^\dagger \gamma_2 S^\dagger - \frac{P^\dagger \nu}{S^\dagger} \sigma r^1 \xi'(r^1) \right] \\
-r^1 (\kappa_1 - \kappa_2) \left[ S^\dagger g'(S^\dagger) P^\dagger \gamma_2 S^\dagger + S^\dagger \sigma h'(r^1) \frac{P^\dagger \nu}{S^\dagger} \right] \\
r^1 P^\dagger \left[ \kappa_1 \nu \sigma (\xi'(r^1) - h'(r^1)) + \kappa_2 ((S^\dagger)^2 g'(S^\dagger) \gamma_2 + \nu \sigma h'(r^1)) \right] \\
r^1 P^\dagger \Delta(r^1, S^\dagger),
\]

where \( \frac{\nu}{\gamma_1 + \gamma_2 r^\dagger} = S^\dagger \) is used for readability. Therefore, if \( \Delta(r^1, S^\dagger) > 0 \), then the determinant will be positive while the trace remains negative. Since the product of a matrix’s eigenvalues is the determinant of the matrix and the trace is the sum of its eigenvalues, there must be exactly one (real) eigenvalue with positive real part. This implies the second assertion.

Now suppose that \( \Delta(r^1, S^\dagger) < 0 \). Then \( \text{Det}(J) < 0 \), so we can use the Routh-Hurwitz criterion to determine the stability. In preparation for Routh-Hurwitz, we calculate the first principle minors:

\[
A_1 = -P^\dagger \gamma_2 S^\dagger r^1(\kappa_1 - \kappa_2), \quad A_2 = \kappa_1 S^\dagger (\gamma_1 P^\dagger + \gamma_2 r^1 P^\dagger), \quad \text{and}
\]
\[
A_3 = S^\dagger g'(S^\dagger) \sigma r^1 \xi'(r^1) - S^\dagger g'(S^\dagger) r^1 \sigma h'(r^1) = S^\dagger g'(S^\dagger) \sigma r^1 (\xi'(r^1) - h'(r^1)) > 0.
\]

Note that \( A_1 + A_2 = P^\dagger (\kappa_2 \gamma_2 S^\dagger r^1 + \kappa_1 \gamma_1 S^\dagger) > 0 \). Thus the Routh-Hurwitz coefficient [18] is (using that \( \nu = S^\dagger (\gamma_1 + \gamma_2 r^\dagger) \))

\[
h = \text{Det}(J) - Tr(J)(A_1 + A_2 + A_3) \geq \text{Det}(J) - Tr(J)(A_1 + A_2)
\]
\[
= r^1 P^\dagger \left[ \kappa_1 S^\dagger (\gamma_1 + \gamma_2 r^1) \sigma \xi'(r^1) + (\kappa_2 - \kappa_1) \nu \sigma h'(r^1) + \kappa_2 \gamma_2 S^\dagger r^1 g'(S^\dagger) \right] \\
- P^\dagger (S^\dagger g'(S^\dagger) + \sigma r^1 \xi'(r^1))(\kappa_2 \gamma_2 S^\dagger r^1 + \kappa_1 \gamma_1 S^\dagger) \\
= P^\dagger \left[ -\kappa_1 \gamma_1 S^\dagger r^1 g'(S^\dagger) + \sigma \kappa_2 (\kappa_2 - \kappa_1) \nu h'(r^1) - \gamma_2 r^1 S^\dagger \xi'(r^1) \right].
\]

Since all terms in the above sum are positive (recall that \( h' - \xi' \) is strictly positive and that \( \kappa_2 - \kappa_1 \) is possibly zero), \( h > 0 \) and local asymptotic stability of the interior equilibrium when \( \Delta(r^1, S^\dagger) < 0 \) [18]. \qed
Proof of Theorem 10.3. Recall from Theorem 8.1 and Theorem 7.7, that the hypotheses imply that both \((S^*, r^*, 0)\) and \((S^0, 0, P^0)\) are locally asymptotically stable. By Lemma 15.5 (a1) and (d), \(E(0) < \mu < E(r^*)\) and \(D_2(r^*) = 0\).

