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*Research article*

## **Can infectious diseases eradicate host species? The effect of infection-age structure**

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**Abstract:** It is a fundamental question in mathematical epidemiology whether deadly infectious diseases only lead to a mere decline of their host populations or whether they can cause their complete disappearance. Upper density-dependent incidences do not lead to host extinction in simple, deterministic SI or SIS (susceptible-infectious) epidemic models. Infection-age structure is introduced into SIS models because of the biological accuracy offered by considering arbitrarily distributed infectious periods. In an SIS model with infection-age structure, survival of the susceptible host population is established for incidences that depend on the infection-age density in a general way. This confirms previous host persistence results without infection-age for incidence functions that are not generalizations of frequency-dependent transmission. For certain power incidences, hosts persist if some infected individuals leave the infected class and become susceptible again and the return rate dominates the infection-age dependent infectivity in a sufficient way. The hosts may be driven into extinction by the infectious disease if there is no return into the susceptible class at all.

**Keywords:** Host persistence; Host extinction; Uniform weak persistence; Incidence function; Kermack; McKendrick; A priori estimates; Integral equations; Volterra functional equations; Laplace transform

**Dedicated to Stephan Luckhaus on the occasion of his 70th birthday.**

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### **1. Introduction**

It is a fundamental question in mathematical epidemiology whether deadly infectious diseases only lead to a mere decline of their host populations or whether they can also cause their complete disappearance. This question has become particularly relevant for the possible role of infectious diseases in amphibian decline and disappearance (see [1, 2] and the references therein).

Deterministic mathematical models have shown the importance of how the disease incidence, the

rate of new infections, denoted by  $f(S, I)$ , depends on the numbers of susceptible,  $S$ , and infected individuals,  $I$ . The function  $f$  is called the *incidence function*.

### 1.1. Density and frequency dependent incidence

Density dependent (or mass action) incidence  $f(S, I) = SI$  typically does not lead to host extinction [3, 4] unless there is a reservoir for the disease [5–7] or the population is subject to an Allee effect [8–10].

Frequency dependent incidence is of the form  $f(S, I) = \frac{SI}{N}$ , where  $N$  is the total population size, and  $f(S, I) = \frac{SI}{S+I}$  if the population only consists of susceptible and infective individuals (i.e. the model is of SI or SIS type). Infectious disease models with frequency-dependent (or standard) incidence are mathematically known to show both decline and disappearance of the host in different parameter regions, [4, 11–21], and [22, Sec.4.4]. However, empirical evidence of a species or population eliminated by frequency-dependent parasites seems elusive [23, 24].

Many more incidence forms have been suggested, and many of those, though not all, have been fitted to the infection experiments involving tiger salamander larvae and ranavirus in [25]. See also [1]. Both density- and frequency-dependent incidence do not fare well in these fits.

In [1] and [26], epidemic models are considered that consist of two ordinary differential equations for the densities of susceptible and infective hosts; they have general incidence functions and rather general host population dynamics. In [1], all infective hosts die from the disease (unless they die from natural causes first), while in [26] some infective hosts recover from the disease and become susceptible again.

Two types of incidence functions were identified:

- Incidence functions that are *mildly upper density-dependent*,

$$\begin{aligned} f(0, I) = 0 = f(S, 0), \quad S, I \geq 0, \\ \frac{f(S, I)}{S + I} \rightarrow 0, \quad S, I \geq 0, \quad 0 < S + I \rightarrow 0, \end{aligned} \quad (1.1)$$

(i.e.,  $f$  is differentiable at  $(0, 0)$  with zero derivative).

- Incidence functions that are *positively homogeneous of degree one*.

An incidence function  $f$  is *positively homogeneous of degree*  $\zeta > 0$  [27, Sec.6.53] if

$$f(rS, rI) = r^\zeta f(S, I), \quad S, I, r \geq 0. \quad (1.2)$$

The density-dependent incidence  $f(S, I) = SI$  is mildly upper density-dependent, while the frequency-dependent incidence  $f(S, I) = \frac{SI}{S+I}$  is homogeneous of degree one.

In these ODE models, incidence functions that are *mildly upper density-dependent* lead to mere (though possibly substantial) host decline (with one subtlety for certain power incidences), while incidence functions that are *positively homogeneous of degree one* can cause host extinction.

For power incidence functions  $f(S, I) = S^q I^p$  with  $p, q > 0$ ,  $q < 1 < q + p$  (which are mildly upper density-dependent), though, it makes a big difference whether or not infective individuals can become susceptible again. If the disease is universally fatal, there is always initial-value dependent extinction of both host and disease [1, Thm.5.8]. If infective individuals can become susceptible again, both host and disease always persist [26].

### 1.2. The case for infection-age

In these ODE models, infective individuals die or become susceptible again at constant per capita rates so that the sojourn of hosts in the infectious stage (which is influenced by the extra death rate due the disease and, possibly, by the return rate into the susceptible class) is exponentially distributed. It is long known that this is far from reality. Sardwell [28, 29], for instance, has fitted lognormal distributions to the length of incubation periods of various diseases. The distribution of the time from infection to disease death in infection experiments involving salamander larvae and ranavirus [25] looks very different from an exponential distribution [2]. A lognormal distribution fits better than a Gamma distribution which in turn fits better than a Weibull distribution. The case has been made that assuming exponential stage distributions rather than more realistic distributions can lead to wrong epidemiological conclusions [30].

We therefore will study whether the feature that mildly upper density-dependent incidence functions do not lead to host disappearance remains valid if the length of the infectious period has an arbitrary distribution. In other words, we will introduce infection-age structure into the model. Such model have already been considered by Kermack and McKendrick [31, 32] though they apparently did not use the term “infection-age” but talked about “the duration of the illness”. They also (as we will) let the infectivity of infective hosts depend on their infection-age (“The infectivity of the disease is a function of the period of illness”), which turned out to be an important feature of HIV infection [33].

Kermack and McKendrick [31, 32] even let the susceptibility of a recovered host be a “function of the period which has elapsed since the time of” recovery (of the recovery-age) which we will not assume. See [34, Sec.8.2] [35, 13.3] [36]). Infection-age and recovery-age are special cases of epidemiological class-age [37]. Covid-19 models with two or more infection-ages have been considered for households of two hosts [38] and for groups with successive multiple infections [39]. Class-age needs to be distinguished from chronological age, time since birth. While there can be good reason to consider both age types [34, Sec.6.5] [40, Sec.5.3.2], we will concentrate on infection-age in this paper. One reason is that, if both type of ages are considered, our message will drown in technicalities. Another is that chronological age may be epidemiologically less important for some animal populations (like ungulates affected by an infectious eye disease [41], see end of Section 1.6) than for human populations. For amphibian populations, different developmental stages would be more important [42].

Finally, let us mention that Kermack and McKendrick [31] did not only already consider epidemic outbreaks like in [43, 44] but also the “Problem of Endemicity” which in our model is caused by a per capita host growth rate.

### 1.3. The sojourn function

Let  $P(a)$  denote the probability that a previously infected host is still infected (i.e., has not died from the disease or from other causes and not returned into the susceptible stage) at infection age  $a$ , i.e.  $a$  time units after infection with the disease. Then the sojourn function  $P : \mathbb{R}_+ \rightarrow [0, 1]$  of the infected stage is decreasing,

$$P(0) = 1, \quad D(0) = \int_0^{\infty} P(a) da < \infty. \quad (1.3)$$

$D(0)$  is the expected duration of the infected stage. See [45, Chap.12] [2].

There are two cases:

**Table 1.** Parameters and model variables.

Symbol	Definition
$S(t)$	number of susceptible hosts at time $t$
$I(t)$	number of infected hosts at time $t$
$R(t)$	rate of infected hosts returning to the $S$ class at time $t$
$B(t)$	incidence, rate of new infections at time $t$
$J(t)$	infective impact at time $t$
$P(a)$	probability that an infectious host remains infected at infection-age $a$
$b$	maximal infection-age
$g(S)$	per capita growth rate of $S$ susceptible hosts
$f$	incidence function
$u(t, \cdot)$	infection-age density of infected hosts at time $t$
$\kappa(a)$	infectivity of an infected host at infection-age $a$
$\gamma(a)$	rate at which an infected individual leaves the infected stage at infection-age $a$
$\alpha(a)$	per capita rate at which an infected host ceases to be infected at infection-age $a$ and returns to the $S$ class
$\vartheta(a)$	is the per capita rate at which infected hosts die from the disease at infection-age $a$
$\nu$	per capita natural death rate
$K$	population's carrying capacity, $g(K) = 0$

- (i)  $P(a) > 0$  for all  $a \in \mathbb{R}_+$ .  
(ii) There is some  $b \in (0, \infty)$  (which is uniquely determined) such that  $P(a) > 0$  for  $a \in [0, b)$  and  $P(a) = 0$  for  $a \in [b, \infty)$ .

If  $b \in (0, \infty)$ ,  $b$  has the interpretation of the maximal infection age.

To consider both cases simultaneously, we allow  $b = \infty$ . If the duration of the infected stage is Gamma, lognormal or Weibull distributed,  $b = \infty$ . For numerical purposes, it may be convenient to assume  $b \in (0, \infty)$ .

#### 1.4. Infection-age stratification

Let  $I(t)$  denote the number of infected hosts at time  $t \geq 0$  where  $t = 0$  marks the start of the epidemic. If infection-age is considered,

$$I(t) = \int_0^b u(t, a) da, \quad t \geq 0, \quad (1.4)$$

where  $u(t, a)$ , as a function of  $a$ , is the infection-age density, loosely speaking the number of infected hosts at time  $t$  with infection-age  $a$ , i.e., those hosts that have been infected  $a$  time units ago.

The number of infected hosts needs to be distinguished from the *infective impact*,

$$J(t) = \int_0^b \kappa(a)u(t, a)da, \quad (1.5)$$

where  $\kappa(a)$  is the infectivity of an infected host with infection-age  $a$ , for instance the amount of infective particles that an infective host releases. Our notation follows [46, chap.9]. In [26],  $i$  has been used instead of  $u$  and  $W$  instead of  $J$ . In [2],  $I$  and  $J$  have been switched and  $j$  been used instead of  $u$ .

### 1.5. Infection-age stratified incidence

The incidence function  $f$  provides the functional relationship between the rate of new infections at time  $t$ ,  $B(t)$ , on the one hand and the number of susceptible hosts,  $S(t)$ , and the infection-age density of infected hosts,  $u(t, \cdot)$ , on the other hand,

$$B(t) = f(S(t), u(t, \cdot)). \quad (1.6)$$

Here,  $f : \mathbb{R}_+ \times L_+^1[0, b) \rightarrow \mathbb{R}_+$ .  $X = L^1[0, b)$  is the Banach space of Lebesgue integrable functions on  $[0, b)$  with values in  $[-\infty, \infty]$  (more precisely of the appropriate a.e. equivalence classes) and  $X_+ = L_+^1[0, b)$  is the cone of nonnegative functions in  $X$ . The norm on  $X$  is  $\|w\|_1 = \int_0^b |w(a)|da$ ,  $w \in X_+$ , which is the number of infected hosts if  $w \in X_+$ .

We assume that  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}$  is continuous, where the norm on  $\mathbb{R} \times X$  is  $\|(S, w)\| = |S| + \|w\|_1$ ,  $S \in \mathbb{R}_+$  and  $w \in X_+$ , which is the number of hosts.

If  $B$  is the disease incidence, the rate of new infections, and  $u_0 \in X_+$  is the density of infected host at time 0, we have the relation

$$u(t, a) = \begin{cases} B(t-a)P(a), & 0 \leq a < t \\ u_0(a-t)\frac{P(a)}{P(a-t)}, & 0 \leq t < a \end{cases} \quad t \geq 0, \quad a \in [0, b). \quad (1.7)$$

$\frac{P(a)}{P(a-t)}$  is the conditional probability to be still infected at infection age  $a$  provided one was already infected at infection-age  $a-t$ . See [45, Sec.13.1].

If  $B$  is continuous and  $u_0 \in X_+$ , then  $u(t, \cdot)$  is a continuous function of  $t$  with values in  $X_+$  [2] (Lemma 7.1).

The straightforward extension of the density-dependent incidence function to infection-age models is

$$f(S, w) = SJ, \quad J = \int_0^b \kappa(a)w(a)da, \quad S \in \mathbb{R}_+, w \in X_+, \quad (1.8)$$

with infective impact  $J$  and infection-age dependent per capita infectivity  $\kappa \in L_+^\infty[0, b)$ . Notice that if  $u(t, \cdot)$  is a continuous function of  $t$  with values in  $X_+$ , then the infective impact  $J(t) = \int_0^b \kappa(a)u(t, a)da$  is also a continuous function of  $t$ .

$L^\infty[0, b)$  is the Banach space of essentially bounded Borel measurable functions (more precisely, their equivalence classes) with the essential supremum norm  $\|w\|_\infty$ ,  $w \in L^\infty[0, b)$ .

Density-dependent incidence yields a very poor fit in [1,25,47]. Another possible incidence function is

$$f(S, w) = SJ / (1 + kI + \sqrt{1 + 2kI}), \quad S \in \mathbb{R}_+, w \in X_+, \\ I = \int_0^b w(a)da, \quad J = \int_0^b \kappa(a)w(a)da. \quad (1.9)$$

In the special case without infection age, where  $J = \sigma I$ , this incidence function is an adaptation of the contact incidence in [48] and performs quite well in the fitting comparisons in [1, 47]. Notice that, compared to [2],  $J$  and  $I$  have been switched. In [26], incidence functions

$$f(S, w) = S J h(S + I), \quad I = \int_0^b w(a) da, \quad J = \int_0^b \kappa(a) w(a) da, \quad (1.10)$$

with a decreasing continuous function  $h : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  were considered. Cf. [2, (1.6)].

### 1.6. Uniform weak persistence of susceptible hosts

Since we will consider general incidence functions in this paper, survival of the susceptible host population is established in the form of uniform weak persistence and not in form of the more desirable uniform persistence.

Uniform persistence means that there is an initial-value independent level above which the susceptible host density settles given enough time:

There is some  $\epsilon > 0$  such that  $\liminf_{t \rightarrow \infty} S(t) \geq \epsilon$  for any nonnegative solution on  $\mathbb{R}_+$  with  $S(0) > 0$ .

Uniform weak persistence (in which the  $\liminf$  is replaced by the  $\limsup$ ) means that there is an initial-value independent level above which the host density always returns though it can become arbitrarily low at times.

**Definition 1.1.** The susceptible hosts *persist uniformly weakly* if there exists some  $\epsilon > 0$  such that for all solutions of our model system on  $\mathbb{R}_+$  the number of susceptible hosts  $S(t)$  at time  $t \geq 0$  satisfies the following implication:

$$S(0) > 0 \implies \limsup_{t \rightarrow \infty} S(t) > \epsilon.$$

In detailed words, the susceptible hosts  $S$  persist uniformly weakly if there is some  $\epsilon > 0$  such that, whenever  $S(0) > 0$  and  $s > 0$ , there is some  $t > s$  such that  $S(t) > \epsilon$ .

For general persistence concepts, see [46, 49, 50] and the references therein. See also Section 8.1 about possible roads from uniform weak to uniform persistence. To give a taste of what we want to accomplish in this paper, we present a special case of Theorem 4.1 which covers many incidence functions, in particular those we just mentioned. More general results would involve more terminology than we want to present in the introduction (Section 2.5).

**Corollary 1.2.** Assume that there exists a function  $\tilde{f} : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  such that

$$f(S, w) = S \tilde{f}(S, w), \quad S, w \geq 0, S \in \mathbb{R}_+, w \in X_+,$$

where  $\tilde{f}$  is continuous at  $(0, 0)$  and is bounded on bounded sets and  $\tilde{f}(0, 0) = 0$ .

Then the susceptible hosts persist uniformly weakly.

The function  $\tilde{f}$  is often called the *force of infection* [51] [52, Sec.1] [53, 54] [35, 6.2.2], not to be confused with *infective impact*, (1.5), which is a term specific for infection-age structured models; for density-dependent incidence, the two can coincide [34, Sec.5.3].

