

Infinite ODE Systems Modeling Size-Structured Metapopulations, Macroparasitic Diseases, and Prion Proliferation

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Summary. Infinite systems of ordinary differential equations can describe:

- Spatially implicit metapopulation models with discrete patch-size structure
- Host-macroparasite models that distinguish hosts by their parasite loads
- Prion proliferation models that distinguish protease-resistant protein aggregates by the number of prion units they contain

It is the aim of this chapter to develop a theory for infinite ODE systems in sufficient generality (based on operator semigroups) and, besides well-posedness, to establish conditions for the solution semiflow to be dissipative and have a compact attractor for bounded sets. For metapopulations, we present conditions for uniform persistence on the one hand and prove on the other hand that a metapopulation dies out, if there is no emigration from birth patches or if empty patches are not colonized.

2.1 Introduction

Infinite systems of ordinary differential equations,

$$\begin{aligned} w' &= f(t, w, x), \\ x'_j &= \sum_{k=0}^{\infty} \alpha_{jk} x_k + g_j(t, w, x), \quad j = 0, 1, 2, \dots \end{aligned} \tag{2.1}$$

where $x(t)$ is the sequence of functions $(x_j(t))_{j=0}^{\infty}$, can describe:

- Spatially implicit metapopulation models with discrete patch-size structure [2, 5, 7, 38, 42]
- Host-macroparasite models which distinguish hosts by their parasite loads [6, 13, 24, 25, 33, 34, 48, 49]
- Prion proliferation models which distinguish protease-resistant protein aggregates by the number of prion units they contain [41, 45]

Spatially Implicit Metapopulation Models

A metapopulation is a group of populations of the same species which occupy separate areas (patches) and are connected by dispersal. Each separate population in the metapopulation is referred to as a local population. Metapopulations occur naturally or by human activity as a result of habitat loss and fragmentation.

In system (2.1), x_j denotes the number of patches with j occupants and w the average number of migrating individuals, or wanderers. The coefficients α_{jk} describe the transition from patches with k occupants to patches with j occupants due to deaths, births and emigration of occupants. The function f gives the rate of change of the number of dispersers due to patch emigration, immigration and disperser death. The functions g_j describe the rate of change of the numbers of patches with j occupants due to the immigration of dispersers. The coefficients α_{jk} have the properties typical for infinite transition matrices in stochastic processes with continuous time and discrete state (continuous-time birth and death chains, e.g., see [1] and the references therein). Since they form an unbounded set, existence and uniqueness of solutions to (2.1) is non-trivial. It is the aim of this chapter to develop a this-related theory in sufficient generality and also establish conditions for the solution semiflow to be dissipative [26], have a compact attractor for bounded sets [26, 52], and be uniformly persistent [5, 27, 56, 58]. We also prove that a metapopulation dies out, if nobody emigrates from its birth patch or if empty patches are not colonized.

It is worth mentioning that, though the linear special case $x'_j = \sum_{k=0}^{\infty} \alpha_{jk} x_k$ can be interpreted as a stochastic model for a population that is not distributed over patches [39], the model (2.1) is a deterministic model. It inherits the property though that subpopulations on individual patches can become extinct at finite time which is an important feature of real metapopulations. As a trade-off, the metapopulation model (2.1) is spatially implicit and not able to take spatial heterogeneities into account. A spatially explicit metapopulation model would be a finite system of ordinary differential equations $y'_j = \sum_{k=1}^N d_{jk} y_k + f_j(t, y)$, $j = 1, \dots, N$, where N is the number of patches and y_j the size of the local population on patch j . The coefficients d_{jk} would describe the movement from patch k to patch j and the non-linearities f_j the local demographics on patch j due to births and deaths. An example of a spatially explicit metapopulation model (underlying an epidemic model) can be found in Chap. 4. Spatially explicit models can take account of how

the patches are situated relatively to each other and of differences between the patches, but do not have the property that a local population can become extinct in finite time. The most basic spatially implicit metapopulation model is the Levins model [36, 37] which only considers empty and occupied patches. Incorporating a structure which distinguishes between patches according to local population size makes it possible, e.g., to compare emigration strategies which are based on how crowded a patch is [38].

Alternatively, spatially implicit metapopulation models can be structured by a continuous rather than a discrete variable. This leads to non-local partial differential equations or integral equations [23]. The partial differential equations one obtains are similar to those considered in Chap. 1, but have non-linear terms in the derivative with respect to the size-structure variable. For general information on mathematical metapopulation theory we refer to [20, 28, 38].

Host-Macroparasite Models

The connection between metapopulation and host-macroparasite models is not incidental as a macroparasite population is a metapopulation with the hosts being the patches and the parasites in single hosts forming the local populations. In the epidemiology of infectious diseases, the Levins metapopulation model corresponds to a prevalence model that only considers susceptible and infective individuals. Such models (possibly after adding classes which take account of incubation and immunity) are quite adequate for microparasitic (viral, bacterial, fungal) diseases where the infectious agents multiply rapidly and it basically only matters whether a host is infectious or not. Macroparasitic (worm, e.g.) diseases, however, are characterized by highly variable parasite loads in individual hosts with very different effects on host health. Models like (2.1), called density models in [13], can take these into account with x_j denoting the number of hosts with j parasites and w denoting the average number of free-living parasites. The coefficients α_{jk} describe the transition from hosts with k parasites to hosts with j parasites due to deaths, births and release of parasites. The function f gives the rate of change of the number of free-living parasites due to death and the entry into or exit from hosts. The functions g_j describe the rate of change of the numbers of hosts with j parasites due to the acquisition of parasites from the pool of free-living parasites.

Since parasite loads often depend on the age of the host, host age has been included into density models [6, 13, 24, 25, 34, 49]. This leads to an infinite system of partial differential equations. The analysis of these models uses moment generating functions. The use of a generating function would convert the system (2.1) into a single partial differential equation. An infinite system of partial differential equations incorporating age dependence would also be converted into a single partial differential equation, however with one more

variable and partial derivative. This approach yields impressive and illuminating results, but requires the transition matrix to correspond to a simple birth and death process (possibly with catastrophes). Levins type metapopulation models with patch age have been considered in [19].

Models for Prion Proliferation

Prion proteins have been linked to fatal diseases called transmissible spongiform encephalopathies (TSE) including Creutzfeldt–Jakob disease (CJD), kuru, scrapie, and bovine spongiform encephalopathy (BSE, “mad cow disease”). The prion diseases in an individual host are associated with the accumulation of single prion proteins (monomers) into prion protein aggregates (polymers). An aggregate is a stringlike formation possibly containing several thousand units with each unit being a former monomer. Monomers are considered healthy because they can easily be degraded by proteinase while polymers are much more proteinase-resistant and are neurotoxic. The system (2.1), with some modification, covers the models of prion proliferation suggested in [41, 45]. Since a detailed derivation of a special metapopulation model can already be found in [38] (cf. Sect. 2.12), we explain the prion model in some more detail here.

The amount of aggregates which contain j prion units (former monomers) is represented by x_j while the amount of (healthy) prion monomers is w . We assume that aggregates grow by adding one monomer at a time, the respective rate is σ_j for an aggregate to grow from j to $j + 1$ units. This process is sometimes called polymerization. An aggregate of size k can break into two pieces of sizes j and $k - j$: the respective per unit rate is b_{jk} if $j \leq k - j$ and $b_{k-j,k}$ if $j \geq k - j$. Aggregates of size j are chemically degraded at a rate κ_j while single monomers are degraded at a rate δ . Monomers are produced at a constant rate Λ . The model in [41] has the form

$$\begin{aligned} w' &= \Lambda - w \sum_{k=1}^{\infty} \sigma_k x_k - \delta w, \\ x_j' &= w(\sigma_{j-1} x_{j-1} - \sigma_j x_j) - \kappa_j x_j + \sum_{k=j+1}^{\infty} (b_{jk} + b_{k-j,k}) x_k - x_j \sum_{k=1}^{j-1} b_{kj}, \\ j &= 1, 2, \dots, \quad \sigma_0 = 0. \end{aligned} \tag{2.2}$$

Notice that the polymerization rate is of mass action type as it involves the product of the amount of monomers w and the amount of polymers containing $j - 1$ or j units respectively. There is no equation for x_0 because aggregates containing 0 units do not exist, differently from empty patches in metapopulations or hosts without worms in macroparasite diseases. To fit (2.2) into (2.1), without an x_0 -equation, we set

$$\alpha_{jk} = \begin{cases} b_{jk} + b_{k-j,k}, & 1 \leq j \leq k-1, \\ -\kappa_k - \sum_{i=1}^{k-1} b_{ik}, & 1 \leq j = k, \\ 0, & j > k \geq 1. \end{cases} \quad (2.3)$$

The model in [45] (see also [41, App.A]) allows for the fact that small aggregates below a certain minimum size, m , are unstable. So, if an aggregate splits and one of the pieces has a size less than m , it immediately disintegrates into monomers,

$$\begin{aligned} w' &= \Lambda - w \sum_{k=1}^{\infty} \sigma_k x_k - \delta w + \sum_{j=1}^{m-1} j \sum_{k=m}^{\infty} (b_{jk} + b_{j-k,k}) x_k, \\ x_j' &= w(\sigma_{j-1} x_{j-1} - \sigma_j x_j) - \kappa_j x_j + \sum_{k=j+1}^{\infty} (b_{jk} + b_{k-j,k}) x_k - x_j \sum_{k=1}^{j-1} b_{kj}, \\ j &= m, m+1, \dots, \quad \sigma_{m-1} = 0. \end{aligned} \quad (2.4)$$

The system (2.1) can be adapted to this model by striking the equations for x_0, \dots, x_{m-1} and defining the coefficients $(\alpha_{jk})_{j,k=m}^{\infty}$ as in (2.3) with the modification that $j \geq m$ and $k \geq m$. Analogous models where the amount of units in an aggregate are modeled by a continuous rather than a discrete variable have been considered in [15, 21, 35, 47, 53, 61]. Saturation effects in polymerization have been incorporated in [22].

The system (2.4) includes the special case that b_{jk} is constant for $1 < m \leq j < k$ which may be a reasonable approximation of reality, while the assumption that b_{jk} is constant for $1 \leq j < k$ is clearly unrealistic. This special case allows a moment closure which reduces the infinite system of ODEs to a system of three ODEs which can be completely analyzed (cf. [47]). Since we consider the case of variable b_{jk} here, it is not clear whether to favor system (2.2) or system (2.4). Notice that there is another conceptual difference between the systems. System (2.2) distinguishes between monomers which have been part of an aggregate before (in other words aggregates consisting of one unit), represented by the variable x_1 , and the “virgin” monomers represented by w . Only virgin monomers are attached to the aggregates. Such a distinction between monomers and single unit aggregates is not made in system (2.4) where the monomers resulting from aggregate disintegration return to the monomer class represented by w . A drawback of system (2.4) may be that it could be very difficult to assign a specific value to m . Thinking along the lines that polymer splitting can result in complete disintegration, it seems to be more realistic (and mathematically more difficult) to assume that for each $j \in \mathbb{N}$ there is a probability $q_j \in [0, 1]$ of a piece of j units to disintegrate into monomers after polymer splitting,

$$\begin{aligned}
w' &= \Lambda - w \sum_{k=1}^{\infty} \sigma_k x_k - \delta w + \sum_{j=1}^{\infty} j q_j \sum_{k=j+1}^{\infty} (b_{jk} + b_{j-k,k}) x_k, \\
x'_j &= w(\sigma_{j-1} x_{j-1} - \sigma_j x_j) - \kappa_j x_j \\
&\quad + (1 - q_j) \sum_{k=j+1}^{\infty} (b_{jk} + b_{k-j,k}) x_k - x_j \sum_{k=1}^{j-1} b_k, \\
j &= 1, 2, \dots, \quad \sigma_0 = 0.
\end{aligned} \tag{2.5}$$

Obviously this system encompasses the two previous ones.

Outline of the Mathematical Approach

For the mathematical treatment of (2.1), we choose a somewhat more abstract approach than the ones in [2] and [5] from which we have received much inspiration in order to include a variety of models (in Sect. 2.12 and [38] we assume that only juveniles migrate) and to include state transitions which are not of nearest-neighbor type like in the prion proliferation models. The biological interpretation (restricted here to metapopulation and host-macroparasite systems) gives us guidance how to choose the appropriate state space. Assuming that meaningful solutions are non-negative, the number of patches (hosts) is given by $\sum_{j=0}^{\infty} x_j$ and the number of occupants (in-host parasites) by $\sum_{j=1}^{\infty} j x_j$. Recall the sequence space

$$\ell^1 = \left\{ (x_j)_{j=0}^{\infty}; x_j \in \mathbb{R}, \sum_{j=0}^{\infty} |x_j| < \infty \right\} \tag{2.6}$$

with norm

$$\|x\| = \sum_{j=0}^{\infty} |x_j|, \quad x = (x_j)_{j=0}^{\infty}. \tag{2.7}$$

We introduce the subspace

$$\ell^{11} = \left\{ (x_j)_{j=0}^{\infty}; x_j \in \mathbb{R}, \sum_{j=0}^{\infty} j |x_j| < \infty \right\} \tag{2.8}$$

which becomes a Banach space of its own under the norm

$$\|x\|_1 = \sum_{j=0}^{\infty} (1+j) |x_j|, \quad x = (x_j)_{j=0}^{\infty}. \tag{2.9}$$

Other, equivalent, choices are possible, of course. We treat (2.1) as a semilinear operator differential equation

$$w' = f(t, w, x), \quad x' = A_1 x + g(t, w, x)$$

on the non-negative cone of the Banach space $\mathbb{R} \times \ell^{11}$ where A_1 is the infinitesimal generator of a positive C_0 -semigroup on ℓ^{11} and the functions f and $g(\sqcup) = (g_j(\sqcup))_{j=0}^\infty$ are locally Lipschitz continuous.

The main body of the chapter is structured as follows.

- 2.2. The homogeneous linear system: Kolmogorov's differential equation
- 2.3. Solution to the semilinear system
- 2.4. General metapopulation models and boundedness of solutions
- 2.5. Extinction without migration or colonization of empty patches
- 2.6. A more specific metapopulation model
- 2.7. Compact attractors
- 2.8. Towards the stability of equilibria
- 2.9. Instability of every other equilibrium: general result
- 2.10. Existence of equilibria and instability of every other equilibrium
- 2.11. Stability of the extinction equilibrium versus metapopulation persistence
- 2.12. Application to special metapopulation models
- 2.13. Special host-macroparasite models and existence of solutions
- 2.14. Application to prion proliferation
 - A. Non-differentiability of the simple birth process semigroup

2.2 The Homogeneous Linear System: Kolmogorov's Differential Equation

The linear special case of (2.1),

$$x'_j = \sum_{k=0}^{\infty} \alpha_{jk} x_k, \quad j \in \mathbb{Z}_+, \quad (2.10)$$

is known as Kolmogorov's differential equation [31] and has been widely studied [17, XVII.9] [18, XIV.7] [29, Sects. 23.10–23.12] [16, 30, 50, 51]. See [4] and [59] for more references. We write \mathbb{Z}_+ for the set of non-negative integers and \mathbb{N} for the natural numbers starting at 1, $\mathbb{Z}_+ = \mathbb{N} \cup \{0\}$. We review results proved in [39].

Assumption 1 We make the following assumptions concerning the coefficients α_{jk} , $j, k \in \mathbb{Z}_+$.

