Persistence of vertically transmitted parasite strains which protect against more virulent horizontally transmitted strains

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Abstract

The question whether a vertically and a horizontally transmitted parasite strain can coexist under complete cross protection is investigated in a host-parasite model with susceptibles and infectives only. It is shown that coexistence is possible even if the vertically transmitted strain would go extinct on its own provided that it is considerably less virulent than the horizontally transmitted strain. While the vertical transmitted strain is without benefit to the host as such, it protects the host against the more harmful horizontally transmitted strain. The coexistence is shown in the form of uniform strong persistence of the host and both parasite strains.

1 Introduction

There is a wide range of pathogens which are both horizontally and vertically transmitted (see [2, 6, 7, 8, 9] and the references mentioned there). Common sense suggests and mathematical models prove that a parasite which is only vertically transmitted cannot persist (unless it is beneficial to its host under certain circumstances, i.e. it is not always parasitic). In this paper we will demonstrate that a parasitic strain

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which is only vertically transmitted can persist in the presence of a more virulent horizontally (and also perhaps vertically) transmitted strain if the two strains provide complete cross-protection against each other, i.e. a host which is infected by one strain cannot be infected by the other strain. Cross-protection that is at least partially effective has been found in the woodland grass *Brachypodium sylvaticum* where vertical infection by the fungus *Epichloë sylvatica* makes the plants less susceptible to infection by horizontally transmitted strains [8].

Coexistence of the two strains (and the host) has numerically been observed for mass action incidence [7]. Coexistence at equilibrium has analytically been established first for mass action incidence and a logistic birth rate [7] and later for general incidence (including standard incidence) and general birth and death rates [3]. Here we will prove dynamic coexistence (uniform strong persistence of the host and both parasite strains). We also show global stability of the coexistence equilibrium for standard incidence and a host birth rate which linearly depends on host density. If the host birth rate is nonlinear, the coexistence equilibrium is unstable in certain parameter regions. (See Subsection 5.1 for more more details, though proof and discussion of the local stability results will be presented in another publication.)

The coexistence of the vertically strain and the horizontally transmitted strain is of interest for parasite evolution. At carrying host capacity (in absence of the parasite), the vertically transmitted strain has a replacement ratio which is strictly smaller than 1 while the horizontally transmitted strain has a replacement ratio which exceeds 1. The coexistence of the two strains is a counterexample to the principle of $\mathcal{R}_0$-maximization that strains with higher basic replacement ratio drive strains with lower basic replacement ratio into extinction (see [12] for a survey). In view of the competitive exclusion principle, there are two consumers (the two parasite strains) and one resource (the host); still the two consumers coexist because horizontal and vertical transmission offer two different routes of resource utilization.

We mention an apparent paradox [3]: at endemic equilibrium, the ratio of infections by the horizontally transmitted strain to infections by the vertically transmitted strain is a *decreasing* function of the coefficient of horizontal transmission. An analogous paradox has been observed in one-strain models where, at equilibrium, the ratio of horizontal infections to vertical infections is a decreasing function of the coefficient of horizontal transmission [6, 3].

2 A model with horizontal and vertical transmission

To set the stage we first formulate a one-strain model. Without the disease, the population with density $N(t)$ at time t develops as

$$N' = (\beta(N) - \mu(N))N. \tag{2.1}$$

where $\beta(N)$ and $\mu(N)$ are the per capita reproduction and mortality rates (of healthy individuals).

Assumption 2.1. $\beta(N)$ is a decreasing positive function of $N \geq 0$, $\mu(N)$ is an increasing positive functions of $N \geq 0$. Both are continuously differentiable, $\beta'(N) - \mu'(N) < 0$ for all $N > 0$. $\beta(N) - \mu(N)$ is positive for $N = 0$ and negative for large $N > 0$.

It follows from these assumptions that there exists a unique number $K > 0$ such that

$$\beta(K) - \mu(K) = 0. \tag{2.2}$$

K is called the *carrying capacity* of the host population in absence of the disease, because $N(t) \to K$ as $t \to \infty$ provided $N(0) > 0$.

The disease divides the population into a susceptible part, with density $S(t)$, and an infective part, with density $I(t)$.

$$\begin{aligned} N =& S + I, \\ S' =& \beta(N)\big(S + q(1-p)I\big) - \mu(N)S - \frac{\sigma C(N)SI}{N}, \\ I' =& \frac{\sigma C(N)SI}{N} + qp\beta(N)I - \mu(N)I - \alpha I. \end{aligned} \tag{2.3}$$

The infection is vertically transmitted at the probability p, $p \in [0,1]$. Infected individuals reproduce at the reduced rate $q\beta(N)$, $q \in [0,1]$. α is the additional per capita rate of dying from the disease.

The parameter σ is a compound parameter whose exact interpretation depends on the specific transmission mode of the parasite. In fungal plant diseases, σ factors in the average spore production of a typical infected plant and the conditional probability that an infection occurs once a spore has landed on a susceptible plant. In sexually transmitted diseases, σ combines the average sexual activity of a typical sexually active person and the conditional probability that a given sexual contact between a susceptible and an infective individual actually leads to an infection. The parameter σ will be of central importance in our analysis, and we call it the *horizontal transmission coefficient.*

The contact function $C(N)$ describes how the per capita amount or rate of contacts depend on the host population density N. These may be direct contacts as in sexually transmitted diseases or indirect contacts as through spores in fungal plant diseases. Again the precise interpretation depends on the type of disease.

I/N is the conditional probability that a given contact made by a susceptible individual actually occurs with an infective individual.

In fungal plant diseases, $C(N)$ is proportional to the probability at which a given spore lands on host plants rather than on the soil (or somewhere else where it is wasted) provided that the host plant density is N. At low host plant densities, this probability should be roughly proportional to the plant density which suggests that $C(0) = 0$. In sexually transmitted diseases, $C(N)$ is proportional to the number of sexual contacts a typical sexually active person makes in a population with density N. Some models assume that $C(N)$ is basically independent of N unless the population density is so low that a deterministic model like ours is not valid anyway. This assumption results in what is sometimes called *standard incidence* [5, 2.1] and is a special case of assuming $C(0) > 0$. The studies in [6, 7] assume *mass action incidence* where $C(N)$ is proportional to N such that $C(N)/N$ does not depend on host density. Our analysis includes both standard and mass action incidence and all reasonable interpolations between these two extremes. A collection of contact functions that have been used in the literature can be found in [11, Sec.19.1]; another example, $C(N) = \zeta \ln(a + \nu N)$, has been suggested for insect diseases [1, App.B].

We replace the equation for S by an equation for N,

$$\begin{aligned} N' &= \big(\beta(N) - \mu(N)\big)N - \big((1-q)\beta(N) + \alpha\big)I, \\ I' &= \frac{\sigma C(N)(N-I)I}{N} + qp\beta(N)I - \mu(N)I - \alpha I. \end{aligned} \tag{2.4}$$

We introduce the fraction of infective individuals,

$$f = \frac{I}{N}. \tag{2.5}$$

By the quotient rule, $f' = \frac{I'}{N} - f\frac{N'}{N} = f(\frac{I'}{I} - \frac{N'}{N})$. The model takes the following form in terms of N and f,

$$\begin{aligned} N' &= N\Big(\beta(N) - \mu(N) - \big((1-q)\beta(N) + \alpha\big)f\Big), \\ f' &= f\Big(\Big[\sigma C(N) - \alpha - (1-q)\beta(N)\Big](1-f) - q(1-p)\beta(N)\Big). \end{aligned} \tag{2.6}$$

Assumption 2.2. All parameters are non-negative, $q > 0$ (the disease does not sterilize), $p < 1$ (vertical transmission typically is imperfect).

$C(N)$ is an increasing function of $N \geq 0$, $C(N) > 0$ for $N > 0$. $C(N)$ is continuously differentiable at $N > 0$.

3 The persistence equilibrium

The origin is an equilibrium where both the host and the parasite are extinct. Potentially there are equilibria of three other types: the parasite extinction equilibrium $(K, 0)$ with the carrying host capacity $K > 0$, the host extinction equilibrium $(0, f^\#)$ with $f^\# > 0$, where the host is extinct and the parasite persists (not in absolute density but in proportion), and the *persistence equilibrium* (N^*, f^*) where both host and parasite persist.

3.1 Uniqueness and existence

There is at most one persistence equilibrium [3]. We restrict our consideration to imperfect vertical transmission, $p < 1$. This excludes that all hosts are infective at equilibrium.

The following equation can be derived for the persistence equilibrium,

$$\sigma^* := \sigma C(N^*) = \left(\frac{q(1-p)\beta^*}{\mu^* + \alpha - q\beta^*} + 1 \right) \big((1-q)\beta^* + \alpha \big) \tag{3.1}$$

where $\beta^* = \beta(N^*)$ is a decreasing and $\mu^* = \mu(N^*)$ an increasing function of N^* and $\beta(N^*) - \mu(N^*)$ is a strictly decreasing function of N^* (Assumption 2.1). For details see [3]. We define

$$\mathcal{R}(N) = \frac{\sigma C(N) + qp\beta(N)}{\mu(N) + \alpha}. \tag{3.2}$$

$\mathcal{R}(N)$ is the basic replacement ratio of the parasite at host population density N, i.e., the average number of new infective hosts produced by one infective host in a completely susceptible population of density N. Notice that $\frac{1}{\mu(N)+\alpha}$ is the mean length of the infective period. $\sigma C(N)$ is the average rate at which a typical infective individual produces new infections by horizontal transmission if it is introduced into a completely susceptible population of density N. $qp\beta(N)$ is the average rate at which a typical infective individual produces new infections by vertical transmission if the population density is N. Recall the carrying host capacity K in (2.2).

Theorem 3.1 ([3]). *Then there exists at most one equilibrium (N^*, f^*) at which both host and parasite persist, $N^*, f^* > 0$. If the persistence equilibrium exists, N^* depends in a strictly decreasing way on σ while the fraction of infectives f^* depends in a strictly increasing way on σ.*

The persistence equilibrium exists, with $0 < N^* < K$, if and only if the following two conditions are satisfied:

(a) $\mathcal{R}(K) > 1$,

(b) either $\mu(0) + \alpha - q\beta(0) \le 0$

$$\text{or } \begin{cases} \mu(0) + \alpha - q\beta(0) > 0 \text{ and} \\ \sigma C(0) < \left(\dfrac{q(1-p)\beta(0)}{\mu(0) + \alpha - q\beta(0)} + 1\right)\big((1-q)\beta(0) + \alpha\big). \end{cases}$$

Notice that condition (b) is satisfied if $C(0) = 0$ which includes the case of mass action incidence. Condition (a) guarantees that $f^* > 0$ while (b) guarantees that $N^* > 0$. If (a) holds but not (b), then the disease drives the host into extinction [14, 3].