Once again, the Laplace transform will be a useful tool for proving uniform weak persistence in age-structured population models [45, 46, 55]. Corollary 1.2 follows from Corollary 2.5.

**Example 1.3.** Let

$$f(S, w) = \frac{S J_1}{1 + \kappa_0 S + J_2}, \quad J_j = \int_0^b \kappa_j(a) w(a) da, \quad j = 1, 2.$$

Here  $\kappa_0 \in (0, \infty)$  is the mixing activity of a susceptible host.  $\kappa_2(a)$  is the mixing activity of an infected host,  $\kappa_1(a) = \sigma(a)\kappa_2(a)$  is the effective infectivity of an infected host at infection-age  $a$  and  $\sigma(a)$  is the amount of infectious particles that an infected host releases at infection-age  $a$ . We assume that  $\sigma, \kappa_j \in L_+^\infty[0, b)$ ,  $j = 1, 2$ .

The fraction  $\frac{J_2}{1 + \kappa_0 S + J_2}$  is the chance that a random contact of a susceptible host actually occurs with an infected host and  $J_1/J_2$  is the average effective infectivity of active infected hosts. The force of infection is

$$\tilde{f}(S, w) = \frac{J_1}{1 + \kappa_0 S + J_2}, \quad \tilde{f}(0, 0) = 0,$$

$\tilde{f}$  is continuous at  $(0, 0)$  and bounded on bounded subsets on  $X_+$ . By Corollary 1.2, the susceptible hosts persist uniformly weakly.

These examples should not distract from the fact that the incidence function is allowed to depend on the infection-age distribution in a very general way which we do not remember to have seen in the literature. However an incidence function is derived, by first principles or from data, chances are that it is covered by this paper unless it is a generalization of frequency-dependent incidence. In spite of this generality, the outcome is the same as for the analogous model without infection-age: the disease does not drive the host into extinction, as long as the incidence function leads to a proper force of infection, like in Corollary 1.2 and differently from power incidences

$$f(S, w) = S^q J^p, \quad J = \int_0^b \kappa(a) w(a) da, \quad \text{with } q \in (0, 1) \text{ or } p \in (0, 1). \quad (1.11)$$

As a trade-off for the generality concerning the incidence function, our assumptions concerning the effect of the disease on the growth of the host population are somewhat restrictive: Only susceptible hosts reproduce and compete for resources effectively. These assumptions are sometimes made (the first more frequently than the second) in ecoepidemic models, which have a predator in addition to a parasite and to a host that is also a prey. See [41, 56] [35, 10.4.2] and the literature cited therein; see [57] for other assumptions. To our knowledge, ecoepidemic models rarely mention concrete predator – prey/host – parasite systems. An exception is a highly infective *Mycoplasma* disease affecting the eyes of wild ungulates (chamois, ibex, mouflon) on high mountain pastures [41]. All age groups and both sexes are affected. The disease can either heal or lead to total blindness. In the case of wild ungulates, the disease leads to a change of behavior as the affected animals can no longer follow their herd. They become insecure and unable to feed and may fall from precipices. The disease should make it difficult to find a mate and, if reproduction occurs nevertheless, to keep offspring alive. Finally, it seems a valid assumption that diseased hosts have little or no impact on the food supply of susceptible hosts.

The assumption that infected individuals do not effectively reproduce or compete seems acceptable for diseases that do not last for a long time because either recovery or disease death occurs fast or that cause severe symptoms interfering with feeding, mating, giving birth, or keeping neonates alive.

This assumption does not only save us from mathematical difficulties but also from some modeling issues. While it is not too difficult to model the influence of infected individuals on population growth

without infection age [51, 57–59], the incorporation of infection-age raises many questions such as, if there is vertical transmission (from mother to unborn child), how is infection-age inherited?

### 1.7. Organization of the paper

The epidemic model will be introduced in three equivalent versions in Section 2. In Section 3, we derive a priori properties of the model solutions. First, we establish upper bounds for nonnegative solutions; interestingly enough, they do not depend on the incidence function. Incidentally, the assumption that infected individuals do not compete for resources makes finding upper bounds more difficult. This was already challenging without infection-age [26] but is more so with infection-age.

Secondly, we find conditions for the number of susceptible hosts to stay strictly positive. Clearly, this helps the persistence of susceptible hosts; those conditions involve the incidence function.

Section 4 is the core of this paper, where we establish conditions for uniform weak host persistence. If this were a movie, we could have called it “The return of the Laplace transform”.

In Section 5 and 6, we present two special cases in which our assumptions for host persistence turn out to be necessary.

Finally, in Section 7, we establish existence and uniqueness for nonnegative solutions of our model system. We do this at the end of the paper for two reasons. First, the proofs turn out to be the most technical of this paper, though as one expects, they ultimately rely on standard arguments: the contraction mapping theorem, an approximation procedure and Arzela-Ascoli type arguments. Therefore, we want to convince ourselves that we can gain epidemiological insights which give us enough motivation to tackle them. Second, the a priori considerations in Section 3 will be helpful. As the incidence function is allowed to depend on the infection-age distribution in a general way, we make a fixed point argument within a fixed point argument, which may be a novel feature.

We will show existence but not uniqueness of solutions for power incidences (1.11) because they are not Lipschitz continuous at the origin. In spite of this mathematical deficiency, power incidence functions keep popping up in the literature (see [52, 60–62] and the references therein). They fit the infection experiments in [25] very well [1]. With due caution, one has to say, though, that it is difficult to estimate incidence functions for very few susceptible and infective hosts, which is the range relevant for host survival.

## 2. The model

For introductions to mathematical epidemiology in book form, we refer to [22, 30, 34, 35, 40, 51, 52, 63–67] and [68, Chap.6], [69, Chap.9,10], [45, Part 3].

We assume that, with respect to the infectious disease, the hosts are in one of two stages:

They are susceptible to the disease or they are infected by the disease. They leave the susceptible stage by being infected and leave the infected stage either by dying from natural causes, dying from the disease or by becoming susceptible again.

We do not consider the case where infected individuals recover from the disease and have acquired permanent immunity to it. Infected hosts are not necessarily infective: they may be still in a latent period or have recovered enough to be no longer infective and no longer subject to death from the disease. But we assume that they still have symptoms severe enough that they do not reproduce or are not able to keep their offspring alive and that prevent them from competing for resources.



Rather than introducing classes of infected hosts that are in the latency period or have recovered from the disease (without having become susceptible again yet), in the spirit of [31, 32] we introduce infection-age as the time since the moment of infection and assume that the infectivity of infected hosts depends on their infection-age. We also assume that the per capita rate at which infected hosts die from the disease or become susceptible again depends on their infection-age.

### 2.1. More on the sojourn function

Let  $P : \mathbb{R}_+ \rightarrow [0, 1]$  be the sojourn function of the infected stage (Section 1.3). Since  $P$  is decreasing,  $P$  is differentiable a.e. on  $\mathbb{R}_+$  with nonpositive a.e. derivative  $P'$  and  $P'$  is finitely integrable [70, Thm.6.4]. Recall the maximal infection age  $b \in (0, \infty]$  (Section 1.3). If  $b < \infty$ ,  $P'(a) = 0$  for a.a.  $a \in (b, \infty)$ .

**Assumption 2.1.** We assume throughout this paper that  $P$  is absolutely continuous on  $\mathbb{R}_+$  and  $P(0) = 1$ , i.e.,

$$P(a) - P(0) = P(a) - 1 = \int_0^a P'(s)ds, \quad a \in \mathbb{R}_+. \quad (2.1)$$

**Lemma 2.2.** If  $b < \infty$  and  $P : \mathbb{R}_+ \rightarrow [0, 1]$  is continuous, then  $P$  is absolutely continuous on  $\mathbb{R}_+$  if and only if  $P$  is absolutely continuous on  $[0, b)$ .

**Example 2.3** ([70, Thm.6.6]). Let  $b \in (0, \infty]$ .  $P$  is absolutely continuous on  $\mathbb{R}_+$  if  $P$  is continuous on  $\mathbb{R}_+$  and Lipschitz continuous on every proper subinterval of  $[0, b)$ .

Assume that  $a \geq 0$ ,  $h > 0$ . Then  $\frac{P(a) - P(a+h)}{P(a)}$  is the probability of leaving the infected stage during the age interval  $[a, a+h)$ . So, for almost all  $a \geq 0$ ,

$$\gamma(a) := -P'(a)/P(a), \quad \text{a.e. } a \in [0, b), \quad (2.2)$$

is the rate at which an infected individual leaves the infected stage at infection age  $a$ . By a chain rule for absolute continuity (Lemma 8.1),  $\ln P$  is absolutely continuous on  $[0, b)$  and  $(\ln P)' = -\gamma$  a.e. on  $[0, b)$ ,

$$P(a) = \exp\left(-\int_0^a \gamma(s)ds\right), \quad a \in [0, b).$$

Infected individuals leave the infected stage either by returning to the susceptible class, by death from the disease, or by disease-unrelated (“natural”) death,

$$\gamma(a) = \alpha(a) + \vartheta(a) + \nu, \quad a \geq 0. \quad (2.3)$$

Here  $\alpha(a)$  is the per capita rate of becoming susceptible again,  $\vartheta(a)$  the per capita disease death-rate and  $\nu$  the natural death rate (which does not depend on infection-age).

The function  $\gamma, \alpha : [0, b) \rightarrow \mathbb{R}_+$  are assumed to be Borel measurable, and  $\gamma$  is assumed to be bounded away from 0 a.e.

If we do not like the explicit formula (2.6), we simply assume that there is some  $\nu > 0$  such that

$$\gamma(a) \geq \alpha(a) + \nu, \quad a \in [0, b), \quad (2.4)$$

where  $\nu > 0$  is related to the natural mortality of hosts. As for susceptible hosts, the natural mortality has been incorporated into  $g$ .

Let, at time  $t \geq 0$ , denote

- $S(t)$  the amount of susceptible hosts,
- $I(t)$  the amount of infected hosts,
- $u(t, \cdot)$  the infection-age density of infected hosts,
- $R(t)$  the rate of infected hosts returning into the susceptible class,
- $B(t)$  the incidence, the rate of new infections.

We choose the letter  $B$  for the incidence because it is the birth rate of the disease. See Table 1 for a more complete list of symbols. The disease dynamics can be mathematically described in various equivalent ways.

## 2.2. The differential equations model (in the spirit of McKendrick [71])

This model formulation consists of an integro-differential equation and a partial differential equation,

$$\begin{aligned} S' &= Sg(S) - B + R \quad \text{a.e. on } (0, \infty), \\ (\partial_t + \partial_a)u(t, a) &= -\gamma(a)u(t, a), \quad t \in \mathbb{R}_+, a \in [0, b), a \neq t, \\ u(t, 0) &= B(t) = f(S(t), u(t, \cdot)), \\ R(t) &= \int_0^b \alpha(a)u(t, a)da. \end{aligned} \tag{2.5}$$

Further, there are initial conditions,

$$S(0) = S_0, \quad u(0, a) = u_0(a), \quad a \in [0, b).$$

In (2.5),  $S$  is assumed to be absolutely continuous. There,  $\gamma(a)$  is the rate at which infected hosts, at infection age  $a$ , cease to be infected by either natural death, disease death, or by becoming susceptible again;  $\alpha(a)$  is the per capita rate at which infected hosts cease to be infected at infection age  $a$  and become susceptible again; more precisely

$$\gamma(a) = \alpha(a) + \vartheta(a) + \nu, \quad a \geq 0, \tag{2.6}$$

where  $\vartheta$  is the per capita rate at which infected hosts die from the disease and  $\nu > 0$  is the per capita rate of natural death, which does not depend on infection age.

For  $S \geq 0$ ,  $g(S)$  is the per capita growth rate of susceptible hosts if their amount is  $S$ . The model formulation implicitly assumes that infected individuals do not reproduce or are not able to keep their offspring alive and that they do not compete for resources (cf. [10]). This assumption allows to reduce the problem to one for just two independent variables: the number of susceptibles,  $S$ , and the incidence of the disease,  $B$ .

As described in Section 1.5,  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$ ,  $X_+ = L_+^1[0, b)$ , is the incidence function, i.e., the entity  $f(S, w)$  is the rate of new infections if the amount of susceptible hosts is  $S \in \mathbb{R}_+$  and the infection-age density of infected hosts is  $w \in X_+$ .

The per capita host growth rate  $g$  has the following properties.

**Assumption 2.4.** The function  $g : \mathbb{R}_+ \rightarrow \mathbb{R}$  is Lipschitz continuous on bounded subsets of  $\mathbb{R}_+$ : For any  $c \in (0, \infty)$ , there exists some  $\Lambda_c \in (0, \infty)$  such that

$$|g(S) - g(\tilde{S})| \leq \Lambda_c |S - \tilde{S}|, \quad S, \tilde{S} \in [0, c].$$

Further  $g$  is decreasing,  $g(0) > 0$ , and  $g(S) < 0$  for large  $S > 0$ .

In fact, we assume that there is a unique  $K > 0$  such that  $g(K) = 0$  and that  $g$  is continuously differentiable on  $(0, K + \delta)$  with some  $\delta > 0$ ,  $g'(S) < 0$  for  $S \in (0, K]$  and  $Sg'(S) \rightarrow 0$  as  $S \rightarrow 0+$ .

In particular,  $g$  is a decreasing function of the size of the susceptible part of the population due to resource competition.

$K$  is called the *carrying capacity* for the host population. The term ‘‘carrying capacity’’ originates from the fact that the host population size converges to it in the absence of the disease.

If  $f(K, u) = 0$  when  $u$  is the zero function,  $(K, u)$  with  $u = 0$  is an equilibrium of (2.5), called the *disease-free equilibrium*, DFE, for short.

### 2.3. The formulation in the spirit of Lotka [72]

This formulation takes the sojourn function  $P$  for the infection stage as a starting point.  $P(a)$  is the probability at which a host that has been infected is still alive and infected  $a$  time units after the moment of infection. See Section 1.3.

Let  $u_0 : [0, b) \rightarrow \mathbb{R}_+$  be the initial density of infected hosts,  $\int_0^b u_0(a) da < \infty$ . The model is a system consisting of a differential equation and Volterra functional equations,

$$\begin{aligned} S' &= Sg(S) - B + R \quad \text{a.e. on } (0, \infty), \\ B(t) &= f(S(t), u(t, \cdot)), \\ u(t, a) &= \begin{cases} B(t-a)P(a), & t > a \geq 0 \\ u_0(a-t)\frac{P(a)}{P(a-t)}, & 0 \leq t < a \end{cases} \quad 0 \leq a < b, \\ R(t) &= \int_0^b \alpha(a)u(t, a)da. \end{aligned} \quad (2.7)$$

Further, there is the initial condition for the susceptible hosts,  $S(0) = S_0$ .

Since there are a lot of variables in this system, let us clarify that  $S_0, u_0, P, \alpha, g, f$  are given and a continuous function  $B$  and an absolutely continuous function  $S$  are wanted. The auxiliary variable  $u$  is determined by  $B$  and  $u_0$  in the spirit of Lotka [72]. See (1.7).

The assumption (2.4) takes the form

$$\gamma(a) := -\frac{P'(a)}{P(a)} \geq \alpha(a) + \nu \quad \text{for a.a. } a \in [0, b). \quad (2.8)$$

The Lotka formulation can be derived from the McKendrick formulation by integration along characteristics [45, Sec.13.2]. The function  $u$  satisfies the PDE in the McKendrick formulation if  $B, u_0$  and  $P$  are differentiable and  $\gamma$  is given by (2.8) [45, Sec.13.2]. Otherwise, the PDE is satisfied in an appropriate generalized sense.