(a) $\alpha_{jj} \leq 0 \leq \alpha_{jk}, \quad k \neq j.$

(b) $\alpha^\diamond := \sup_{k=0}^\infty \sum_{j=0}^\infty \alpha_{jk} < \infty.$

(c) There exist constants $c_0, c_1 > 0, \epsilon > 0$ such that

$$\sum_{j=1}^{\infty} j \alpha_{jk} \leq c_0 + c_1 k - \epsilon |\alpha_{kk}| \quad \forall k \in \mathbb{Z}_+.$$

Notice that the sequence $|\alpha_{jj}|$ may be unbounded and is so in many applications. Let ℓ^1 denote the Banach space of real sequences $x = (x_k)_{k=0}^{\infty}$ with $\|x\| := \sum_{k=0}^{\infty} |x_k| < \infty$. ℓ_+^1 denotes the cone of non-negative sequences in ℓ^1 .

Recall that a C_0 -semigroup on a Banach space X is a family of bounded linear operators on X , $\{S(t); t \geq 0\}$, such that $S(t+s) = S(t)S(s)$ for all $t, s \geq 0$ and $S(t)x \xrightarrow{t \rightarrow 0} x = S(0)x$ for all $x \in X$. It follows that $S(t)x$ is a continuous function of $t \geq 0$ for all $x \in X$.

The *infinitesimal generator* of the C_0 -semigroup S , A , is defined by

$$A = \lim_{h \rightarrow 0+} \frac{1}{h} (S(h)x - x), \quad x \in D(A),$$

where $D(A)$ is the subspace of elements x where this limit exists. $D(A)$ is dense in X and A is a closed operator. If $x \in D(A)$, then $S(t)x$ is differentiable in $t \geq 0$ and

$$\frac{d}{dt} S(t)x = AS(t)x = S(t)Ax.$$

Notice that the first equation can be interpreted as an abstract linear differential equation. For this and more see the textbooks [4, 9, 14, 29, 32, 40, 46, 52].

Theorem 2. Let $x^{[n]} = (x_j^{[n]})_{j=0}^{\infty}$ be the unique componentwise solution of the (essentially finite) linear system of ordinary differential equations

$$\begin{aligned} \frac{d}{dt} x_j^{[n]} &= \sum_{k=0}^n \alpha_{jk} x_k^{[n]}, & j = 0, \dots, n, \\ \frac{d}{dt} x_j^{[n]} &= \alpha_{jj} x_j^{[n]}, & j > n, \end{aligned} \quad (2.11)$$

with initial data $x^{[n]}(0) = \check{x}$. Then $S^{[n]}(t)\check{x} = x^{[n]}(t)$ defines a sequence of C_0 -semigroups $S^{[n]}$ on ℓ^1 . There exists a C_0 -semigroup S on ℓ^1 such that $S^{[n]}(t)\check{x} \rightarrow S(t)\check{x}$ in ℓ^1 for every $\check{x} \in \ell^1$, $t \geq 0$. If $\check{x} \in \ell_+^1$, $S^{[n]}(t)\check{x} \in \ell_+^1$, $S(t)\check{x} \in \ell_+^1$, and the convergence of $S^{[n]}(t)\check{x}$ to $S(t)\check{x}$ as $n \rightarrow \infty$ is monotone increasing. The domain of the infinitesimal generator $A^{[n]}$ of $S^{[n]}$ is

$$D(A^{[n]}) = \left\{ x \in \ell^1; \sum_{j=0}^{\infty} |\alpha_{jj}| |x_j| < \infty \right\} =: D_0, \quad (2.12)$$

and $A^{[n]}x = \left(\sum_{k=0}^{\infty} \alpha_{jk}^{[n]} x_k \right)_{j=0}^{\infty}$, $x = (x_k)_{k=0}^{\infty}$, with

$$\alpha_{jk}^{[n]} = \begin{cases} \alpha_{jk}; & j, k \leq n \\ \alpha_{jj}; & j = k > n \\ 0; & \text{otherwise} \end{cases}, \quad j, k \in \mathbb{Z}_+. \quad (2.13)$$

The following estimates hold

$$\|S^{[n]}(t)\| \leq \|S(t)\| \leq e^{\alpha^\diamond t}, \quad t \geq 0.$$

On the subspace D_0 introduced in (2.12) we define a linear operator \check{A} ,

$$\check{A}x = \left(\sum_{k=0}^{\infty} \alpha_{jk} x_k \right)_{j=0}^{\infty}, \quad x \in D_0. \quad (2.14)$$

Lemma 1. *Let the Assumption 1 be satisfied. Then D_0 is dense in ℓ^1 , $\check{A} : D_0 \rightarrow \ell^1$ is well-defined and linear and $\|(\lambda - \check{A})x\| \geq (\lambda - \alpha^\diamond)\|x\|$ for all $x \in D_0$, $\lambda \in \mathbb{R}$. The closure of \check{A} is the infinitesimal generator of the semigroup S in Theorem 2 and $\sum_{j=0}^{\infty} (\check{A}x)_j = \sum_{k=0}^{\infty} \left(\sum_{j=0}^{\infty} \alpha_{jk} \right) x_k$ for all $x \in D_0$.*

Remark 1. That S is generated by the closure of \check{A} is proved in [59]. Without part (c) in Assumption 1, the semigroup S still exists and its infinitesimal generator extends \check{A} [59] but it may no longer coincide with the closure of \check{A} [4, Theorem 7.11]. Further, without (c), solutions to (2.10) may no longer be uniquely determined by their initial data [50, Sect. 6].

In our context, the space of main interest is

$$\ell^{11} = \left\{ x \in \ell^1; \sum_{j=1}^{\infty} j|x_j| < \infty \right\}$$

with norm $\|x\|_1 = \|x\| + \sum_{j=1}^{\infty} j|x_j|$ which allows us to address the total number of patch occupants in the context of metapopulations or the total number of in-host parasites in the context of macroparasitic diseases.

Theorem 3. *Let the Assumption 1 be satisfied. Then the following hold:*

- (a) *The semigroup S in Theorem 2 leaves ℓ^{11} invariant and the restrictions of $S(t)$ to ℓ^{11} , $S_1(t)$, form a C_0 -semigroup on ℓ^{11} which is generated by the part of \check{A} in ℓ^{11} , denoted by A_1 , i.e. A_1 is the restriction of \check{A} to*

$$D(A_1) = \{x \in \ell^{11} \cap D_0; \check{A}x \in \ell^{11}\}.$$

Further $\|S_1(t)\|_1 \leq e^{\omega t}$ for all $t \geq 0$, with $\omega = \max\{c_1, \alpha^\diamond + c_0\}$.

- (b) *The semigroups $S^{[n]}$ in Theorem 2 leave ℓ^{11} invariant. Their restrictions to ℓ^{11} , $S_1^{[n]}$, form C_0 -semigroups on ℓ^{11} and also satisfy the estimate $\|S_1^{[n]}(t)\|_1 \leq e^{\omega t}$ for all $t \geq 0$. Their infinitesimal generators, $A_1^{[n]}$, have the same domain*

$$D(A_1^{[n]}) = \left\{ x \in \ell^{11}; \sum_{j=1}^{\infty} j |a_{jj}| |x_j| < \infty \right\} =: D_1.$$

Finally, for all $\check{x} \in \ell^{11}$, $S_1^{[n]}(t)\check{x} \rightarrow S_1(t)\check{x}$ in ℓ^{11} , with the convergence being uniform in bounded intervals in \mathbb{R}_+ .

Lemma 2. *Let the Assumption 1 be satisfied. Then $D_1 \subseteq D(A_1)$ and $\sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j |\alpha_{jk}| \right) |x_k| < \infty$ for all $x \in D_1$.*

Several other approximations of the semigroups S and S_1 have been suggested [4, 16, 30, 50, 60]; the one used here has the advantage that it is easy to show that the approximating semigroups are differentiable. It is closely related to the approach in [51], but the construction there does not really yield approximating semigroups on the same Banach space.

Lemma 3. *Let the Assumption 1 be satisfied. Then the semigroups $S^{[n]}(t)$ on ℓ^1 and $S_1^{[n]}(t)$ on ℓ^{11} are differentiable for $t > 0$. Further there exist constants $c_n > 0$ such that*

$$\left. \begin{aligned} \left\| \frac{d}{dt} S^{[n]}(t) \right\| &\leq c_n + (et)^{-1}, \\ \left\| \frac{d}{dt} S_1^{[n]}(t) \right\|_1 &\leq c_n + (et)^{-1} \end{aligned} \right\} \quad \forall t \in (0, 1). \quad (2.15)$$

Proof. We only give the proof for $S^{[n]}$; the proof for $S_1^{[n]}$ is completely analogous. Equivalently we show that $S^{[n]}(t)$ maps ℓ^1 into $D(A^{[n]})$. By construction, (2.11), $[S^{[n]}(t)x]_j = e^{\alpha_{jj}t} x_j$ for $j > n$. Hence, with appropriate constants $c_n > 0$, for $t > 0$,

$$\sum_{j=n+1}^{\infty} |\alpha_{jj}| [S^{[n]}(t)x]_j \leq \sum_{j=n+1}^{\infty} |\alpha_{jj}| e^{-|\alpha_{jj}|t} x_j \leq \frac{1}{et} \|x\|.$$

By (2.12) and (2.13), $S(t)$ maps ℓ^1 into $D(A^{[n]})$ for $t > 0$ and

$$\begin{aligned} \|A^{[n]} S^{[n]}(t)x\| &\leq \sum_{j,k=1}^n |\alpha_{jk}| |S^{[n]}(t)x| + \sum_{j=n+1}^{\infty} |\alpha_{jj}| [S^{[n]}(t)x]_j \\ &\leq c_n \|x\| + (et)^{-1} \|x\| \quad \forall t \in (0, 1), \end{aligned}$$

with appropriate constants $c_n > 0$. \square

We conjecture that the semigroups in Lemma 3 are analytic, but the estimate in the proof does not completely match [46, Chap. 2, Theorem 5.2(d)]. In general, neither the semigroup S nor the semigroup S_1 are differentiable for all $t > 0$. As an example we consider the simple death process,

$$\alpha_{k-1,k} = k = -\alpha_{kk}, \quad k \in \mathbb{N}, \quad \alpha_{jk} = 0 \quad \text{otherwise.} \quad (2.16)$$

Let $e^{[n]} = (\delta_{kn})_{k=0}^\infty$ (the Kronecker symbols) be the sequence where all terms are 0 except the n th term which is 1. It is well-known [1, 6.4.2] that $[S(t)e^{[n]}]_j = 0$ for $j > n$ and

$$[S(t)e^{[n]}]_j = \binom{n}{j} e^{-jt} (1 - e^{-t})^{n-j}, \quad j = 0, \dots, n. \quad (2.17)$$

Since $e^{[n]}$ is an element of both D_0 and $D(A_1)$ (notice $\|e^{[n]}\| = 1$ and $\|e^{[n]}\|_1 = n + 1$), we can differentiate $S(t)e^{[n]}$ and $S_1(t)e^{[n]}$ and

$$\left[\frac{d}{dt} S(t)e^{[n]} \right]_j = \begin{cases} 0; & j > n, \\ [S(t)e^{[n]}]_j \frac{ne^{-t} - j}{1 - e^{-t}}; & j = 0, \dots, n. \end{cases} \quad (2.18)$$

We choose $\bar{t} = \ln 2$ such that $e^{-\bar{t}} = 1/2$ for $t = \bar{t}$. As we show in the appendix

$$2 \frac{\left\| \frac{d}{dt} S_1(\bar{t})e^{[2n]} \right\|_1}{\|e^{[2n]}\|_1} \geq \left\| \frac{d}{dt} S(\bar{t})e^{[2n]} \right\| = 2n \binom{2n}{n} 2^{-2n} \quad (2.19)$$

$$\geq \sqrt{n-1} e^{-1/2}, \quad \bar{t} = \ln 2, n \geq 2. \quad (2.20)$$

This implies that $S(t)$ is not strongly differentiable at any $t \leq \ln 2$. Otherwise $S'(\bar{t}) = AS(\bar{t})$ would be a bounded linear operator [46, 2.4] contradicting this estimate because $\|e^{[2n]}\| = 1$. Similarly, $S_1(t)$ is not differentiable at any $t \leq \ln 2$.

2.3 Solution to the Semilinear System

We can formally rewrite (2.1) as a semilinear Cauchy problem

$$\begin{aligned} w' &= f(t, w, x), \\ x' &= A_1 x + g(t, w, x), \end{aligned} \quad (2.21)$$

where

$$g(t, w, x) = (g_j(t, w, x))_{j=0}^\infty$$

and A_1 is the infinitesimal generator of the semigroup S_1 considered in Theorem 3. Since in general the semigroup S_1 is not differentiable (see the discussion at the end of the previous section), we cannot expect to find a solution of (2.21) in the strict sense if $x(0) = \check{x} \in \ell_+^{11}$ rather than $x(0) \in D(A_1)$. The pair of continuous functions $w : [0, \tau) \rightarrow \mathbb{R}_+$ and $x : [0, \tau) \rightarrow \ell_+^{11}$ is called an *integral solution* of (2.21) with initial condition $w(0) = \check{w}$, $x(0) = \check{x}$ if

$$\begin{aligned} w' &= f(t, w, x), \quad t \in [0, \tau), \quad w(0) = \check{w}, \\ x(t) &= \check{x} + A_1 \int_0^t x(s) ds + \int_0^t g(s, w(s), x(s)) ds, \quad t \in [0, \tau), \end{aligned} \quad (2.22)$$

with the understanding that $\int_0^t x(s)ds \in D(A_1)$ for all $t \in [0, \tau)$. Equivalently to the second equation in (2.22), x is a *mild solution* of $x' = A_1 x + g(t, w, x)$, if it satisfies the integral equation

$$x(t) = S_1(t)\check{x} + \int_0^t S_1(t-s)g(s, w(s), x(s))ds, \quad t \in [0, \tau), \quad (2.23)$$

where S_1 is the C_0 -semigroup generated by A_1 on ℓ^{11} [4, Proposition 3.31].

2.3.1 Local Existence

A standard approach to local existence of solutions consists in assuming that the non-linearities satisfy a Lipschitz condition. We also need assumptions which make the solutions preserve positivity.

Assumption 4 $f : \mathbb{R}_+^2 \times \ell_+^{11} \rightarrow \mathbb{R}$ and $g : \mathbb{R}_+^2 \times \ell_+^{11} \rightarrow \ell^{11}$ are continuous and have the following properties:

- (a) $f(t, 0, x) \geq 0$ for all $x \in \ell_+^{11}$, $t \geq 0$.
- (b) For every $j \in \mathbb{Z}_+$, $g_j(t, w, x) \geq 0$ whenever $w \geq 0$, $x \in \ell_+^{11}$, $x_j = 0$, $t \geq 0$.
- (c) For every $r > 0$ there exists a Lipschitz constant A_r such that

$$\left. \begin{aligned} &|f(t, w, x) - f(t, \tilde{w}, \tilde{x})| \\ &\|g(t, w, x) - g(t, \tilde{w}, \tilde{x})\|_1 \end{aligned} \right\} \leq A_r(|w - \tilde{w}| + \|x - \tilde{x}\|_1),$$

whenever $t \in [0, r]$, $w, \tilde{w} \in [0, r]$, $x, \tilde{x} \in \ell_+^{11}$, $\|x\|_1, \|\tilde{x}\|_1 \leq r$.

Theorem 5. *Under the Assumptions 1, and 4, for every $\check{w} \in \mathbb{R}_+$ and $\check{x} \in \ell_+^{11}$, there exists some $\tau \in [0, \infty]$ and a unique continuous solution $w : [0, \tau) \rightarrow [0, \infty)$, $x : [0, \tau) \rightarrow \ell_+^{11}$ of (2.22).*

Remark 2. $\tau \in [0, \infty)$ can be chosen in such a way that the solution (w, x) cannot be extended to a solution on a larger open interval.