By the intermediate value theorem, there exists some \(r^\dagger \in (0, r^*)\) such that \(E(r^\dagger) = \mu\). Since \(D_2\) is strictly decreasing, \(D_2(r^\dagger) > 0\). So \(r^\dagger\) is associated with an interior equilibrium.

By Remark 15.4, for almost all \(\mu > 0\) for which the assumptions of this theorem are satisfied (which imply \(E(0) > \mu\)) the interior equilibrium with the smallest \(r^\dagger\) value is a saddle. \(\square\)

Remark 15.7. The conditions of Theorem 10.3 take the form

\[
\frac{\mu}{h'(0)} < \sigma < \frac{g(0)}{h(g(0)/\mu)} ,
\]

\[
g(S^0) > 0, \quad 0 < S^*[1 + \gamma r^*] < S^0 ,
\]

\[
\sigma < \frac{\mu + \kappa g(S^0)}{h'(0)} .
\]

To show that they are feasible, we first choose \(\sigma > 0\) such that the first inequality is satisfied. Then the host-parasite boundary equilibrium \((S^*, r^*, 0)\) exists with \(g(S^*) > 0\). Then we choose \(S^0\) slightly larger than \(S^*\) such that \(g(S^0) > 0\) and then choose \(\gamma > 0\) small enough that the second inequality holds. Finally we choose \(\kappa > 0\) large enough that the last inequality holds.

So the condition are mathematically feasible; it is debatable whether the choice of a small \(\gamma\) and a large \(\kappa\) makes biological sense.

Proof of Theorem 10.5. Here we will apply Theorem 6.2 from [57]. Let \(X = \mathbb{R}^3_+\) and \(\rho(S, r, P) = \min\{S, r, P\}\), so we check its assumptions. First we check that \(\rho\) is concave. We do so by showing the minimum function is superadditive and homogeneous.

Let \(x \in \mathbb{R}^n_+\), for some \(n \in \mathbb{N}\), \(n \geq 1\), with \(x_i\) the \(i\)th component of \(x\). Let \(k\) be the index such that \(\min x = \min_i x_i = x_k\). Then for any \(\alpha \in \mathbb{R}\),

\[
\alpha(\min x) = \alpha(x_k) = \alpha x_k = \min \alpha x ,
\]

thus the minimum function is homogeneous. Let \(y \in \mathbb{R}^n_+\), with \(y_j\) as its minimal component, and define \(z = x + y\), with \(z_m\) is its minimal component. Then

\[
\min (x + y) = \min z = z_m = x_m + y_m \geq x_k + y = \min x + \min y ,
\]

so the minimum function is superadditive. Therefore the minimum function is concave, and so \(\rho\) is as well.

Next, note that these the assumptions of this theorem satisfy the assumptions of Theorem 9.9 or Theorem 9.10; thus there is uniform \(\rho\) persistence. By Theorems 3.1 and 5.3, a bounded attracting set exists. Since we are considering a finite dimensional system of equations, a bounded attractor implies that the induced semiflow is condensing. Finally once \(S, r, \) or \(P\) become 0, they will stay zero, so there is no possibility of \(\rho\) going from zero to a non-zero quantity. Thus all conditions of [57, Theorem 6.2] are met, so there is an interior equilibrium which we denote \((S^\dagger, r^\dagger, P^\dagger)\) with \(\rho(S^\dagger, r^\dagger, P^\dagger) = \min\{S^\dagger, r^\dagger, P^\dagger\} > 0\), thus an interior equilibrium will exist.