#### 2.4. A system of differential and Volterra integral equations in the spirit of Kermack and McKendrick

As a special case of (2.7), we consider

$$\begin{aligned} f(S, w) &= \check{f}(S, J_1, \dots, J_n), \quad w \in L_+^1[0, b), \\ \check{f} : \mathbb{R}_+^{n+1} &\rightarrow \mathbb{R}_+, \quad J_j = \int_0^b \kappa_j(a)w(a)da, \quad \kappa_j \in L_+^\infty[0, b). \end{aligned} \quad (2.9)$$

The  $J_j$  are various *impacts by infectious hosts* associated with infection-age dependent per capita infectivities  $\kappa_j \in L_+^\infty[0, b)$ . If  $\kappa_1 = 1$ , then  $J_1 = I$  is the amount of infective individuals.

Several infectious impacts may occur if the infection can take different routes like the eye disease of chamois, ibex and mouflon [41] that we mentioned towards the end of Section 1.5: It spreads not only through direct contact but also by airborne particles and through vectors such as flies. Also see Example 1.3.

If  $b \in (0, \infty)$ , we extend  $\kappa_j$  and  $\alpha$  to  $\mathbb{R}_+$  by  $\kappa_j(a) = 0 = \alpha(a)$ ,  $a \in (b, \infty)$ ,  $b \in (0, \infty]$ . We substitute the formula for  $u$  in (2.7) into  $J_j(t) = \int_0^b \kappa_j(a)u(t, a)da$  and obtain a system of one differential equation and several Volterra integral equations,

$$\begin{aligned} S' &= Sg(S) - B + R \quad \text{a.e. on } (0, \infty), \\ B(t) &= \check{f}(S(t), J_1(t), \dots, J_n(t)), \\ J_j(t) &= \int_0^t \kappa_j(a)P(a)B(t-a)da + J_{j0}(t), \\ R(t) &= \int_0^t \alpha(a)P(a)B(t-a)da + R_0(t), \end{aligned} \quad (2.10)$$

with the given functions

$$\begin{aligned} J_{j0}(t) &= \int_0^b \kappa_j(s+t) \frac{P(s+t)}{P(s)} u_0(s) ds, \\ R_0(t) &= \int_0^b \alpha(s+t) \frac{P(s+t)}{P(s)} u_0(s) ds. \end{aligned} \quad (2.11)$$

If  $0 < t < b < \infty$ , since  $P(a) = 0$  for  $a > b$ ,

$$R_0(t) = \int_0^{b-t} \alpha(s+t) \frac{P(s+t)}{P(s)} u_0(s) ds,$$

and similar formulas hold for  $J_{j0}$ . If  $b \leq t < \infty$ ,  $R_0(t) = 0 = J_{j0}(t)$ .

Under our assumptions so far, it cannot be excluded that  $R_0$  takes infinite values; however  $R_0$  is finitely integrable on  $\mathbb{R}_+$ . Indeed, by Tonelli's theorem and (2.8),

$$\begin{aligned} \int_0^\infty R_0(t) dt &\leq \int_0^\infty \left( \int_0^b \gamma(s+t) \frac{P(s+t)}{P(s)} u_0(s) ds \right) dt \\ &= \int_0^b \left( \int_0^\infty -P'(s+t) dt \right) \frac{u_0(s)}{P(s)} ds = \int_0^b u_0(s) ds. \end{aligned} \quad (2.12)$$

We give this special case extra consideration because we could not prove existence of solutions to (2.7) without a Lipschitz conditions for  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  (Section 7.1) whereas (2.10) can be solved for  $\check{f} : \mathbb{R}_+^{n+1} \rightarrow \mathbb{R}_+$  that are just continuous (Section 7.2). See Example 2.8.

## 2.5. More preview

We now have developed enough terminology to give a preview of some more results. The following one generalizes Corollary 1.2 and follows from Theorem 4.1. Recall that  $X_+ = L_+^1[0, b)$ .

**Corollary 2.5.** *Assume that there exists a function  $\tilde{f} : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  such that  $f(S, w) = S \tilde{f}(S, w)$  for all  $S \geq 0$ ,  $w \in X_+$ , where  $\tilde{f}$  is continuous at  $(0, 0)$  and is bounded on bounded sets. Then, if*

$$g(0) > \left(1 - \int_0^b \alpha(a)P(a)da\right)\tilde{f}(0, 0), \quad (2.13)$$

*the susceptible hosts persist uniformly weakly. In particular, if  $\tilde{f}(0, 0) = 0$ , the susceptible hosts persist uniformly weakly.*

The function  $\tilde{f}$  is often called the *force of infection* [51] [52, Sec.1] [54] [35, 6.2.2], not to be confused with *infective impact* which is a term specific for infection-age structured models; for density-dependent incidence, the two can coincide [34, Sec.5.3]. The term  $\tilde{f}(S, 0)$  represents the force of infection coming from reservoirs of the disease.

**Remark 2.6.** By (2.8),

$$\wp := \int_0^b \alpha(a)P(a)da \leq - \int_0^b \nu P(a)da - \int_0^b P'(a)da.$$

By the fundamental theorem of calculus,

$$\wp \leq 1 - \nu D < 1, \quad (2.14)$$

where  $D$  is the expected sojourn time in the infection period (natural death included). Recall that  $1/\nu > D$  is the life expectation of a healthy host. We owe to one of the referees the insight that  $\wp$  can be interpreted as the probability that a susceptible host just infected will turn susceptible again and how to reformulate (2.13) in terms of a *basic host reproduction number*,  $\mathcal{H}_0$ . The number  $1 - \wp \in (0, 1]$  is the probability that a susceptible host just infected will not turn susceptible again. Let  $g(0) = \beta - \mu$  with  $\mu$  the per capita death rate of healthy hosts and  $\beta$  the per capita birth rate without competition for resources. Then (2.13) can be rewritten as

$$1 < \mathcal{H}_0 = \frac{\beta}{\tilde{f}(0, 0)(1 - \wp) + \mu}. \quad (2.15)$$

Notice that  $(\tilde{f}(0, 0)(1 - \wp) + \mu)^{-1}$  is the average time a host is alive and susceptible if very few hosts (susceptible or infective) are around.

**Theorem 2.7.** *Assume that  $f(S, w) = \check{f}(S, J)$  with  $J = \int_0^b \kappa(a)w(a)da$ , where  $\kappa \in L^\infty[0, b)$  and  $\check{f} : \mathbb{R}_+^2 \rightarrow \mathbb{R}$  is differentiable at  $(0, 0)$ ,  $\check{f}(0, J) = 0$  for all  $J \geq 0$  and  $\partial_1 \check{f}(0, 0) = 0$ .*

*Further assume that there is some  $\eta_0 > 0$  such that*

$$\alpha(a) \geq \eta_0 \kappa(a), \quad a \in [0, b). \quad (2.16)$$

*Then the susceptible hosts,  $S$ , persist uniformly weakly.*

This theorem is proved at the end of Section 4.2.

Condition 2.16 implies that, at whatever infection-age, if some infected individuals are infectious there are also some infected individuals that leave the infected class and become susceptible again.

**Example 2.8.** Let  $f(S, w) = S^q J^p = \check{f}(S, J)$  with  $q \in (0, 1)$  and  $p > 0$  and  $q + p > 1$ ,  $J = \int_0^b \kappa(a)w(a)da$ ,  $S \in \mathbb{R}_+$ ,  $w \in X_+$ ; further  $\kappa \in L_+^\infty[0, b)$ .

Assume that there is some  $\eta_0 > 0$  such that

$$\alpha(a) \geq \eta_0 \kappa(a), \quad \text{for a.a. } a \in [0, b).$$

Since

$$\check{f}(S, J) \leq (S + J)^{p+q}, \quad S, J \geq 0,$$

with  $p + q > 1$ ,  $\check{f}$  is differentiable at  $(0, 0)$  with zero derivative, and the susceptible hosts persist uniformly weakly under this incidence function and assumption (2.16).

We mention that the model in Section 2 has non-negative solutions under these assumption (Section 7.2) though they may not be unique.

This result should be compared with the next one in which host persistence fails if assumption (2.16) is violated in the extreme form that  $\alpha(a) = 0$  for all  $a \geq 0$  and  $\kappa$  is a positive constant.

**Theorem 2.9.** Let  $\alpha, \gamma, \kappa$  be nonnegative constants and  $\alpha = 0 < \gamma$  and  $f(S, w) \geq S^q J^p$ ,  $S \geq 0$ ,  $J = \kappa \int_0^b w(a)da$  with  $q \in (0, 1)$  and  $p \geq 0$ . Assume that  $S(0) > 0$  and  $I(0) > 0$  satisfy

$$\frac{(S(0))^{1-q}}{(I(0))^p} < \frac{(1-q)\kappa^p}{(1-q)g(0) + p\gamma}.$$

Then  $S(t)$  becomes 0 at finite time and stays zero thereafter, and  $I(t) \rightarrow 0$  as  $t \rightarrow \infty$ .

For the proof see Section 6. Theorem 2.9 shows that the assumption 2.16 in Theorem 2.7 cannot be completely abandoned.

## 2.6. Should the per capita return rate be bounded?

One may like to turn to numerical calculations to explore the grey zone between Theorem 2.7 and Theorem 2.9.

We fix a natural per capita host mortality rate  $\nu > 0$ , i.e.,  $1/\nu$  is the life expectation of a healthy host. Then we choose a sojourn function  $Q$  for the infection period (natural death disregarded) such that  $P(a) = e^{-\nu a}Q(a)$ . To find the per capita rates of disease death on the one hand and of return into the susceptible class on the other hand, we use the concept of a *case fatality ratio* (usually but falsely called a rate) [16], which we assume to be independent of infection age and is denoted by  $\varpi \in (0, 1)$ : If an individual leaves the infection period, it leaves by disease death with probability  $1 - \varpi$  and leaves by return into the susceptible class with probability  $\varpi$ . This means that

$$\alpha(a) = -\varpi \frac{Q'(a)}{Q(a)}, \quad 0 \leq a < b. \quad (2.17)$$

If  $b = \infty$ , boundedness of  $\alpha$  on  $\mathbb{R}_+$  may not be a bad assumption. Let us take a look at the sojourn functions which have been fitted in [2] to the infection experiments involving salamander larvae and

ranavirus [25]. We should mention that all infected larvae (their number was 446) died from the disease and that they were all dead by the 23rd day. Since they were larvae and not yet terrestrial salamanders, reproduction was not an issue.

If the duration of the infection stage (neglecting natural death) is lognormally or Gamma distributed  $-Q'/Q$  is bounded on  $\mathbb{R}_+$  for the associated sojourn function  $Q$ .

If the length of the infection period (neglecting natural death) is lognormally distributed, the probability density of the sojourn function is given by

$$-(2\pi)^{1/2}Q'(a) = e^{-b(a)^2/2} \frac{1}{\zeta a}, \quad b(a) = (1/\zeta) \ln(a/m), \quad a \geq 0,$$

with parameters  $\zeta, m > 0$  [45, Sec.12.8]. By the chain rule,

$$(2\pi)^{1/2}Q''(a) = e^{-b(a)^2/2} \left( b(a) \frac{1}{(\zeta a)^2} + \frac{1}{\zeta a^2} \right) = \frac{e^{-b(a)^2/2}}{\zeta^3 a^2} (\ln(a/m) + \zeta^2).$$

Notice that  $Q(a)$ ,  $Q'(a)$  and  $Q''(a)$  are different from 0 if  $a/m > e^{-\zeta^2}$ . Further,  $Q''(a) \rightarrow 0$ ,  $Q'(a) \rightarrow 0$  and  $Q(a) \rightarrow 0$  as  $a \rightarrow \infty$ . Since  $Q$  is decreasing, actually  $Q'(a) < 0$  for all  $a > 0$ . So

$$\lim_{a \rightarrow \infty} -\frac{Q'(a)}{Q(a)} = \lim_{a \rightarrow \infty} -\frac{Q''(a)}{Q'(a)} = 0$$

by a l'Hôpital type argument [2, Thm.7.2]. This implies that  $-\frac{Q'}{Q}$  is bounded on  $\mathbb{R}_+$ .

Similar arguments show that this also holds if the infection period is Gamma-distributed.

However, for the Weibull distribution,  $Q(a) = e^{-\xi a^\zeta}$ ,  $a \geq 0$ , with  $\xi > 0$  and  $\zeta \geq 1$ , we have

$$-\frac{Q'(a)}{Q(a)} = \xi \zeta a^{\zeta-1}, \quad a > 0,$$

which is unbounded on  $(0, \infty)$ , unless  $\zeta = 1$ , the special case of an exponential distribution.

If  $b \in (0, \infty)$ , after normalization  $b = 1$ , then  $Q(a) = (1 - a^m)^n$  with  $n, m > 1$  would have a plausible shape. (See the figures in [2]). Then

$$-\frac{Q'(a)}{Q(a)} = n(1 - a^m)^{-1} m a^{m-1}, \quad a \in [0, 1),$$

goes to infinity if  $a \rightarrow 1-$ .

In view of these findings, we will try to avoid assuming essential boundedness of  $\alpha$  as much as we can. Instead, we will try to exploit (2.8) which gives us for  $0 \leq a_1 < a_2 \leq \infty$  that

$$\begin{aligned} \int_{a_1}^{a_2} \alpha(a)P(a)da &\leq \int_{a_1}^{a_2} \gamma(a)P(a)da - \nu \int_{a_1}^{a_2} P(a)da \\ &= - \int_{a_1}^{a_2} P'(a)da - \nu \int_{a_1}^{a_2} P(a)da = P(a_1) - P(a_2) - \nu \int_{a_1}^{a_2} P(a)da. \end{aligned}$$

In the limit  $a_1 \rightarrow 0$  and  $a_2 \rightarrow b$ ,

$$\int_0^\infty \alpha(a)P(a)da \leq 1 - \nu \int_0^b P(a)da. \quad (2.18)$$

Assuming that  $\alpha$  is not essentially bounded, has the unpleasant technical complication that the return rate  $R(t)$  is not continuous in  $t$  and that the differential equation for  $S$  in (2.7) holds only a.e..

### 3. A priori properties of solutions

Before we discuss the existence of solutions of either of the systems, we derive some of their properties provided that they exist. We will need these properties to discuss the dynamics of the system, and later this information will help us in setting up the existence proof.

Since  $u(t, \cdot)$  is the infection-age density of infected hosts, the total number of infected hosts is given by

$$I(t) = \int_0^b u(t, a) da, \quad t \geq 0. \quad (3.1)$$

The total number of hosts,  $H$ , is

$$H(t) = S(t) + I(t), \quad t \geq 0. \quad (3.2)$$

By (2.7),

$$I(t) = \int_0^t P(t-s)B(s)ds + \int_0^b \frac{P(t+s)}{P(s)} u_0(s) ds. \quad (3.3)$$

In particular,

$$I(0) = \int_0^b u_0(a) da. \quad (3.4)$$

Assume that the number of susceptibles  $S$  is absolutely continuous and that the disease incidence  $B$  is continuous. Further, we assume that  $S$ ,  $B$ ,  $u_0$  are nonnegative. Then  $I$  in (3.3) and  $R$  in (2.10) are nonnegative.