Since we want our solutions to preserve positivity, we do not refer for the proof to general results which use Banach's fixed point theorem [46, Chap. 6 Theorem 1.2] [52, Theorem 46.1], but to results which use generalizations of the explicit Euler approximation to solve ordinary differential equations [11, Chap. 1 Theorem 1.1].

Proof. We apply [40, VIII.2, Theorem 2.1] (or [55, Sect. 2]). We set $D = \mathbb{R}_+ \times \ell_+^{11}$. Notice that (2.23) can be rewritten in terms of $y(t) = (w(t), x(t))$ and $\check{y} = (\check{w}, \check{x})$ as

$$y(t) = \bar{S}(t)\check{y} + \int_0^t \bar{S}(t-s)\bar{f}(s, y(s))ds$$

with the C_0 -semigroup $\bar{S}(t)\check{y} = (\check{w}, S_1(t)\check{x})$ on $\mathbb{R} \times \ell^{11}$ and the non-linearity $\bar{f}(s, \check{y}) = (f(s, \check{y}), g(s, \check{y}))$. The local existence of solutions with values in D follows once we have checked the subtangential condition

$$\frac{1}{h}d(y + h\bar{f}(t, y), D) \rightarrow 0, \quad h \rightarrow 0+, y \in D,$$

where $d(z, D)$ is the distance from the point z to the set D . This subtangential condition can be broken up into two tangential conditions,

$$\left. \begin{aligned} \frac{1}{h}d(w + hf(t, w, x), \mathbb{R}_+) &\rightarrow 0 \\ \frac{1}{h}d(x + hg(t, w, x), \ell_+^{11}) &\rightarrow 0 \end{aligned} \right\} \quad h \rightarrow 0+, w \in \mathbb{R}_+, x \in \ell_+^{11}.$$

In a Banach lattice Z with positive cone Z_+ ,

$$d(z, Z_+) \leq \|z - z^+\| = \|z^-\|,$$

where z^+ and z^- are the positive and negative part of the vector z . Since, for $z \in Z_+$, $\|z^-\| = 0$,

$$\begin{aligned} \limsup_{h \rightarrow 0+} \frac{1}{h}d(z + h\tilde{z}, Z_+) &\leq \limsup_{h \rightarrow 0+} \frac{1}{h}\|[z + h\tilde{z}]^-\| \\ &= \lim_{h \rightarrow 0+} \frac{1}{h}(\|[z + h\tilde{z}]^-\| - \|z^-\|) \\ &=: D_+\|z^-\|\tilde{z}, \end{aligned}$$

which is the right derivative of the convex functional $z \mapsto \|z^-\|$ at z in the direction of \tilde{z} [40, II.5]. If $Z = \mathbb{R}$,

$$\begin{aligned} D_+\|z^-\|\tilde{z} &= D_+z^-\tilde{z} = \lim_{h \rightarrow 0+} \frac{1}{h}([z + h\tilde{z}]^- - z^-) \\ &= \left\{ \begin{aligned} \lim_{h \rightarrow 0+} \frac{1}{h}(0 - 0); &z > 0 \\ \lim_{h \rightarrow 0+} \frac{1}{h}[h\tilde{z}]^-; &z = 0 \\ \lim_{h \rightarrow 0+} \frac{1}{h}(-z - h\tilde{z} + z); &z < 0 \end{aligned} \right\} = \left\{ \begin{aligned} 0; &z > 0 \\ \tilde{z}^-; &z = 0 \\ -\tilde{z}; &z < 0 \end{aligned} \right\}. \end{aligned}$$

For $z \in \mathbb{R}_+$ $\tilde{z} \in \mathbb{R}$,

$$\limsup_{h \rightarrow 0+} \frac{1}{h}d(z + h\tilde{z}, \mathbb{R}_+) \leq \begin{cases} 0; & z > 0, \\ \tilde{z}^-; & z = 0. \end{cases}$$

For $z, \tilde{z} \in \ell^1$,

$$D_+\|z^-\|\tilde{z} = \sum_{j=0}^{\infty} \lim_{h \rightarrow 0+} \frac{1}{h}([z_j + h\tilde{z}_j]^- - z_j^-) = \sum_{j=0}^{\infty} D_+z_j^-\tilde{z}_j.$$

For $z, \tilde{z} \in \ell^{11}$,

$$D_+ \|z^-\|_1 \tilde{z} = \sum_{j=0}^{\infty} (1+j) D_+ z_j^- \tilde{z}_j.$$

We summarize. For $w \in \mathbb{R}_+$ and $x \in \ell_+^{11}$,

$$\lim_{h \rightarrow 0+} \frac{1}{h} d(w + hf(t, w, x), \mathbb{R}^+) \leq \begin{cases} 0; & w > 0 \\ [f(t, w, x)]^-; & w = 0 \end{cases}$$

and

$$\lim_{h \rightarrow 0+} \frac{1}{h} d(x + hg(t, w, x), \ell_+^{11}) \leq \sum_{j=0}^{\infty} (1+j) \begin{cases} 0; & x_j > 0 \\ [g_j(t, w, x)]^-; & x_j = 0 \end{cases}.$$

By Assumption 4 (a) and (b), these expressions are 0 and the subtangential condition is satisfied. \square

2.3.2 Global Existence

In order to establish global existence we make the following additional assumptions. Recall D_1 in Theorem 3,

$$D_1 = \left\{ x \in \ell^{11}; \sum_{j=1}^{\infty} j |\alpha_{jj}| |x_j| < \infty \right\}.$$

Assumption 6 There exist constants $c_2, c_3 \geq 0$ such that for all $t \geq 0, w \geq 0$ and $x \in \ell_+^{11} \cap D_1$ the following hold:

- $\sum_{j=0}^{\infty} g_j(t, w, x) \leq c_3 \|x\|.$
- $f(t, w, x) + \sum_{j=1}^{\infty} j g_j(t, w, x) \leq c_2(w + \|x\|_1).$

Theorem 7. *Let Assumptions 1, 4, and 6 be satisfied. Then, for every $\check{w} \in [0, \infty)$ and $\check{x} \in \ell_+^{11}$, there exists a unique continuous solution $w : [0, \infty) \rightarrow \mathbb{R}_+$, $x : [0, \infty) \rightarrow \ell_+^{11}$ of (2.22). The solution satisfies the estimates*

$$\|x(t)\| \leq \|\check{x}\| e^{\alpha^\diamond t}, \quad |w(t)| + \|x(t)\|_1 \leq (\check{w} + \|\check{x}\|_1) e^{\omega_2 t}$$

where α^\diamond is from Assumption 1 and $\omega_2 \in \mathbb{R}$ is an appropriate constant.

Remark 3. On every bounded subinterval of $[0, \infty)$, the solution x is the uniform limit of solutions $x^{[n]}$ on $[0, \infty)$ with values in ℓ_+^{11} which solve the system

$$\begin{aligned} \frac{d}{dt}w^{[n]}(t) &= f(t, w^{[n]}(t), x^{[n]}(t)), & w^{[n]}(0) &= \check{w}, \\ \frac{d}{dt}x_j^{[n]}(t) - g_j(t, w^{[n]}(t), x^{[n]}(t)) &= \begin{cases} \sum_{k=0}^n \alpha_{jk} x_k^{[n]}(t), & j = 0, \dots, n, \\ \alpha_{jj} x_j^{[n]}(t), & j > n, \end{cases} & (2.24) \\ x^{[n]}(0) &= \check{x}, \end{aligned}$$

and satisfy

$$\sum_{j=1}^{\infty} j |a_{jj}| \int_0^t x_j^{[n]}(s) ds < \infty. \quad (2.25)$$

The following estimates will be used frequently for $m = 0, 1$ and $0^0 := 1$,

$$\begin{aligned} \sum_{j=0}^{\infty} j^m x_j^{[n]}(t) &\leq \sum_{j=0}^{\infty} j^m \check{x}_j + \sum_{k=0}^{\infty} \left(\sum_{j=0}^{\infty} j^m \alpha_{jk} \right) \int_0^t x_k^{[n]}(s) ds \\ &\quad + \int_0^t \sum_{j=0}^{\infty} j^m g_j(s, w^{[n]}(s), x^{[n]}(s)) ds. \end{aligned} \quad (2.26)$$

Proof. In order to derive the estimates which imply global existence of solutions we consider the approximating problems where the infinite matrix (α_{jk}) is replaced by the infinite matrices $(\alpha_{jk}^{[n]})$ in (2.13) because this will allow us to interchange the order of summation freely. The matrices also satisfy the assumptions of Theorem 5. So, for every $n \in \mathbb{N}$, there exists some $\tau_n \in [0, \infty]$ and a solution on $[0, \tau_n)$ of

$$\begin{aligned} \frac{d}{dt}w^{[n]} &= f(t, w^{[n]}, x^{[n]}), & w^{[n]}(0) &= \check{w}, \\ x^{[n]}(t) &= \check{x} + A_1^{[n]} \int_0^t x^{[n]}(s) ds + \int_0^t g(s, w^{[n]}(s), x^{[n]}(s)) ds, \end{aligned}$$

with the understanding that $\int_0^t x^{[n]}(s) ds \in D(A_1^{[n]}) = D_1$. (2.25) follows from the definition of D_1 .

Again $\tau_n \in [0, \infty]$ can be chosen such that the solution $(w^{[n]}, x^{[n]})$ cannot be extended to a solution on a larger interval.

If we spell the equation for $x^{[n]}$ out componentwise for x , we see that $w^{[n]}$ and $x_j^{[n]}$ can be differentiated and satisfy (2.24). Since the $x^{[n]}$ are non-negative, for $m = 0, 1$,

$$\begin{aligned} &\sum_{j=0}^{\infty} j^m x_j^{[n]}(t) \\ &= \sum_{j=0}^{\infty} j^m \check{x}_j + \sum_{j=0}^n j^m \left(\sum_{k=0}^n \alpha_{jk} \int_0^t x_k^{[n]}(s) ds \right) + \sum_{j=n+1}^{\infty} j^m \alpha_{jj} \int_0^t x_j^{[n]}(s) ds \\ &\quad + \sum_{j=0}^{\infty} j^m \int_0^t g_j(s, w^{[n]}, x^{[n]}) ds. \end{aligned}$$

We can change the order of summations, use that $\alpha_{jk} \geq 0$ for $j \neq k$, and obtain the estimate (2.26) which implies

$$\begin{aligned} & w^{[n]}(t) + \|x^{[n]}(t)\|_1 \\ & \leq \check{w} + \|\check{x}\|_1 + \int_0^t f(s, w^{[n]}(s), x^{[n]}(s)) ds \\ & \quad + \sum_{k=0}^{\infty} \left(\sum_{j=0}^{\infty} (1+j) \alpha_{jk} \right) \int_0^t x_k^{[n]}(s) ds \\ & \quad + \int_0^t \sum_{j=0}^{\infty} (1+j) g_j(s, w^{[n]}, x^{[n]}) ds. \end{aligned}$$

By Assumptions 1, 4, and 6,

$$\begin{aligned} & w^{[n]}(t) + \|x^{[n]}(t)\|_1 \\ & \leq \check{w} + \|\check{x}\|_1 + (\alpha^\diamond + c_0 + c_3) \int_0^t \|x^{[n]}(s)\| ds \\ & \quad + c_2 \int_0^t w^{[n]}(s) ds + (c_1 + c_2) \int_0^t \|x^{[n]}(s)\|_1 ds \\ & \leq \omega_2 \left(\int_0^t w^{[n]}(s) ds + \int_0^t \|x^{[n]}(s)\|_1 ds \right) \end{aligned}$$

with an appropriate $\omega_2 > 0$. By Gronwall's inequality,

$$w^{[n]}(t) + \|x^{[n]}(t)\|_1 \leq e^{\omega_2 t} (\check{w} + \|\check{x}\|_1).$$

Suppose $\tau_n < \infty$. The growth bounds in Assumption 6 imply that $g(t, w^{[n]}, x^{[n]})$ and $f(t, w^{[n]}, x^{[n]})$ are bounded on $[0, \tau_n)$. It follows from the variation of parameters formula,

$$\begin{aligned} w^{[n]}(t) &= \check{w} + \int_0^t f(s, w^{[n]}(s), x^{[n]}(s)) ds, \\ x^{[n]}(t) &= S_1^{[n]}(t) \check{x} + \int_0^t S_1^{[n]}(t-s) g(s, w^{[n]}(s), x^{[n]}(s)) ds, \end{aligned}$$

that $w^{[n]}$ and $x^{[n]}$ can be continuously extended to $[0, \tau_n]$. By the local existence theorem they can be extended to an interval larger than $[0, \tau_n]$, contradicting the maximality of the solution.

We return to the solution (w, x) in Theorem 5 which, by (2.23), is given by

$$\begin{aligned} w(t) &= \check{w} + \int_0^t f(s, w(s), x(s)) ds, \\ x(t) &= S_1(t) \check{x} + \int_0^t S_1(t-s) g(s, w(s), x(s)) ds. \end{aligned}$$

We subtract this system of equations from the previous,

$$|w(t) - w^{[n]}(t)| \leq \int_0^t |f(s, w(s), x(s)) - f(s, w^{[n]}(s), x^{[n]}(s))| ds$$

and

$$\begin{aligned} & \|x(t) - x^{[n]}(t)\| \\ & \leq \| [S_1(t) - S_1^{[n]}(t)] \check{x} \|_1 \\ & \quad + \int_0^t \| [S_1(t-s) - S_1^{[n]}(t-s)] g(s, w(s), x(s)) \|_1 ds \\ & \quad + \int_0^t \| S_1^{[n]}(t-s) \|_1 \| g(s, w(s), x(s)) - g(s, w^{[n]}(s), x^{[n]}(s)) \|_1 ds. \end{aligned}$$

We use $\|S_1^{[n]}(t)\|_1 \leq e^{\omega t}$ (Theorem 3) and the Lipschitz conditions for f and g in Assumption 4. For every $r \in (0, \tau)$, we find a Lipschitz constant A_r such that

$$\begin{aligned} & |w(t) - w^{[n]}(t)| + \|x(t) - x^{[n]}(t)\|_1 \\ & \leq \| [S_1(t) - S_1^{[n]}(t)] \check{x} \|_1 \\ & \quad + \int_0^t \| [S_1(t-s) - S_1^{[n]}(t-s)] g(s, w(s), x(s)) \|_1 ds \\ & \quad + A_r \int_0^t e^{\omega(t-s)} (|w(s) - w^{[n]}(s)| + \|x(s) - x^{[n]}(s)\|_1) ds. \end{aligned}$$

Since

$$\| [S_1^{[n]}(t) - S_1(t)] \check{x} \|_1 \rightarrow 0, \quad n \rightarrow \infty, t \geq 0, \check{x} \in \ell_+^{11}$$

by Theorem 3, Lebesgue's theorem of dominated convergence implies that second summand on the right hand side of the last inequality converges to 0 for all $t \geq 0$. A Gronwall argument implies that

$$|w(t) - w^{[n]}(t)| + \|x(t) - x^{[n]}(t)\|_1 \rightarrow 0, \quad n \rightarrow \infty,$$

uniformly for t in every compact subinterval of $[0, \tau)$. This implies that

$$w(t) + \|x(t)\|_1 \leq e^{\omega_2 t} (\check{w} + \|\check{x}\|_1), \quad t \in [0, \tau).$$

A similar argument as before implies that $\tau = \infty$. \square

2.3.3 A Semiflow

A map $\Phi : \mathbb{R}_+ \times \ell_+^{11} \rightarrow \ell_+^{11}$ is called a *semiflow* on ℓ_+^{11} if $\Phi(t+s, \check{x}) = \Phi(t, \Phi(s, \check{x}))$ for all $t, s \geq 0$ and $\Phi(0, \check{x}) = \check{x}$ whenever $\check{x} \in \ell_+^{11}$. If Φ is continuous, it is called a *continuous semiflow*. The following theorem is essentially proved in the same way as the continuous dependence of solutions of ODEs on initial data with the Gronwall inequality playing a crucial role [52, Theorem 46.4] [55, Sect. 3].