3.2 Global stability of the persistence equilibrium

We state that the persistence equilibrium, when it exists, represents the long term behavior of the host-parasite dynamics.

Theorem 3.2. *Let the assumptions (a) and (b) of Theorem 3.1 be satisfied. Then the persistence equilibrium* (N^*, f^*) *is locally stable and all solutions* N, f *of (2.6) with* $N(0) > 0$ *and* $f(0) \in (0, 1]$ *satisfy* $N(t) \to N^*$ *and* $f(t) \to f^*$ *for* $t \to \infty$.

Proof. The local stability of (N^*, f^*) follows by linearization and a straightforward application of the Routh-Hurwitz criterion. The convergence of f and N is proved in [14, Sec.3].

□

The proofs of the following global results can be found in [14, Sec.3]. The local results follow from standard linearized stability arguments in two dimensions.

Theorem 3.3. *Assume that* $\mathcal{R}(K) < 1$. *Then the equilibrium* $(K, 0)$ *is locally asymptotically stable and* $f(t) \to 0$ *and* $N(t) \to K$ *for every solution of (2.6) with* $N(0) > 0$, $f(0) \in [0, 1]$.

Corollary 3.4. *A completely vertically transmitted parasite* ($\sigma = 0$) *dies out, unless vertical transmission is perfect,* $p = 1$, *and the parasite is completely harmless,* $q = 1$ *and* $\alpha = 0$.

Proof. Let $\sigma = 0$. Recall that $\beta(K) = \mu(K)$. So the sufficient condition for parasite extinction in Theorem 3.3 is satisfied if $0 < (1-pq)\mu(K)+\alpha$, i.e., if $pq < 1$ or $\alpha > 0$. □

Theorem 3.5. *Assume that* $\mathcal{R}(K) > 1$. *Let* $\sigma_0 = \sigma C(0)$, $\beta_0 = \beta(0)$ *and* $\mu_0 = \mu(0)$ *and also assume* $\mu_0 + \alpha - q\beta_0 > 0$ *and*

$$\sigma_0 > \left(\frac{q(1-p)\beta_0}{\mu_0 + \alpha - q\beta_0} + 1\right)\big((1-q)\beta_0 + \alpha\big).$$

Then $N(t) \to 0$ as $t \to \infty$ and

$$f(t) \longrightarrow f^{\#} := \frac{\sigma_0 - (1-qp)\beta_0 - \alpha}{\sigma_0 - (1-q)\beta_0 - \alpha} > 0$$

for every solution with $N(0) \geq 0$ and $f(0) \in (0,1]$.

4 The multiple strain model

We extend our model to allow for multiple strains of the parasite. We assume that there is cross-protection between the strains, i.e., a host that has been infected by one strain cannot be infected by another strain. We also assume that a host that has been infected one way (horizontally or vertically) cannot be again infected by the same strain the other way. In this section, we will consider arbitrarily many strains, let us say n, for some basic investigations. But soon we will restrict the consideration to two strains with the second strain only vertically transmitting. We will see that, if the horizontal transmission coefficient of the first strain is sufficiently high and the second strain is less virulent, the two strains can coexist. As before, N denotes the total density of hosts, S the denisty of susceptible, uninfected, hosts, I the total density of infected hosts, while I_j denotes the density of hosts infected with strain j.

$$\begin{cases} N = S + \sum_{j=1}^{n} I_j, \\ S' = \Big(S + \sum_{k=1}^{n} q_k(1-p_k)I_k\Big)\beta(N) - \mu(N)S \\ \qquad -\dfrac{C(N)S}{N}\sum_{k=1}^{n}\sigma_k I_k, \\ I_j' = I_j\Big(\dfrac{C(N)S}{N}\sigma_j + q_j p_j \beta(N) - \mu(N) - \alpha_j\Big). \end{cases} \tag{4.1}$$

The parameters and parameter functions have the same meaning as before, but the epidemiologic parameters now carry an index which denotes the parasite strain. In the same way as for the one-strain model, we rewrite the system in terms of the total host density,

$$\begin{aligned} N' &= N\big(\beta(N) - \mu(N)\big) - \sum_{k=1}^{n} I_k\big((1-q_k)\beta(N) + \alpha_k\big), \\ I_j' &= I_j\Big(\sigma_j C(N)\frac{N - \sum_{k=1}^{n} I_k}{N} + q_j p_j \beta(N) - \mu(N) - \alpha_j\Big). \end{aligned} \tag{4.2}$$

We introduce the fraction of strain j infective individuals,

$$f_j = \frac{I_j}{N}, \tag{4.3}$$

and the fraction of infective individuals

$$\bar{f} = \sum_{k=1}^{n} f_k. \tag{4.4}$$

By the quotient rule, $f_j' = f_j\big(\frac{I_j'}{I_j} - \frac{N'}{N}\big)$. We rewrite the system in terms of the total host density and the fractions of strain j parasites,

$$\begin{aligned} N' =& N\Big(\beta(N) - \mu(N) - \sum_{k=1}^{n} f_k\big((1-q_k)\beta(N) + \alpha_k\big)\Big), \\ f_j' =& f_j\Big(\sigma_j C(N)\big(1-\bar{f}\big) - (1-q_jp_j)\beta(N) - \alpha_j \\ & + \sum_{k=1}^{n} f_k\big((1-q_k)\beta(N) + \alpha_k\big)\Big). \end{aligned} \tag{4.5}$$

We derive a differential equation for the fraction of infected hosts, $\bar{f}$,

$$\begin{aligned} \bar{f}' =& \Big(\sum_{j=1}^{n} \sigma_j f_j\Big) C(N)(1-\bar{f}) - (1-\bar{f})\sum_{j=1}^{n} f_j(1-q_jp_j)\beta(N) \\ & - \bar{f}\beta(N)\sum_{j=1}^{n} q_j(1-p_j) f_j - (1-\bar{f})\sum_{j=1}^{n} \alpha_j f_j. \end{aligned} \tag{4.6}$$

Theorem 4.1. *Let $\breve{N}$ and $\breve{f}_1, \dots, \breve{f}_n$ be non-negative numbers, $\sum_{j=1}^n \breve{f}_j \le 1$. Then there exists a unique non-negative solution of (4.5) on $\mathbb{R}_+$ such that $N(0) = \breve{N}$, $f_j(0) = \breve{f}_j$ for $j = 1, \dots, n$. Moreover $\sum_{j=1}^n f_j(t) \le 1$ for all $t \ge 0$ and $N(t) \le \max\{\breve{N}, K\}$ where K is the carrying capacity for the parasite-free host population, $\beta(K) = \mu(K)$. Finally $\limsup_{t\to\infty} N(t) \le K$.*

Proof. We notice that

$$N' = NG_0(N, f_1, \dots, f_n) \text{ and } f_j' = f_jG_j(N, f_1, \dots, f_n)$$

with locally Lipschitz continuous functions $G_j : \mathbb{R}_+^n \to \mathbb{R}$. So we a have an ODE system with a locally Lipschitz continous vector field and a unique solution on a maximal interval $[0, b)$. By the form of the equations, $f_j(t) = f_j(0)\exp(\int_0^t \phi_j(s)ds)$ with $\phi_j = G_j(N, f_1, \dots, f_n)$ as long as the solution exist. So $f_j \ge 0$ as long as the solution exists and the same holds for N. So $b > 0$ can be chosen such that $\limsup_{t\to b}\big(N(t) + \sum_{j=1}^n f_j(t)\big) = \infty$ if $b < \infty$. We employ (4.6) and use $p_j \le 1$, $f_j \ge 0$, to obtain the differential inequality

$$\begin{aligned}\bar f' \le & \Big(\sum_{j=1}^n \sigma_j f_j\Big) C(N)(1-\bar f) - (1-\bar f)\beta(N)\sum_{j=1}^n (1-q_j p_j) f_j \\ & - (1-\bar f)\sum_{j=1}^n \alpha_j f_j .\end{aligned} \tag{4.7}$$

This implies that, as long as the solution of (4.5) exists,

$$\frac{d}{dt}(1-\bar f) \ge (1-\bar f)\phi(t)$$

with a continuous function $\phi : [0,b) \to \mathbb{R}$. We solve the differential inequality,

$$1 - \bar f(t) \ge (1-\bar f(0)) \exp\Big(\int_0^t \phi(s) ds\Big).$$

Since $1 - \bar f(0) \ge 0$, also $1 - \bar f(t) \ge 0$ for all $t \in [0,b)$. N satisfies the differential inequality,

$$N' \le N(\beta(N) - \mu(N)).$$

Let $t \in (0,b)$ and $\tilde N = \max_{[0,t]} N(t)$. By [11, Lemma A.6], $\tilde N = N(0)$ or there exists some $s \in (0,t]$ such that $N'(s) \ge 0$ and $N(s) = \tilde N$. So $0 \le N'(s) = \tilde N(\beta(\tilde N) - \mu(\tilde N))$. Since $\beta(N) - \mu(N) < 0$ for $N > K$, $\tilde N \le K$. So $\tilde N \le \max\{N(0), K\}$. Since this estimate does not depend on $t \in [0,b)$, N is bounded on $[0,b)$ and $N(t) \le \max\{N(0),K\}$ for all $t \in [0,b)$. This implies that $b = \infty$ and the estimate holds for all $t \ge 0$. By the fluctuation method [4] [11, Prop.A.22], there exists a sequence $t_j \to \infty$, $N(t_j) \to N^\infty$, $N'(t_j) \to 0$ as $j \to \infty$. This implies $0 \le N^\infty(\beta(N^\infty) - \mu(N^\infty))$. Since the right hand side of this inequality would be negative for $N^\infty > K$, $N^\infty \le K$. □

In the remainder of this paper we assume that no strain sterilizes the host and that every strain has imperfect vertical transmission, i.e.,

- $q_j > 0$ and $p_j < 1$ for all $j = 1, \dots, n$.

Theorem 4.2. *There exists some $\varepsilon > 0$ such that*

$$\limsup_{t\to\infty} \sum_{j=1}^n f_j(t) \le 1 - \varepsilon$$

for all solutions of (4.5) with $N(0) \ge 0$, $f_j(0) \ge 0$, $j = 1, \dots, n$, and $\sum_{j=1}^n f_j(0) \le 1$.

A formula for $\varepsilon > 0$ is found in the subsequent proof, see (4.8).