Since  $P$  is absolutely continuous,  $I$  is absolutely continuous and, for a.a.  $t \geq 0$ , by (3.3),

$$I'(t) = B(t) + \int_0^t P'(t-s)B(s)ds + \int_0^b \frac{P'(t+s)}{P(s)} u_0(s) ds. \quad (3.5)$$

As for the first two expressions after the equality sign, one checks that integrating them in time yields the first expression in (3.3) by Tonelli's theorem. Indeed, since the integrand is non-positive a.e.,

$$\begin{aligned} \int_0^T \left( \int_0^t P'(t-s)B(s)ds \right) dt &= \int_0^T \left( \int_s^T P'(t-s)dt \right) B(s) ds \\ &= \int_0^T (P(T-s) - P(0)) B(s) ds = \int_0^T P(T-s) B(s) ds - \int_0^T B(s) ds. \end{aligned}$$

As for the third expression, one checks that integrating it in time yields the second expression in (3.3) after the equality sign by Tonelli's theorem. Indeed, for any  $T > 0$ , since the integrand is non-negative, by Tonelli's theorem,

$$\begin{aligned} \int_0^T \left( \int_0^b \frac{-P'(t+s)}{P(s)} u_0(s) ds \right) dt &= \int_0^b \frac{u_0(s)}{P(s)} \left( \int_0^T -P'(t+s) dt \right) ds \\ &= \int_0^b \frac{u_0(s)}{P(s)} (P(s) - P(T+s)) ds = \int_0^b u_0(s) ds - \int_0^b \frac{P(T+s)}{P(s)} u_0(s) ds. \end{aligned}$$



By (1.7) and (3.5), for a.a.  $t > 0$ ,

$$\begin{aligned} I'(t) &= B(t) - \int_0^t \gamma(a)P(a)B(t-a)ds - \int_0^b \gamma(t+s)\frac{P(t+s)}{P(s)}u_0(s)ds \\ &= B(t) - \int_0^b \gamma(a)u(t,a)da. \end{aligned}$$

Since we have assumed that  $S$  is absolutely continuous,  $H$  is absolutely continuous and by (2.7), for a.a.  $t > 0$ ,

$$H'(t) = S(t)g(S(t)) + \int_0^b [\alpha(a) - \gamma(a)]u(t,a)da.$$

### 3.1. Estimates from above

By (2.8),

$$H'(t) \leq S(t)g(S(t)) - \nu I(t) \quad a.e.$$

By (3.2), this can be rewritten as

$$H' \leq S(g(S) + \nu) - \nu H \quad a.e.$$

Let

$$\psi(t) = S(t)[g(S(t)) + \nu], \quad t \geq 0. \quad (3.6)$$

Then, for a.a.  $t > 0$ ,

$$H'(t) + \nu H(t) \leq \psi(t).$$

This implies

$$\int_0^t e^{-\nu(t-s)}\psi(s)ds \geq \int_0^t e^{-\nu(t-s)}H'(s)ds + \int_0^t \nu e^{-\nu(t-s)}H(s)ds.$$

By the integration by parts formula for absolutely continuous functions [73, Cor.18.20], for all  $t \geq 0$ ,

$$\int_0^t e^{-\nu(t-s)}\psi(s)ds \geq H(t) - H(0)e^{-\nu t}. \quad (3.7)$$

Let  $T > 0$  and  $\psi_T = \sup \psi([0, T])$  and  $H_T = \sup H([0, T])$ . For  $t \in [0, T]$ ,

$$H(t) \leq \psi_T \frac{1}{\nu}(1 - e^{-\nu t}) + H(0)e^{-\nu t} \leq \max \left\{ \frac{1}{\nu}\psi_T, H(0) \right\}.$$

Taking the maximum for  $t \in [0, T]$ ,

$$H_T \leq \max \left\{ \frac{1}{\nu}\psi_T, H(0) \right\}.$$

By (3.6),

$$H_T \leq \max \left\{ H(0), \frac{1}{\nu} \max_{0 \leq S \leq S_T} S(g(S) + \nu) \right\}.$$

Suppose that  $H_T > H(0)$ . Then there exists some  $\tilde{S} \in [0, S_T]$  such that

$$H_T \leq \frac{1}{\nu} \tilde{S} (g(\tilde{S}) + \nu).$$

Suppose that  $\tilde{S} > K$ . Then  $g(\tilde{S}) < 0$  and  $H_T < \tilde{S} \leq S_T$ , a contradiction. So  $\tilde{S} \leq K$  and

$$H_T \leq \max \left\{ H(0), \frac{1}{\nu} \max_{0 \leq S \leq K} S (g(S) + \nu) \right\}. \quad (3.8)$$

Since the right hand side of this inequality does not depend on  $T > 0$ ,  $H$  is bounded on  $\mathbb{R}_+$  and

$$\begin{aligned} H(t) &\leq \max \left\{ H(0), \frac{1}{\nu} \max_{0 \leq S \leq K} S (g(S) + \nu) \right\}, \quad t \geq 0, \\ H(0) &= S_0 + \int_0^\infty u_0(a) da. \end{aligned} \quad (3.9)$$

Once we know that  $H$  is bounded on  $\mathbb{R}_+$ , we also know that  $S \leq H$  is bounded and  $\psi$  in (3.6) is bounded.

In the following, we use the following notation:

$$H^\infty = \limsup_{t \rightarrow \infty} H(t) = \inf_{s \geq 0} \sup_{t \geq s} H(t). \quad (3.10)$$

$S^\infty$  and  $\psi^\infty$  and  $J^\infty$  are defined analogously. By (3.7),

$$H^\infty \leq \limsup_{t \rightarrow \infty} \int_0^t e^{-\nu s} \psi(t-s) ds.$$

This can be written as

$$H^\infty \leq \limsup_{t \rightarrow \infty} \int_0^\infty e^{-\nu s} H_0(t-s) \psi(t-s) ds$$

with the Heaviside function  $H_0(s) = 1$  if  $s \geq 0$  and  $H_0(s) = 0$  if  $s < 0$ . By a generalization of the Lebesgue-Fatou lemma [45, p.468],

$$H^\infty \leq \int_0^\infty \limsup_{t \rightarrow \infty} H_0(t-s) \psi(t-s) e^{-\nu s} ds \leq \psi^\infty \int_0^\infty e^{-\nu s} ds = \frac{\psi^\infty}{\nu}. \quad (3.11)$$

By (3.6),

$$\psi^\infty = \limsup_{t \rightarrow \infty} S(t) [g(S(t)) + \nu] = \lim_{n \rightarrow \infty} S(t_n) [g(S(t_n)) + \nu]$$

for an appropriate sequence  $(t_n)$  with  $t_n \rightarrow \infty$  as  $n \rightarrow \infty$ . Since  $S$  is bounded, after choosing a subsequence,  $S(t_n) \rightarrow \tilde{S}$  as  $n \rightarrow \infty$  for some  $\tilde{S} \in [0, S^\infty]$ . So,  $\psi^\infty = \tilde{S} [g(\tilde{S}) + \nu]$ . By (3.11),

$$H^\infty \leq \frac{1}{\nu} \tilde{S} [g(\tilde{S}) + \nu] \quad (3.12)$$

with some  $\tilde{S} \in [0, S^\infty]$ . If  $\tilde{S} > K$ , then  $g(\tilde{S}) < 0$  and  $H^\infty < \tilde{S} \leq S^\infty$ , a contradiction because  $H(t) \geq S(t)$  for all  $t \geq 0$ . Hence,  $\tilde{S} \leq K$  and

$$H^\infty \leq \frac{1}{\nu} \max_{0 \leq S \leq K} S [g(S) + \nu] =: H^\circ. \quad (3.13)$$

We also get from (3.12) that

$$H^\infty \leq \frac{S^\infty}{\nu} [g(0) + \nu]. \quad (3.14)$$

Assume  $\kappa \in L_+^\infty[0, b)$  and

$$\kappa^\diamond = \|\kappa\|_\infty. \quad (3.15)$$

Then the infective impact  $J$  associated with  $\kappa$  via (1.5) is bounded and

$$J(t) \leq \kappa^\diamond I(t), \quad t \geq 0. \quad (3.16)$$

By (3.13),

$$J^\infty \leq \frac{\kappa^\diamond}{\nu} \max_{0 \leq S \leq K} S [g(S) + \nu]. \quad (3.17)$$

By (3.14),

$$J^\infty \leq S^\infty \frac{\kappa^\diamond}{\nu} [g(0) + \nu]. \quad (3.18)$$

### 3.2. Positivity of susceptibles

Uniform weak persistence of susceptible hosts is certainly facilitated if all nonnegative solutions  $S$  and  $B$  of (2.7) on  $\mathbb{R}_+$  with  $S(0) > 0$  satisfy  $S(t) > 0$  for all  $t \in \mathbb{R}_+$ . In this section we will derive conditions for this to hold.

**Lemma 3.1.** *Assume that for any  $c > 0$  there is some  $\tilde{c} > 0$  such that*

$$f(S, w) \leq \tilde{c}S, \quad 0 \leq S, \|w\|_1 \leq c, w \in X_+. \quad (3.19)$$

*Then the following hold.*

- (a) *If  $T \in (0, \infty)$  and there is a continuous nonnegative solution of (2.7) on  $[0, T]$  with  $S(t) > 0$  for all  $t \in [0, T)$ , then  $S(T) > 0$ .*
- (b) *If there is a continuous solution of (2.7) on  $[0, \infty)$  and  $S(0) > 0$ , then  $S(t) > 0$  for all  $t \geq 0$ .*

*Proof.* (a) Let  $S(0) > 0$  and  $S(t) > 0$  for  $t \in [0, T)$ .

Suppose that  $S(T) = 0$ . By (3.8), there is some  $c > 0$  such that  $S(t) \leq c, I(t) = \int_0^b u(t, a) da \leq c$  for all  $t \in [0, T]$ . By assumption (3.19), there is some  $\tilde{c} > 0$  such that the function  $\psi(t) = f(S(t), u(t, \cdot))/S(t), t \in [0, T)$ , satisfies  $\psi(t) \leq \tilde{c}$  for all  $t \in [0, T)$ . Further, by (2.7),

$$S'(t) \geq S(t)[g(S(t)) - \tilde{c}], \quad \text{for a.a. } t \in [0, T].$$

We use an integrating factor,

$$S(t) \geq S(0) \exp\left(\int_0^t [g(S(s)) - \tilde{c}] ds\right) > 0 = S(T), \quad 0 \leq t < T,$$

contradicting the continuity of  $S$  at  $T$ .

Part (b) follows from part (a). □

The next positivity result involves the per capita return rate  $\alpha$  in (2.7) of infected hosts into the susceptible class. Return into the susceptible class keeps the number of susceptible hosts away from zero provided there is some relation between the infectivity and the per capita return rate of infected hosts. See Theorem 2.7 and Example 2.8. Recall that we do not assume that  $\alpha \in L_+^\infty[0, b]$  (Section 2.6).

**Lemma 3.2.** *Let  $\kappa \in L_+^\infty[0, b]$  and  $\eta_0 \in (0, 1)$  such that*

$$\alpha(a) \geq \eta_0 \kappa(a), \quad \text{for a.a. } a \in [0, b]. \quad (3.20)$$

*Assume that there are  $c, \delta > 0$  such that*

$$\begin{aligned} S \in \mathbb{R}_+, w \in X_+, J &= \int_0^b \kappa(a)w(a)da, S + J \leq \delta \\ \implies f(S, w) &\leq cS + \eta_0 J. \end{aligned} \quad (3.21)$$

*Then, if  $T \in (0, \infty)$  and  $S, B$  is a continuous nonnegative solution of (2.7) on  $[0, T]$  and  $S(t) > 0$  for all  $t \in [0, T)$ , then  $S(T) > 0$ .*

*Proof.* Let  $T \in (0, \infty)$  and  $S(t) > 0$  for all  $t \in [0, T)$ . Suppose  $S(T) = 0$ .

By (3.20),

$$R(t) = \int_0^b \alpha(a)u(t, a)da \geq \int_0^b \eta_0 \kappa(a)u(t, a)da = \eta_0 J(t), \quad t \in [0, T]. \quad (3.22)$$

We integrate the differential equation for  $S$  in (2.7); for all  $t \in (0, T)$ ,

$$0 \geq S(T) - S(t) \geq \int_t^T S(s)g(S(s))ds - \int_t^T B(s)ds + \eta_0 \int_t^T J(s)ds.$$

We divide by  $T - t > 0$  and take the limit  $t \rightarrow T$ . Since  $S, J$  and  $B$  are continuous and  $J(T) \geq 0 = S(T)$ ,

$$0 \geq S(T)g(S(T)) - B(T) + \eta_0 J(T).$$

Since  $B(T) = f(S(T), u(T, \cdot)) = 0$ , we have  $J(T) = 0$ .

Since  $S$  and  $J$  are continuous, there is some  $s \in (0, T)$  such that  $S(t) + J(t) < \delta$  for all  $t \in [s, T]$  with  $\delta > 0$  from (3.21).

By (3.21) and (3.22),

$$f(S(t), u(t, \cdot)) \leq cS(t) + \eta_0 J(t) \leq cS(t) + R(t), \quad t \in [s, T].$$

By (2.7),

$$S'(t) \geq -cS(t) \text{ for almost all } t \in [s, T].$$

Hence  $S(T) \geq S(s)e^{c(s-T)} > 0$ , a contradiction.  $\square$

#### 4. Uniform weak persistence of susceptible hosts

Recall the definition of uniform weak persistence of susceptible hosts (Definition 1.6). The following persistence considerations are very much facilitated by using the Laplace transform.

Let  $S : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  be Borel measurable and be bounded or finitely integrable. Then

$$\hat{S}(\lambda) = \int_0^{\infty} e^{-\lambda t} S(t) dt, \quad \lambda > 0. \quad (4.1)$$

The Laplace transform is useful in this context because it converts convolutions into products.

Let  $B : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  be Borel measurable and be bounded or finitely integrable and  $\kappa \in L^1_+(\mathbb{R}_+)$ .

Then the convolution of  $B$  and  $\kappa$  is defined by

$$(B * \kappa)(t) = \int_0^t B(t-s)\kappa(s)ds, \quad t \in \mathbb{R}_+. \quad (4.2)$$

Respectively,  $B * \kappa$  is bounded or finitely integrable on  $\mathbb{R}_+$  and

$$\widehat{B * \kappa}(\lambda) = \hat{B}(\lambda)\hat{\kappa}(\lambda), \quad \lambda > 0. \quad (4.3)$$

See [74, Sec.2.2].

##### 4.1. Incidences that depend on the infection-age density in a general way

**Theorem 4.1.** *Let Assumption 2.4 be satisfied. Assume that for any  $c > 0$  there is some  $\tilde{c} > 0$  such that  $f(S, w) \leq \tilde{c}S$  for all  $S \in [0, c]$  and all  $w \in X_+$  with  $\|w\|_1 = \int_0^b w(a)da \leq c$ . Further assume that*

$$\left(1 - \int_0^b \alpha(a)P(a)da\right) \limsup_{S, w \rightarrow 0} \frac{f(S, w)}{S} < g(0). \quad (4.4)$$

*Then the susceptible hosts persist uniformly weakly.*

Condition (4.4) is equivalent to the existence of some  $\delta \in (0, g(0))$  such that

$$\left(1 - \int_0^b \alpha(a)P(a)da\right) \frac{f(S, w)}{S} \leq g(0) - \delta, \quad 0 < S \leq \delta, \quad w \in X_+, \quad \|w\|_1 \leq \delta. \quad (4.5)$$

**Remark 4.2.** Under the assumptions of Theorem 4.1, for any  $S_0 \in (0, \infty)$  and any  $u_0 \in X_+$ , there exists a unique solution to (2.7) provided that  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  is Lipschitz continuous on bounded subsets of  $\mathbb{R}_+ \times X_+$ :

For any  $c \in (0, \infty)$ , there exists some  $\Lambda_c \in (0, \infty)$  (called a Lipschitz constant) such that

$$\begin{aligned} |f(S, w) - f(\tilde{S}, \tilde{w})| &\leq \Lambda_c(|S - \tilde{S}| + |w - \tilde{w}|), \\ S, \tilde{S} &\in [0, c], \quad w, \tilde{w} \in X_+, \quad \|w - \tilde{w}\|_1 \leq c. \end{aligned} \quad (4.6)$$

See Section 7.1.  $f$  is called Lipschitz continuous if there is some  $\Lambda = \Lambda_c$  that does not depend on  $c > 0$ .