Theorem 8. *Let the assumptions of Theorem 7 be satisfied and f and g_j not depend on time t . Then the map $\Phi : \mathbb{R}_+ \times \mathbb{R}_+ \times \ell_+^{11} \rightarrow \mathbb{R}_+ \times \ell_+^{11}$ defined by $\Phi(t, (\check{w}, \check{x})) = (w(t), x(t))$ with x being a solution of (2.22) is a continuous semiflow.*

2.4 General Metapopulation Models and Boundedness of Solutions

In the following we concentrate on metapopulations to derive boundedness results. A special feature of a certain class of metapopulation models is that the number of patches (islands) does not increase.

2.4.1 Decrease or Constancy of Patch Number

We formulate the Assumption that guarantees this feature.

Assumption 9 (a) $\sum_{j=0}^{\infty} \alpha_{jk} \leq 0$ for all $k \in \mathbb{Z}_+$
 (b) $\sum_{j=0}^{\infty} g_j(t, w, x) \leq 0$ for all $t \geq 0$, $w \geq 0$, $x \in \ell_+^{11}$.

Proposition 1. *Let the Assumptions of Theorem 7 and Assumption 9 be satisfied. Then $\|x(t)\| \leq \|\check{x}\|$ for all $t \geq 0$ for every non-negative solution of (2.22).*

Proof. Recall that x solves

$$x(t) = \check{x} + A_1 \int_0^t x(s) ds + \int_0^t g(s, w(s), x(s)) ds.$$

Since $x(t) \in \ell_+^{11}$,

$$\begin{aligned} \|x(t)\| &= \sum_{j=0}^{\infty} x_j(t) \\ &= \|\check{x}\| + \sum_{j=0}^{\infty} \left(A_1 \int_0^t x(s) ds \right)_j + \int_0^t \sum_{j=0}^{\infty} g_j(s, w(s), x(s)) ds. \end{aligned}$$

By Lemma 1 and Assumption 9, $\|x(t)\| \leq \|\check{x}\|$ because $\alpha^\diamond \leq 0$. \square

The same proof yields the following result.

Corollary 1. *Let the Assumptions of Theorem 7 be satisfied and $\sum_{j=0}^{\infty} \alpha_{jk} = 0$ for all $k \in \mathbb{Z}_+$ and $\sum_{j=0}^{\infty} g_j(t, w, x) = 0$ for all $t, w \geq 0$, $x \in \ell_+^{11}$. Then $\|x(t)\| = \|x(0)\|$ for all $t > 0$ and all solutions of (2.22).*

2.4.2 Uniform Eventual Boundedness of Solutions

Assumption 10 *There exist constants $c_4, c_5, \epsilon_4 > 0$ such that, for all $w \geq 0$, $x \in D_1 \cap \ell_+^{11}$,*

$$\begin{aligned} f(t, w, x) + \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j \alpha_{jk} \right) x_k + \sum_{j=1}^{\infty} j g_j(t, w, x) \\ \leq c_4 \|x\| + c_5 - \epsilon_4 \left(w + \sum_{j=1}^{\infty} j x_j \right). \end{aligned}$$

By Lemma 2, the series in the second term exist. If the previous assumptions are added, the solutions of the model equations are uniformly eventually bounded and the solution semiflow is called *dissipative*.

Theorem 11. *Let Assumptions 1, 4, 9, and 10 be satisfied. Then, with the constants c_4, c_5, ϵ_4 from Assumption 10,*

$$w(t) + \sum_{j=1}^{\infty} j x_j(t) \leq \left(\check{w} + \sum_{j=1}^{\infty} j \check{x}_j \right) e^{-\epsilon_4 t} + \frac{c_4 \|\check{x}\| + c_5}{\epsilon_4}$$

for all solutions (w, x) of (2.1) with initial data $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$.

Proof. The Assumptions 9 and 10 imply Assumption 6, and we have global solutions for the initial values in question by Theorem 7. By Proposition 1, $\|x(t)\| \leq \|\check{x}\|$ for all $t \geq 0$. We consider the functions $x^{[n]}$ on $[0, \infty)$ in (2.24) which approximate x by Remark 3. By estimate (2.26),

$$\begin{aligned} & \left(w^{[n]}(t) + \sum_{j=1}^{\infty} j x_j^{[n]}(t) \right) \\ & \leq \check{w} + \sum_{j=1}^{\infty} j \check{x}_j + \int_0^t f(s, w^{[n]}(s), x^{[n]}(s)) ds \\ & \quad + \sum_{k=0}^{\infty} \left(\sum_{j=0}^{\infty} j \alpha_{jk} \right) \int_0^t x_k^{[n]}(s) ds + \int_0^t \sum_{j=0}^{\infty} j g_j(s, w^{[n]}(s), x^{[n]}(s)) ds. \end{aligned}$$

By Lemma 2, the double series exists absolutely. Since the functions $x_k^{[n]}$ are non-negative, we can interchange the series and the integral. By Assumption 10 (notice that $\int_0^t x^{[n]}(s) ds \in D_1$),

$$\begin{aligned} w^{[n]}(t) + \sum_{j=1}^{\infty} j x_j^{[n]}(t) & \leq \check{w} + \sum_{j=1}^{\infty} j \check{x}_j + c_4 \int_0^t \|x^{[n]}(s)\| ds + c_5 t \\ & \quad - \epsilon_4 \left(\int_0^t w^{[n]}(s) ds + \int_0^t \left(\sum_{j=1}^{\infty} j x_j^{[n]}(s) \right) ds \right). \end{aligned}$$

By Gronwall's inequality,

$$\begin{aligned} w^{[n]}(t) + \sum_{j=1}^{\infty} jx^{[n]}(t) &\leq e^{-\epsilon_4 t} \left(\check{w} + \sum_{j=1}^{\infty} j\check{x}_j \right) + \frac{c_5}{\epsilon_4} \\ &\quad + c_4 \int_0^t \|x^{[n]}(t-s)\| e^{-\epsilon_4 s} ds. \end{aligned}$$

We take the limit $n \rightarrow \infty$, use $\|x(t)\| \leq \|\check{x}\|$ and obtain the statement of this theorem. \square

2.5 Extinction Without Migration or Colonization of Empty Patches

If there is no emigration from the patches, we can assume that the average number of migrating individuals (wanderers), $w(t)$, is exponentially decreasing, more generally, w is bounded on $[0, \infty)$, $\int_0^\infty w(t)dt < \infty$. In this section we derive conditions such that this implies that the solutions of (2.22) satisfy

$$\sum_{j=1}^{\infty} jx_j(t) \rightarrow 0 \quad \text{as} \quad t \rightarrow \infty,$$

i.e., the occupant part of the population goes extinct together with its migrating part. We also show that the occupant population goes extinct if empty patches are not colonized.

Assumption 12 (a) $\sum_{j=0}^{\infty} \alpha_{jk} \leq 0$, $k = 0, 1, 2, \dots$

(b) For all $k \in \mathbb{N}$ there is some $j \in \mathbb{Z}_+$, $j < k$, such that $\alpha_{jk} > 0$.

(c) $g_j(0, x) = 0$ for all $x \in \ell_+^{11}$, $j = 0, 1, \dots$

(d) $\sum_{j=0}^{\infty} g_j(w, x) \leq 0$ for all $w \geq 0$, $x \in \ell_+^{11}$.

(e) There exists a constant $c > 0$ such that

$$\sum_{j=1}^{\infty} jg_j(w, x) \leq cw\|x\| \text{ for all } w \geq 0, x \in \ell_+^{11}.$$

(f) $\limsup_{k \rightarrow \infty} \sum_{j=0}^{\infty} \frac{j\alpha_{jk}}{k} < 0$.

If the Assumptions 1, 4 (for g), 10, and 12 are satisfied, then also the Assumption 9 is satisfied and unique solutions exist to (2.22) which are defined and bounded on $[0, \infty)$.

Proposition 2. *Let the Assumptions 1, 4, 10, and 12 be satisfied. Let $c > 0$ be the number in Assumption 12. Then there exist $m \in \mathbb{N}$ and $\epsilon_1 > 0$ such that for every solution x of (2.22) with $\check{x} \in \ell_+^{11}$,*

$$\begin{aligned} \sum_{j=1}^{\infty} jx_j(t) &\leq e^{-\epsilon_1 t} \sum_{j=1}^{\infty} j\check{x}_j + \int_0^t e^{-\epsilon_1(t-s)} \sum_{k=0}^{m-1} \xi_k x_k(s) ds \\ &\quad + c\|\check{x}\| \int_0^t e^{-\epsilon_1(t-s)} w(s) ds, \end{aligned}$$

where $\xi_k = \sum_{j=1}^{\infty} \alpha_{jk} + \epsilon_1 k$.

Proof. Let $x^{[n]}$ be the solutions of (2.24) which approximate x . By (2.26),

$$\begin{aligned} \|x^{[n]}(t)\| &\leq \|\check{x}\|, \\ \sum_{j=1}^{\infty} jx_j^{[n]}(t) &\leq \sum_{j=1}^{\infty} j\check{x}_j + \sum_{k=0}^{\infty} \tilde{\xi}_k \int_0^t x_k^{[n]}(s) ds \\ &\quad + \int_0^t \left(\sum_{j=1}^{\infty} jg_j(w(s), x^{[n]}(s)) \right) ds. \end{aligned}$$

By part (f) of Assumption 12, $\tilde{\xi}_k \leq -\epsilon_1 k$ for $k \geq m$ with appropriate $\epsilon_1 > 0$, $m \in \mathbb{N}$, and, by part (e),

$$\begin{aligned} \sum_{j=1}^{\infty} jx_j^{[n]}(t) &\leq \sum_{j=1}^{\infty} j\check{x}_j + \sum_{k=0}^{m-1} \tilde{\xi}_k \int_0^t x_k^{[n]}(s) ds - \epsilon_1 \sum_{k=m}^{\infty} k \int_0^t x_k^{[n]}(s) ds \\ &\quad + \int_0^t \left(\sum_{j=0}^{\infty} cw(s)x_j^{[n]}(s) \right) ds \\ &= \sum_{j=1}^{\infty} j\check{x}_j + \sum_{k=0}^{m-1} \xi_k \int_0^t x_k^{[n]}(s) ds - \epsilon_1 \sum_{k=0}^{\infty} k \int_0^t x_k^{[n]}(s) ds \\ &\quad + \int_0^t cw(s)\|x^{[n]}(s)\| ds, \end{aligned}$$

with $\xi_k = \tilde{\xi}_k + \epsilon_1 k$. We take the limit as $n \rightarrow \infty$, obtain $\|x(t)\| \leq \|\check{x}\|$ and

$$\begin{aligned} \sum_{j=1}^{\infty} jx_j(t) &\leq \sum_{j=1}^{\infty} j\check{x}_j + \sum_{k=0}^{m-1} \xi_k \int_0^t x_k(s) ds - \epsilon_1 \int_0^t \sum_{k=1}^{\infty} kx_k(s) ds \\ &\quad + \int_0^t cw(s)\|\check{x}\| ds. \end{aligned}$$

Gronwall's inequality implies the assertion. \square

Next we show that the size of the occupant population tends to zero as $t \rightarrow \infty$ if there is no emigration from patches and the migrating part of the metapopulation decreases exponentially as a result.

Theorem 13. *Let Assumptions 1, 4, 10, and 12 be valid. Further let $\alpha_{00} = 0$. Let w, x be a solution of (2.22) on $[0, \infty)$ such that w is bounded on \mathbb{R}_+ and $\int_0^\infty w(t)dt < \infty$. Then*

$$\sum_{k=1}^{\infty} k \int_0^\infty x_k(s)ds < \infty \quad \text{and} \quad \sum_{k=1}^{\infty} kx_k(t) \rightarrow 0, \quad t \rightarrow \infty.$$

We mention that the assumption $\alpha_{00} = 0$ together with the other assumptions on the coefficients α_{jk} implies that $\alpha_{j0} = 0$ for all $j \in \mathbb{Z}_+$.

Proof. Recall that x is an integral solution,

$$x(t) - \check{x} = A_1 \int_0^t x(s)ds + \int_0^t g(w(s), x(s))ds.$$

For the single terms this means that

$$x_j(t) - \check{x}_j = \sum_{k=1}^{\infty} \alpha_{jk} \int_0^t x_k(s)ds + \int_0^t g_j(w(s), x(s))ds.$$

Recall that x_k is non-negative, $\alpha_{jk} \geq 0$ for $j \neq k$, and $x_j(t) \leq \|\check{x}\|$. By Theorem 11, the functions w and x (with values in ℓ_+^{11}) are bounded. Since $g_j(0, x) = 0$ and g_j are locally Lipschitz continuous, there exist constants $\Lambda_j > 0$ such that, for all $j, k \in \mathbb{Z}_+$, $j \neq k$, $t \geq 0$,

$$\alpha_{j,k} \int_0^t x_k(s)ds \leq |\alpha_{jj}| \int_0^t x_j(s)ds + \|\check{x}\| + \Lambda_j \int_0^t w(s)ds.$$

Let $k \in \mathbb{N}$ be arbitrary. By successive application of Assumption 12 (b) we find numbers $k_0 < \dots < k_m$ such that $k_0 = 0$, $k_m = k$ and $\alpha_{k_i, k_{i+1}} > 0$ for $i = 0, \dots, m-1$. Since $\alpha_{00} = 0$,

$$\alpha_{0k_1} \int_0^t x_{k_1}(s)ds \leq \|\check{x}\| + \Lambda_0 \int_0^t w(s)ds.$$

Since $\int_0^\infty w(s)ds < \infty$, also $\int_0^\infty x_{k_1}(s)ds < \infty$. Since $\alpha_{k_i, k_{i+1}} > 0$, we obtain step by step that

$$\int_0^\infty x_{k_i}(s)ds < \infty \quad \forall i = 1, 2, \dots, m,$$

in particular $\int_0^\infty x_k(s)ds < \infty$ where $k \in \mathbb{N}$ has been arbitrary. The claims now follow from the inequality in Proposition 2, the first by integrating it, the second by applying Lebesgue's theorem of dominated convergence. Notice that $\xi_0 = 0$ because $\alpha_{j0} = 0$ for all $j \in \mathbb{Z}_+$. \square

We turn to the case that empty patches are not colonized. This is mathematically captured in the assumption that the function g_0 is non-negative.

Theorem 14. *Let Assumptions 1, 4, 10, and 12 be valid. Further let $\alpha_{00} = 0$ and $g_0(w, x) \geq 0$ for all $w \geq 0, x \in \ell_+^{11}$. Let x be a solution of (2.22) on $[0, \infty)$ with values in ℓ_+^{11} . Then*

$$\sum_{k=1}^{\infty} k \int_0^{\infty} x_k(s) ds < \infty \quad \text{and} \quad \sum_{k=1}^{\infty} k x_k(t) \rightarrow 0, \quad t \rightarrow \infty.$$

Proof. We revisit the proof of Theorem 13. From the integral equation for x_0 , we obtain the inequality,

$$\alpha_{01} \int_0^t x_1(s) ds \leq \|\check{x}\| - \int_0^t g_0(w(s), x(s)) ds \leq \|\check{x}\| \quad \forall t \geq 0.$$

Except for this modification, the proof proceeds in exactly the same way. \square

2.6 A More Specific Metapopulation Model

For the rest of the chapter we restrict our considerations which concern qualitative aspects of metapopulation models (compact attractors, (in)stability of equilibria, persistence) to a somewhat more specific model framework in order to cut down on obscuring technicalities,

$$\begin{aligned} w' &= \sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k - \delta w, \\ x_j' &= \sum_{k=0}^{\infty} \alpha_{jk} x_k + w \sum_{k=0}^{\infty} \gamma_{jk} x_k, \quad j = 0, 1, \dots \end{aligned} \tag{2.27}$$

The coefficients γ_{jk} describe the transition from patches with k occupants to patches with j occupants due to immigrating dispersers. The terms σ_k describe the average loss rate of dispersers due to settlement on a patch with k occupants. Below we will impose a balance equation or inequality linking γ_{jk} and σ_k . The coefficients η_k describe the rate at which individuals emigrate from a patch with k occupants. $\delta > 0$ is the per capita mortality rate of dispersers. We assume the following.