Proof. Set $\xi = \min_{j=1}^n q_j(1-p_j)$ and $\breve{\sigma} = \max_{j=1}^n \sigma_j$. Then $\xi > 0$ and the following inequality is obtained from (4.6),

$$\bar{f}' \leq \breve{\sigma} C(N)(1-\bar{f}) - \xi\beta(N)\bar{f}.$$

Let $\bar{f}^\infty = \limsup_{t\to\infty} \bar{f}(t)$. By the fluctuation method ([4] or [11, Prop.A.22]), there exists a sequence $t_k \to \infty$ such that $\bar{f}(t_k) \to \bar{f}^\infty$ and $\bar{f}'(t_k) \to 0$ as $k \to \infty$. Since $\limsup_{t\to\infty} N(t) \leq K$ and C is increasing and β decreasing,

$$0 \leq \breve{\sigma} C(K)(1-\bar{f}^\infty) - \xi\beta(K)\bar{f}^\infty.$$

We solve this inequality for $\bar{f}^\infty$,

$$\bar{f}^\infty \leq \frac{\breve{\sigma} C(K)}{\breve{\sigma} C(K) + \xi\beta(K)} < 1. \tag{4.8}$$

□

Lemma 4.3. *Let* $\sigma_j C(0) \leq (1-q_j p_j)\beta(0) + \alpha_j$ *for* $j = 1, \dots, n$. *Then, for all solutions with* $N(0) = 0$, $f_j(t) \to 0$ *as* $t \to \infty$, $j = 1, \dots, n$,

Proof. Let $N(0) = 0$. Then $N(t) = 0$ for all $t \geq 0$ and (4.6) can be written as

$$\begin{aligned} \bar{f}' =& \sum_{j=1}^n f_j \Big(\sigma_j C(0)(1-\bar{f}) - (1-\bar{f})\beta(0)(1-q_j p_j) \\ & - \bar{f} q_j(1-p_j)\beta(0) - (1-\bar{f})\alpha_j \Big). \end{aligned} \tag{4.9}$$

By assumption,

$$\bar{f}' \leq -\sum_{j=1}^n f_j q_j (1-p_j)\beta(0)\bar{f}.$$

Set $\xi = \min_{j=1,\dots,n} q_j(1-p_j)$. Then $\xi > 0$ and $\bar{f}' \leq -\xi \bar{f}^2$. This implies that $\bar{f}(t) \to 0$ as $t \to \infty$. □

Theorem 4.4. *Let* $\sigma_j C(0) \leq (1-q_j p_j)\beta(0) + \alpha_j$ *for* $j = 1, \dots, n$. *Then the host population is uniformly persistent: there exists some* $\varepsilon > 0$ *such that* $\liminf_{t\to\infty} N(t) \geq \varepsilon$ *for all solutions with* $N(0) > 0$.

Proof. We use the language and the results in Section A. Our state space is $X = \{(N, f_1, \dots, f_n) \in \mathbb{R}_+^{n+1}, \sum_{j=1}^n f_j \leq 1\}$. We split up X as $X = X_1 \uplus X_2$ (disjoint union) with $X_1 = \{N > 0\} \cap X$ and $X_2 = \{N = 0\} \cap X$. Then X is closed and X_2 is compact. Both X_1 and X_2 are forward invariant. By Lemma 4.3, $(0,\dots,0)$ is globally asymptotically stable for X_2. By Theorem 4.1, every solution in X tends to the compact set $X \cap \{N \le K\}$. System (4.5) has the form of Lemma A.7 with $x = (N, f_1, \dots, f_n)$. By assumption, $g_1(0,\dots,0) = \beta(0) - \mu(0) > 0$. By Lemma A.7, $(0,\dots,0)$ is a uniform weak repeller for $X \cap \{x_1 > 0\} = X \cap \{N > 0\} = X_1$. By Proposition A.6, the singleton set containing $(0,\dots,0)$ is an isolated invariant set for X. By Theorem A.4, X_2 is a uniform strong repeller for X_1 which is equivalent to the statement of the theorem.

□

5 The two strain model with one strain only vertically transmitted

We restrict our consideration to two parasite strains. The second strain is only vertically transmitted while the first strain is transmitted horizontally and possibly vertically too. Somewhat imprecisely, we will speak about the first strain as the horizontally transmitted strain (HT strain) and about the second strain as the vertically transmitted strain (VT strain). System (4.2) specializes to

$$\begin{aligned}
N' &= N\big(\beta(N) - \mu(N)\big) - \sum_{k=1}^{2} I_k\big((1-q_k)\beta(N) + \alpha_k\big),\\
I_1' &= I_1\Big(\sigma C(N)\frac{N - \sum_{k=1}^{2} I_k}{N} + q_1 p_1 \beta(N) - \mu(N) - \alpha_1\Big),\\
I_2' &= I_2\Big(q_2 p_2 \beta(N) - \mu(N) - \alpha_2\Big),
\end{aligned} \tag{5.1}$$

and the system (4.5) specializes to

$$\begin{aligned}
N' &= N\Big(\beta(N) - \mu(N) - \sum_{k=1}^{2} f_k\big((1-q_k)\beta(N) + \alpha_k\big)\Big),\\
f_1' &= f_1\Big(\sigma C(N)(1 - f_1 - f_2) - (1 - q_1 p_1)\beta(N) - \alpha_1\\
&\qquad + \sum_{k=1}^{2} f_k\big((1-q_k)\beta(N) + \alpha_k\big)\Big),\\
f_2' &= f_2\Big(-(1 - q_2 p_2)\beta(N) - \alpha_2\\
&\qquad + \sum_{k=1}^{2} f_k\big((1-q_k)\beta(N) + \alpha_k\big)\Big).
\end{aligned} \tag{5.2}$$

σ is again called the *coefficient of horizontal transmission.* We assume that both strains do some harm to the host, $\alpha_j > 0$ or $q_j < 1$ for $j = 1, 2$. However, neither strain sterilizes the host, i.e. $q_j > 0$ for $j = 1, 2$. Further vertical transmission is imperfect for both strains, $p_j < 1$ for $j = 1, 2$.

5.1 Coexistence equilibrium

By the last equation of (5.1), an equilibrium where both parasite strains and the host coexist satisfies

$$0 = q_2 p_2 \beta(N^*) - \mu(N^*) - \alpha_2. \tag{5.3}$$

Since the right hand side of this equation is strictly decreasing, we learn that N^* is uniquely determined and does not depend on σ. We write $\sigma^* = \sigma C(N^*)$, $\beta^* = \beta(N^*)$, $\mu^* = \mu(N^*)$. So β^* and μ^* do not depend on σ either, while σ^* is proportional to σ. We define

$$\mathcal{R}_2(N) = \frac{q_2 p_2 \beta(N)}{\mu(N) + \alpha_2}. \tag{5.4}$$

$\mathcal{R}_2(N)$ is the basic replacement number of the VT strain at population density N and is the special case of (3.2) for the VT strain ($\sigma = 0$). The following is shown in [3].

Theorem 5.1. *A (uniquely determined) coexistence equilibrium exists if and only if the following assumptions are satisfied:*

(a) $\mathcal{R}_2(0) > 1$.

(b) The vertically transmitted second strain is less harmful than the horizontally transmitted first strain in the following way,

$$(q_2 p_2 - q_1)\beta(N^*) + \alpha_1 - \alpha_2 > 0,$$

where N^* *is the unique solution of* $\mathcal{R}_2(N^*) = 1$.

(c) The horizontal transmission coefficient is large enough,

$$\sigma C(N^*) > \frac{(q_2 p_2 - q_1 p_1)\beta(N^*) + \alpha_1 - \alpha_2}{(q_2 p_2 - q_1)\beta(N^*) + \alpha_1 - \alpha_2}\big((1 - q_1)\beta(N^*) + \alpha_1\big).$$

Remark 5.2. The equation $\mathcal{R}_2(N^*) = 1$ in Theorem 5.1 (b) is equivalent to (5.3) by which the condition in Theorem 5.1 (b) is equivalent to

$$\mu(N^*) + \alpha_1 - q_1 \beta(N^*) > 0. \tag{5.5}$$

The condition in Theorem 5.1 (c) is equivalent to

$$1 > \left(1 + \frac{q_1(1-p_1)\beta(N^*)}{\mu(N^*) + \alpha_1 - q_1\beta(N^*)}\right)\frac{(1-q_1)\beta(N^*) + \alpha_1}{\sigma C(N^*)}. \tag{5.6}$$

Notice that the right hand side of this inequality is strictly decreasing. Since $N^* \le K$, (5.6) also holds if N^* is replaced by K. Since $\beta(K) = \mu(K)$, the condition in Theorem 5.1 (c) implies that

$$\sigma C(K) > (1 - p_1 q_1)\beta(K) + \alpha_1 \tag{5.7}$$

which is equivalent to condition (a) in Theorem 3.1 for $q = q_1$, $p = p_1$. Let us assume that condition (b) in Theorem 3.1 also holds. Then we have a boundary equilibrium $(\mathbb{N}^\sharp, f_1^\sharp, 0)$ where only the HT strain is present. By (3.1),

$$1 = \left(1 + \frac{q_1(1-p_1)\beta(N^\sharp)}{\mu(N^\sharp) + \alpha_1 - q_1\beta(N^\sharp)}\right)\frac{(1-q_1)\beta(N^\sharp) + \alpha_1}{\sigma C(N^\sharp)}. \tag{5.8}$$

Since the right hand side of this equation is decreasing, $N^\sharp < N^*$.

We have the following stability results which will be proved and discussed elsewhere.

Theorem 5.3. *If the coexistence equilibrium exists, i.e. conditions (a), (b), (c) in Theorem 5.1 hold, it is locally asymptotically stable if*

(i) *the horizontal transmission coefficient σ is sufficiently large,*

or

(ii) *the per capita birth rate β does not depend on the population density N.*

Under standard incidence, i.e. if the contact function C is constant, the coexistence equilibrium can be unstable for the following scenario:

- p_2 and q_2 are close enough to 1, i.e. the VT strain is almost perfectly vertically transmitted and causes almost no fertility reduction,

and

- $q_1(1-p_1)$ is close enough to 0, i.e. the HT strain is almost perfectly vertically transmitted or sterilizes the host almost completely.

Differently from the case of standard incidence, the coexistence equilibrium is locally asymptotically stable under mass action incidence (i.e. $C(N)/N$ does not depend on N) if p_2 is sufficiently close to 1. Whether or not the coexistence equilibrium is locally asymptotically stable whenever it exists is still an open question for mass action incidence.

5.2 Dynamic coexistence

The criteria for coexistence of both parasite strains and the host at equilibrium which were proved in Theorem 5.1 also guarantee dynamic coexistence.

Theorem 5.4. *The following are equivalent:*

(i) There exists a coexistence equilibrium.

(ii) The horizontally and vertically transmitted strains coexist in the sense that there exists some $\varepsilon > 0$ *such that*

$$\liminf_{t\to\infty} I_j(t) \geq \varepsilon, \qquad j = 1, 2,$$

for all solutions of (5.1) with $I_1(0) > 0$, $I_2(0) > 0$, $N(0) \geq I_1(0) + I_2(0)$.