*Proof of Theorem 4.1.* Suppose that the susceptible hosts do not persist uniformly weakly. Then, for any  $\epsilon > 0$ , there exists a solution with  $S(0) > 0$  and  $S^\infty < \epsilon$ . If  $b \in (0, \infty)$ , extend  $\alpha$  to  $\mathbb{R}_+$  by  $\alpha(a) = 0$  for  $a \in [b, \infty)$ . By assumption (4.5), there exists some  $\delta > 0$  (by making it smaller if needed) such that

$$\left(1 - \int_0^\infty \alpha(a)P(a)da\right) \frac{f(S, w)}{S} < g(\delta) - \delta, \quad S \in (0, \delta], \quad w \in X_+, \|w\|_1 \leq \delta. \quad (4.7)$$

Since the susceptible hosts do not persist uniformly weakly, there exists a solution with  $S(0) > 0$  and  $S^\infty < \epsilon$ . By (3.14), if  $\epsilon \in (0, \delta)$  is chosen small enough,  $S^\infty < \delta$ ,  $I^\infty < \delta$ ,  $I(t) = \int_0^b u(t, a)da$ . By Lemma 3.1,  $S(t) > 0$  for all  $t \geq 0$ . So there exists some  $r > 0$  such that  $0 < S(t) < \delta$  and  $I(t) < \delta$  for all  $t \geq r$ . We write some of the model equations in the form

$$S' = Sg(S) - B + R, \quad R(t) \geq \int_0^t \alpha(a)P(a)B(t-a)da. \quad (4.8)$$

We introduce the translations  $S_r(t) = S(r+t)$ ,  $B_r(t) = B(r+t)$ ,  $I_r(t) = I(r+t)$  for  $r, t \geq 0$ . Further  $x(t) \in X_+$  is defined by  $x(t)(a) = u(t, a)$  for  $t \geq 0$ ,  $a \in [0, b)$  and  $x_r(t) = x(r+t)$  for  $t, r \geq 0$ . Notice that  $I_r(t) = \|x_r(t)\|_1$ . By (4.8), since  $B$  is nonnegative,

$$\begin{aligned} \delta &\geq S_r(t), \|x_r(t)\|_1, \quad t \geq 0, & S'_r &= S_r g(S_r) - B_r + R_r, \\ R_r(t) &\geq \int_0^t \alpha(a)P(a)B_r(t-a)da. \end{aligned} \quad (4.9)$$

We take Laplace transforms which convert convolutions into products, (4.3),

$$\hat{S}_r(\lambda) = \int_0^\infty e^{-\lambda t} S_r(t) dt, \quad \lambda > 0.$$

For all  $\lambda > 0$ ,

$$\lambda \hat{S}_r(\lambda) \geq S_r \widehat{g(S_r)}(\lambda) - \hat{B}_r(\lambda) + \hat{R}_r(\lambda), \quad \hat{R}_r(\lambda) \geq \widehat{\alpha P}(\lambda) \hat{B}_r(\lambda).$$

We substitute the second inequality into the first,

$$\lambda \hat{S}_r(\lambda) \geq S_r \widehat{g(S_r)}(\lambda) - (1 - \widehat{\alpha P}(\lambda)) \hat{B}_r(\lambda). \quad (4.10)$$

Since  $S_r(t), \|x_r(t)\|_1 \leq \delta$  and  $S_r(t) > 0$  for all  $t \geq 0$ ,

$$\begin{aligned} \hat{B}_r(\lambda) &= \int_0^\infty e^{-\lambda t} S_r(t) \frac{f(S_r(t), x_r(t))}{S_r(t)} dt \\ &\leq \hat{S}_r(\lambda) \sup_{t \geq 0} \frac{f(S_r(t), x_r(t))}{S_r(t)} \leq \hat{S}_r(\lambda) \sup_{0 < S \leq \delta, \|w\|_1 \leq \delta} \frac{f(S, w)}{S}. \end{aligned}$$

Similarly, since  $g$  is decreasing,

$$S_r \widehat{g(S_r)}(\lambda) \geq \hat{S}_r(\lambda) g(\delta), \quad \lambda > 0.$$

We substitute these inequalities into (4.10) and divide by  $0 < \hat{S}_r(\lambda) < \infty$ ,

$$\lambda \geq g(\delta) - (1 - \widehat{\alpha P}(\lambda)) \sup_{0 < S \leq \delta, \|w\|_1 \leq \delta} \frac{f(S, w)}{S}, \quad \lambda > 0.$$

This inequality does not depend on the solution of our system and holds for all  $\lambda > 0$ . We take the limit of this inequality as  $\lambda \rightarrow 0$ ,

$$0 \geq g(\delta) - \left(1 - \int_0^\infty \alpha(a)P(a)da\right) \sup_{0 < S \leq \delta, 0 \leq \|w\|_1 \leq \delta} \frac{f(S, w)}{S} \geq \delta > 0,$$

with the last, contradictory, inequality following from (4.7).  $\square$

Corollary 2.5 is a consequence of Theorem 4.1.

**Remark 4.3.** If  $f(S, w) = S^q J^p$ ,  $J = \int_0^b \kappa(a)w(a)da$ ,  $0 < q < 1$ ,  $p > 0$ ,  $\kappa \in L^\infty[0, b]$ ,  $\|\kappa\|_\infty > 0$ , then

$$\limsup_{S, w \rightarrow 0} \frac{f(S, w)}{S} = \infty.$$

So this power incidence function does not satisfy (4.4) and Theorem 4.1 does not apply. Compare Example 2.8 which will follow from our next next persistence result (Theorem 4.4).

*Proof.* Choose a sequence  $(w_n)$  in  $X_+ = L_+^1[0, b)$  with

$$0 < J_n \rightarrow 0, \quad n \rightarrow \infty, \quad J_n = \int_0^b \kappa(a)w_n(a)da.$$

This is possible because  $\|\kappa\|_\infty > 0$ . Choose  $S_n = J_n^r$  with some  $r > 0$  to be chosen later. Then

$$\frac{f(S_n, J_n)}{S_n} = S_n^{q-1} J_n = J_n^{r(q-1)+1}.$$

If  $r > 0$  is chosen large enough,  $r(q-1)+1 < 0$  and the right hand side of the last inequality tends to infinity as  $n \rightarrow \infty$ .  $\square$

Remark 4.3 motivates the next general persistence result.

**Theorem 4.4.** Assume that any continuous nonnegative solutions  $S, B$  of (2.7 with  $S(0) > 0$  satisfies  $S(t_n) > 0$  for a sequence  $(t_n)$  in  $\mathbb{R}_+$  with  $t_n \rightarrow \infty$  as  $n \rightarrow \infty$ .

Assume there is some  $\zeta \in (0, \infty)$  with the following properties:

(i) For any  $\eta > 0$  there exists some  $\tilde{\epsilon} > 0$  such that

$$\begin{aligned} S \in \mathbb{R}_+, w \in X_+, \quad S + \|w\|_1 \leq \tilde{\epsilon} \\ \implies f(S, w) \leq (\zeta + \eta)S + \eta R, \quad R = \int_0^b \alpha(a)w(a)da; \end{aligned} \quad (4.11)$$

(ii)

$$\zeta \left(1 - \int_0^b \alpha(a)P(a)da\right) < g(0). \quad (4.12)$$

Then the susceptible hosts persist uniformly weakly.

Notice that, by  $\gamma = -P'/P$  and  $P(0) = 1$ ,

$$1 - \int_0^b \alpha(a)P(a)da = \int_0^b [\gamma(a) - \alpha(a)]P(a)da > 0. \quad (4.13)$$

*Proof.* If  $b \in (0, \infty)$ , we extend  $\alpha : [0, b) \rightarrow \mathbb{R}_+$  to  $\mathbb{R}_+$  by  $\alpha(a) = 0$  for  $a \in [b, \infty)$ . By (4.12), there is some  $\delta \in (0, 1) \cap (0, g(0))$ , such that

$$(\zeta + \delta)\left(1 - (1 - \delta) \int_0^\infty \alpha(a)P(a)da\right) < g(\delta) - \delta. \quad (4.14)$$

We write some of the model equations in the form

$$\begin{aligned} S' &= Sg(S) - B + \delta R + (1 - \delta)R \text{ a.e.}, \\ R(t) &= \int_0^b \alpha(a)u(t, a)da \geq \int_0^t \alpha(a)P(a)B(t - a)da. \end{aligned} \quad (4.15)$$

Suppose that the susceptibles do not persist uniformly weakly.

Then, for arbitrary  $\epsilon > 0$ , which can be chosen as small as needed to generate a contradiction, there exists a solution such that  $S(0) > 0$  and  $S^\infty < \epsilon$ . By assumption,  $S(t_n) > 0$  for a sequence  $(t_n)$  with  $t_n \rightarrow \infty$  as  $n \rightarrow \infty$ . By (3.14),

$$(S + I)^\infty < \frac{\epsilon}{\nu}[g(0) + \nu]. \quad (4.16)$$

We can assume  $\epsilon < \delta$ . See (4.14). There exists  $r > 0$  ( $r = t_n$  for some sufficiently large  $n$ ) such that  $S(r) > 0$  and

$$0 < S(t) < \epsilon, \quad I(t) = \|u(t, \cdot)\|_1 < \frac{\epsilon}{\nu}[g(0) + \nu], \quad t \geq r, \quad (4.17)$$

We introduce that translations  $S_r(t) = S(r + t)$ ,  $R_r(t) = R(r + t)$ ,  $B_r(t) = B(r + t)$  for  $r, t \geq 0$ . By (4.15),

$$\begin{aligned} S'_r &\geq S_r g(\delta) - B_r + \delta R_r + (1 - \delta)R_r \text{ a.e.}, \\ R_r(t) &\geq \int_0^t \alpha(a)P(a)B_r(t - a)da. \end{aligned} \quad (4.18)$$

We take Laplace transforms which convert convolutions into products. For all  $\lambda > 0$ , we obtain

$$\hat{R}_r(\lambda) \geq \hat{B}_r(\lambda)\widehat{\alpha P}(\lambda) \quad (4.19)$$

and

$$\lambda \hat{S}_r(\lambda) \geq \hat{S}_r(\lambda)g(\delta) - \hat{B}_r(\lambda)(1 - (1 - \delta)\widehat{\alpha P}) + \delta \hat{R}_r(\lambda). \quad (4.20)$$

By (4.11) there exists some  $\tilde{\epsilon} > 0$  such that

$$f(S, w) \leq (\zeta + \eta)S + \eta R, \quad S, \|w\|_1 \in [0, \tilde{\epsilon}]. \quad (4.21)$$

Let  $\epsilon \in (0, \tilde{\epsilon})$  and  $\frac{\epsilon}{\nu}[g(0) + \nu] < \tilde{\epsilon}$ . By (4.17), for all  $t \geq 0$ ,  $0 < S_r(t) < \tilde{\epsilon}$  and  $I_r(t) < \tilde{\epsilon}$  and, by (4.21),

$$B_r(t) \leq (\zeta + \eta)S_r(t) + \eta R_r(t).$$

Since the Laplace transform is a linear operation,

$$\hat{B}_r(\lambda) \leq (\zeta + \eta)\hat{S}_r(\lambda) + \eta\hat{R}_r(\lambda).$$



We substitute this inequality into (4.20),

$$\lambda \hat{S}_r(\lambda) \geq \hat{S}_r(\lambda)g(\epsilon) - ((\zeta + \eta)\hat{S}_r - \eta\hat{R}_r(\lambda))(1 - (1 - \delta)\widehat{\alpha P}) + \eta\hat{R}_r(\lambda).$$

This implies

$$\lambda \hat{S}_r(\lambda) \geq \hat{S}_r(\lambda)g(\epsilon) - ((\zeta + \eta)\hat{S}_r(\lambda))(1 - (1 - \delta)\widehat{\alpha P}). \quad (4.22)$$

Since  $\hat{S}_r(\lambda) > 0$  because  $S_r(0) > 0$ , we can divide by it,

$$\lambda \geq g(\epsilon) - ((\zeta + \eta))(1 - (1 - \delta)\widehat{\alpha P}). \quad (4.23)$$

Now, this inequality holds for any  $\lambda > 0$  and so it holds in the limit  $\lambda = 0$ ,

$$0 \geq g(\epsilon) - (\zeta + \eta)(1 - (1 - \delta) \int_0^\infty \alpha(a)P(a)da). \quad (4.24)$$

Since  $\epsilon \leq \delta$  and  $\eta \leq \delta$ , this inequality contradicts inequality (4.14).  $\square$

We combine Lemma 3.2 and Theorem 4.4.

**Corollary 4.5.** *Let  $\kappa \in L_+^\infty[0, b]$  and  $\eta_0 \in (0, 1)$  such that*

$$\alpha(a) \geq \eta_0 \kappa(a), \quad \text{for a.a. } a \in [0, b]. \quad (4.25)$$

*Assume there is some  $\zeta \in (0, \infty)$  with the following properties:*

(a) *For any  $\check{\eta} > 0$  there exists some  $\check{\epsilon} > 0$  such that*

$$\begin{aligned} S \in \mathbb{R}_+, w \in X_+, \quad S + J \leq \check{\epsilon}, \quad J = \int_0^b \kappa(a)w(a)da \\ \implies f(S, w) \leq (\zeta + \check{\eta})S + \check{\eta}J; \end{aligned}$$

(b)

$$\zeta \left(1 - \int_0^b \alpha(a)P(a)da\right) < g(0).$$

*Then the susceptible hosts persist uniformly weakly.*

*Proof.* Observe that for all  $w \in X_+$ , we have  $J \leq \|\kappa\|_\infty \|w\|_1$  and, by (4.25),  $\int_0^b \alpha(a)w(a)da = R \geq \eta_0 J$ .

Some tedious but elementary considerations then show that the assumptions (a) and (b) imply the assumptions of Lemma 3.2 and Theorem 4.4.

Lemma 3.2 implies that  $S(0) > 0$  implies  $S(t) > 0$  for all  $t > 0$  for all solutions of (2.7) on  $\mathbb{R}_+$ . Apply Theorem 4.4.  $\square$

#### 4.2. Incidences depending on susceptibles and one infective impact only

We assume that

$$f(S, w) = \check{f}(S, J), \quad S \in \mathbb{R}_+, w \in X_+, \quad J = \int_0^b \kappa(a)w(a)da, \quad (4.26)$$

where  $\kappa \in L_+^\infty[0, b]$ ,

$$\check{f}(0, J) = 0, \quad J \in \mathbb{R}_+. \quad (4.27)$$

Then the partial derivative  $0 = \partial_2 f(0, 0)$  with respect to  $J$  exists.

**Corollary 4.6.** Assume that the partial derivative  $\partial_1 \check{f}$  with respect to  $S$  exists on  $\mathbb{R}_+^2$  and is bounded on bounded subsets of  $\mathbb{R}_+$  and is continuous at  $(0, 0)$  with

$$\left(1 - \int_0^b \alpha(a)P(a)da\right) \partial_1 \check{f}(0, 0) < g(0). \quad (4.28)$$

Then the susceptible hosts persists uniformly weakly.

*Proof.* By the mean value theorem, for  $S > 0$  and  $J \geq 0$ ,

$$\frac{\check{f}(S, J)}{S} = \partial_1 \check{f}(\tilde{S}, J) \quad (4.29)$$

with some  $\tilde{S} \in (0, S)$ . Let  $c > 0$ . Since  $\partial_1 \check{f}$  is bounded on bounded sets, there exists some  $\tilde{c} > 0$  such that  $\partial_1 \check{f}(\tilde{S}, J) \leq \tilde{c}$  for all  $\tilde{S}, J \in [0, c]$ . By (4.29),  $\check{f}(S, J) \leq \tilde{c}S$  for all  $S, J \in [0, c]$ . Since  $\partial_1 \check{f}$  is assumed to be continuous at  $(0, 0)$ ,

$$\frac{\check{f}(S, J)}{S} \rightarrow \partial_1 \check{f}(0, 0), \quad S, J \rightarrow 0,$$

and (4.28) implies (4.4). The assertion now follows from Theorem 4.1.  $\square$

*Proof of Theorem 2.7.* The assumptions of Corollary 4.5 are satisfied with  $\zeta = \partial_1 \check{f}(0, 0) = 0$ .  $\square$

## 5. The constant risk incidence

The constant risk incidence has the form

$$f(S, w) = \sigma S, \quad S, w \in X_+. \quad (5.1)$$

This means that the per capita risk of a susceptible host to be infected does not depend on the number of infected hosts. It is the only incidence that is differentiable at  $(0, 0)$  and is positively homogeneous of degree 1. The constant risk incidence is a simplistic way to model an infection reservoir. Surprisingly, it did not fare so bad in the fits in [1] of the infection experiments in [25] as one might expect. As unrealistic as constant risk may appear, we consider this incidence in order to put our other results into perspective and to present an example in which our persistence results are sharp. Notice that the constant risk incidence is infinitely often differentiable and has the partial derivatives

$$\partial_1 f(S, w) = \sigma, \quad \partial_2 f(S, w) = 0. \quad (5.2)$$

As a special case of Corollary 2.5 or 4.6 we obtain the following result.