Assumption 15 (a) $\alpha_{jj}, \gamma_{jj} \leq 0 \leq \alpha_{jk}, \gamma_{jk}$ for $j \neq k, j, k \in \mathbb{Z}_+$. Further

$$\sum_{j=0}^{\infty} \alpha_{jk} \leq 0 \text{ and } \sum_{j=0}^{\infty} \gamma_{jk} \leq 0 \text{ for all } k \in \mathbb{Z}_+.$$

(b) There exist constants $c_0, c_1 > 0, \epsilon > 0$ such that

$$\sum_{j=1}^{\infty} j \alpha_{jk} \leq c_0 + c_1 k - \epsilon |\alpha_{kk}| \quad \forall k \in \mathbb{Z}_+.$$

- (c) There exists a constant $c_7 > 0$ such that $0 \leq \eta_k, \sigma_k \leq c_7 k$ for all $k \in \mathbb{N}$.
- (d) There exists a constant $c_8 > 0$ such that $\sum_{j=1}^{\infty} j |\gamma_{jk}| \leq c_8(1+k)$ for all $k \in \mathbb{Z}_+$.
- (e) $\sum_{j=1}^{\infty} j \gamma_{jk} \leq \sigma_k$ for all $k \in \mathbb{Z}_+$.

Part (e) of the last assumption expresses a balance law which guarantees that the rate at which a patch with k occupants gains new occupants through immigration of dispersers does not exceed the rate at which dispersers leave the disperser pool to settle on a patch with k occupants. A strict inequality means that some dispersers die during the immigration. Mathematically part (e), together with part (c), implies that the second part of Assumption 6 is satisfied. The first part of that assumption, with $c_3 = 0$, is satisfied by Assumption 15 (a). The other parts of Assumption 15 either repeat the Assumption 1 or make sure that the functions f and g in Assumption 4 are well-defined and satisfy the Lipschitz conditions. Theorem 7 implies the following result.

Theorem 16. *Let the Assumption 15 be satisfied. Then, for every $\check{w} \in [0, \infty)$ and $\check{x} \in \ell_+^{11}$, there exists a unique integral solution $w : [0, \infty) \rightarrow \mathbb{R}_+$, $x : [0, \infty) \rightarrow \ell_+^{11}$ of (2.27),*

$$\begin{aligned} w' &= \sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k - \delta w, \\ x_j(t) - \check{x}_j &= \sum_{k=0}^{\infty} \alpha_{jk} \int_0^t x_k(s) ds + \sum_{k=0}^{\infty} \gamma_{jk} \int_0^t w(s) x_k(s) ds, \\ j &= 0, 1, \dots \end{aligned} \tag{2.28}$$

The solution satisfies the estimates

$$\|x(t)\| \leq \|\check{x}\|, \quad |w(t)| + \|x(t)\|_1 \leq (\check{w} + \|\check{x}\|_1) e^{\omega_2 t}$$

with some $\omega_2 > 0$.

We add an assumption to obtain uniform eventual boundedness of solutions.

Assumption 17 There exists constants $c_4 > 0$ and $\epsilon_4 > 0$ such that

$$\eta_k + \sum_{j=1}^{\infty} j \alpha_{jk} \leq c_4 - \epsilon_4 k \quad \forall k \in \mathbb{Z}_+.$$

In order to check Assumption 10, we observe that, by Lemma 2, for $x \in D_1$,

$$\begin{aligned} \sum_{k=0}^{\infty} \eta_k x_k + \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j \alpha_{jk} \right) x_k &= \sum_{k=0}^{\infty} \left(\eta_k + \sum_{j=1}^{\infty} j \alpha_{jk} \right) x_k \\ &\leq c_4 \|x\| - \epsilon_4 \sum_{k=1}^{\infty} k x_k. \end{aligned}$$

If we combine this inequality with the one in Assumptions 15(e), 10 follows with $c_5 = 0$. One readily checks that the other assumptions of Theorem 11 are satisfied.

Theorem 18. *Let the Assumptions 15 and 17 be satisfied. Then, with the constants c_4 and $\epsilon_4 > 0$ from Assumption 17,*

$$w(t) + \sum_{j=1}^{\infty} j x_j(t) \leq \left(\check{w} + \sum_{j=1}^{\infty} j \check{x}_j \right) e^{-\epsilon_4 t} + \frac{c_4 \|\check{x}\|}{\epsilon_4}$$

for all solutions (w, x) of (2.1) with initial data $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$. Further $\|x(t)\| \leq \|\check{x}\|$ for all $t \geq 0$.

2.6.1 Extinction Without Migration or Colonization

The metapopulation in system (2.27) dies out, if there is no emigration from the patches or if empty patches are not colonized.

Corollary 2. *Let Assumptions 15 and 17 be valid. Assume that $\alpha_{00} = 0$ and that for all $k \in \mathbb{N}$ there is some $j \in \mathbb{Z}_+$, $j < k$, such that $\alpha_{jk} > 0$. Further let (σ_j) be a bounded sequence and $\limsup_{k \rightarrow \infty} \sum_{j=1}^{\infty} \frac{j \alpha_{jk}}{k} < 0$. Finally and most importantly let $\gamma_{00} = 0$ or $\eta_j = 0$ for all $j \in \mathbb{N}$. Then, for model (2.27),*

$$\sum_{k=1}^{\infty} k \int_0^{\infty} x_k(s) ds < \infty \quad \text{and} \quad \lim_{t \rightarrow \infty} \sum_{k=1}^{\infty} k x_k(t) = 0.$$

Proof. If $\gamma_{00} = 0$, the statement follows from Theorem 14. If $\eta_j = 0$ for all $j \in \mathbb{N}$, then $w' \leq -\delta w$ by (2.27) and $\int_0^{\infty} w(t) dt < \infty$ and w is bounded on \mathbb{R}_+ . The statement now follows from Theorem 13. \square

2.6.2 An a Priori Estimate for Equilibria

An equilibrium of (2.27) is a time-independent solution of (2.27). Equivalently it is a time-independent solution of (2.28). In either case, an equilibrium (w, x) , $w \geq 0$, $x = (x_k) \in \ell_+^{11}$ satisfies $x \in D(A_1)$ and

$$\begin{aligned}\delta w &= \sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k, \\ 0 &= A_1 x + w \Gamma x,\end{aligned}\tag{2.29}$$

where $[A_1 x]_j = \sum_{k=0}^{\infty} \alpha_{jk} x_k$, $x \in D(A_1)$, and $[\Gamma x]_j = \sum_{k=0}^{\infty} \gamma_{jk} x_k$, $x \in \ell^{11}$. Γ maps ℓ_+^{11} into ℓ_+^{11} by Assumption 15.

Theorem 19. *Let the Assumptions 15 and 17 be satisfied. Then, for every solution $x \in D(A_1) \cap \ell_+^{11}$ of $0 = A_1 x + w \Gamma x$, where $w \geq 0$ is given, we have the estimate*

$$\sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k \leq c_4,$$

with c_4 from Assumption 17. If (w, x) is an equilibrium of (2.27), we also have $\delta w \leq c_4$.

Proof. Let $x \in \ell_+^{11} \cap D(A_1)$ satisfy $A_1 x + w \Gamma x = 0$. Then

$$\int_0^t S_1(s) w \Gamma x ds = - \int_0^t S_1(s) A_1 x ds = x - S_1(t) x.$$

By Theorem 3, for every $t \geq 0$, $x = \lim_{n \rightarrow \infty} x^{[n]}(t)$ where

$$x^{[n]}(t) = S_1^{[n]}(t) x + w \int_0^t S_1^{[n]}(s) \Gamma x ds.$$

Since the semigroups $S_1^{[n]}$ are differentiable (Lemma 3), we can differentiate $x^{[n]}(t)$ in ℓ^{11} for $t > 0$ and

$$\frac{d}{dt} x^{[n]}(t) = A_1^{[n]} x^{[n]}(t) + w \Gamma x.$$

By (2.11), Assumptions 15 and 17,

$$\begin{aligned}& \frac{d}{dt} \sum_{j=1}^{\infty} j x_j^{[n]}(t) \\&= \sum_{k=0}^n \left(\sum_{j=1}^n j \alpha_{jk} \right) x_k^{[n]}(t) + \sum_{j=n+1}^{\infty} j \alpha_{jj} x_j^{[n]}(t) + w \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j \gamma_{jk} \right) x_k \\&\leq \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j \alpha_{jk} \right) x_k^{[n]}(t) + w \sum_{k=0}^{\infty} \sigma_k x_k \\&\leq \sum_{k=0}^{\infty} (c_4 - \epsilon_4 k - \eta_k) x_k^{[n]}(t) + w \sum_{k=0}^{\infty} \sigma_k x_k.\end{aligned}$$

We integrate this inequality,

$$\begin{aligned} \sum_{j=1}^n jx_j^{[n]}(t) &\leq \sum_{j=1}^n jx_j e^{-\epsilon_4 t} + \frac{c_4}{\epsilon_4} - \int_0^t \sum_{k=0}^n \eta_k x_k^{[n]}(t-s) e^{-\epsilon_4 s} ds \\ &\quad + w \int_0^t \sum_{k=0}^{\infty} \sigma_k x_k e^{-\epsilon_4 s} ds. \end{aligned}$$

We first take the limit $n \rightarrow \infty$ and then the limit $t \rightarrow \infty$,

$$\sum_{j=1}^{\infty} jx_j \leq \frac{c_4}{\epsilon_4} - \frac{1}{\epsilon_4} \sum_{k=0}^{\infty} \eta_k x_k + \frac{w}{\epsilon_4} \sum_{k=0}^{\infty} \sigma_k x_k.$$

In particular,

$$\sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k \leq c_4.$$

□

2.7 Compact Attractors

We continue to study the metapopulation model (2.27) under the Assumptions 15 and 17. We now fix the number of initial patches to be $N \in \mathbb{N}$ and choose the state space

$$X_N = \{(w, x) \in \mathbb{R}_+ \times \ell_+^{11}; \|x\| \leq N\}.$$

We let f and g be independent of time. By Theorems 8 and 16,

$$\Phi(t, (\check{w}, \check{x})) = (w(t), x(t)), \quad t \geq 0,$$

is a continuous semiflow on X_N . In the following it is convenient to introduce the notation $\Phi_t(x) = \Phi(t, x)$ for $t \geq 0$, $x \in X_N$. This way we obtain a family of maps $\{\Phi_t; t \geq 0\}$ on X_N with the property $\Phi_t \circ \Phi_s = \Phi_{t+s}$ in non-linear analogy to operator semigroups.

Let $B \subseteq X_N$. A non-empty compact invariant subset C of X_N is called a *compact attractor* of B if for every open set U , $C \subseteq U \subseteq X_N$, there exists some $r \geq 0$ such that $\Phi_t(B) \subseteq U$ for all $t \geq r$.

Equivalently, $d(\Phi_t(x), C) \rightarrow 0$ as $t \rightarrow \infty$, uniformly in $x \in B$. Here $d(y, B) = \inf\{d(y, z); z \in B\}$ is the distance from the point y to the set B .

A non-empty compact invariant subset C of X_N is called the *compact attractor of bounded subsets* of X_N if C is a compact attractor of every bounded subset B of X_N . Obviously, by its invariance, a compact attractor of bounded subsets is uniquely determined.

General results concerning compact attractors of bounded sets can be found in [26] and [52]. They involve concepts like dissipativity and asymptotic smoothness of the semiflow. For this particular semiflow a more direct approach seems to work better. We need some additional assumptions.

Assumption 20 (a) $\sup_{k \in \mathbb{N}} \frac{|\alpha_{jk}|}{k} < \infty$ for all $j \in \mathbb{Z}_+$.
 (b) $\sup_{k \in \mathbb{N}} \frac{|\gamma_{jk}|}{k} < \infty$ for all $j \in \mathbb{Z}_+$.
 (c) $\sup_{k \in \mathbb{N}} \sigma_k < \infty$.

Our main tool is the *separation measure of non-compactness* [3, II.3], α_s , which has the following sequential characterization in a metric space (X, d) . If $Y \subseteq X$,

$$\alpha_s(Y) = \inf \left\{ c > 0; \text{ each sequence } (x_n) \text{ in } Y \text{ has a} \right. \\ \left. \text{subsequence } (x_{n_j}) \text{ with } \limsup_{j, k \rightarrow \infty} d(x_{n_j}, x_{n_k}) \leq c \right\}. \quad (2.30)$$

It is related to the Kuratowski and the Hausdorff measures of non-compactness, α_K and α_H , by

$$\alpha_H(Y) \leq \alpha_s(Y) \leq \alpha_K(Y) \leq 2\alpha_H(Y), \quad Y \subseteq X. \quad (2.31)$$

We will use the following two of its properties:

Lemma 4. (a) $\alpha_s(B) = \alpha_s(\bar{B})$ for any bounded subset B of X and its closure \bar{B} .

(b) Let (X, d) be a complete metric space. If B_t is a family of non-empty, closed, bounded sets defined for $t > r$ that satisfy $B_t \subseteq B_s$ whenever $s \leq t$ and $\alpha_s(B_t) \rightarrow 0$ as $t \rightarrow \infty$, then $\cap_{t>r} B_t$ is a non-empty compact set.

(a) follows from (2.30), while (b) is a consequence of the inequality (2.31) and the fact that α_H and α_K satisfy (b) [3, II.2].

Lemma 5. Let Φ be a semiflow and B a bounded set and $r \geq 0$ such $\Phi_t(B) \subseteq B$ for all $t \geq r$, $\alpha_s(\Phi_t(B)) \rightarrow 0$ for $r \leq t \rightarrow \infty$. Then B has a compact attractor, namely

$$\omega(B) = \bigcap_{t \geq 0} \overline{\bigcup_{s \geq t} \Phi_s(B)}.$$

This result holds for any measure of non-compactness.