Existence of a coexistence equilibrium is necessary for the dynamic coexistence in (b) due to a general result [13, Thm.1.3.7]. The sufficiency is shown in Section 7. A global stability result can be shown if C and β do not depend on the population density N.

Theorem 5.5. *Assume that* C *and* β *are positive constants and that the coexistence equilibrium* $x^* = (N^*, I_1^*, I_2^*)$ *with* $N^*, I_1^*, I_2^* > 0$ *exists. Then all solutions of (5.1) with* $I_1(0), I_2(0) > 0$, $N(0) \geq I_1(0) + I_2(0)$ *converge towards the coexistence equilibrium.*

The proof will be given in the next section.

6 Global stability for constant contact function and per capita birth rate

We consider the special case that $C(N)$ and $\beta(N)$ do not depend on N. Notice that Assumption 2.1 implies that $\mu'(N) > 0$ for all $N > 0$. In the following we show that whenever an endemic equilibrium exists where the VT strain is present (i.e. $f_2^\diamond > 0$), then this equilibrium attracts all solutions with $f_1(0) > 0$ and $f_2(0) > 0$. Depending on a further threshold condition the host population goes extinct or converges to a positive limit.

The equations for the strain fractions (5.2) become independent of the host equation,

$$\begin{aligned} f_1' &= f_1\Big((1 - f_1 - f_2)\sigma C + f_1\gamma_1 + f_2\gamma_2 - \hat\gamma_1\Big), \\ f_2' &= f_2\Big(f_1\gamma_1 + f_2\gamma_2 - \hat\gamma_2\Big), \end{aligned} \tag{6.1}$$

where

$$\begin{aligned}\gamma_j =&(1-q_j)\beta+\alpha_j,\\ \hat{\gamma}_j =&\gamma_j+q_j(1-p_j)\beta=(1-q_jp_j)\beta+\alpha_j.\end{aligned} \tag{6.2}$$

Notice that $\hat{\gamma}_j > \gamma_j$.

Lemma 6.1. *The equilibrium* $(f_1^{\#},0)$ *with* $0 < f_1^{\#} \leqslant 1$ *exists if and only if* $\sigma C - \hat{\gamma}_1 > 0$*, in which case,*

$$f_1^{\#} = \frac{\sigma C - \hat{\gamma}_1}{\sigma C - \gamma_1} < 1. \tag{6.3}$$

Proof. $(f_1^{\#},0)$ exists with $0 < f_1^{\#}$ if and only if $(1-f_1^{\#})\sigma C + f_1^{\#}\gamma_1 - \hat{\gamma}_1 = 0$ if and only if $f_1^{\#} = \frac{\sigma C - \hat{\gamma}_1}{\sigma C - \gamma_1} > 0$ and numerator and denominator have the same sign. Since $\hat{\sigma}_1 > \sigma_1$, $f_1^{\#} \leq 1$ if and only if $\sigma C - \hat{\gamma}_1 > 0$, in which case $f_1^{\#} < 1$. ☐

Lemma 6.2. *An equilibrium* $(f_1^{\diamond}, f_2^{\diamond})$ *with* $f_1^{\diamond} > 0$*,* $f_2^{\diamond} > 0$ *and* $f_1^{\diamond}+f_2^{\diamond} \leqslant 1$ *exists if and only if*

1. *the equilibrium* $(f_1^{\#},0)$ *in Lemma 6.1 exists, and*
2. $f_1^{\#}\gamma_1 - \hat{\gamma}_2 > 0$*, where* $f_1^{\#}$ *is given by* (6.3)*.*

The equilibrium is unique. In case $(f_1^{\diamond}, f_2^{\diamond})$ *exists, we have* $\hat{\gamma}_1 > \gamma_1 > \hat{\gamma}_2 > \gamma_2$*,* $f_1^{\diamond}\gamma_1 + f_2^{\diamond}\gamma_2 = \hat{\gamma}_2$*, and* $f_1^{\diamond} + f_2^{\diamond} < 1$*.*

Proof. Suppose the equilibrium $(f_1^{\#},0)$ exists and $f_1^{\#}\gamma_1 - \hat{\gamma}_2 > 0$. Since $0 < f_1^{\#} \leqslant 1$, we have $\hat{\gamma}_1 > \gamma_1 > \hat{\gamma}_2 > \gamma_2$. Since

$$\begin{aligned}0 < f_1^{\#}\gamma_1 - \hat{\gamma}_2 &= \frac{\sigma C - \hat{\gamma}_1}{\sigma C - \gamma_1}\gamma_1 - \hat{\gamma}_2 = \frac{(\sigma C - \hat{\gamma}_1)\gamma_1 - (\sigma C - \gamma_1)\hat{\gamma}_2}{\sigma C - \gamma_1}\\ &= \frac{\sigma C(\gamma_1 - \hat{\gamma}_2) - \gamma_1(\hat{\gamma}_1 - \hat{\gamma}_2)}{\sigma C - \gamma_1},\end{aligned}$$

we have $\sigma C(\gamma_1 - \hat{\gamma}_2) - \gamma_1(\hat{\gamma}_1 - \hat{\gamma}_2) > 0$. Define

$$f_2^{\diamond} = \frac{\sigma C(\gamma_1 - \hat{\gamma}_2) - \gamma_1(\hat{\gamma}_1 - \hat{\gamma}_2)}{\sigma C(\gamma_1 - \gamma_2)} > 0. \tag{6.4}$$

Since

$$\begin{aligned}\sigma C(\gamma_1 - \hat{\gamma}_2) - \gamma_1(\hat{\gamma}_1 - \hat{\gamma}_2) &< \sigma C(\gamma_1 - \gamma_2) - \gamma_1(\hat{\gamma}_1 - \hat{\gamma}_2)\\ &< \sigma C(\gamma_1 - \gamma_2),\end{aligned}$$

we also have $f_2^\diamond < 1$. Define $f_1^\diamond$ to be such that $f_1^\diamond \gamma_1 + f_2^\diamond \gamma_2 - \hat\gamma_2 = 0$, i.e.,

$$f_1^\diamond = \frac{\hat\gamma_2 - f_2^\diamond \gamma_2}{\gamma_1}. \tag{6.5}$$

Then we have $f_1^\diamond > \frac{\gamma_2 - f_2^\diamond \gamma_2}{\gamma_1} = (1 - f_2^\diamond)\frac{\gamma_2}{\gamma_1} > 0$. $(f_1^\diamond, f_2^\diamond)$ is an equilibrium because

$$\begin{aligned}
&(1 - f_1^\diamond - f_2^\diamond)\sigma C + f_1^\diamond \gamma_1 + f_2^\diamond \gamma_2 - \hat\gamma_1\\
&= (1 - f_1^\diamond - f_2^\diamond)\sigma C - (\hat\gamma_1 - \hat\gamma_2) \quad \text{(by (6.5))}\\
&= \Big(1 - \frac{\hat\gamma_2 - f_2^\diamond \gamma_2}{\gamma_1} - f_2^\diamond\Big)\sigma C - (\hat\gamma_1 - \hat\gamma_2) \quad \text{(by (6.5))}\\
&= \frac{\big(\gamma_1 - \hat\gamma_2 - f_2^\diamond(\gamma_1 - \gamma_2)\big)\sigma C - \gamma_1(\hat\gamma_1 - \hat\gamma_2)}{\gamma_1}\\
&= \frac{(\gamma_1 - \hat\gamma_2)\sigma C - (\hat\gamma_1 - \hat\gamma_2) - \gamma_1(\gamma_1 - \gamma_2)\sigma C f_2^\diamond}{\gamma_1} = 0 \quad \text{(by (6.4))}.
\end{aligned}$$

Since $(1 - f_1^\diamond - f_2^\diamond)\sigma C = \hat\gamma_1 - \hat\gamma_2 > 0$, we have $f_1^\diamond + f_2^\diamond < 1$.

Conversely, suppose the equilibrium $(f_1^\diamond, f_2^\diamond)$ exists with $f_1^\diamond > 0$, $f_2^\diamond > 0$, and $f_1^\diamond + f_2^\diamond \leqslant 1$. Then

$$(1 - f_1^\diamond - f_2^\diamond)\sigma C + f_1^\diamond \gamma_1 + f_2^\diamond \gamma_2 - \hat\gamma_1 = 0 \quad \text{and} \tag{6.6}$$

$$f_1^\diamond \gamma_1 + f_2^\diamond \gamma_2 - \hat\gamma_2 = 0. \tag{6.7}$$

We rewrite (6.7) as $(1 - f_2^\diamond)(\gamma_1 - \hat\gamma_2) = (1 - f_1^\diamond - f_2^\diamond)\gamma_1 + f_2^\diamond(\hat\gamma_2 - \gamma_2)$ and see that $\hat\gamma_1 > \gamma_1 > \hat\gamma_2 > \gamma_2$. We combine (6.6) and (6.7),

$$(1 - f_1^\diamond - f_2^\diamond)\sigma C - (\hat\gamma_1 - \hat\gamma_2) = 0. \tag{6.8}$$

We rearrange (6.7) as

$$(1 - f_1^\diamond - f_2^\diamond)\gamma_1 = -f_2^\diamond(\gamma_1 - \gamma_2) + \gamma_1 - \hat\gamma_2. \tag{6.9}$$

We combine (6.8) and (6.9),

$$\big(-f_2^\diamond(\gamma_1 - \gamma_2) + \gamma_1 - \hat\gamma_2\big)\sigma C - \gamma_1(\hat\gamma_1 - \hat\gamma_2) = 0, \tag{6.10}$$

which we rearrange as

$$f_2^\diamond \sigma C(\gamma_1 - \gamma_2) = \sigma C(\gamma_1 - \hat\gamma_2) - \gamma_1(\hat\gamma_1 - \hat\gamma_2). \tag{6.11}$$

Since $\gamma_1 > \hat\gamma_2$, we have

$$\sigma C > \frac{\gamma_1(\hat\gamma_1 - \hat\gamma_2)}{\gamma_1 - \hat\gamma_2} = \frac{\hat\gamma_1(\gamma_1 - \hat\gamma_2) + \hat\gamma_2(\hat\gamma_1 - \gamma_1)}{\gamma_1 - \hat\gamma_2} > \hat\gamma_1,$$

and so the equilibrium $(f_1^\#, 0)$ in Lemma 6.1 exists. By (6.11),

$$f_1^\# \gamma_1 - \hat\gamma_2 = \frac{\sigma C - \hat\gamma_1}{\sigma C - \gamma_1}\gamma_1 - \hat\gamma_2 = \frac{\sigma C(\gamma_1 - \hat\gamma_2) - \gamma_1(\hat\gamma_1 - \hat\gamma_2)}{\sigma C - \gamma_1} > 0. \quad \square$$

Lemma 6.3. *Every solution* $f_1(t), f_2(t)$ *with*

$$\liminf_{t\to\infty} f_1(t) > 0, \quad \liminf_{t\to\infty} f_2(t) > 0, \qquad \textit{and}$$
$$\limsup_{t\to\infty} \bar{f}(t) = \limsup_{t\to\infty} \big(f_1(t) + f_2(t)\big) < 1,$$

converges to the interior equilibrium $(f_1^\diamond, f_2^\diamond)$.