**Theorem 5.1.** Let  $g(0) > \sigma \left(1 - \int_0^\infty \alpha(a)P(a)da\right)$ . Then the susceptible hosts persist uniformly weakly.

In the following we show that this result is sharp. The system (2.10) decouples

$$\begin{aligned} S' &= S g(S) - \sigma S + R(t), \\ R(t) &= \int_0^t \alpha(a) \sigma S(t-a) P(a) da + R_0(t), \\ R_0(t) &= \int_0^b \alpha(s+t) u_0(s) \frac{P(s+t)}{P(s)} ds. \end{aligned} \quad (5.3)$$

The equation for the infected hosts takes the form

$$\begin{aligned} I(t) &= \int_0^t \sigma S(t-a)P(a)da + I_0(t), \\ I_0(t) &= \int_0^\infty u_0(s) \frac{P(s+t)}{P(s)} ds. \end{aligned} \quad (5.4)$$

Since the solutions are bounded by (3.9), we can apply the fluctuation method [75] [45, Prop.A.22]: There exists a sequence  $(t_n)$  with  $t_n \rightarrow \infty$  and  $S(t_n) \rightarrow S^\infty$  and  $S'(t_n) \rightarrow 0$  as  $n \rightarrow \infty$ . This yields

$$0 = S^\infty g(S^\infty) - \sigma S^\infty + \lim_{n \rightarrow \infty} \int_0^{t_n} \alpha(a) \sigma S(t_n - a) P(a) da + \limsup_{n \rightarrow \infty} R_0(t_n).$$

By the Lebesgue-Fatou's lemma [45, p.468],

$$0 \leq S^\infty g(S^\infty) - \sigma S^\infty + \int_0^\infty \alpha(a) \sigma \limsup_{n \rightarrow \infty} S(t_n - a) P(a) da + R_0^\infty.$$

Now  $\limsup_{n \rightarrow \infty} S(t_n - a) \leq S^\infty$  for any  $a \geq 0$ . If  $b < \infty$ ,  $R_0(t) = 0$  for  $t \geq b$ . If  $\alpha$  is bounded,  $R_0(t_n) \rightarrow 0$  as  $n \rightarrow \infty$  by the almost everywhere version of the dominated convergence theorem [70, Thm.4.9]. In either case,

$$0 \leq S^\infty \left( g(S^\infty) - \sigma + \sigma \int_0^\infty \alpha(a) P(a) da \right). \quad (5.5)$$

Recall (2.14),

$$\wp = \int_0^\infty \alpha(a) P(a) da \leq 1 - \nu D,$$

where  $D$  is the expected sojourn time in the infection period (natural death included). Remember that  $1/\nu > D$  is the life expectation of a healthy host.

**Theorem 5.2.** *Let  $g(0) \leq \sigma \left( 1 - \int_0^\infty \alpha(a) P(a) da \right)$  and let  $b < \infty$  or  $\alpha$  be bounded. Then the hosts die out.*

*Proof.* Suppose the susceptible hosts do not die out. Then  $S^\infty > 0$  and  $g(0) > g(S^\infty)$  and  $g(S^\infty) \geq \sigma \left( 1 - \int_0^\infty \alpha(a) P(a) da \right)$  by (5.5), a contradiction to the assumption of this theorem. So  $S^\infty = 0$ . Another application of Fatou's lemma, this time to (5.4), shows that  $I^\infty = 0$ .  $\square$

## 6. The special case of infection-age independence

If the rates  $\gamma$ ,  $\alpha$  and  $\kappa$  do not depend on infection-age, we have  $R(t) = \alpha I(t)$  and  $J(t) = \kappa I(t)$  with  $I$  given by (3.1), and  $P(a) = e^{-\gamma a}$ . The system (2.10) takes the form

$$\begin{aligned} S' &= S g(S) - \check{f}(S, \kappa I) + \alpha I, \\ I(t) &= \int_0^t e^{-\gamma(t-a)} \check{f}(S(a), \kappa I(a)) da + I_0(t), \\ I_0(t) &= e^{-\gamma t} \int_0^\infty u_0(s) ds. \end{aligned} \quad (6.1)$$

$S$  and  $I$  satisfy the ODE system

$$S' = Sg(S) - \check{f}(S, \kappa I) + \alpha I, \quad I' = \check{f}(S, \kappa I) - \gamma I, \quad (6.2)$$

with  $I(0) = \int_0^\infty u_0(a)da$  and  $S(0) = S_0$ . Theorem 2.9 now follows from [1, Thm.5.8]. In turn, any solution  $S, I$  of (6.2) can be written in the form of (6.1) with

$$I_0(t) = I(0)e^{-\gamma t} = e^{-\gamma t} \int_0^\infty u_0(s)ds, \quad u_0(s) = \gamma I(0)e^{-\gamma s}. \quad (6.3)$$

If  $\alpha > 0$ , by Example 2.8, we obtain that the susceptible hosts persist uniformly weakly in model (6.2). Actually, the persistence is uniform by [26, Exp.2.13].

## 7. Existence of solutions

We establish the existence of solutions to the model formulations in Section 2.3 and Section 2.4. The formulation in 2.3 is equivalent to the one in 2.2. Existence of solutions to the model formulations in Section 2.3 is proved under the assumption that the incidence function  $f : \mathbb{R}_+ \times L_+^1[0, b) \rightarrow \mathbb{R}_+$  is Lipschitz continuous on bounded subsets of its domain. The proof involves a fixed point argument within a fixed point argument.

Existence of solutions to the model formulations in Section 2.2 is proved in the case that  $f$  does not necessarily satisfy a Lipschitz condition but is of the special form

$$\begin{aligned} f(S, w) &= \check{f}(S, J), \quad J = \int_0^b \kappa(a)w(a)da, \quad \kappa \in L_+^\infty[0, b), \\ \check{f} : \mathbb{R}_+^2 &\rightarrow \mathbb{R}_+ \text{ continuous.} \end{aligned} \quad (7.1)$$

The proof for more infectious impacts than just  $J$  is similar.

### 7.1. Lotka version, incidence functions Lipschitz continuous on bounded sets

We rewrite (2.7) in integrated form,

$$\begin{aligned} S(t) &= \left[ S_0 + \int_0^t S(s)g(S(s))ds - \int_0^t B(s)ds + \int_0^t R(s)ds \right]_+, \\ R(t) &= \int_0^t \alpha(a)B(t-a)P(a)da + \int_0^b \alpha(r+t)u_0(r) \frac{P(r+t)}{P(r)} dr. \end{aligned} \quad (7.2)$$

Here,  $[\cdot]_+$  is the positive part of a real number  $r \in \mathbb{R}$ ,  $[r]_+ = \max\{r, 0\}$ , and is used because we want  $S(t) \geq 0$  whereas the right hand side may be negative. Further, we use the notation  $x(t)(a) = u(t, a)$ ,  $t, a \in \mathbb{R}_+$ ,  $x(t) \in X_+ = L_+^1[0, b)$ , for a more rigorous mathematical treatment,

$$\begin{aligned} B(t) &= f(S(t), x(t)), \quad x(t) \in L_+^1[0, b), \\ x(t)(a) &= \begin{cases} B(t-a)P(a), & 0 \leq a < t \\ u_0(a-t) \frac{P(a)}{P(a-t)}, & 0 \leq t < a \end{cases} \quad a \in [0, b). \end{aligned} \quad (7.3)$$

Notice that  $x(0) = u_0$  in  $L_+^1[0, b) = X_+$ . Our approach consists in considering this system as a fixed-point problem for  $S$  and  $B$  and apply the contraction mapping theorem (Banach's fixed point theorem). The subsystem (7.3) seems to make it difficult to apply the existence results for functional equations in [74, Sec.12.2]. We will deal with subsystem (7.3) as a fixed point problem within a fixed point problem (Section 7.1.1).

Then we will show that solutions to (7.2) and (7.3) are solutions to (2.7).

Our first step consists in eliminating  $R$  for the equation for  $S$  in (7.2). We change the order of integration,

$$\begin{aligned} \int_0^t R(s)ds &= \int_0^t \left( \int_0^s \alpha(s-r)P(s-r)B(r)dr \right) ds \\ &\quad + \int_0^t \left( \int_0^b \alpha(r+s)u_0(r) \frac{P(r+s)}{P(r)} dr \right) ds \\ &= \int_0^t \left( \int_r^t \alpha(s-r)P(s-r)ds \right) B(r)dr \\ &\quad + \int_0^b (u_0(r)/P(r)) \left( \int_0^t \alpha(r+s)P(r+s)ds \right) dr. \end{aligned}$$

After a substitution,

$$\int_0^t R(s)ds = \int_0^t A(t-r)B(r)dr + v_0(t) \quad (7.4)$$

with

$$\begin{aligned} A(t) &= \int_0^t \alpha(s)P(s)ds, & v_0(t) &= \int_0^b u_0(r)\tilde{A}(t,r)dr, \\ \tilde{A}(t,r) &= (1/P(r)) \int_r^{t+r} \alpha(s)P(s)ds, & 0 \leq r, t. \end{aligned}$$

Since  $\alpha(s) \leq \gamma(s) = -P'(s)/P(s)$ ,

$$A(t) \leq 1 - P(t), \quad \tilde{A}(t,r) \leq 1. \quad (7.5)$$

We substitute (7.4) into (7.2),

$$S(t) = \left[ S_0 + \int_0^t S(s)g(S(s))ds - \int_0^t (1 - A(t-s))B(s)ds + v_0(t) \right]_+ \quad (7.6)$$

where  $B$  satisfies (7.3).

In the next two sections, we will find solutions  $S$  and  $B$  to (7.6) and (7.3) by a fixed point argument. We will first assume that the incidence function  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  is Lipschitz continuous rather than just Lipschitz continuous on bounded subsets (Remark 4.2). The argument will then be extended to incidence functions that are Lipschitz continuous on bounded subsets in Section 7.1.3 by using retractions, and solutions to the original system (2.7) will be established.

### 7.1.1. Lipschitz continuous incidence functions: the incidence, a fixed point problem within a fixed point problem

Let  $u_0 \in L_+^1[0, b) = X_+$  be fixed. For given  $S$ , we treat (7.3) as a fixed point problem for  $B$  and then study how  $B$  depends on  $S$ .

Let  $T \in (0, \infty)$ . Consider the vector space  $C[0, T]$  of real-valued continuous functions on  $[0, T]$  and let  $C_+[0, T]$  be the cone on non-negative continuous functions.

**Lemma 7.1.** For given  $B \in C_+[0, T]$ ,  $x(t)$ ,  $t \in [0, T]$ , in (7.3) is an element in  $L_+^1[0, b)$  and

$$\|x(t)\|_1 \leq \int_0^t B(s)ds + \|u_0\|_1, \quad 0 \leq t < \infty. \quad (7.7)$$

Further,  $x : [0, T] \rightarrow L_+^1[0, b) = X_+$  in (7.3) is a continuous function of  $t \in [0, T]$  with values in  $L_+^1[0, b)$ .

*Proof.* If  $b \in (0, \infty)$ , we extend  $u_0 \in L_+^1[0, b)$  from  $[0, b)$  to  $[0, \infty)$  by  $u_0(a) = 0$  for  $t \in [b, \infty)$ . The extended  $u_0$  is an element of  $L_+^1[0, \infty)$ . We also define  $\frac{u_0}{P}(a) = 0$  for  $a \in [b, \infty)$ . To show the continuity (cf. [2]), we let  $t \in [0, T]$  and  $(t_n)$  and  $(s_n)$  be sequences in  $[0, T]$  with  $t_n, s_n \rightarrow t$  and  $s_n \leq t_n$  for all  $n \in \mathbb{N}$  and show that  $\|x(t_n) - x(s_n)\|_1 \rightarrow 0$  as  $n \rightarrow \infty$ . Indeed, for each  $n \in \mathbb{N}$ ,

$$\begin{aligned} \|x(t_n) - x(s_n)\|_1 &\leq \int_0^{s_n} |B(t_n - a) - B(s_n - a)|P(a)da \\ &\quad + \int_{s_n}^{t_n} B(t_n - a)P(a)da + \int_{s_n}^{t_n} \frac{u_0(a - s_n)}{P(a - s_n)}P(a)da \\ &\quad + \int_{t_n}^{\infty} \left| \frac{u_0(a - t_n)}{P(a - t_n)} - \frac{u_0(a - s_n)}{P(a - s_n)} \right| P(a)da. \end{aligned}$$

Since  $P$  is decreasing and takes values in  $[0, 1]$ , after some changes of variables,

$$\begin{aligned} \|x(t_n) - x(s_n)\|_1 &\leq \int_0^{s_n} |B(t_n - s_n + a) - B(a)|da \\ &\quad + \int_0^{t_n - s_n} B(a)da + \int_0^{t_n - s_n} u_0(a)da \\ &\quad + \int_{t_n}^{\infty} \left| \frac{u_0}{P}(a - t_n) - \frac{u_0}{P}(a - s_n) \right| P(a)da. \end{aligned}$$

As  $n \rightarrow \infty$  and  $t_n, s_n \rightarrow t$ , all these integrals converge to 0 except possibly the last one. By the triangle inequality, the last integral satisfies

$$\begin{aligned} &\leq \int_{t_n}^{\infty} |u_0(a - t_n) - u_0(a - s_n)|P(a)da \\ &\quad + \int_{t_n \wedge b}^b u_0(a - t_n) \left| \frac{1}{P(a - t_n)} - \frac{1}{P(a - s_n)} \right| P(a)da, \end{aligned}$$

with  $t_n \wedge b = \min\{t_n, b\}$ . After some changes of variables, this expression can be estimated by

$$\begin{aligned} &\leq \int_0^{\infty} |u_0(a) - u_0(a + t_n - s_n)|da \\ &\quad + \int_0^{[b - t_n]_+} u_0(a) \left| \frac{1}{P(a)} - \frac{1}{P(a + t_n - s_n)} \right| P(a + t_n)da. \end{aligned}$$

The first integral tends to 0 because  $u_0 \in L_1(\mathbb{R}_+)$  [76, X.1], and the second by the a.e. dominated convergence theorem. Since  $P$  is decreasing and bounded,  $P$  is continuous a.e. and the integrands in the second integral tend to 0 for a.e.  $a \geq 0$ . Further, the integrands are dominated by the finitely integrable function  $2u_0$ .  $\square$

In order to obtain a strict contraction for the fixed point problem (7.3), we consider exponentially weighted supremum norms on  $C[0, T]$ . Cf. [77, Sec.3.3] [46, Sec.9.1.2]. For  $\lambda \in (0, \infty)$  (the “weight” of the norm), let

$$\|B\|_\lambda = \sup_{t \in [0, T]} e^{-\lambda t} |B(t)|, \quad B \in C[0, T]. \quad (7.8)$$

For  $\lambda = 0$ , this is the supremum norm. One readily checks that  $\|\cdot\|_\lambda$  is a norm on  $C[0, T]$ . Since  $e^{-\lambda T} \|B\|_0 \leq \|B\|_\lambda \leq \|B\|_0$ ,  $\|\cdot\|_\lambda$  is equivalent to the supremum norm, and  $C[0, T]$  is a Banach space under  $\|\cdot\|_\lambda$  and  $C_+[0, T]$  is a complete metric space under the metric induced by  $\|\cdot\|_\lambda$ .