By Lemma 15.5 (a), \(E(0) > \mu\). By Remark 15.4, for almost all \(\mu > 0\) for which the assumptions of this theorem are satisfied, the interior equilibrium with the smallest \(r^\dagger\)-value is locally asymptotically stable. \(\square\)
Proof of Theorem 10.6. By Lemma 15.5 (a) and (b), \( E(0) < \mu < E(g(0)/\mu) \) and \( D_2(g(0)/\mu) \geq 0 \).

By the intermediate value theorem, there exists some \( r^\dagger \in (0, g(0)/\mu) \) such that \( E(r^\dagger) = \mu \). Since \( E(0) < \mu \), there exists some \( r^\ddagger \in (0, r^\dagger] \) such that \( E(r) < \mu = E(r^\dagger) \) for all \( r \in [0, r^\dagger] \) and so \( E'(r^\dagger) \geq 0 \). By Remark 15.4, \( E'(r^\dagger) > 0 \) for almost all \( \mu \).

Since \( r^\dagger < g(0)/\mu \) and \( D_2 \) is strictly decreasing, \( D_2(r^\dagger) > D_2(\gamma(0)/\mu) \geq 0 \), and \( r^\dagger \) is associated with an interior equilibrium by Proposition 15.1.

\[ \square \]

Proof of Theorem 10.7. By Lemma 15.5 (a), \( E(0) > \mu \).

By Lemma 15.5 (b), \( E(g(0)/\mu) > \mu \) and \( D_2(g(0)/\mu) > 0 \).

Since \( g(0)/\mu > 1 \) and \( 1 + \gamma(g(0)/\mu) > 0 \), also \( 1 + \gamma > 0 \).

By Lemma 15.5 (c), \( E(1) < \mu \).

By the intermediate value theorem, there are \( 0 < r^\ddagger_1 < 1 < r^\ddagger_2 < g(0)/\mu \) such that \( \mu = E(r^\ddagger_j) \) for \( j = 1, 2 \).

Since \( D_2 \) is decreasing, \( D_2(g(0)/\mu) > 0 \), and \( r^\ddagger_1 < g(0)/\mu \) for \( j = 1, 2, D_2(r^\ddagger_j) > 0 \) for \( j = 1, 2 \). By Remark 15.4, for almost all \( \mu > 0 \) for which the assumptions of this theorem are satisfied, the interior equilibrium with the smallest \( r^\dagger \)-value is a saddle and the interior equilibrium with the second smallest \( r^\dagger \)-value is locally asymptotically stable.

Uniform persistence of the ratio of infected to susceptible hosts follows from Theorem 9.5. Notice that \( g(0) < \sigma h(g(0)/\mu) \) implies \( g(0) + \mu < \sigma \xi(g(0)/\mu) \leq \sigma \xi(0) = \sigma h'(0) \).

\[ \square \]

Remark 15.8. To see that the conditions of Theorem 10.7 (i.e. inequalities (45) and (46)) are feasible, consider the special case that susceptible and infective prey have the same nutritional value for the predator but that infective prey are much easier to catch than susceptible prey,

\[ \kappa = \kappa_2/\kappa_1 = \gamma_2/\gamma_1 > 1. \]

Choose \( \sigma > 0 \) such that

\[ \sigma h(1) < g(0) < \sigma h(\infty) \]

and \( S^\circ > 0 \) large enough that \( g(S^\circ) < 0 \) (no predator-prey boundary equilibrium). Then \( g(0)/\mu > 1 \) and \( \mu < \sigma h(1) < g(0) < \sigma h(g(0)/\mu) \) can be satisfied by choosing \( \mu > 0 \) small enough. The other part of inequality (46) takes the form \( \sigma h(1)(1 + \kappa) - \kappa g \left( \frac{S^\circ}{1 + \kappa} \right) < \mu \) which can be satisfied by choosing \( \kappa > 0 \) large enough (recall \( \sigma h(1) < g(0) \)). We can even choose \( \kappa \) so large that \( \sigma h(1)(1 + \kappa) - \kappa g \left( \frac{S^\circ}{1 + \kappa} \right) \leq 0 \).

\[ \square \]

Proof of Theorem 10.9. By Lemma 15.5 (a) and (d), \( E(0) < \mu \) and \( E(r^*) < \mu \) and \( D_2(r^*) = 0 \).