Proof. We have $f_1' = F_1$, $f_2' = F_2$, where

$$\begin{aligned} F_1(f_1, f_2) =& f_1\Big((1 - f_1 - f_2)\sigma C + f_1\gamma_1 + f_2\gamma_2 - \gamma_1 - q_1(1 - p_1)\beta\Big) \\ =& f_1\Big((1 - f_1 - f_2)(\sigma C - \gamma_1) - f_2(\gamma_1 - \gamma_2) - q_1(1 - p_1)\beta\Big), \\ F_2(f_1, f_2) =& f_2\Big(f_1\gamma_1 + f_2\gamma_2 - \gamma_2 - q_2(1 - p_2)\beta\Big) \\ =& f_2\Big(-(1 - f_1 - f_2)\gamma_2 + f_1(\gamma_1 - \gamma_2) - q_2(1 - p_2)\beta\Big). \end{aligned}$$

From the assumption, the ω-limit of the solution is contained in

$$D = \{(f_1, f_2) \in \mathbb{R}^2 \,:\, 0 < f_1,\ 0 < f_2,\ f_1 + f_2 < 1\}.$$

Define $\rho : D \to \mathbb{R}$ by $\rho(f_1, f_2) = \frac{1}{f_1 f_2(1-f_1-f_2)}$. Then

$$\begin{aligned} \rho F_1 &= \frac{\sigma C - \gamma_1}{f_2} - \frac{\gamma_1 - \gamma_2}{1 - f_1 - f_2} - \frac{q_1(1 - p_1)\beta}{f_2(1 - f_1 - f_2)}, \\ \rho F_2 &= -\frac{\gamma_2}{f_1} + \frac{\gamma_1 - \gamma_2}{1 - f_1 - f_2} - \frac{q_2(1 - p_2)\beta}{f_1(1 - f_1 - f_2)}, \end{aligned}$$

and so

$$\begin{aligned} \frac{\partial \rho F_1}{\partial f_1} &= -\frac{\gamma_1 - \gamma_2}{(1 - f_1 - f_2)^2} - \frac{q_1(1 - p_1)\beta}{f_2(1 - f_1 - f_2)^2}, \\ \frac{\partial \rho F_2}{\partial f_2} &= \frac{\gamma_1 - \gamma_2}{(1 - f_1 - f_2)^2} - \frac{q_2(1 - p_2)\beta}{f_1(1 - f_1 - f_2)^2}. \end{aligned}$$

Hence

$$\frac{\partial \rho F_1}{\partial f_1} + \frac{\partial \rho F_2}{\partial f_2} = -\frac{q_1(1 - p_1)\beta}{f_2(1 - f_1 - f_2)^2} - \frac{q_2(1 - p_2)\beta}{f_1(1 - f_1 - f_2)^2} < 0.$$

Since this is a planar system and is dissipative, the solution converges toward an equilibrium in D, hence converges to $(f_1^\diamond, f_2^\diamond)$ since there is only one interior equilibrium. ☐

Lemma 6.4. *For every solution, we have* $\limsup_{t\to\infty} \bar{f}(t) < 1$. *If the interior equilibrium* $(f_1^\diamond, f_2^\diamond)$ *exists, we also have* $\liminf_{t\to\infty} f_1(t) > 0$ *and* $\liminf_{t\to\infty} f_2(t) > 0$ *whenever* $f_1(0), f_2(0) > 0$.

Proof. The first assertion follows from Theorem 4.2. Now assume that the interior equilibrium $(f_1^\diamond, f_2^\diamond)$ exists. Let

$$\begin{aligned} X &= \{(f_1, f_2) \in \mathbb{R}^2 \,:\, 0 \leqslant f_1,\ 0 \leqslant f_2,\ f_1 + f_2 \leqslant 1\},\\ X_1 &= \{(f_1, f_2) \in X \,:\, f_1 > 0, f_2 > 0\},\\ X_2 &= \{(f_1, f_2) \in X \,:\, f_1 = 0 \text{ or } f_2 = 0\}. \end{aligned}$$

There are two equilibria in X_2, $(0,0)$ and $(f_1^\#, 0)$. Every solution in X with $f_1(0) = 0$ converges $(0,0)$ and every solution in X with $f_2(0) = 0$, $f_1(0) > 0$ converges to $(f_1^\#, 0)$. In particular, the two equilibria form an acyclic set in X_2. We rewrite system (6.1) in the form of Lemma A.7. From Lemma 6.1 and Lemma 6.2, we have

$$g_1(0,0) = \sigma C - \hat{\gamma}_1 > 0 \quad \text{and} \quad g_2(f_1^\#, 0) = f_1^\# \gamma_1 - \hat{\gamma}_2 > 0.$$

By Lemma A.7, $(0,0)$ is a uniform weak repeller for $X \cap \{f_1 > 0\}$ and $(f_1^\#, 0)$ a uniform weak repeller for $X \cap \{f_2 > 0\}$. On $X \cap \{f_1 = 0\}$ we have

$$f_2' = f_2\big((f_2 - 1)\gamma_2 - q_2(1 - p_2)\big)$$

which is negative whenever $f_2 \in (0,1]$. Hence $(0,0)$ is locally asymptotically stable for $X \cap \{f_1 = 0\}$. By Proposition A.6, $(0,0)$ is an isolated invariant set for X.

It is easy to see that $(f_1^\#, 0)$ is locally asymptotically stable for $X \cap \{f_2 = 0\}$. Since $(f_1^\#, 0)$ is a uniform weak repeller for $X \cap \{f_2 > 0\}$, $(f_1^\#, 0)$ is an isolated invariant set for X by Proposition A.6.

By Theorem A.4, X_2 is a uniform strong repeller for X_1, in particular $\liminf_{t\to\infty} f_1(t) > 0$ and $\liminf_{t\to\infty} f_2(t) > 0$ whenever $f_1(0) > 0$ and $f_2(0) > 0$. □

Theorem 6.5. *If the unique equilibrium $(f_1^\diamond, f_2^\diamond)$ with $f_1^\diamond > 0$, $f_2^\diamond > 0$, $f_1^\diamond + f_2^\diamond \leqslant 1$ exists (i.e. if conditions in Lemma 6.2 are satisfied), then it is locally asymptotically stable and every solution of (6.1) with $f_1(0) > 0$ and $f_2(0) > 0$ converges to this equilibrium.*

Proof. The local stability follows from a standard linearized stability analysis in two dimensions. The convergence results follow from Lemma 6.3 and Lemma 6.4. □

We return to the full system (5.2) which, by (6.2), can be rewritten in this special case as

$$\begin{aligned} N' &= N\Big(\beta - \mu(N) - f_1\gamma_1 - f_2\gamma_2\Big),\\ f_1' &= f_1\Big((1 - f_1 - f_2)\sigma C + f_1\gamma_1 + f_2\gamma_2 - \hat{\gamma}_1\Big),\\ f_2' &= f_2\Big(f_1\gamma_1 + f_2\gamma_2 - \hat{\gamma}_2\Big). \end{aligned} \tag{6.12}$$

Corollary 6.6. *The unique coexistence equilibrium* (N^*, f_1^*, f_2^*) *of (5.2) with* $f_1^* > 0$, $f_2^* > 0$, $f_1^* + f_2^* \leqslant 1$, *and* $N^* > 0$ *exists if and only if* $q_2 p_2 \beta > \mu(0) + \alpha_2$ *and the unique equilibrium* $(f_1^\diamond, f_2^\diamond)$ *of (6.1) exists with* $f_j^\diamond > 0$ *and* $f_1^\diamond + f_2^\diamond \leqslant 1$. *Actually* $f_1^* = f_1^\diamond$ *and* $f_2^* = f_2^\diamond$.

If this equilibrium exists, every solution of (5.2) with $f_1(0) > 0$, $f_2(0) > 0$ *and* $N(0) > 0$ *converges to this equilibrium as* $t \to \infty$.

Proof. By (6.2) and Lemma 6.2, $q_2 p_2 \beta > \mu(0) + \alpha_2$ is equivalent to $\beta - \mu(0) - \hat{\gamma}_2 > 0$ and to

$$\beta - \mu(0) - f_1^\diamond \gamma_1 - f_2^\diamond \gamma_2 > 0 \tag{6.13}$$

which is a necessary and sufficient condition for the existence of a solution $N^* > 0$ to the equation

$$0 = \beta - \mu(N^*) - f_1^\diamond \gamma_1 - f_2^\diamond \gamma_2. \tag{6.14}$$

Cf. the first equation in (6.12). By Theorem 6.5, $f_1(t) \to f_1^\diamond$ and $f_2(t) \to f_2^\diamond$. By (6.13) there exist $T \geqslant 0$ and $\varepsilon > 0$ such that $\beta - \mu(0) - f_1(t)\gamma_1 - f_2(t)\gamma_2 \geqslant \varepsilon$ for $t \geqslant T$. Since μ is continuous, there is $\delta > 0$ such that $\beta - \mu(x) - f_1(t)\gamma_1 - f_2(t)\gamma_2 \geqslant \varepsilon/2 > 0$ for $x \in [0, \delta]$ and $t \geqslant T$. Since $N' = N\big(\beta - \mu(N) - f_1\gamma_1 - f_2\gamma_2\big)$ and since $N(t) > 0$ for all t, we must have $N_\infty \geqslant \delta > 0$.

By the fluctuation method [4] [11, Prop.A.22] and (6.7) and (6.2), we have

$$\begin{aligned} 0 =& N^\infty \Big(\beta - \mu(N^\infty) - f_1^\diamond \gamma_1 - f_2^\diamond \gamma_2\Big) \\ =& N_\infty \Big(\beta - \mu(N_\infty) - f_1^\diamond \gamma_1 - f_2^\diamond \gamma_2\Big). \end{aligned}$$

Since $N^\infty \geqslant N_\infty > 0$, (6.14) holds for both N^∞ and N_∞ in place of N^*. Since N^* is the unique solution of (6.14), we have $N^\infty = N_\infty = N^*$ which implies that $N(t) \to N^*$ as $t \to \infty$. □

Corollary 6.7. *If* $q_2 p_2 \beta \leqslant \mu(0) + \alpha_2$ *and the equilibrium* $(f_1^\diamond, f_2^\diamond)$ *of (6.1) with* $f_1^\diamond > 0$, $f_2^\diamond > 0$ *and* $f_1^\diamond + f_2^\diamond \leqslant 1$ *exists, then every solution of (5.2) with* $f_1(0) > 0$, $f_2(0) > 0$ *and* $N(0) \geqslant 0$ *satisfies* $N(t) \to 0$, $f_1(t) \to f_1^\diamond$, $f_2(t) \to f_2^\diamond$ *as* $t \to \infty$.