We also assume that  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  is Lipschitz continuous (Remark 4.2). In Section 7.1.3, we will extend the existence proof to cover incidence functions that are only Lipschitz continuous on bounded sets.

**Lemma 7.2.** *Let  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  be Lipschitz continuous (Remark 4.2). Let  $T \in (0, \infty)$  and  $S \in C_+[0, T]$  and  $u_0 \in X_+$  be given. Then the equation (7.3) has a unique solution  $B = \beta(S) \in C_+[0, T]$  which is a Lipschitz continuous function of  $S$ . Further, the function  $x : [0, T] \rightarrow L_+^1[0, b)$  defined by (7.3) is continuous.*

*Further, if  $\Lambda > 0$  is a Lipschitz constant for  $f$  and  $\lambda > \Lambda$ , then*

$$\|\beta(S) - \beta(\tilde{S})\|_\lambda \leq \frac{\Lambda \lambda}{\lambda - \Lambda} \|S - \tilde{S}\|_\lambda, \quad S, \tilde{S} \in C_+[0, T]. \quad (7.9)$$

*Proof.* Let  $S \in C_+[0, T]$  be given. Let  $F_S : C_+[0, T] \rightarrow C_+[0, T]$  be defined by

$$F_S(B)(t) = f(S(t), x(t)) \quad (7.10)$$

where

$$x(t)(a) = \begin{cases} B(t-a)P(a), & 0 \leq a < t, \\ u_0(a-t) \frac{P(a)}{P(a-t)}, & 0 \leq t < a. \end{cases} \quad 0 \leq a < b. \quad (7.11)$$

Then  $x : [0, T] \rightarrow L_+^1[0, b)$  is continuous [2] (Lemma 7.1) and  $F_S$  maps  $C_+[0, T]$  into itself by Lemma 7.1.  $F_S$  will turn out to be a strict contraction and the solution  $B$  of (7.3) its fixed point. Let  $B, \tilde{B} \in C[0, T]$  and  $\tilde{x} \in L_+^1[0, b)$  be given by (7.11) with  $\tilde{B}$  replacing  $B$ . By (7.11),

$$\|x(t) - \tilde{x}(t)\|_1 \leq \int_0^t |B(t-a) - \tilde{B}(t-a)| P(a) da. \quad (7.12)$$

By (7.10),

$$|F_S(B)(t) - F_S(\tilde{B})(t)| = |f(S(t), x(t)) - f(S(t), \tilde{x}(t))|.$$

Let  $\Lambda > 0$  be a Lipschitz constant for  $f$ ; for  $t \in [0, T]$ ,

$$\begin{aligned} |F_S(B)(t) - F_S(\tilde{B})(t)| &\leq \Lambda \|x(t) - \tilde{x}(t)\|_1 \\ &\leq \Lambda \int_0^t |B(t-a) - \tilde{B}(t-a)| P(a) da \leq \Lambda \int_0^t |B(t-a) - \tilde{B}(t-a)| da. \end{aligned} \quad (7.13)$$

Here, we have used that  $P(a) \leq 1$  for all  $a \in \mathbb{R}_+$ . As mentioned above, the norm  $\|\cdot\|_\lambda$  defined in (7.8) is equivalent to the supremum norm on  $C[0, T]$  and thus makes  $C_+[0, T]$  a complete metric space. By (7.13),

$$\|F_S(B) - F_S(\tilde{B})\|_\lambda = \|f(S, x) - f(S, \tilde{x})\|_\lambda \leq \frac{\Lambda}{\lambda} \|B - \tilde{B}\|_\lambda. \quad (7.14)$$

So, for  $\lambda > \Lambda$ ,  $F_S$  becomes a strict contraction with respect to  $\|\cdot\|_\lambda$  and has a fixed point

$$B = \beta(S) = f(S, x) \in C_+[0, T], \quad (7.15)$$

which solves (7.3).

To show (7.9), let  $S, \tilde{S} \in C_+[0, T]$  and  $B = \beta(S)$  and  $\tilde{B} = \beta(\tilde{S})$ . For all  $t \in [0, T]$ ,

$$|B(t) - \tilde{B}(t)| = |f(S(t), x(t)) - f(\tilde{S}(t), \tilde{x}(t))| \leq \Lambda |S(t) - \tilde{S}(t)| + \Lambda \|x(t) - \tilde{x}(t)\|_1,$$

where  $\tilde{x}$  is given by (7.11) with  $\tilde{B}$  replacing  $B$ . By (7.11),

$$|B(t) - \tilde{B}(t)| \leq \Lambda |S(t) - \tilde{S}(t)| + \Lambda \int_0^t |B(t-a) - \tilde{B}(t-a)| da.$$

By (7.8),

$$\|B - \tilde{B}\|_\lambda \leq \Lambda \|S - \tilde{S}\|_\lambda + (\Lambda/\lambda) \|B - \tilde{B}\|_\lambda.$$

We solve this inequality for  $\|B - \tilde{B}\|_\lambda$  and obtain (7.9).  $\square$

### 7.1.2. Finishing the full fixed point problem for Lipschitz continuous incidence function

Let  $T > 0$ . On  $[0, T]$ , using  $\beta : C_+[0, T] \rightarrow C_+[0, T]$  from Lemma 7.2, (7.6) becomes

$$\begin{aligned} S(t) &= \left[ S_0 + \int_0^t S(s)g(S(s))ds - \int_0^t (1 - A(t-s))\beta(S)(s)ds + v_0(t) \right]_+ \\ &=: \tilde{F}(S)(t), \quad t \in [0, T]. \end{aligned} \quad (7.16)$$

Assume that  $s \mapsto sg(s)$  is Lipschitz continuous from  $\mathbb{R}_+$  to  $\mathbb{R}_+$  with a Lipschitz constant  $\tilde{\Lambda}$ . By Lemma 7.2, for  $S, \tilde{S} \in C_+[0, T]$ ,

$$\|\tilde{F}(S) - \tilde{F}(\tilde{S})\|_\lambda \leq \frac{\tilde{\Lambda}}{\lambda} \|S - \tilde{S}\|_\lambda + \lambda^{-1} \|\beta(S) - \beta(\tilde{S})\|_\lambda \leq \left( \frac{\tilde{\Lambda}}{\lambda} + \frac{\Lambda}{\lambda - \Lambda} \right) \|S - \tilde{S}\|_\lambda.$$

By choosing  $\lambda > 0$  large enough,  $\tilde{F}$  becomes a strict contraction on  $C_+[0, T]$  under  $\|\cdot\|_\lambda$  and has a unique fixed point  $S$  by Banach's fixed point theorem, which is a unique solution of (7.16) on  $[0, T]$ . Since our arguments did not depend on  $T \in (0, \infty)$ , we find a unique solution of (7.16) on  $[0, T]$  for every  $T \in (0, \infty)$ .

Notice that a solution of (7.16) on  $[0, T]$  is also a solution of (7.16) on  $[0, \tilde{T}]$  for any  $\tilde{T} \in (0, T)$ . Since the solutions are unique, the restriction of the solution on  $[0, T]$  to the subinterval  $[0, \tilde{T}]$ ,  $\tilde{T} < T$ , is the unique solution on  $[0, \tilde{T}]$ .

Then we also have a unique solution  $S, B$  of (7.16) on  $[0, \infty)$  and thus of (7.6) and of (7.2) with (7.3).

Let us summarize what we have established so far.



**Proposition 7.3.** Assume that  $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  is Lipschitz continuous, there exists some  $\Lambda \in (0, \infty)$  such that

$$|f(S, w) - f(\tilde{S}, \tilde{w})| \leq \Lambda(|S - \tilde{S}| + \|w - \tilde{w}\|_1), \quad S, \tilde{S} \in \mathbb{R}_+, \quad w, \tilde{w} \in X_+. \quad (7.17)$$

Assume that  $s \mapsto sg(s)$  is Lipschitz continuous from  $\mathbb{R}_+$  to  $\mathbb{R}_+$ .

Then, for any  $S_0 \in (0, \infty)$  and  $u_0 \in X_+$ , there exists a unique solution  $S, B : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  of (7.2) and (7.3).

### 7.1.3. Incidence functions Lipschitz continuous on bounded subsets

Unfortunately, many incidence functions are not Lipschitz continuous, but only Lipschitz continuous on bounded subsets of  $\mathbb{R}_+ \times X_+$  (Remark 4.2).

**Theorem 7.4.** Assume that  $g$  is Lipschitz continuous on every bounded subset of  $\mathbb{R}_+$  and that  $f$  is Lipschitz continuous on every bounded subset of  $\mathbb{R}_+ \times X_+$  (Remark 4.2). Further, assume that  $f$  satisfies the following additional assumption: For any  $c_1 > 1$  there is some  $c_2 > 0$  such that

$$f(S, w) \leq c_2 S, \quad 0 \leq S, \|w\|_1 \leq c_1. \quad (7.18)$$

Then, for any  $S_0 \in (0, \infty)$  and  $u_0 \in X_+$ , there exists a unique solution  $S, B : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  of (2.7) with  $S(t) > 0$  for all  $t \geq 0$ .

**Remark 7.5.** The assumption involving (7.18) can be replaced by the assumptions of Lemma 3.2.

*Proof.* Guided by the a priori estimates in Section 3.1, we proceed as follows.

Let  $S_0 > 0$  and  $u_0 \in X_+$ . Set

$$c = \max \left\{ H(0), K + 1, \frac{1}{\nu} \max_{0 \leq S \leq K} S(g(S) + \nu) \right\}, \quad H(0) = S_0 + \|u_0\|_1. \quad (7.19)$$

We define the retraction  $\xi_c : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+ \times X_+$  by

$$\xi_c(S, w) = \begin{cases} (S, x), & |S| + \|w\|_1 \leq c, \\ \frac{c}{S + \|w\|_1}(S, w), & |S| + \|w\|_1 \geq c. \end{cases} \quad (7.20)$$

By the proof of [78, Lem.19.8].  $\xi_c$  is Lipschitz continuous with a Lipschitz constant 2. Further,  $\xi_c$  maps  $\mathbb{R}_+ \times X_+$  into a bounded subset of itself.

We define  $f_c = f \circ \xi_c$  on  $\mathbb{R}_+ \times X_+$  with  $c$  in (7.19). Since  $f$  is Lipschitz continuous on bounded subsets of  $\mathbb{R}_+ \times X_+$ ,  $f_c$  is Lipschitz continuous on  $\mathbb{R}_+ \times X_+$  and  $f_c(S, w) = f(S, w)$  if  $S \in \mathbb{R}_+$ ,  $w \in X_+$  and  $S + \|w\|_1 \leq c$ .

Further, we define  $g_c : \mathbb{R}_+ \rightarrow \mathbb{R}$  by

$$g_c(S) = \max\{g(S), g(c)\}, \quad S \in \mathbb{R}_+. \quad (7.21)$$

Since  $g$  is decreasing,  $g_c(S) = g(S)$  for  $S \in [0, c]$  and  $g_c(S) = g(c)$  for  $S \geq c$ . Then  $g_c$  also satisfies the Assumptions 2.4, but in addition  $S \mapsto Sg_c(S)$  is Lipschitz continuous on  $\mathbb{R}_+$  with  $c\Lambda_c + |g(c)|$  being a Lipschitz constant for  $S \mapsto Sg_c$  on  $\mathbb{R}_+$  where  $\Lambda_c$  is a Lipschitz constant for  $g$  on  $[0, c]$ .

By Proposition 7.3, (7.2) and (7.3) with  $f$  replaced by  $f_c$  and  $g$  replaced by  $g_c$ , has a unique solution  $S, B$  on  $[0, \infty)$  with  $S(t) \geq 0$  and  $B(t) \geq 0$  for all  $t > 0$ .

Suppose that  $S(t) > 0$  does not hold for all  $t > 0$ . Then there exists some  $T > 0$  such that

$$S(t) > 0, \quad t \in [0, T], \quad \text{and } S(T) = 0. \quad (7.22)$$

By (7.2),

$$S(t) = S_0 + \int_0^t S(s)g_c(S(s))ds - \int_0^t B(s)ds + \int_0^t R(s)ds, \quad t \in [0, T].$$

Then  $S$  is absolutely continuous on  $[0, T]$  and

$$S'(t) = S(t)g_c(S(t)) - B(t) + R(t), \quad B(t) = f_c(S(t), x(t)) \quad \text{for a.a. } t \in [0, T].$$

Our a priori estimates in Section 3 also hold for the modified equation on  $\mathbb{R}_+$  because they were independent of the incidence function and

$$\frac{1}{\nu} \max_{0 \leq S \leq K} S(g(S) + \nu)$$

does not change if  $g$  is replaced by  $g_c$  because  $c \geq K + 1$  by (7.19). This implies that  $S(t) + \|x(t)\|_1 \leq c$  for  $t \in [0, T]$ . So  $S$  and  $B$  are solutions of the original system (2.7) with  $g$  and  $f$  on  $[0, T]$ . Then  $S(T) > 0$  by Lemma 3.1. This is a contradiction to (7.22) and so  $S(t) > 0$  for all  $t > 0$ .

(Alternatively, one argues with Remark 7.5 and Lemma 3.2.)

By repeating the previous argument on  $[0, \infty)$  instead of  $[0, T]$ ,  $S$  and  $u(t, \cdot) = x(t)$  satisfy the a priori estimates in Section 3.1 on  $\mathbb{R}_+$  and are solutions of the original system (2.7) with  $g$  on  $f$  on  $\mathbb{R}_+$  and  $S(t) > 0$  and  $B(t) \geq 0$  for all  $t \geq 0$ .  $\square$

## 7.2. Incidence functions not Lipschitz continuous on bounded sets

With the contraction mapping theorem no longer at our disposal, we consider the Volterra equations formulation of our system (Section 2.4), which is a special case of the Lotka formulation (Section 2.3). For ease of presentation, we only consider one infectious impact, but the case of finitely many infectious impacts can be done analogously. Let

$$f(S, w) = \check{f}(S, J), \quad J = \int_0^b \kappa(a)w(a)da, \quad \kappa \in L_+^\infty[0, b], \quad (7.23)$$

$$\check{f} : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+ \text{ continuous.}$$

Since we want to cover  $\check{f}(S, J) = S^q J^p$  with  $q, p > 0$ ,  $p + q > 1$  and  $p < 1$  or  $q < 1$ , we do not assume that  $\check{f}$  is Lipschitz continuous on bounded subsets of  $\mathbb{R}_+^2$ .

We could try to use some appropriate version of Schauder's or Tychonov's fixed point theorem [79, Thm.8.8,10.1] or to check the assumptions of the existence results for functional equations in [74, Sec.12.2]. Instead, we take advantage of the work we did for Lipschitz continuous incidence functions and use an approximation procedure and Arzela-Ascoli type arguments [70, Sec.8.3]. Notice that we do not assume that  $\alpha \in L_+^\infty[0, b)$ . See Section 2.6. This will lead to some technical complications.

Choose a sequence  $\check{f}_n : \mathbb{R}_+^2 \rightarrow \mathbb{R}_+$ ,  $n \in \mathbb{N}$ , that are Lipschitz continuous and  $\check{f}_n \rightarrow \check{f}$  as  $n \rightarrow \infty$  uniformly on bounded subsets of  $\mathbb{R}_+^2$ . This is possible by the following result.

Let  $M$  be a metric space with metric  $d$ . For a function  $\check{f} : M \rightarrow \mathbb{R}_+$ , define the sequence  $(\check{f}_n)$  of functions  $\check{f}_n : M \rightarrow \mathbb{R}_+$  by

$$\check{f}_n(x) = \inf \{ \check{f}(y) + nd(x, y); y \in M \}, \quad x \in M, n \in \mathbb{N}. \quad (7.24)$$

[80, Thm.3.13] [81].