By Lemma 15.5 (c), \( D_2(1) > 0 \) and \( E(1) > \mu \).

By the intermediate value theorem, there exist \( r^\dagger_1 \) and \( r^\dagger_2 \) with \( 0 < r^\dagger_1 < 1 < r^\dagger_2 < r^* \) with \( E(r^\dagger_1) = \mu = E(r^\dagger_2) \). Since \( D_2 \) is strictly decreasing and \( D_2(r^*) = 0 \), \( D_2(r^\dagger_j) > 0 \). Finally \( 1 + \gamma r^\dagger_j > 0 \) for \( j = 1, 2 \).

By Proposition 15.1, \( r^\dagger_1 \) and \( r^\dagger_2 \) are associated with interior equilibria. By Remark 15.4, for almost all \( \mu \) that satisfy the conditions of the theorem, the interior equilibrium with the smallest \( r^\dagger \)-value is a saddle and the interior equilibrium with the second smallest \( r^\dagger \)-value is locally asymptotically stable.

\[ \square \]
Remark 15.9. To verify that the assumptions of Theorem 10.9 are feasible, we assume that \( \gamma_2 > 0 \) and \( \gamma_2/\gamma_1 =: \gamma \). Then the assumptions take the form
\[
\begin{align*}
\sigma h'(0) &< \kappa g(S^\circ) + \mu, \quad S^\circ < S^*(1 + \gamma r^*), \\
\sigma h(g(0)/\mu) &< g(0), \quad \sigma h(1) > \mu, \\
\sigma h(1)[1 + \kappa] - \kappa g\left(\frac{S^\circ}{1 + \gamma}\right) &> \mu.
\end{align*}
\]
We fix \( \sigma > 0 \) such that
\[
\begin{align*}
\sigma h(\infty) &< g(0), \quad \sigma h'(0) < g(0), \quad 2\sigma h(1) < g(0), \quad (67)
\end{align*}
\]
which is possible because \( h(\infty) \) and \( h'(0) \) are finite. We consider \( \mu \in (0, \sigma h(1)) \) to be chosen sufficiently small later. Then \( \sigma h(g(0)/\mu) < g(0) \) and \( \mu < \sigma h'(0) \) (recall that \( h(r)/r \) is decreasing). The remaining inequalities can be rewritten as
\[
\begin{align*}
S^\circ &< g^{-1}\left(\frac{\sigma h'(0) - \mu}{\kappa}\right), \quad S^\circ < S^*(1 + \gamma r^*) \\
S^\circ &> (1 + \gamma)g^{-1}\left(\sigma h(1)\frac{1 + \kappa}{\kappa} - \frac{\mu}{\kappa}\right). \quad (68)
\end{align*}
\]
Choosing \( \kappa > 1 \) large and \( \gamma > 0 \) small enough, we can achieve that \( \sigma h(1) \frac{1 + \kappa}{\kappa} < g(0) \) and
\[
\begin{align*}
g^{-1}\left(\frac{\sigma h'(0)}{\kappa}\right) &> (1 + \gamma)g^{-1}\left(\sigma h(1)\frac{1 + \kappa}{\kappa}\right),
\end{align*}
\]
and we can fit some \( S^\circ \) strictly in between the two. Now \( r^* > 0 \) and \( S^* > 0 \) with \( \sigma h(r^*) = \mu r^* = g(S^*) \) depend on \( \mu \in (0, \sigma h(1)) \). Since \( h(r)/r \to 0 \) as \( r \to \infty \),
\[
\begin{align*}
r^* \xrightarrow{\mu \to 0} \infty, \quad S^* \xrightarrow{\mu \to 0} g^{-1}(\sigma h(\infty)) > 0.
\end{align*}
\]
So (68) can be satisfied by choosing \( \mu > 0 \) small enough.