Proof. Let $f_1(t), f_2(t), N(t)$ be the solution with $f_1(0) > 0$, $f_2(0) > 0$ and $N(0) \geqslant 0$. From Theorem 6.5 we have $(f_1, f_2) \to (f_1^\diamond, f_2^\diamond)$. By Lemma 6.2, we have $f_1^\diamond \gamma_1 + f_2^\diamond \gamma_2 = \hat{\gamma}_2$. By the fluctuation method [4] [11, Prop.A.22], we have from Lemma 6.2 and (6.2)

$$\begin{aligned} 0 &= N^\infty \Big(\beta - \mu(N^\infty) - f_1^\diamond \gamma_1 - f_2^\diamond \gamma_2\Big) = N^\infty \Big(\beta - \mu(N^\infty) - \hat{\gamma}_2\Big) \\ &= N^\infty \Big(-\mu(N^\infty) + q_2 p_2 \beta - \alpha_2\Big). \end{aligned}$$

Since μ is strictly increasing, we have $q_2 p_2 \beta - \mu(x) - \alpha < 0$ for $x > 0$. Hence $N^\infty = 0$ and so $N(t) \to 0$. $\square$

7 Uniform strong coexistence

This section is devoted to the proof that the HT and VT strain and the host uniformly coexist, whenever the coexistence equilibrium exists.

By assumption we always have three equilibria: the origin $(0, 0, 0)$, $(K, 0, 0)$ and the coexistence equilibrium (N^*, f_1^*, f_2^*) where all components are positive.

Another possible equilibrium is $(N^\sharp, f_1^\sharp, 0)$ at which the host and the HT strain persist, i.e., the first two components are positive. This equilibrium corresponds to the equilibrium (N^*, f^*) for the one strain model considered in Section 2 and Section 3. The dynamics of the two-strain model on the invariant set $\{f_2 = 0\}$ are the same as the dynamics of the one-strain model.

If $C(0) > 0$, there are two more possible boundary equilibria: $(0, f_1^{\#}, 0)$ and $(0, f_1^\diamond, f_2^\diamond)$. We will use the results of Section 6 for the invariant set $\{N = 0\}$. The parameters γ_j and $\hat{\gamma}_j$, β and C in Section 6 must then be understood as being evaluated at $N = 0$, and the equilibrium coordinates $f_1^{\#}$ and $f_1^\diamond, f_2^\diamond$ in Section 6 are the same as in the boundary equilibria just mentioned. The dynamics of the host-parasite model with two strains restricted to the invariant set $\{N = 0\}$ are the same as the dynamics of two dimensional model considered in Section 6 (with the exception of Corollary 6.6 and Corollary 6.7).

Let us summarize some previous results (Corollary 3.4, Theorem 3.2 Theorem 3.5). Consult Definition A.5.

Lemma 7.1. (a) *Solutions with* $N(0) > 0, f_1(0) = 0, f_2(0) \geq 0$ *converge to* $(K, 0, 0)$. $(K, 0, 0)$ *is locally asymptotically stable for* $\{f_1 = 0\}$.

(b) *There exists at most one equilibrium* $(N^\sharp, f^\sharp, 0)$ *with* $N^\sharp, f^\sharp > 0$. *If it exists, it attracts all solutions with* $N(0) > 0, f_1(0) > 0, f_2(0) = 0$ *and is locally asymptotically stable for* $\{f_2 = 0\}$.

(c) *There exists at most one equilibrium* $(0, f_1^\diamond, f_2^\diamond)$ *with* $f_j^\diamond > 0$. *If it exists, it attracts all solutions with* $N(0) = 0$, $f_1(0) > 0$, $f_2(0) > 0$ *and is locally asymptotically stable for* $\{N = 0\}$.

(d) *There exists at most one equilibrium* $(0, f_1^{\#}, 0)$ *with* $f_1^{\#} > 0$. *If it exists, it attracts all solutions with* $N(0) = 0 = f_2(0)$ *and* $f_1(0) > 0$.

If it exists and $(N^\sharp, f_1^\sharp, 0)$ *does not exist, it attracts all solutions with* $f_2(0) = 0$ *and* $f_1(0) > 0$ *and is locally asymptotically stable for* $\{f_2 = 0\}$.

If it exists and $(0, f_1^\diamond, f_2^\diamond)$ *does not exist, then it attracts all solutions with* $N(0) = 0$ *and* $f_1(0) > 0$ *and is locally asymptotically stable for* $\{N = 0\}$.

The last statement can be derived from the Poincaré-Bendixson theory and a standard linearized stability analysis in the plane. For the next results consult Definition A.1.

Lemma 7.2. *For the purpose of this lemma, let* $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \leq 1\}$. *If* (N^*, f_1^*, f_2^*) *exists, then:*

(a) $(K, 0, 0)$ *is a uniform weak repeller for* $X \cap \{f_1 > 0\}$. $(0, 0, 0)$ *is a uniform weak repeller for* $X \cap \{N > 0\}$,

(b) *Let* $(N^\sharp, f_1^\sharp, 0)$ *exists. Then it is a uniform weak repeller for* $X \cap \{f_2 > 0\}$.

(c) *Let* $(0, f_1^{\#}, 0)$ *exist. Then* $(0, 0, 0)$ *is a uniform weak repeller for* $X \cap \{f_1 > 0\}$. *If* $(0, f_1^\diamond, f_2^\diamond)$ *does not exist,* $(0, f_1^{\#}, 0)$ *is also a uniform weak repeller for* $X \cap \{N > 0\}$.

(d) *If* $(0, f_1^\diamond, f_2^\diamond)$ *exists, it is a uniform weak repeller for* $X \cap \{N > 0\}$ *and* $(0, f_1^{\#}, 0)$ *is a uniform weak repeller for* $X \cap \{f_2 > 0\}$.

Proof. The system (5.2) has the form in Lemma A.7 with $x = (N, f_1, f_2)$.

(a) As mentioned in Remark 5.2, the existence of the coexistence equilibrium implies that

$$g_2(K, 0, 0) = \sigma C(K) - (1 - q_1 p_1)\beta(K) - \alpha_1 > 0.$$

By Lemma A.7, $(K, 0, 0)$ is a uniform weak repeller for $X \cap \{x_2 > 0\} = X \cap \{f_1 > 0\}$.

Let us turn to (0,0,0). By assumption, $g_1(0, 0, 0) = \beta(0) - \mu(0) > 0$. By Lemma A.7, $(0, 0, 0)$ is a uniform weak repeller for $X \cap \{x_1 > 0\} = X \cap \{N > 0\}$.

(b) As mentioned in Remark 5.2, $N^\sharp < N^*$. Since N^* satisfies $q_2 p_2 \beta(N^*) - \mu(N^*) - \alpha_2 = 0$, this implies

$$q_2 p_2 \beta^\sharp - \mu^\sharp - \alpha_2 > 0,$$

where $\beta^\sharp = \beta(N^\sharp)$ and $\mu^\sharp = \mu(N^\sharp)$. Then

$$\begin{aligned} g_3(N^\sharp, f_1^\sharp, 0) &= -\,(1 - q_2 p_2)\beta^\sharp - \alpha_2 + f_1^\sharp((1 - q_1)\beta^\sharp + \alpha_1) \\ &> -\,\beta^\sharp + \mu^\sharp + f_1^\sharp((1 - q_1)\beta^\sharp + \alpha_1) = 0, \end{aligned}$$

with the last equality following from the first equation in (5.2) which is evaluated for $N = N^\sharp$ and $f_1 = f_1^\sharp$, $f_2 = 0$. By Lemma A.7, $(N^\sharp, f_1^\sharp, 0)$ is a uniform weak repeller for $X \cap \{x_3 > 0\} = X \cap \{f_2 > 0\}$.

(c) Since $(0, f_1^{\#}, 0)$ exists, $\sigma C(0) - \hat{\gamma}_1 > 0$ by Lemma 6.1. By the second equation in (5.2),

$$g_2(0,0,0) = \sigma C(0) - \hat{\gamma}_1 > 0.$$

By Lemma A.7, $(0,0,0)$ is a uniform weak repeller for $X \cap \{x_2 > 0\} = X \cap \{f_1 > 0\}$.

If $(0, f_1^\diamond, f_2^\diamond)$ does not exist, then $f_1^{\#}\gamma_1 \le \hat{\gamma}_2$ by Lemma 6.2. Since the coexistence equilibrium exists,$\mathcal{R}_2(0) > 1$ and $q_2p_2\beta(0) - \mu(0) - \alpha_2 > 0$ by Theorem 5.1. Then

$$\begin{aligned} g_1(0, f_1^{\#}, 0) =& \beta(0) + \mu(0) - f_1^{\#}\gamma_1 \ge \beta(0) - \mu(0) - \hat{\gamma}_2 \\ =& q_2p_2\beta(0) - \mu(0) - \alpha_2 > 0. \end{aligned}$$

By Lemma A.7, $(0, f_1^{\#}, 0)$ is a uniform weak repeller for $X \cap \{x_1 > 0\} = X \cap \{N > 0\}$.

(d) In this case, $\sigma C(0) > \hat{\gamma}_1$ and $f_1^{\#}\gamma_1 > \hat{\gamma}_2$. Then

$$g_3(0, f_1^{\#}, 0) = -(1 - q_2p_2)\beta(0) - \alpha_2 + f_1^{\#}\gamma_1 = -\hat{\gamma}_2 + f_1^{\#}\gamma_1 > 0.$$

By Lemma A.7, $(0, f_1^{\#}, 0)$ is a uniform weak repeller for $X \cap \{x_3 > 0\} = X \cap \{f_2 > 0\}$. Further

$$g_1(0, f_1^\diamond, f_2^\diamond) = \beta(0) - \mu(0) - \sum_{k=1}^{2} f_k^\diamond((1 - q_k)\beta(0) + \alpha_k).$$

Since $N = 0$, $f_j = f_j^\diamond$ solve the third equation in (5.2),

$$g_1(0, f_1^\diamond, f_2^\diamond) = q_2p_2\beta(0) - \mu(0) - \alpha_2 > 0$$

by Theorem 5.1 (a). By Lemma A.7, $(0, f_1^\diamond, f_2^\diamond)$ is a uniform weak repeller for $X \cap \{x_1 > 0\} = X \cap \{N > 0\}$. ☐

Proposition 7.3. *If* $(0, f_1^{\#}, 0)$ *does not exist, there is some* $\varepsilon > 0$ *such that*

(i) $\liminf_{t\to\infty} N(t) \ge \varepsilon$ *for all solutions with* $N(0) > 0$.