Proof. Let $B_t = \overline{\bigcup_{s \geq t} \Phi_s(B)}$. Then $B_t \subseteq B$ for $t \geq r$. By definition B_t is a decreasing family of subsets of B_0 . For $t \geq r$,

$$B_t = \overline{\Phi_{t-r} \left(\bigcup_{s \geq t} \Phi_{s+r-t}(B) \right)} \subseteq \overline{\Phi_{t-r}(B)}.$$

By Lemma 4 (a),

$$\alpha_s(B_t) \leq \alpha_s(\Phi_{t-r}(B)) \rightarrow 0, \quad r \leq t \rightarrow \infty.$$

By Lemma 4 (b), $\omega(B) = \bigcap_{t \geq 0} B_t$ is non-empty and compact. Suppose that $\omega(B)$ does not attract B . Then there exist sequences $x_n \in B$ and $t_n \rightarrow \infty$ as $n \rightarrow \infty$ and $\epsilon > 0$ such that $d(\Phi(t_n, x_n), \omega(B)) > \epsilon$. Define

$$C_m = \overline{\{\Phi(t_n, x_n); n \geq m\}}.$$

Then $C_{m+1} \subseteq C_m$ for all $m \in \mathbb{N}$. Further

$$C_m = \overline{\Phi_{t_m-r}(\{\Phi(t_n + r - t_m, x_n); n \geq m\})} \subseteq \overline{\Phi_{t_m-r}(B)}.$$

By assumption, $\alpha_s(C_m) \rightarrow 0$ as $m \rightarrow \infty$. So $\bigcap_{m \in \mathbb{N}} C_m$ is non-empty and compact. Choose z in this intersection. Then $z \in \omega(B)$ and $d(\Phi(t_n, x_n), z) < \epsilon$ for some $n \in \mathbb{N}$, a contradiction. Since $\omega(B)$ is compact and attracts B , it is invariant [26, Lemma 3.3.1]. \square

Theorem 21. *Let the Assumptions 15, 17, and 20 be satisfied. Then the semi-flow Φ on X_N induced by the solutions of (2.27) has a compact attractor of all bounded subsets of X_N .*

Proof. Let B_0 be the following bounded set.

$$B_0 = \left\{ (w, x) \in X_N; w + \sum_{j=1}^{\infty} jx_j \leq \frac{c_4 N}{\epsilon_4} + 1 \right\},$$

where c_4 and ϵ_4 are the constants from Theorem 18. By Theorem 18, for every bounded set B there exists some $r > 0$ such that $\Phi_t(B) \subseteq B_0$ for all $t \geq r$. So it is sufficient to prove that the set B_0 has a compact attractor. There exists some $r_0 > 0$ such that $\Phi_t(B_0) \subseteq B_0$ for all $t \geq r_0$. By Lemma 5 it is sufficient to show that $\alpha_s(\Phi_t(B_0)) \rightarrow 0$.

Let $y, \tilde{y} \in \mathbb{R}$. Then, for sufficiently small $|h|$,

$$|y + h\tilde{y}| - |y| = \begin{cases} h\tilde{y}, & y > 0, \\ |h||\tilde{y}|, & y = 0, \\ -h\tilde{y}, & y < 0. \end{cases}$$

We divide by h and take the limit $h \rightarrow 0$ either from the right or the left,

$$D_{\pm}|y|\tilde{y} := \lim_{h \rightarrow 0 \pm} \frac{|y + h\tilde{y}| - |y|}{h} = \begin{cases} \tilde{y}, & y > 0, \\ \pm|\tilde{y}|, & y = 0, \\ -\tilde{y}, & y < 0. \end{cases}$$

In particular,

$$D_-|y|\tilde{y} \leq \tilde{y} \operatorname{sign}_0(y) \quad \text{where} \quad \operatorname{sign}_0(y) = \begin{cases} 1, & y > 0, \\ 0, & y = 0, \\ -1, & y < 0. \end{cases}$$

Let $\check{x}, \tilde{x} \in B_0$ and $x^{[n]}$ and $\tilde{x}^{[n]}$ be the approximating solutions of $\Phi(\sqcup, \check{x})$ and $\Phi(\sqcup, \tilde{x})$ as in Remark 3. By [40, VI.4],

$$\begin{aligned} \frac{d_-}{dt} |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| &= D_- |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| \left(\frac{d}{dt} x_j^{[n]}(t) - \frac{d}{dt} \tilde{x}_j^{[n]}(t) \right) \\ &\leq \left(\frac{d}{dt} x_j^{[n]}(t) - \frac{d}{dt} \tilde{x}_j^{[n]}(t) \right) \text{sign}_0(x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)). \end{aligned}$$

Here $\frac{d_-}{dt}$ denotes the left derivative. Notice that $y \text{sign}_0(y) = |y|$. By (2.24) and (2.27), for $j = 1, \dots, n$,

$$\begin{aligned} \frac{d_-}{dt} |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| &\leq \sum_{k=0}^n \alpha_{jk} |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| \\ &\quad + w^{[n]}(t) \sum_{k=0}^{\infty} \gamma_{jk} |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| \\ &\quad + |w^{[n]}(t) - \tilde{w}^{[n]}(t)| \sum_{k=0}^{\infty} |\gamma_{jk}| |\tilde{x}_k^{[n]}(t)|. \end{aligned}$$

We multiply this inequality by j , add over $j = 1, \dots, n$, change the order of summation and use $\alpha_{jk} \geq 0$ for $j \neq k$,

$$\begin{aligned} \frac{d_-}{dt} \sum_{j=1}^n j |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| &\leq \sum_{k=0}^n \left(\sum_{j=1}^{\infty} j \alpha_{jk} \right) |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| \\ &\quad + w^{[n]}(t) \sum_{k=0}^{\infty} \left(\sum_{j=1}^n j \gamma_{jk} \right) |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| \\ &\quad + |w^{[n]}(t) - \tilde{w}^{[n]}(t)| \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j |\gamma_{jk}| \right) |\tilde{x}_k^{[n]}(t)|. \end{aligned}$$

Notice that $\sum_{j=1}^{\infty} j |\gamma_{jk}| \leq c_8(k+1)$ for all $k \in \mathbb{Z}_+$ by Assumption 15(d). By Assumption 17, we can choose $\epsilon > 0$ and $m \in \mathbb{N}$ such that $\sum_{j=1}^{\infty} j \alpha_{jk} \leq -\epsilon k$ for all $k > m$. Set $\xi_k = \sum_{j=1}^{\infty} j \alpha_{jk} + \epsilon k$. For $n > m$,

$$\begin{aligned}
& \frac{d_-}{dt} \sum_{j=1}^n j |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| \\
& \leq \sum_{k=0}^m \xi_k |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| - \epsilon \sum_{j=1}^n j |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| \\
& \quad + w^{[n]}(t) \sum_{k=0}^{\infty} \left(\sum_{j=1}^n j \gamma_{jk} \right) |x_k^{[n]}(t) - \tilde{x}_k^{[n]}(t)| \\
& \quad + |w^{[n]}(t) - \tilde{w}^{[n]}(t)| \sum_{k=0}^{\infty} c_8 (1+k) |\tilde{x}_k^{[n]}(t)|.
\end{aligned}$$

We integrate this differential inequality,

$$\begin{aligned}
& \sum_{j=1}^n j |x_j^{[n]}(t) - \tilde{x}_j^{[n]}(t)| \\
& \leq e^{-\epsilon t} \sum_{j=1}^n j |x_j^{[n]}(0) - \tilde{x}_j^{[n]}(0)| + \int_0^t e^{-\epsilon(t-s)} \sum_{k=0}^m \xi_k |x_k^{[n]}(s) - \tilde{x}_k^{[n]}(s)| ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} w^{[n]}(s) \sum_{k=0}^{\infty} \left(\sum_{j=1}^n j \gamma_{jk} \right) |x_k^{[n]}(s) - \tilde{x}_k^{[n]}(s)| ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} |w^{[n]}(s) - \tilde{w}^{[n]}(s)| c_8 \|\tilde{x}^{[n]}(s)\|_1 ds.
\end{aligned}$$

The infinite matrices $(\alpha_{jk}^{[n]})$ satisfy the same assumptions as the infinite matrix (α_{jk}) with the same constants. So $w^{[n]}, x^{[n]}$ satisfy the estimates in Theorem 18 with the same constants as w, x . By Lebesgue's theorem of dominated convergence (first applied to the sum and then to the integral), we can take the limit as $n \rightarrow \infty$,

$$\begin{aligned}
& \sum_{j=1}^{\infty} j |x_j(t) - \tilde{x}_j(t)| \\
& \leq e^{-\epsilon t} \sum_{j=1}^{\infty} j |x_j(0) - \tilde{x}_j(0)| + \int_0^t e^{-\epsilon(t-s)} \sum_{k=0}^m \xi_k |x_k(s) - \tilde{x}_k(s)| ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} w(s) \sum_{k=0}^{\infty} \left(\sum_{j=1}^{\infty} j \gamma_{jk} \right) |x_k(s) - \tilde{x}_k(s)| ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} |w(s) - \tilde{w}(s)| c_8 \|\tilde{x}(s)\|_1 ds.
\end{aligned}$$

By Assumptions 15(e) and 20(c), there exists some $c_9 > 0$ such that $\sum_{j=1}^{\infty} j \gamma_{jk} \leq c_9$ for all $k \in \mathbb{Z}_+$. We split up the last but one sum in the last inequality at $k = i$ where $i \in \mathbb{N}$ is arbitrary. Then

$$\begin{aligned}
& \sum_{j=1}^{\infty} j |x_j(t) - \tilde{x}_j(t)| \\
& \leq e^{-\epsilon t} \|x(0) - \tilde{x}(0)\|_1 + \int_0^t e^{-\epsilon(t-s)} \sum_{k=0}^m \xi_k |x_k(s) - \tilde{x}_k(s)| ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} w(s) \sum_{k=0}^i c_9 |x_k(s) - \tilde{x}_k(s)| ds \\
& \quad + \frac{c_9}{i} \int_0^t e^{-\epsilon(t-s)} w(s) \|x(s) - \tilde{x}(s)\|_1 ds \\
& \quad + \int_0^t e^{-\epsilon(t-s)} |w(s) - \tilde{w}(s)| c_8 \|\tilde{x}(s)\|_1 ds.
\end{aligned}$$

Let $((\check{w}^{\{n\}}, \check{x}^{\{n\}}))$ be a sequence in B_0 and $(w^{\{n\}}(t), x^{\{n\}}(t)) = \Phi(t, (\check{w}^{\{n\}}, \check{x}^{\{n\}}))$. It follows from (2.28), Assumption 20(a, b), and Theorem 18 that $w^{\{n\}}$ and, for each $j \in \mathbb{Z}_+$, $x_j^{\{n\}}$ are equi-bounded and equi-continuous with respect to n on every finite interval in \mathbb{R}_+ . By the Arzela–Ascoli theorem and a diagonalization procedure, after choosing subsequences, $w^{\{n\}}, x_j^{\{n\}}$ are Cauchy sequences for each j uniformly on every finite interval in \mathbb{R}_+ . We set $x = x^{\{l\}}$ and $\tilde{x} = x^{\{n\}}$ in the inequality above. Then

$$\begin{aligned}
& \limsup_{l,n \rightarrow \infty} \sum_{j=1}^{\infty} j |x_j^{\{l\}}(t) - x_j^{\{n\}}(t)| \\
& \leq e^{-\epsilon t} \limsup_{l,n \rightarrow \infty} \|x^{\{l\}}(0) - x^{\{n\}}(0)\|_1 \\
& \quad + \frac{c_9}{i} \limsup_{l,n \rightarrow \infty} \int_0^t e^{-\epsilon(t-s)} w^{\{l\}}(s) \|x^{\{l\}}(s) - x^{\{n\}}(s)\|_1 ds.
\end{aligned}$$

Since this estimate holds for every $i \in \mathbb{N}$ and each $x^{\{n\}}$ satisfies the estimates in Theorem 18, with the same constants, we can take the limit $i \rightarrow \infty$ and

$$\limsup_{l,n \rightarrow \infty} \sum_{j=1}^{\infty} j |x_j^{\{l\}}(t) - x_j^{\{n\}}(t)| \leq e^{-\epsilon t} \limsup_{l,n \rightarrow \infty} \|x^{\{l\}}(0) - x^{\{n\}}(0)\|_1.$$

Since $\|x\|_1 \leq |x_0| + 2 \sum_{j=1}^{\infty} j |x_j|$,

$$\limsup_{l,n \rightarrow \infty} \|\Phi_t(\check{x}^{\{l\}}) - \Phi_t(\check{x}^{\{n\}})\|_1 \leq 2e^{-\epsilon t} \|\check{x}^{\{l\}} - \check{x}^{\{n\}}\|_1 \leq 4e^{-\epsilon t} \|B_0\|_1$$

where $\|B_0\|_1 = \sup_{\check{x} \in B_0} \|\check{x}\|_1$. By (2.30), $\alpha_s(\Phi_t(B_0)) \leq 4e^{-\epsilon t} \|B_0\|_1 \rightarrow 0$ as $t \rightarrow \infty$. This finishes the proof. \square

2.8 Towards the Stability of Equilibria

For the metapopulation model (2.27) we make assumptions which guarantee that the number of patches does not change in time.

Assumption 22 Assume

(a) For all $k \in \mathbb{N}$ there is some $j \in \mathbb{Z}_+$, $j < k$, with $\alpha_{jk} > 0$, $\alpha_{00} = 0$, and

$$\sum_{j=0}^{\infty} \alpha_{jk} = 0 = \sum_{j=0}^{\infty} \gamma_{jk} \quad \forall k \in \mathbb{Z}_+.$$

(b) $\limsup_{k \rightarrow \infty} \sum_{j=0}^{\infty} \frac{j \alpha_{jk}}{k} < 0$.

Occasionally we will also assume the following.

Assumption 23 (a) The sequence (σ_n) is bounded.

(b) There exist positive constants c_0, c_1, ϵ such that

$$\sum_{j=1}^{\infty} j \gamma_{jk} \leq c_0 + c_1 k - \epsilon |\gamma_{kk}| \quad \text{for all } k \in \mathbb{N}.$$

By Corollary 1, $\|x(t)\| = \|\tilde{x}\|$. We fix the initial patch number to be N and obtain $\sum_{j=0}^{\infty} x_j(t) = N$. We will use this equality to eliminate x_0 . Notice that Assumption 15(a) and 22(a) imply that $\alpha_{j0} = 0$ for all $j \in \mathbb{Z}_+$. We equivalently rewrite (2.27) as

$$\begin{aligned} w' &= \sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=1}^{\infty} (\sigma_k - \sigma_0) x_k - (N\sigma_0 + \delta)w, \\ x_j' &= \sum_{k=1}^{\infty} \alpha_{jk} x_k + w \left(\gamma_{j0} N + \sum_{k=1}^{\infty} (\gamma_{jk} - \gamma_{j0}) x_k \right), \quad j = 1, 2, \dots \end{aligned} \quad (2.32)$$

This system can be cast in more condensed notation,

$$w' = \langle x, x^* \rangle - \xi w + w \langle x, y^* \rangle, \quad x' = \tilde{A}x + wz + w\Gamma_0 x, \quad (2.33)$$

with $x(t) = (x_j(t))_{j=1}^{\infty}$.