Proof of Theorem 10.11. By Lemma 15.5, \( E(0) > \mu > E(1) \) and \( E(r^*) > \mu \). By the intermediate value theorem, there exist at least two interior equilibria \((S, r, P)\) whose \( r \)-values are in \((0, 1)\) and \((1, r^*)\), respectively. Let \( r^*_1 \) be the \( r \)-value of an interior equilibrium that is closest to 0 and \( r^*_2 > 1 \) be the \( r \)-value of an interior equilibrium that is closest to 1. Then, for almost all \( \mu > 0 \) such that the assumed inequalities are satisfied, \( E'(r^*_1) < 0 \) and the associated interior equilibrium is locally asymptotically stable, while \( E'(r^*_2) > 0 \) and the associated interior equilibrium is a saddle. The first directly follows from Remark 15.4, while the second follows analogously with \( E(1) \) replacing \( E(0) \).

Remark 15.10. To show that the conditions of Theorem 10.11 are feasible, we find \( S^\circ > 0, \gamma > 0, \kappa \geq 1, \mu > 0, \sigma > 0 \) such that all the subsequent inequalities hold:
\[
\begin{align*}
\frac{\mu}{h(1)} < \sigma &< \frac{g(0)}{h(g(0)/\mu)}, \quad 1 < g(0)/\mu, \\
\frac{\mu + \kappa g(S^\circ)}{h'(0)} < \sigma &< \frac{\mu + \kappa g\left(\frac{S^\circ}{1 + \gamma}\right)}{h(1)(1 + \kappa)} , \\
\mu r^* = \sigma h(r^*) = g(S^*) , \quad 1 < r^* < g(0)/\mu, \\
S^\circ &> S^*(1 + \gamma r^*).
\end{align*}
\]
Recall that $h(r)/r$ is a strictly decreasing function, which implies that $\frac{g(0)}{\mu h'(0)} < \frac{g(0)}{h(g(0)/\mu)}$ is equivalent to $1 < g(0)/\mu$. We choose $S^o = K$. Then the inequalities take the form

$$\frac{\mu}{h(1)} < \sigma < \frac{g(0)}{h(g(0)/\mu)}, \quad 0 < \mu < g(0),$$

$$\frac{\mu}{h'(0)} < \sigma < \frac{\mu + \kappa g\left(\frac{1}{1 + \gamma}\right)}{h(1)(1 + \kappa)},$$

$$\mu r^* = \sigma h(r^*) = g(S^o), \quad 1 < r^* < g(0)/\mu,$$

$$K > S^o(1 + \gamma r^*).$$

As $\kappa \to \infty$, the second inequality takes the limiting form

$$\frac{\mu}{h'(0)} < \sigma < \frac{g\left(\frac{1}{1 + \gamma}\right)}{h(1)}.$$

Since $h(1) < h(g(0)/\mu)$, we can and do choose some sufficiently large $\gamma > 0$ such that

$$\frac{g(0)}{h(g(0)/\mu)} < \frac{g\left(\frac{1}{1 + \gamma}\right)}{h(1)}.$$ 

For sufficiently large $\kappa > 0$,

$$\frac{g(0)}{h(g(0)/\mu)} < \frac{\mu + \kappa g\left(\frac{1}{1 + \gamma}\right)}{h(1)(1 + \kappa)}.$$ 

Since $h(1) < h'(0)$, we now consider $\sigma \in \left(\frac{\mu}{h(1)}, \frac{g(0)}{h(g(0)/\mu)}\right)$ and look at the limiting case $\sigma \nearrow \frac{g(0)}{h(g(0)/\mu)}$. Then $r^* \nearrow g(0)/\mu$ and $S^o \searrow \gamma$. For $\sigma$ close enough to $\frac{g(0)}{h(g(0)/\mu)}$, $K > S^o(1 + \gamma r^*)$ holds.