(ii) $\liminf_{t\to\infty} f_1(t) \ge \varepsilon$ *for all solutions with* $N(0) > 0$, $f_1(0) > 0$.

(iii) $\liminf_{t\to\infty} f_2(t) \ge \varepsilon$ *for all solutions with* $N(0) > 0$,$f_1(0) > 0$, $f_2(0) > 0$.

Proof. Assume that $(0, f_1^{\#}, 0)$ does not exist. By Lemma 6.1, $\sigma C(0) \le (1 - q_1p_1)\beta(0) + \alpha_1$ and (i) follows from Theorem 4.4 with $\sigma_2 = 0$.

For (ii), we choose the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \le 1; N > 0\}$. By (i) and Theorem 4.1, all solutions in X are absorbed in a compact set which is contained in X. We split $X = X_1 \uplus X_2$ with $X_1 = X \cap \{f_1 > 0\}$ and $X_2 = X \cap \{f_1 = 0\}$. The only equilibrium contained in X_2 is $(K, 0, 0)$. $(K, 0, 0)$ is globally stable for X_2 by Lemma 7.1 (a) and a uniform weak repeller for X_1 by Lemma 7.2 (a). By Proposition A.6, it forms an isolated invariant set for X which is trivially acyclic. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies (ii).

For (iii), we choose the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \leq 1; N > 0, f_1 > 0\}$. By (i) and (ii) and Theorem 4.1, all solutions in X tend to a compact set which is contained in X. We split $X = X_1 \uplus X_2$ with $X_1 = X \cap \{f_2 > 0\}$ and $X_2 = X \cap \{f_2 = 0\}$. It follows from (i) and (ii) and [13, Thm.1.3.7] that the equilibrium $(N^\sharp, f_1^\sharp, 0)$ exists. It is the only equilibrium contained in X_2 and is globally asymptotically stable for X_2 by Lemma 7.1 (b). By Lemma 7.2 (b), it is a uniform weak repeller for X_1 and so forms an isolated invariant set by Proposition A.6 which is trivially acyclic. By Theorem A.4, X_2 is a uniform strong repeller for X_1 which implies (iii).

$\square$

Proposition 7.4. *If* $(0, f_1^{\#}, 0)$ *exists, there is some* $\varepsilon > 0$ *such that* $\liminf_{t\to\infty} f_1(t) \geq \varepsilon$ *for all solutions with* $f_1(0) > 0$.

Proof. We split up the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+, f_1 + f_2 \leq 0\}$ as $X = X_1 \uplus X_2$ with $X_1 = \{(N, f_1, f_2) \in X; f_1 > 0\}$ and $X_2 = \{(N, f_1, f_2) \in X; f_1 = 0\}$. By Theorem 4.1, all solutions in X tend to the compact set $X \cap \{N \leq K\}$. X_2 only contains the equilibria $(0, 0, 0)$ and $(K, 0, 0)$. By Lemma 7.1 (a), all solutions in X_2 with $N(0) > 0$ converge towards $(K, 0, 0)$ and $(K, 0, 0)$ is locally asymptotically stable for X_2. By Lemma 7.2 (a), $(K, 0, 0)$ is a uniform weak repeller for X_1 and thus an isolated invariant set for X by Proposition A.6. One readily checks that all solutions in X_2 with $N(0) = 0$ converge to (0,0,0), and (0,0,0) is locally asymptotically stable for $X_2 \cap \{N = 0\}$. By Lemma 7.2 (a), $(0, 0, 0)$ is a uniform weak repeller for $\{N > 0\}$. Under the assumptions of this proposition, it is also a uniform weak repeller for $\{f_1 > 0\}$ by Lemma 7.2 (c). So $\{(0, 0, 0)\}$ is an isolated invariant set for X by Proposition A.6. Obviously $M = \{(0, 0, 0), (K, 0, 0)\}$ is acyclic. By Theorem A.4, X_2 is a uniform strong repeller for X_1 which implies the statement.

$\square$

Proposition 7.5. *If* $(0, f_1^{\#}, 0)$ *exists, but not* $(0, f_1^{\diamond}, f_2^{\diamond})$*, then there is some* $\varepsilon > 0$ *such that*

(i) $\liminf_{t\to\infty} f_1(t) \geq \varepsilon$ *for all solutions with* $f_1(0) > 0$,

(ii) $\liminf_{t\to\infty} N(t) \geq \varepsilon$ *for all solutions with* $f_1(0) > 0$, $N(0) > 0$,

(iii) $\liminf_{t\to\infty} f_2(t) \ge \varepsilon$ *for all solutions with* $f_1(0) > 0$, $N(0) > 0$, $f_2(0) > 0$.

Proof. (i) follows from Proposition 7.4. For (ii), we take the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \le 1, f_1 > 0\}$. By Proposition 7.4 and Theorem 4.1, X contains a compact set to which all solutions in X tend. We split up $X = X_1 \uplus X_2$ with $X_1 = \{(N, f_1, f_2) \in X; N > 0\}$ and $X_2 = \{(N, f_1, f_2) \in X; N = 0\}$. All solutions in X_2 converge to $(0, f_1^{\#}, 0)$ and $(0, f_1^{\#}, 0)$ is locally asymptotically stable for $\{N = 0\}$. Since $(0, f_1^\diamond, f_2^\diamond)$ does not exist, $(0, f_1^{\#}, 0)$ is a uniform weak repeller for $\{N > 0\}$ and in particular for X_1 by Lemma 7.2 (c). By Proposition A.6, $\{(0, f_1^{\#}, 0)\}$ is an isolated invariant set and obviously acyclic. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies assertion (ii).

For (iii), we take the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \le 1, N > 0, f_1 > 0\}$. We split up $X = X_1 \uplus X_2$ with $X_1 = \{(N, f_1, f_2) \in X; f_2 > 0\}$ and $X_2 = \{(N, f_1, f_2) \in X; f_2 = 0\}$. By (i) and (ii) and Theorem 4.1, all solutions in X tend to a compact set contained in X. X_2 contains the equilibrium $(N^\sharp, f_1^\sharp, 0)$ which exists by (ii) and [13, Thm.1.3.7] and is globally asymptotically stable for X_2. By Lemma 7.2 (b), $(N^\sharp, f_1^\sharp, 0)$ is a uniform weak repeller for X_1 and so an isolated invariant set for X. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies the assertion. □

Proposition 7.6. *Assume that the equilibria* $(0, f_1^{\#}, 0)$ *and* $(0, f_1^\diamond, f_2^\diamond)$ *exist, but not* $(N^\sharp, f_1^\sharp, 0)$. *Then there exists some* $\varepsilon > 0$ *such that*

(i) $\liminf_{t\to\infty} f_1(t) \ge \varepsilon$ *for all solutions with* $f_1(0) > 0$,

(ii) $\liminf_{t\to\infty} f_2(t) \ge \varepsilon$ *for all solutions with* $f_1(0) > 0$, $f_2(0) > 0$.

(iii) $\liminf_{t\to\infty} N(t) \ge \varepsilon$ *for all solutions with* $f_1(0) > 0$, $f_2(0) > 0$, $N(0) > 0$,

Proof. (i) follows from Proposition 7.4. For (ii), we take the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \le 1, f_1 > 0\}$. By Proposition 7.4 and Theorem 4.1, all solutions in X converge to a compact set which is contained in X. We split $X = X_1 \uplus X_2$ with $X_1 = X \cap \{f_2 > 0\}$ and $X_2 = X \cap \{f_2 = 0\}$. Since $(N^\sharp, f_1^\sharp, 0)$ does not exist, $(0, f^{\#}, 0)$ is globally asymptotically stable for X_2 by Lemma 7.1 (d). By Lemma 7.2 (d), it is a uniform weak repeller for X_2 and so forms an isolated invariant set for X. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies (ii).

For (iii), we choose the state space $X = \{(N, f_1, f_2) \in \mathbb{R}^3_+; f_1 + f_2 \le 1, f_1 > 0, f_2 > 0$. By (ii) and Theorem 4.1, all solutions in X tend to a compact set which is contained in X. We split $X = X_1 \uplus X_2$ with

$X_1 = X \cap \{N > 0\}$ and $X_2 = X \cap \{N = 0\}$. By Lemma 7.1 (c), $(0, f_1^\diamond, f_2^\diamond)$ is globally asymptotically stable for X_2. By Lemma 7.2 (d), it is a uniform weak repeller for X_1 and so forms an isolated invariant set by Proposition A.6. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies (iii).

□

Proposition 7.7. *Assume that* $(0, f_1^{\#}, 0)$, $(0, f_1^\diamond, f_2^\diamond)$ *and* $(N^\sharp, f_1^\sharp, 0)$ *exist. Then there exists some* $\varepsilon > 0$ *such that*

(i) $\liminf_{t\to\infty} f_1(t) \geq \varepsilon$ *for all solutions with* $f_1(0) > 0$,

(ii) $\liminf_{t\to\infty} N(t) \geq \varepsilon$ *and* $\liminf_{t\to\infty} f_2(t) \geq \varepsilon$ *for all solutions with* $f_1(0) > 0$, $f_2(0) > 0$ *and* $N(0) > 0$,

Proof. (i) follows from Proposition 7.4. For (ii), we take the state space $X = \{(N, f_1, f_2) \in \mathbb{R}_+^3; f_1 + f_2 \leq 1, f_1 > 0\}$. By Proposition 7.4, all solutions in X converge to a compact set which is contained in X. We split $X = X_1 \uplus X_2$ with $X_1 = X \cap \{N > 0, f_2 > 0\}$ and $X_2 = X \cap \{N = 0 \text{ or } f_2 = 0\}$. By Lemma 7.1, $(0, f_1^\diamond, f_2^\diamond)$ is globally asymptotically stable for $X \cap \{N = 0, f_2 > 0\}$, $(N^\sharp, f_1^\sharp, 0)$ is globally asymptotically stable for $X \cap \{N > 0, f_2 = 0\}$ and $(0, f_1^{\#}, 0)$ is globally asymptotically stable for $X \cap \{N = 0, f_2 = 0\}$. This implies that $(0, f_1^{\#}, 0)$ is a uniform weak repeller for $\{N > 0\}$ and $\{f_2 > 0\}$ and thus an isolated invariant set for X. By Lemma 7.2 (d), $(0, f_1^\diamond, f_2^\diamond)$ is a uniform weak repeller for $\{N > 0\}$ and forms an isolated invariant set for X. $(N^\sharp, f_1^\sharp, 0)$ is locally asymptotically stable for $X \cap \{f_2 = 0\}$ by Lemma 7.1 (b) and a uniform weak repeller for $X \cap \{f_2 > 0\}$ by Lemma 7.2 (b). By Proposition A.6, it forms an isolated invariant set for X. The set M consisting of these three equilibria is acyclic in X_2 as one can see from the dynamics described before. By Theorem A.4, X_2 is a uniform strong repeller for X_1. This implies (ii). □

A Elements of persistence theory

Let $F : \mathbb{R}_+^n \to \mathbb{R}^n$ be locally Lipschitz and consider the ODE system $x' = F(x)$. A set $X \subset \mathbb{R}_+^n$ is called *forward invariant*, if all solutions with $x(0) \in X$ are defined for all $t \geq 0$ and $x(t) \in X$ for all $t \geq 0$. X is called *invariant*, if all solutions with $x(0) \in X$ are defined for all $t \in \mathbb{R}$ and $x(t) \in X$ for all $t \in \mathbb{R}$.