Remark 4. $x(t)$ takes values in $\tilde{\ell}^{11}$, the space of sequences $x = (x_j)_{j=1}^{\infty}$ with norm $\|x\|_1^{\sim} = \sum_{j=1}^{\infty} j|x_j|$. Further

$$\xi = N\sigma_0 + \delta, \quad u = (\gamma_{j0})_{j=1}^{\infty}, \quad z = Nu,$$

x^* and y^* in the dual space of $\tilde{\ell}^{11}$,

$$\langle x, x^* \rangle = \sum_{k=1}^{\infty} \eta_k x_k, \quad \langle x, y^* \rangle = \sum_{k=1}^{\infty} (\sigma_0 - \sigma_k) x_k.$$

Finally

$$\tilde{A}x = \left(\sum_{k=1}^{\infty} \alpha_{jk} x_k \right)_{j=1}^{\infty}, \quad \Gamma_0 x = \tilde{\Gamma}x - \langle x, z^* \rangle u$$

with

$$\langle x, z^* \rangle = \sum_{k=1}^{\infty} x_k, \quad \tilde{\Gamma}x = \left(\sum_{k=1}^{\infty} \gamma_{jk} x_k \right)_{j=1}^{\infty}.$$

2.8.1 Stability of Equilibria

Let (\tilde{w}, \tilde{x}) be an equilibrium, i.e. a constant solution of (2.33). $(\tilde{w}, \tilde{x}) = (0, 0)$ is an equilibrium, e.g., called the *extinction equilibrium*. Any other equilibrium in $\mathbb{R}_+ \times \tilde{\ell}_+^{11}$ is called a *persistence equilibrium*. To study the stability of the equilibrium (\tilde{w}, \tilde{x}) , we expand the system about the equilibrium. We set $w = \tilde{w} + v$ and $x = \tilde{x} + y$ and obtain the following equation for v and y , where we have replaced \tilde{x} by x and \tilde{w} by w ,

$$\begin{aligned} v' &= \langle y, x^* \rangle - \xi v + v \langle x, y^* \rangle + w \langle y, y^* \rangle + v \langle y, y^* \rangle, \\ y' &= \tilde{A}y + vz + w\Gamma_0 y + v\Gamma_0 x + v\Gamma_0 y. \end{aligned} \quad (2.34)$$

This is an abstract Cauchy problem (evolution equation)

$$(v, y)' = \mathcal{A}(v, y) + g(v, y), \quad (2.35)$$

where \mathcal{A} is the linear operator defined in ℓ^{11} by

$$\begin{aligned} \mathcal{A}(v, y) &= (\langle y, x^* \rangle - \xi v + v \langle x, y^* \rangle + w \langle y, y^* \rangle, \tilde{A}y + vz + w\Gamma_0 y + v\Gamma_0 x), \\ v &\in \mathbb{R}, y \in \tilde{\ell}^{11}, \end{aligned} \quad (2.36)$$

and g the non-linear map on ℓ^{11} defined by

$$g(v, y) = (v \langle y, y^* \rangle, v\Gamma_0 y). \quad (2.37)$$

Proposition 3. *Let the Assumptions 15 and 22 be satisfied. Let \tilde{A} and $\tilde{\Gamma}$ be as in Remark 4. Let $w \geq 0$. If $w > 0$ also assume Assumption 23. Then $\tilde{A}_w = \tilde{A} + w\tilde{\Gamma}$, with appropriate domain, is the generator of a positive C_0 -semigroup \tilde{S} on $\tilde{\ell}^{11}$ with strictly negative growth bound.*

Proof. Define $\beta_{jk} = \alpha_{jk} + w\gamma_{jk}$ for $j, k \in \mathbb{Z}_+$. The operator \tilde{A}_w is associated with the infinite matrix $(\beta_{jk})_{j,k=1}^{\infty}$. For $k \in \mathbb{N}$,

$$\sum_{j=1}^{\infty} \beta_{jk} = -\alpha_{0k} - w\gamma_{0k}$$

which is non-positive for $k \in \mathbb{N}$ and strictly negative for $k = 1$. Also the other assumptions of [39, Proposition 6.3] are satisfied. It follows that \tilde{A}_w with domain $\{x \in \tilde{\ell}^{11}; \sum_{j=1}^{\infty} |\beta_{jj}| |x_j| < \infty, \tilde{A}_w x \in \tilde{\ell}^{11}\}$ is the generator of a C_0 -semigroup $\tilde{S}(t)$ on $\tilde{\ell}^{11}$ and there exist $\epsilon > 0$, $M \geq 1$ such that $\|\tilde{S}(t)\|_1 \leq Me^{-\epsilon t}$. \square

Proposition 4. *Let $w \geq 0$ and $x \in \tilde{\ell}^{11}$. Let $\Gamma_0 y = \tilde{\Gamma} y + \langle y, z^* \rangle u$ with the ingredients as in Remark 4. Let the Assumptions 15 and 22 be satisfied and, if $w > 0$, also Assumption 23. Then \mathcal{A} is the generator of a C_0 -semigroup T with strictly negative essential growth bound (essential type).*

Proof. $\mathcal{A} = B + C$ where

$$\begin{aligned} B(v, y) &= (-\xi v, \tilde{A}_w y), \\ C(v, y) &= (\langle y, x^* \rangle + v \langle x, y^* \rangle, vz - w \langle y, z^* \rangle u + v \Gamma_0 x) \end{aligned}$$

By Proposition 3, \tilde{A}_w is the generator of a C_0 -semigroup \tilde{S} on $\tilde{\ell}^{11}$ with strictly negative growth bound. B is the generator of the semigroup $S(t)(v, y) = (e^{-\xi t} v, \tilde{S}(t)y)$. S also has a strictly negative growth bound. The linear operator C on ℓ^{11} has finite-dimensional range and therefore is compact. The perturbation $\mathcal{A} = B + C$ generates a C_0 -semigroup T such that $T(t) - S(t)$ is compact for every $t \geq 0$. So the essential growth bound of T does not exceed the growth bound of S and is strictly negative [14, Chap. 4 Proposition 2.12].

□

Theorem 24. *Let the Assumptions 15 and 22 be satisfied and \tilde{w}, \tilde{x} be an equilibrium of (2.32). If $\tilde{w} \neq 0$, also make Assumption 23.*

Then the following hold:

(a) *If all eigenvalues of $\mathcal{A} = B + C$ have strictly negative real part, then the equilibrium (\tilde{w}, \tilde{x}) is locally asymptotically stable in the following sense. There exist $M \geq 1$ and $r > 0$ such that*

$$\|(w(t), x(t)) - (\tilde{w}, \tilde{x})\|_1 \leq M e^{-rt} \|(w(0), x(0)) - (\tilde{w}, \tilde{x})\|_1 \quad \forall t \geq 0,$$

for all solutions of (2.32).

(b) *If $\mathcal{A} = B + C$ has at least one eigenvalue with strictly positive real part, then the equilibrium (\tilde{w}, \tilde{x}) is unstable in the following sense: there exist some $\epsilon > 0$ and a sequence $0 < t_n \rightarrow \infty$ as $n \rightarrow \infty$ and a sequence of solutions w^n, x^n of (2.32) such that $w^n(0) \rightarrow \tilde{w}, x^n(0) \rightarrow \tilde{x}$ as $n \rightarrow \infty$ and $\|(w^n(t_n), x^n(t_n)) - (\tilde{w}, \tilde{x})\|_1 \geq \epsilon$ for all $n \in \mathbb{N}$.*

Proof. We notice that the non-linearity g in (2.35) and (2.37) satisfies $\frac{\|g(v, y)\|_1}{\|(v, y)\|_1} \rightarrow 0$ as $v \rightarrow 0, y \rightarrow 0$. Let $\Phi(t, \check{w}, \check{x})$ be the semiflow induced by the solutions of (2.32) with initial data \check{w} and \check{x} . It follows from standard arguments (essentially from Gronwall's inequality, cf. [55, Sect. 3], e.g.) that, for each $t \geq 0$, $\Phi(t, \cdot)$ is differentiable at (\tilde{w}, \tilde{x}) with derivative $T(t)$ from Proposition 4. The results now follow from [12] along the lines of [55, Sect. 4]. □

2.9 Instability of Every Other Equilibrium: General Result

The following derivation of an instability condition for equilibria is more efficiently done on a somewhat more abstract level and may apply to other

situations where an unstructured (part of the) population [in our case the dispersers] is paired with a structured (part of the) population [in our case the occupants]. We consider the system

$$w' = f(w, x), \quad x' = \Lambda x + g(w, x). \quad (2.38)$$

Here Λ is a closed linear operator in an ordered Banach space X with cone X_+ and $f : \mathbb{R}_+ \times X_+ \rightarrow \mathbb{R}$, $g : \mathbb{R}_+ \times X_+ \rightarrow X$ are continuously differentiable.

We assume that \mathbb{R}_+ is contained in the resolvent set of Λ and also in the resolvent set of $\Lambda + g_x(w, x)$ for each $w \geq 0$ and $x \in X_+$.

g_w and g_x denote the partial derivatives of $g(w, x)$ with respect to w and x . Since Λ^{-1} exists and is bounded, -1 is in the resolvent set of $\Lambda^{-1}g_x(w, x)$ and

$$(\mathbb{I} + \Lambda^{-1}g_x(w, x))^{-1}\Lambda^{-1} = (\Lambda + g_x(w, x))^{-1}. \quad (2.39)$$

2.9.1 The Equilibria

A pair (w, x) is an equilibrium solution of (2.38) if and only if $0 = f(w, x)$ and x satisfies the fixed point equation

$$x = -\Lambda^{-1}g(w, x). \quad (2.40)$$

Assume that for every $w > 0$ there exists a solution $x = \phi(w)$ of (2.40). It follows from our assumptions and the implicit function theorem [8, Chap. 2, Theorem 2.3] that ϕ is differentiable (analytic if g is analytic) and

$$\phi'(w) = -\Lambda^{-1}\left(g_w(w, \phi(w)) + g_x(w, \phi(w))\phi'(w)\right). \quad (2.41)$$

By our assumptions and (2.39),

$$\begin{aligned} \phi'(w) &= -(\mathbb{I} + \Lambda^{-1}g_x(w, \phi(w)))^{-1}\Lambda^{-1}g_w(w, \phi(w)) \\ &= -(\Lambda + g_x(w, \phi(w)))^{-1}g_w(w, \phi(w)). \end{aligned} \quad (2.42)$$

We substitute the solution $x = \phi(w)$ of (2.40) into $0 = f(w, x)$,

$$0 = f(w, \phi(w)) =: F(w). \quad (2.43)$$

Theorem 25. *A pair (w, x) with $w \in \mathbb{R}_+$ and $x \in X_+$ is an equilibrium if and only if $F(w) = 0$ and $x = \phi(w)$. In particular there is a one-to-one correspondence between equilibria and zeros of F . F is analytic if f and g are analytic.*

For later use we differentiate the function F ,

$$F'(w) = f_w(w, \phi(w)) + f_x(w, \phi(w))\phi'(w).$$

We substitute (2.42),

$$F'(w) = f_w(w, x) - f_x(w, x)(\Lambda + g_x(w, x))^{-1}g_w(w, x). \quad (2.44)$$

2.9.2 The Eigenvalue Problem of the Linearized System

We linearize (2.38) around an equilibrium (w, x) ,

$$v' = f_w(w, x)v + f_x(w, x)y, \quad y' = \Lambda y + g_w(w, x)v + g_x(w, x)y. \quad (2.45)$$

The associated eigenvalue problem has the form

$$\begin{aligned} \lambda v &= f_w(w, x)v + f_x(w, x)y, \\ \lambda y &= \Lambda y + g_w(w, x)v + g_x(w, x)y. \end{aligned} \quad (2.46)$$

Consider $\lambda \geq 0$. We solve the second equation for y ,

$$y = (\lambda - \Lambda - g_x(w, x))^{-1} g_w(w, x)v = v(\lambda - \Lambda - g_w(w, x))^{-1} g_w(w, x).$$

We notice that $(v, y) \neq (0, 0)$ if and only if $v \neq 0$. We substitute the expression for y into the first equation of (2.46) and divide by v ,

$$\lambda = f_w(w, x) + f_x(w, x)(\lambda - \Lambda - g_w(w, x))^{-1} g_w(w, x).$$

This leads to the following characteristic equation,

$$0 = Q(\lambda) := \lambda - f_w(w, x) - f_x(w, x)(\lambda - \Lambda - g_w(w, x))^{-1} g_w(w, x).$$

We evaluate $Q(\lambda)$ for $\lambda = 0$ and compare it to (2.44),

$$Q(0) = -f_w(w, x) + f_x(w, x)(\Lambda + g_w(w, x))^{-1} g_w(w, x) = -F'(w).$$

Notice that $Q(\lambda) \rightarrow \infty$ as $\lambda \rightarrow \infty$. If $Q(0) < 0$, the characteristic equation has a root $\lambda > 0$ by the intermediate value theorem.

Theorem 26. *Let (w, x) be an equilibrium of (2.38) and $F'(w) > 0$. Then the associated linear operator has a strictly positive eigenvalue.*

By Theorem 25, we can order the equilibria (w, x) according to their w -component provided that the zeros of F are isolated which is the case, e.g., if f and g and so F are analytic.

Corollary 3. *Assume that the zeros of F are isolated and there is no $w > 0$ with both $F(w) = 0$ and $F'(w) = 0$. Then, for every other equilibrium, the associated linear operator has a strictly positive eigenvalue.*

Proof. If the zeros of F are isolated, then, for every $b > 0$, then we have finitely many equilibria (w_j, x_j) with $0 \leq w_j \leq b$ and can order them like $w_1 < w_2 < \dots$. Since $F'(w_j) \neq 0$, F changes sign at each w_j . So $F'(w_j) > 0$ for every other j and the associated linear operator has a strictly positive eigenvalue by Theorem 26. \square

2.10 Existence of Equilibria and Instability of Every Other Equilibrium

After eliminating the equation for the empty patches, our system can be rewritten in the form (2.32) and then in a more condensed form for $w(t) \in \mathbb{R}_+$ and $x(t) = (x_j(t))_{j=1}^\infty \in \tilde{\ell}_+^{11}$,

$$\begin{aligned} w' &= \langle x, x^* \rangle - w \langle x, y^* \rangle - w(\sigma_0 N + \delta), \\ x' &= \tilde{A}x + w\tilde{\Gamma}x + w(N - \langle x, z^* \rangle)u, \end{aligned} \quad (2.47)$$

which is the same as (2.33). Here u and x^*, y^*, z^* are as in Remark 4 as are the bounded linear quasi-positive operator $\tilde{\Gamma}$ on $\tilde{\ell}^{11}$ and \tilde{A} , the generator of a positive C_0 -semigroup on $\tilde{\ell}^{11}$. The system (2.33) fits into the framework of (2.38) by setting $\Lambda = \tilde{A}$ and

$$\begin{aligned} f(w, x) &= \langle x, x^* \rangle - w \langle x, y^* \rangle - w(\sigma_0 N + \delta), \\ g(w, x) &= w\tilde{\Gamma}x + w(N - \langle x, z^* \rangle)u. \end{aligned} \quad (2.48)$$

For each $w \geq 0$, $\tilde{A}_w = \tilde{A} + w\tilde{\Gamma}$ is also the infinitesimal generator of a positive C_0 -semigroup \tilde{S} on $\tilde{\ell}^{11}$. Notice that we obtain the operator \mathcal{A} in (2.36) when we linearize (2.47) about an equilibrium.

We make the Assumptions 15, 22 and 23. By Proposition 3, \tilde{S} has strictly negative growth bound and so, for each $w \geq 0$, \tilde{A}_w has positive resolvents $(\lambda - \tilde{A}_w)^{-1}$ for all $\lambda \geq 0$. We take the partial derivative of g in (2.48) with respect to x ,

$$g_x(w, x)y = w\tilde{\Gamma}y - w\langle y, z^* \rangle z, \quad z = Nu. \quad (2.49)$$

Lemma 6. *If $\lambda - \tilde{A}_w$ has a bounded positive inverse for $\lambda \geq 0$, $\lambda - \tilde{A} - g_x(w, x)$ has a bounded inverse and*

$$(\lambda - \tilde{A} - g_x(w, x))^{-1}\tilde{x} = (\lambda - \tilde{A}_w)^{-1}\tilde{x} - w\zeta(\lambda - \tilde{A}_w)^{-1}z$$

where

$$\zeta = \frac{\langle (\lambda - \tilde{A}_w)^{-1}\tilde{x}, z^* \rangle}{1 + w\langle (\lambda - \tilde{A}_w)^{-1}z, z^* \rangle}.$$

Proof. In order to find $\hat{x} = (\lambda - \tilde{A} - g_x(w, x))^{-1}\tilde{x}$, we solve the equation

$$\lambda\hat{x} - \tilde{A}\hat{x} - w\tilde{\Gamma}\hat{x} + w\langle \hat{x}, z^* \rangle z = \tilde{x}.$$

See (2.48). This can be rewritten as

$$(\lambda - \tilde{A}_w)\hat{x} = \tilde{x} - w\langle \hat{x}, z^* \rangle z.$$

Since the resolvent exists for \tilde{A}_w ,

$$\hat{x} = (\lambda - \tilde{A}_w)^{-1} \tilde{x} - w \langle \hat{x}, z^* \rangle (\lambda - \tilde{A}_w)^{-1} z.$$

We apply the functional z^* ,

$$\langle x, z^* \rangle = \langle (\lambda - \tilde{A}_w)^{-1} \tilde{x}_w, z^* \rangle - w \langle x, z^* \rangle \langle (\lambda - \tilde{A}_w)^{-1} z, z^* \rangle.$$

We solve for $\zeta := \langle x, z^* \rangle$ and substitute ζ into the equation for x . This yields the assertion. \square

Since f and g are analytic, (w, x) is an equilibrium of (2.47) if and only if $x = \phi(w)$ and $F(w) = 0$ where ϕ and F are analytic functions on \mathbb{R}_+ (see Theorem 25).