**Proposition 7.6.**  $(\check{f}_n)$  is an increasing sequence of bounded Lipschitz continuous functions (with  $n$  being a Lipschitz constant of  $\check{f}_n$ ) such that  $\inf \check{f} \leq \check{f}_n \leq \check{f}$  for all  $n \in \mathbb{N}$ . The following convergence results hold.

- (a) If  $\check{f}$  is lower semi-continuous on  $M$ ,  $\check{f}_n \rightarrow \check{f}$  pointwise on  $M$ .  
 (b) If  $\check{f} \in C_+(M)$ ,  $\check{f}_n \rightarrow \check{f}$  uniformly on compact subsets of  $M$ .

Part (b) follows from part (a) by Dini's lemma. [82, p.225].

We choose  $c \in (0, \infty)$  as in (7.19) and set  $g_c$  as in (7.21). Notice that the functions  $f_n : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}_+$  given by

$$f_n(S, w) = \check{f}_n(S, J), \quad J = \int_0^b \kappa(a)w(a)da, \quad n \in \mathbb{N}, S \in \mathbb{R}_+, w \in X_+,$$

are Lipschitz continuous on  $\mathbb{R}_+ \times X_+$ . By Proposition 7.3, in the Volterra equations formulation (Section 2.4), there are solutions  $S_n, B_n : \mathbb{R}_+ \rightarrow \mathbb{R}_+$  such that

$$\begin{aligned} S_n(t) &= \left[ S_0 + \int_0^t S_n(s)g_c(S(s))ds - \int_0^t B_n(s)ds + \int_0^t R_n(s)ds \right]_+, \\ R_n(t) &= \int_0^t \alpha(a)B_n(t-a)P(a)da + R_0(t), \quad n \in \mathbb{N}, \\ R_0(t) &= \int_0^b \alpha(r+t)u_0(r) \frac{P(r+t)}{P(r)} dr, \end{aligned} \quad (7.25)$$

$$\begin{aligned} B_n(t) &= \check{f}_n(S(t), J_n(t)), \\ J_n(t) &= \int_0^t \kappa(a)B_n(t-a)P(a)da + J_0(t), \quad n \in \mathbb{N}, \\ J_0(t) &= \int_0^b \alpha(r+t)u_0(r) \frac{P(r+t)}{P(r)} dr. \end{aligned} \quad (7.26)$$

**Theorem 7.7.** Let  $g$  be Lipschitz continuous on bounded sets. Assume that there is some  $\eta_0 \in (0, 1)$  such that

$$\alpha(a) \geq \eta_0 \kappa(a), \quad a \in [0, b]. \quad (7.27)$$

Further, assume that there are  $c, \delta > 0$  such that

$$\check{f}(S, J) \leq cS + \eta_0 J, \quad S, J \geq 0, S + J \leq \delta. \quad (7.28)$$

Then, for each  $S_0 > 0$  and  $u_0 \in X_+$ , there exists solution to the model equations on  $\mathbb{R}_+$  with  $S(t) > 0$  and  $J(t) \geq 0$  for all  $t \geq 0$ .

*Proof.* Since  $\check{f}_n \leq \check{f}$ , the approximations  $\check{f}_n$  inherit the inequality (7.28). Arguing as in the proof of Theorem 7.4, using Lemma 3.2, we have

$$0 < S_n(t) = S_0 + \int_0^t S_n(s)g_c(S(s))ds - \int_0^t B_n(s)ds + \int_0^t R_n(s)ds, \quad t \in \mathbb{R}_+. \quad (7.29)$$

These solutions satisfy the a priori estimates in Section 3.1, which do not depend on the incidence functions. So  $\{S_n(t); t \in \mathbb{R}_+, n \in \mathbb{N}\}$  is a bounded subset of  $\mathbb{R}_+$  and  $\{x_n(t); n \in \mathbb{N}, t \in \mathbb{R}_+\}$  is a bounded subset of  $L^1_+[0, b)$ .

Since  $\check{f}_n \leq \check{f}$  and  $\check{f}$  is bounded on bounded subsets of  $\mathbb{R}_+^2$ ,  $\{B_n(t); t \in \mathbb{R}_+, n \in \mathbb{N}\}$  is a bounded subset of  $\mathbb{R}_+$ .

By (7.29),  $\{S_n : \mathbb{R}_+ \rightarrow \mathbb{R}_+; n \in \mathbb{N}\}$  is equicontinuous. Also,  $\{S_n(t) \in \mathbb{N}, t \in \mathbb{R}_+\}$  has compact closure in  $\mathbb{R}_+$ .

By [70, Thm.8.5], after choosing subsequences, we get  $S_n \rightarrow S$ ,  $S : \mathbb{R}_+ \rightarrow \mathbb{R}_+$ , as  $n \rightarrow \infty$ , uniformly on bounded subsets of  $\mathbb{R}^n$ .

Let  $r \in \mathbb{R}_+$  and  $0 \leq r \leq s \leq t$ . After a substitution,

$$\begin{aligned} & R_n(t) - R_n(r) - (R_0(t) - R_0(r)) \\ &= \int_0^t \alpha(t-a)P(t-a)B_n(a)da - \int_0^r \alpha(r-a)P(r-a)B_n(a)da. \end{aligned}$$

By the triangle inequality,

$$\begin{aligned} & |R_n(t) - R(t) - (R_n(r) - R_0(r))| \\ &= \left| \int_0^t \alpha(t-a)P(t-a)B_n(a)da - \int_0^r \alpha(r-a)P(r-a)B_n(a)da \right| \\ &\leq \tilde{c} \int_0^r |\alpha(t-a)P(t-a) - \alpha(r-a)P(r-a)|da + \tilde{c} \int_r^t \alpha(t-a)P(t-a)da, \end{aligned}$$

with some  $\tilde{c} \in (0, \infty)$  that does not depend on  $n$ . Since  $\int_0^\infty \alpha(a)P(a)da \leq 1$  (2.18), the last expression goes to zero as  $t - r \rightarrow 0$  [76, X.1] and does not depend on  $n$ .

So  $\{R_n - R_0; n \in \mathbb{N}\}$  is equicontinuous. Also,  $\{R_n(t) - R_0(t); n \in \mathbb{N}, t \geq 0\}$  are bounded subsets of  $\mathbb{R}$ .

After choosing subsequences, using [70, Thm.8.5],  $R_n \rightarrow R$  as  $n \rightarrow \infty$  uniformly on bounded subsets of  $\mathbb{R}_+$  for some measurable  $R$  on  $\mathbb{R}_+$ . Similarly,  $J_n \rightarrow J$  as  $n \rightarrow \infty$  uniformly on bounded subsets of  $\mathbb{R}_+$  for some measurable  $J$  on  $\mathbb{R}_+$ .

By (7.29),  $\{\tilde{S}_n; n \in \mathbb{N}\}$  with  $\tilde{S}_n(t) = S_n(t) - \int_0^t R_n(s)ds$  is equicontinuous and  $\{\tilde{S}_n(t); n \in \mathbb{N}, t \geq 0\}$  is bounded. After choosing subsequences again, using [70, Thm.8.5] once more,  $\tilde{S}_n \rightarrow \tilde{S}$  as  $n \rightarrow \infty$  uniformly on bounded subsets of  $\mathbb{R}_+$  with a continuous function  $\tilde{S}$ . So  $S_n(t) \rightarrow \tilde{S}(t) + \int_0^t R(s)ds$  as  $n \rightarrow \infty$  uniformly for  $t$  in bounded subsets of  $\mathbb{R}_+$ .

Since the solutions satisfy the a priori estimates of Section 3.1 and  $\check{f}_n \rightarrow \check{f}$  uniformly on bounded subsets of  $\mathbb{R}_+^2$ ,  $B_n = \check{f}_n(S_n, J_n) \rightarrow \check{f}(S, J) =: B$  as  $n \rightarrow \infty$  uniformly on bounded subsets of  $\mathbb{R}$ . Notice that the equations are also satisfied with  $g$  replacing  $g_c$ .

Now we can take limits as  $n \rightarrow \infty$  in (7.25) and (7.26) and obtain

$$\begin{aligned} S(t) &= S_0 + \int_0^t S(s)g(S(s))ds - \int_0^t B(s)ds + \int_0^t R(s)ds, \\ R(t) &= \int_0^t \alpha(a)B(t-a)P(a)da + \int_0^b \alpha(r+t)u_0(r)\frac{P(r+t)}{P(r)}dr. \\ B(t) &= \check{f}(S(t), J(t)), \\ J(t) &= \int_0^t \kappa(a)B(t-a)P(a)da + \int_0^b \kappa(r+t)u_0(r)\frac{P(r+t)}{P(r)}dr. \end{aligned}$$

This is the Volterra equations formulation of our model system (Section 2.4).  $\square$

## 8. Discussion

In this paper, we discuss the fundamental question of whether infectious diseases can drive their host population into extinction.

Previous work [1, 26], using planar SIS type ODEs, shows that this is never the case (in a deterministic setting) if the incidence function is of the generalized density-dependent type (unless the population is subject to an Allee effect or there is a disease reservoir) but that it can happen for generalized frequency-dependent incidence functions.

The choice of general incidence functions is motivated by the fact that density-dependent incidence and frequency-dependent incidence fit the infection experiments for salamander larvae and ranavirus badly.

The results are largely the same whether or not infected individuals can become susceptible again. An exception is the power incidence  $f(S, J) = S^q I^p$  with  $p, q > 0$ ,  $p + q > 1$  and  $q < 1$ .

If infected individuals do not become susceptible again, there is initial-value dependent extinction of the host (Theorem 2.9), but if some infected individuals become susceptible again, the host persists uniformly weakly.

This paper discusses whether the previous results still hold if, more realistically and in the spirit of Kermack and McKendrick [3, 31, 32], infected individuals do not leave the infected stage at a constant per capita rate (exponentially distributed length of the infected stage) but at a per capita rate that depends on infection-age (time since the moment of infection) and if the infectivity of an infected individual also depends on its infection-age.

The findings are that the previous results essentially extend to generalizations of density-dependent incidence functions. Generalizations of frequency-dependent incidence functions were not considered because there are too many different ways to combine frequency-dependence and infection-age.

For certain power incidences, it is sufficient for uniform weak host persistence that, at any infection-age  $a$ , if some infected individuals are infectious at age  $a$  there are also some infected individuals that leave the infected class at age  $a$  and become susceptible again (Example 2.8). This condition seems to be difficult to verify biologically, though it may hold for some diseases. The ODE results show that, mathematically, this assumption cannot be dropped completely (Theorem 2.9). The question is to what degree it is necessary. We could not answer this question analytically; perhaps numerical simulations of some well-chosen special cases can give some insight in the future.

We also mention that, for the host population dynamics, it is assumed (as in [2, 26]) that infected individuals do not give birth and do not compete for resources. This somewhat extreme assumption has been made for mathematical convenience; it allows us to consider the problem in terms of the number of susceptibles and the disease incidence.

### 8.1. Uniform host persistence

In this paper, the survival of the susceptible host population is established in the form of uniform weak persistence and not in the form of the more desirable uniform persistence (see Section 1.6).

The weaker form could be proved because a convenient tool for doing this is available, the Laplace transform. Routes from uniform weak to uniform persistence are described in [46, Chap.4]. Direct routes to uniform persistence can be found in [50, Sec.1.3].

However one proceeds in proving uniform persistence, it is useful to show that the solutions induce a semiflow on  $\mathbb{R}_+ \times X_+$ . This would be facilitated by the uniqueness of solutions, e.g., by the Lipschitz continuity assumptions made in Section 7.2. One can use the model formulation in Section 2.3 and proceed as in [46, Sec.9.4] for the special case of density-dependent incidence. Alternatively, one can interpret the model formulation in Section 2.2 as a Cauchy problem with a non-densely defined operator and use the theory of integrated semigroups [83, 84]. Further, something like a compact attractor is helpful [46, 49, 50]. This should be possible to obtain if the model can be formulated as Volterra integral equations (Section 2.4) proceeding similarly as in the special case of a density-dependent incidence in [46, 9.5].

We conjecture that the uniform persistence of susceptible hosts holds in Theorem 2.7 if  $g$  and  $\check{f}$  are Lipschitz continuous on bounded subsets of  $\mathbb{R}_+$  and  $\mathbb{R}_+^2$ , respectively. We do not know whether the uniform persistence of susceptible hosts holds in Example 2.8, because the incidence function is not Lipschitz continuous in the neighborhood of  $(0, 0)$  and it is difficult to show that the solutions induce a semiflow because they may not be uniquely determined by the initial data.

### Use of AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

### Conflict of interest

The authors declare no conflict of interest.

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## Appendix: A chain rule

**Lemma 8.1.** *Let  $f : [0, b) \rightarrow I \subseteq \mathbb{R}$  be absolutely continuous and  $g : I \rightarrow \mathbb{R}$  be continuously differentiable.*

*Then  $g \circ f$  is absolutely continuous and  $(g \circ f)'(x) = g'(f(x))f'(x)$  for almost all  $x \in [a, b)$ .*

*Proof.* Let  $\tilde{b} \in [0, b)$ . For  $n \in \mathbb{N}$  with  $1/n < b - \tilde{b}$  and  $x \in [0, \tilde{b}]$ , define

$$f_n(x) = n \int_x^{x+(1/n)} f(y)dy = \int_0^1 f(x + (z/n))dz.$$

Then  $f_n$  is continuously differentiable and

$$f'_n(x) = n(f(x + (1/n)) - f(x)) = n \int_x^{x+(1/n)} f'(y)dy = \int_0^1 f'(x + (z/n))dy.$$

Since  $f'$  is finitely integrable.

$$f'_n \rightarrow f', \quad n \rightarrow \infty, \quad a.e.$$

By the chain rule,  $g \circ f_n$  is continuously differentiable and

$$(g \circ f_n)'(x) = g'(f_n(x))f'_n(x).$$

Further,  $f_n(x) \rightarrow f(x)$  as  $n \rightarrow \infty$ . So

$$g(f(x)) - g(f(0)) = \lim_{n \rightarrow \infty} g(f_n(x)) - g(f_n(0)) = \lim_{n \rightarrow \infty} \int_0^x g'(f_n(y))f'_n(y)dy.$$

As for the last expression,

$$\begin{aligned} & \left| \int_0^x g'(f_n(y))f'_n(y)dy - \int_0^x g'(f(y))f'(y)dy \right| \\ & \leq \int_0^x |g'(f_n(y)) - g'(f(y))| |f'_n(y)|dy + \int_0^x |g'(f(y))| |f'(y) - f'_n(y)|dy. \end{aligned}$$

The first expression tends to 0 because  $f_n \rightarrow f$  as  $n \rightarrow \infty$  uniformly on  $[0, x]$  and  $g'$  is uniformly continuous on bounded closed intervals and thus  $g'(f_n(y)) \rightarrow g'(f(y))$  uniformly on  $[0, x]$ . As for the second expression,

$$\begin{aligned} & \int_0^x |g'(f(y))| |f'(y) - f'_n(y)|dy \leq c \int_0^x \left| \int_0^1 (f'(y) - f'(y + (z/n)))dz \right| dy \\ & \leq c \int_0^1 \left( \int_0^x |f'(y) - f'(y + (z/n))|dy \right) dz. \end{aligned}$$

For each  $x$ ,

$$\int_0^x |f'(y) - f'(y + (z/n))|dy \rightarrow 0, \quad n \rightarrow \infty,$$

because  $f'$  is finitely integrable on every subinterval of  $[0, b)$ . By the dominated convergence theorem, it remains to show that these expressions that depend on  $n$  can be dominated by an integrable function. Indeed, for all  $z \in [0, 1]$  and all  $n \in \mathbb{N}$  with  $x + (1/n) < b$ .

$$\begin{aligned} 0 & \leq \int_0^x |f'(y) - f'(y + (z/n))|dy \leq \int_0^x |f'(y)|dy + \int_0^x |f'(y + (z/n))|dy \\ & \leq \int_0^x |f'(y)|dy + \int_{z/n}^{x+(z/n)} |f'(y)|dy \leq 2 \int_0^b |f'(y)|dy. \quad \square \end{aligned}$$