The distance from a point x to a set Y is given by $d(x, Y) = \inf\{\|x - y\|; y \in Y\}$.

Definition A.1. We assume that X is a forward invariant subset of $\mathbb{R}^n_+$, $X = X_1 \cup X_2$, $X_1 \cap X_2 = \emptyset$, with X_2 being a relatively closed subset of X and X_1 forward invariant. Let $Y_2 \subseteq X_2$.

Y_2 is called a *uniform weak repeller* for X_1 if there exists some $\delta > 0$ such that

$$\limsup_{t\to\infty} d(x(t), Y_2)) \geq \delta$$

for all solutions $x(t)$ with $x(0) \in X_1$.

Y_2 is called a *uniform strong repeller* for X_1 if there exists some $\delta > 0$ such that

$$\liminf_{t\to\infty} d(x(t), Y_2)) \geq \delta$$

for all solutions $x(t)$ with $x(0) \in X_1$.

Definition A.2. We assume that X is a forward invariant subset of $\mathbb{R}^n_+$, and $Z \subseteq X$ an invariant set. Then Z is called an *isolated invariant set* in X if there exists some open subset U of $\mathbb{R}^n$ such that $U \cap X$ contains no invariant subset other than Z.

Definition A.3. Let $Y \subseteq \mathbb{R}^n_+$. An equilibrium $x^* \in Y$ is called *chained in* Y to an equilibrium y^* in Y, $x^* \overset{Y}{\mapsto} y^*$, if there exists a solution $x' = F(x)$ which is defined for all $t \in \mathbb{R}$ and takes all its values in Y such that $x(t) \to x^*$ as $t \to -\infty$ and $x(t) \to y^*$ as $t \to \infty$ and there exists some $t \in \mathbb{R}$ such that $x(t) \neq x^*$ and $x(t) \neq y^*$.

A set M of equilibria in Y is called *cyclic in* Y if there exists some $x^* \in M$ with $x^* \overset{Y}{\mapsto} x^*$ or if there exist $x_1^*, \dots, x_k^*$ in M such that $x_1^* \overset{Y}{\mapsto} x_2^* \overset{Y}{\mapsto} \cdots \overset{Y}{\mapsto} x_k^* \overset{Y}{\mapsto} x_1^*$, and acyclic in Y if it is not cyclic in Y.

The following result is a special case of [10, Thm. 4.6].

Theorem A.4. *Let $F : \mathbb{R}^n_+ \to \mathbb{R}^n$ be locally Lipschitz continuous, $X \subseteq \mathbb{R}^n_+$. Assume that X is forward invariant for $x' = F(x)$. Let $X = X_1 \cup X_2$, $X_1 \cap X_2 = \emptyset$, with X_2 being a relatively closed subset of X and X_1 forward invariant.*

Assume that there exists a compact set C in $\mathbb{R}^n$, $C \subseteq X$, to which every solution of $x' = F(x)$ in X tends: $d(x(t), C) \to 0$ as $t \to \infty$.

Let M be a finite set of equilibria in X_2. Assume that every solution that starts in X_2 and stays in X_2 for all forward times converges to one of the equilibria in M. Assume that every equilibrium in M forms an isolated invariant set in X and is a weak repeller for X_1 and that M is acyclic in X_2.

Then X_2 is a uniform strong repeller for X_1.

We present a condition for a set to be an isolated invariant set.

Definition A.5. Let $x^* \in Y \subseteq \mathbb{R}^n_+$ be an equilibrium, $F(x^*) = 0$.

Then x^* is called *locally stable for* Y if the following holds:

(i) For every $\varepsilon > 0$ there exists some $\delta > 0$ with the following property: If $x : \mathbb{R}_+ \to Y$ is a solution of $x' = F(x)$, defined for all $t \geq 0$ with values in Y, and $\|x(0) - x^*\| < \delta$, then $\|x(t) - x^*\| < \varepsilon$ for all $t \geq 0$.

x^* is called *locally asymptotically stable for* Y if is is locally stable and

(ii) There exists some $\delta_0 > 0$ with the following property: If $x : \mathbb{R}_+ \to Y$ is a solution of $x' = F(x)$, defined for all $t \geq 0$ with values in Y, and $\|x(0) - x^*\| < \delta_0$, then $x(t) \to x^*$ for $t \to \infty$.

x^* is called *globally asymptotically stable for* Y if is is locally stable and

(iii) $x(t) \to x^*$ for $t \to \infty$ for all solutions $x : \mathbb{R}_+ \to Y$ of $x' = F(x)$, defined for all $t \geq 0$ with values in Y.

Proposition A.6. *Let* $F : \mathbb{R}^n_+ \to \mathbb{R}^n$ *be locally Lipschitz and* $X \subseteq \mathbb{R}^n_+$ *be forward invariant for the solutions of* $x' = F(x)$*. Assume that* $X = Y_1 \uplus Y_2$ *where* Y_1 *is also forward invariant and* X *and* Y_2 *are closed. Let* $x^* \in Y_2$ *be an equilibrium,* $F(x^*) = 0$*.*

Assume that $\{x^*\}$ *is a uniform weak repeller for* Y_1 *and* x^* *locally asymptotically stable for* Y_2*. Then* $\{x^*\}$ *is an isolated invariant set for* X*.*

Proof. Let $\delta_1 > 0$ be such that $\limsup_{t\to\infty} \|x(t) - x^*\| > \delta_1$ for all solutions $x : \mathbb{R}_+ \to Y_1$. Let $\delta_2 > 0$ be such that $\lim_{t\to\infty} x(t) = x^*$ for all solutions $x : \mathbb{R}_+ \to Y_2$ with $\|x(0) - x^*\| < \delta_2$. Let $\delta = \frac{1}{2}\min(\delta_1, \delta_2)$. Let $M \subset X \cap \overline{B_\delta(x^*)}$ be an invariant set. We have $M \cap Y_1 = \varnothing$ because if $x_0 \in M \cap Y_1$ and $x : \mathbb{R}_+ \to Y_1$ is the solution with $x(0) = x_0$, then there is $t \in \mathbb{R}_+$ such that $\|x(t) - x^*\| > \delta_1 > \delta$, and so $x(t) \notin M$, contradicting the invariance of M. Hence $M \subset Y_2 \cap \overline{B_\delta(x^*)}$.

Now suppose (to get a contradiction) that we can pick $z_0 \in M \subseteq Y_2$, $z_0 \neq x^*$. Let $z : \mathbb{R} \to M$ be the solution (defined on all $\mathbb{R}$) with $z(0) = z_0$. We have $z(t) \in Y_2$ for all $t \in \mathbb{R}$ because if there is $t' \in \mathbb{R}$ such that $z(t') \in Y_1$, then there is $t'' > t'$ with $\|z(t'') - x^*\| > \delta_1 > \delta$, again contradicting the invariance of M. Let $\varepsilon = \frac{1}{2}\|z(0) - x^*\|$ and choose $\delta' > 0$ such that $\|x(t) - x^*\| < \varepsilon$ for every solution $x : \mathbb{R}_+ \to Y_2$ with $\|x(0) - x^*\| < \delta'$.

Since $M \subset \overline{B_\delta(x^*)}$ and $\overline{B_\delta(x^*)}$ is compact, the α-limit set of z, $\alpha(z)$, is not empty and we have $\alpha(z) \subset \overline{M \cap Y_2} \subset X \cap \overline{B_\delta(x^*)}$. Since Y_2 is closed, $\alpha(z) \subset Y_2 \cap \overline{B_\delta(x^*)}$.

Now pick $x_0 \in \alpha(z) \subset Y_2 \cap \overline{B_\delta(x^*)}$ and let $x : \mathbb{R}_+ \to \alpha(z)$ be the solution with $x(0) = x_0$. Then $\lim_{t\to\infty} x(t) = x^*$, and since $\alpha(z)$ is closed, we have $x^* \in \alpha(z)$. Therefore there exists $\bar{t} < 0$ such that $\|z(\bar{t}) - x^*\| < \delta'$. But then we must have $\|z(0) - x^*\| < \varepsilon = \frac{1}{2}\|z(0) - x^*\|$, so we get a contradiction. Therefore $M = \{x^*\}$. □

The following easy lemma will be used again and again to show that a point is uniform weak repeller.

Lemma A.7. *Let $g_j : \mathbb{R}^m_+ \to \mathbb{R}$ be continuous, $j = 1, \ldots, m$. Consider the system of differential equations $x_j' = x_j g_j(x)$, $j = 1, \ldots, m$, $x(t) = (x_1(t), \ldots x_m(t))$. Let $X \subseteq \mathbb{R}^m_+$ be forward invariant. Let $\tilde{x} \in X$, $j \in \{1, \ldots, m\}$, $\tilde{x}_j = 0$, and $g_j(\tilde{x}) > 0$. Then $\tilde{x}$ is a uniform weak repeller for $X \cap \{x_j > 0\}$.*

Proof. Set $\varepsilon = g_j(\tilde{x})/2$. By continuity, choose $\delta > 0$ such that $|g_j(x) - g_j(\tilde{x})| < \varepsilon$ whenever $|x - \tilde{x}| < \delta$. So $g_j(x) \geq \varepsilon$ whenever $|x - \tilde{x}| < \delta$. Suppose that $\tilde{x}$ is not a uniform weak repeller for $X \cap \{x_j > 0\}$. Then there exist a solution with $x_j(t) > 0$ for all $t \geq 0$ and $\limsup_{t\to\infty} |x(t) - \tilde{x}| < \delta$. Then

$$\liminf_{t\to\infty} \frac{x_j'(t)}{x_j(t)} \geq \liminf_{t\to\infty} g_j(x(t)) \geq \varepsilon > 0.$$

This implies $x_j(t) \to \infty$ as $j \to \infty$, a contradiction. □

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