In summary, all the inequalities can be satisfied if $\sigma < \frac{g(0)}{h(g(0)/\mu)}$ is chosen close enough to $\frac{g(0)}{h(g(0)/\mu)}$ and then $\kappa$ is chosen large enough.

**Proof of Theorem 10.13.** By (57) and (13),

$$E(r) = \sigma \xi(r) \left(1 + (\kappa - 1) \frac{r}{r + 1}\right) - \kappa g\left(\frac{S^o}{1 + \gamma r}\right), \quad \gamma = \frac{\gamma_2}{\gamma_1} \geq 0.$$ 

Since $\xi$ is decreasing and $\xi(0) = h'(0)$,

$$E(r) \leq \sigma h'(0) \left(1 + (\kappa - 1) \frac{r}{r + 1}\right) - \kappa g\left(\frac{S^o}{1 + \gamma r}\right).$$ 

Since $\sigma h'(0) < \mu + \kappa g(S^o)$,

$$E(r) - \mu < \sigma h'(0)(\kappa - 1) \frac{r}{r + 1} + \kappa \left(g(S^o) - g\left(\frac{S^o}{1 + \gamma r}\right)\right).$$ 

By the mean value theorem, with some $S$ between $\frac{S^o}{1 + \gamma r}$ and $S^o$,

$$E(r) - \mu < \sigma h'(0)(\kappa - 1) \frac{r}{r + 1} + \kappa g'(S) S^o \frac{\gamma r}{1 + \gamma r}.$$
If \( \kappa \leq 1 \), \( E(r) \leq \mu \) for all \( r > 0 \). So we can assume that \( \kappa > 1 \). In this case, it is assumed that \( g \) is convex and so \( g' \) is increasing on \([0, S^\circ]\) and
\[
E(r) - \mu < \sigma h'(0)(\kappa - 1) \frac{r}{r + 1} + \kappa g'(S^\circ)S^\circ \frac{\gamma r}{1 + \gamma r}.
\]
Assume that \( \gamma \geq 1 \). Then
\[
E(r) - \mu < \sigma h'(0) + \kappa g'(S^\circ)S^\circ \frac{\gamma r}{1 + \gamma r}.
\]
Assume that \( \gamma \leq 1 \). Then
\[
E(r) - \mu < \frac{r}{1 + \gamma r} \left( \sigma h'(0)(\kappa - 1) + \kappa \gamma g'(S^\circ)S^\circ \right).
\]

**Proof of Theorem 10.15.** By Remark 15.6, there is no interior equilibrium if \( g(S^\circ/(1 + \gamma r^*)) \leq 0 \). So we assume \( g(S^\circ/(1 + \gamma r^*)) > 0 \).

Recall that, for any interior equilibrium \((S^\dagger, r^\dagger, P^\dagger)\), the inequality \( r^\dagger < r^* \) holds. So it is sufficient to show that \( E(r) > \mu \) for all \( r \in (0, r^*) \) with \( g(S^\circ/1 + \gamma r) > 0 \). Recall
\[
E(r) = \sigma \xi(r) \left( 1 + (\kappa - 1) \frac{r}{r + 1} \right) - \kappa g(S^\circ/(1 + \gamma r)).
\]
Since \( \kappa \geq 1 \), \( \gamma > 0 \) and \( \xi \) is decreasing and \( g \) is decreasing wherever it is positive, for all relevant \( r \in (0, r^*) \),
\[
E(r) > \sigma \xi(r^*) - \kappa g(S^\circ/1 + \gamma r^*).
\]
Notice that \( \sigma \xi(r^*) = \sigma (h(r^*) + \frac{h(r^*)}{r^*}) = g(S^*) + \mu \). By the assumption for \( \kappa \), for \( r \in (0, r^*) \),
\[
E(r) - \mu \geq g(S^*) - \kappa g(S^\circ/(1 + \gamma r^*)) > 0.
\]

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