2.10.1 Equilibria

To find a concrete expression for the solutions $x = \phi(w)$ of the equation $Ax + g(w, x) = 0$, which is identical to

$$0 = \tilde{A}x + w\tilde{I}x + w(N - \langle x, z^* \rangle)u = \tilde{A}_w x + w(N - \langle x, z^* \rangle)u,$$

we apply the inverse of \tilde{A}_w to the second equation in (2.33),

$$x = -w(N - \langle x, z^* \rangle)\tilde{A}_w^{-1}u. \quad (2.50)$$

In order to calculate $\langle x, z^* \rangle$, we apply the functional z^* to this equation,

$$\langle x, z^* \rangle = -w(N - \langle x, z^* \rangle)\langle \tilde{A}_w^{-1}u, z^* \rangle.$$

We solve for $\langle x, z^* \rangle$,

$$\langle x, z^* \rangle = -wN \frac{\langle \tilde{A}_w^{-1}u, z^* \rangle}{1 - w\langle \tilde{A}_w^{-1}u, z^* \rangle}.$$

Notice that the denominator is positive because $-\tilde{A}_w^{-1}$ is a positive operator. Further

$$\langle x, z^* \rangle \in [0, N]. \quad (2.51)$$

We rewrite

$$\langle x, z^* \rangle = N \left(1 - \frac{1}{1 - w\langle \tilde{A}_w^{-1}u, z^* \rangle} \right). \quad (2.52)$$

We substitute this expression into the one for $x = \phi(w)$, recall $Nu = z$ from Remark 4, and find

$$\begin{aligned} \phi(w) &= w\psi(w), \\ \psi(w) &= -\frac{1}{1 - w\langle \tilde{A}_w^{-1}z, z^* \rangle} \tilde{A}_w^{-1}u \in X_+. \end{aligned} \quad (2.53)$$

By (2.43),

$$\begin{aligned} F(w) &= f(w, \phi(w)) \\ &= \langle \phi(w), x^* \rangle - w \langle \phi(w), y^* \rangle - \sigma_0 w N - \delta w. \end{aligned} \quad (2.54)$$

At this point, we need an estimate for $\phi(w)$. We recall that there is a one-to-one correspondence between equilibria of (2.32) and equilibria of the original system (2.27) with $\|x\| = 1$. This means that $\phi(w) = (x_j)_{j=1}^\infty$ where $x \in \ell_+^{11}$, $A_1 x + w \Gamma x = 0$ and $x_0 = N - \sum_{j=1}^\infty x_j$. By Theorem 19,

$$\sum_{k=1}^\infty \eta_k x_k - w \sum_{k=0}^\infty \sigma_k x_k \leq c_4.$$

After eliminating $x_0 = N - \sum_{k=1}^\infty x_k$ this reads

$$\sum_{k=1}^\infty \eta_k \phi_k(w) - w \sum_{k=1}^\infty [\sigma_k - \sigma_0] \phi_k(w) - w \sigma_0 N \leq c_4.$$

By Remark 4 and (2.54), $F(w) \leq c_4 - \delta w$ and $F(w) < 0$ for large $w > 0$.

We substitute $\phi(w) = w\psi(w)$ into F . For $w > 0$, equation $F(w) = 0$ then takes the form

$$\tilde{F}(w) = \delta$$

with

$$\tilde{F}(w) = \frac{F(w)}{w} + \delta$$

being analytic in $w > 0$ and $\tilde{F}(w) < \delta$ for large $w > 0$ and

$$\tilde{F}(0) = \langle \psi(0), x^* \rangle - \sigma_0 N, \quad \psi(0) = -\tilde{A}^{-1} z.$$

We combine Theorems 24 and 26. The associated linear operator in Theorem 26 coincides with the operator \mathcal{A} in Theorem 24. Notice that, for $w > 0$, $\tilde{F}(w) = \delta$ and $\tilde{F}'(w) = 0$ is equivalent to $F(w) = 0$ and $F'(w) = 0$.

Theorem 27. *Let the Assumptions 15, 22, and 23 be satisfied, $\xi = \sigma_0 N + \delta$.*

(a) *If $\xi < -\langle \tilde{A}^{-1} z, x^* \rangle$, the extinction equilibrium is unstable and there exists a persistence equilibrium. For all but finitely many $\xi < -\langle \tilde{A}^{-1} z, x^* \rangle$, there exists an odd number of persistence equilibria (w_j, x_j) , $w_1 < w_2 < \dots$. Every even-indexed persistence equilibrium is unstable.*

(b) *If $\xi > -\langle \tilde{A}^{-1} z, x^* \rangle$, the extinction equilibrium is stable. For all but finitely many $\xi > -\langle \tilde{A}^{-1} z, x^* \rangle$, there exists no persistence equilibrium or an even number of persistence equilibria (w_j, x_j) , $w_1 < w_2 < \dots$. Every odd-indexed persistence equilibrium is unstable.*

Proof. Assume that $\tilde{F}(w) = \delta$ has a solution. Since $\tilde{F}(w) < \delta$ for large $w > 0$, F is not constant. F is analytic and so is F' . Since F' is not zero everywhere, there is no accumulation of arguments w with $\tilde{F}'(w) = 0$. Since $\tilde{F}(w) < \delta$ for large $w > 0$ there are only finitely many $w > 0$ such that $\tilde{F}(w) = -\delta$ and

$\tilde{F}'(w) = 0$. So for all but finitely many δ , we have $\tilde{F}'(w) \neq 0$ for all $w > 0$ with $\tilde{F}(w) = \delta$.

(a) Here we consider the case $\delta < \tilde{F}(0)$.

As $\tilde{F}(w) < \delta$ for large w , there exists an $w > 0$ such that $\tilde{F}(w) = \delta$ by the intermediate value theorem. For all but finitely many δ , $\tilde{F}'(w) \neq 0$ for all w with $\tilde{F}(w) = \delta$. Choose such a δ . Since $\tilde{F}(w) < \delta$ for sufficiently large $w > 0$, $\tilde{F}(w)$ crosses the line $\tilde{F} = \delta$ an odd number of times, the first time with a negative derivative, the second time with a positive derivative etc. By Theorems 24 and 26, every w with $\tilde{F}'(w) > 0$, i.e., every even-indexed equilibrium, is unstable. (b) is proved similarly. The stability proof for the extinction equilibrium is postponed to Theorem 33. \square

Application of these results to special metapopulation models can be found in [38].

2.11 Stability of the Extinction Equilibrium Versus Metapopulation Persistence

The total population size of the metapopulation is given by the sum of the number of dispersers and the total number of patch occupants,

$$P(t) = w(t) + \sum_{j=1}^{\infty} jx_j(t).$$

The extinction equilibrium is characterized by $P = 0$. The stability of the extinction equilibrium can be formulated in terms of the total population size.

The extinction equilibrium is locally stable if, for every $\epsilon > 0$, there exists some $\delta > 0$ such that $P(t) \leq \epsilon$ whenever $P(0) < \delta$. The extinction equilibrium is locally asymptotically stable, if in addition there exists some $\delta_0 > 0$ such that $P(t) \rightarrow 0$ as $t \rightarrow \infty$ whenever $P(0) < \delta_0$.

The following two concepts imply the instability of the extinction equilibrium.

The metapopulation is called *weakly uniformly persistent* if there exists some $\epsilon > 0$ (independent of the initial conditions) such that

$$\limsup_{t \rightarrow \infty} P(t) > \epsilon \quad \text{whenever} \quad P(0) > 0.$$

The metapopulation is called *(strongly) uniformly persistent* if there exists some $\epsilon > 0$ (independent of the initial conditions) such that

$$\liminf_{t \rightarrow \infty} P(t) > \epsilon \quad \text{whenever} \quad P(0) > 0.$$

Obviously uniform persistence implies weak uniform persistence. The converse holds under additional assumptions the most crucial of which is the existence

of a compact attractor. Actually we will establish uniform persistence in a stronger sense. Material on persistence theory for semiflows on infinite dimensional spaces can be found in [27, 56, 58, 62].

2.11.1 Local Asymptotic Stability of the Extinction Equilibrium

We turn to the stability of the extinction equilibrium for the specific metapopulation model (2.27). After elimination of the empty patches, this is the equilibrium $\tilde{w} = 0$, $\tilde{x} = 0$ for (2.32) or rather its abstract formulation (2.33). Throughout this section, we make the Assumptions 15 and 22. We define a linear operator B_0 (on appropriate domain in ℓ^{11}) and a bounded linear operator C on ℓ^{11} by

$$B_0(w, x) = (-\xi w, \tilde{A}x), \quad C(w, x) = (\langle x, x^* \rangle, wz). \quad (2.55)$$

and a non-linear map g on ℓ^{11} by

$$g(w, x) = (w\langle x, y^* \rangle, w\Gamma_0 x), \quad \Gamma_0 x = \tilde{\Gamma}x - \langle x, z^* \rangle \frac{1}{N}z. \quad (2.56)$$

Then (2.33) can be written as $(w, x)' = (B_0 + C)(w, x) + g(w, x)$. The domain of B_0 is the same as the one of the operator A_1 , $D(B_0) = D(A_1)$, $D_1 \subseteq D(B_0) \subseteq D_0$. For each $\epsilon \geq 0$, (2.32) can be written as the Cauchy problem

$$(w, x)' = \mathcal{A}_\epsilon(w, x) + g_\epsilon(w, x),$$

with

$$\mathcal{A}_\epsilon = B_0 - \epsilon \mathbb{I} + (1 - \epsilon)C, \quad g_\epsilon = \epsilon \mathbb{I} + \epsilon C + g. \quad (2.57)$$

Differently from g , the modified non-linearity g_ϵ , for $\epsilon > 0$, is positivity preserving in a neighborhood of the origin (the size of which depends on ϵ).

Lemma 7. *Let the Assumptions 15 and 22 hold. Then, for any $\epsilon > 0$, there exists some $\epsilon_0 > 0$ such that $g_\epsilon(w, x) \geq 0$ whenever $w \in [0, \epsilon_0]$, $x \in \tilde{\ell}_+^{11}$, $\|x\|_1^\sim \leq \epsilon_0$.*

Proof. Let $w \in [0, \epsilon_0]$, $x \in \tilde{\ell}_+^{11}$, $\|x\|_1^\sim \leq \epsilon_0$. We look at the first component of $g_\epsilon(w, x)$. By (2.56), (2.57), Remark 4, and Assumption 15(c),

$$\begin{aligned} & \epsilon w + \epsilon \langle x, x^* \rangle + w \langle x, y^* \rangle \\ & \geq \epsilon w - w \sum_{k=1}^{\infty} \sigma_k x_k \geq w(\epsilon - c_7 \|x\|_1^\sim) \geq w(\epsilon - c_7 \epsilon_0) \geq 0, \end{aligned}$$

if ϵ_0 is chosen small enough. We look at the second component of g_ϵ . By (2.57) (2.56), and (2.55),

$$\epsilon x + \epsilon w z + w \Gamma_0 x = \epsilon x + w \tilde{\Gamma} x + w \left(\epsilon - \langle x, z^* \rangle \frac{1}{N} \right) z.$$

The term in (\cdot) can be estimated by

$$\geq \epsilon - \|x\|_1 \frac{1}{N} \geq \epsilon - \epsilon_0 \frac{1}{N} \geq 0,$$

if $\epsilon_0 > 0$ is chosen small enough. As for the other term,

$$(\epsilon x + w \tilde{\Gamma} x)_j \geq (\epsilon - w \gamma_{jj}) x_j \geq (\epsilon - w c_8) x_j$$

where c_8 is the constant in Assumption 15(d). The last expression is non-negative if $w \leq \epsilon_0$ and $\epsilon_0 > 0$ is chosen small enough. \square

The operators $(1 - \epsilon)C$ are compact for every $\epsilon \geq 0$. By Proposition 3, \tilde{A} is the generator of a C_0 -semigroup \tilde{S} on $\tilde{\ell}^{11}$ with strictly negative growth bound. The operators $B_0 - \epsilon \mathbb{I}$ generate C_0 -semigroups S^ϵ on ℓ^{11} which have the form

$$S^\epsilon(t)(w, x) = \left(e^{-(\epsilon+\xi)t} w, e^{-\epsilon t} \tilde{S}(t) \tilde{x} \right).$$

Obviously the semigroups S^ϵ have strictly negative growth bounds. For each $\epsilon \geq 0$, the operator $A_\epsilon = B_0 - \epsilon \mathbb{I} + (1 - \epsilon)C$ generates a C_0 -semigroup $\{T^\epsilon(t); t \geq 0\}$ on ℓ^{11} . Since $(1 - \epsilon)C$ is compact, $T^\epsilon(t) - S^\epsilon(t)$ is compact for every $t \geq 0$ and the essential growth bound of T^ϵ equals the essential growth bound of S^ϵ [14, Chap. 4, Proposition 2.12] and is strictly negative. For all $\epsilon \in [0, 1]$, the operators $(1 - \epsilon)C$ are positive, i.e., they map ℓ_+^{11} into itself. Since the semigroup S^ϵ is positive, the standard perturbation formula implies that the semigroup T^ϵ is positive.

Proposition 5. *Let the Assumptions 15 and 22 be satisfied. Assume that there is a spectral value of A_0 with non-negative real part. Then there exists some $\lambda_0 \geq 0$ with the following properties:*

- (i) λ_0 is a pole of the resolvent of A_0 , is isolated in the spectrum of A_0 and an eigenvalue of A_0 with finite algebraic multiplicity.
- (ii) $\lambda_0 \geq \Re \lambda$ for every λ in the spectrum of A_0 .
- (iii) λ_0 is associated with positive eigenvectors of A_0 and A_0^* .

Proof. By assumption, the spectral bound of A_0 ,

$$\lambda_0 = \sup\{\Re \lambda; \lambda \in \sigma(A_0)\},$$

is non-negative. Since $T(t) - S(t)$ is compact for every $t > 0$, $(\lambda - A_0)^{-1} - (\lambda - B_0)^{-1}$ is compact for sufficiently large $\lambda > 0$, i.e., A_0 is resolvent compact relatively to B_0 [57, Def.3.7]. Then the spectral bound λ_0 is non-negative and has the asserted properties [57, Proposition 3.10]. \square

Theorem 28. *Let the Assumptions 22 and 15 be satisfied. Assume that there is no element $v \in \ell_+^{11} \cap D(\mathcal{A}_0)$ such that $v \neq 0$ and $\mathcal{A}_0 v \geq 0$. Then the extinction equilibrium is locally asymptotically stable.*

Proof. It follows from the assumptions and (2.56) that g is continuously differentiable in ℓ_+^{11} and $g'(0) = 0$. Suppose that the spectral bound of \mathcal{A}_0 ,

$$\lambda_0 = \sup\{\Re \lambda; \lambda \in \sigma(\mathcal{A}_0)\},$$

is non-negative. Then the same arguments as in the proof of Proposition 5 imply that λ_0 has the properties (i), (ii), (iii) asserted in Proposition 5, in particular $\mathcal{A}_0 v = \lambda_0 v \geq 0$ with some $v \in \ell_+^{11} \cap D(\mathcal{A}_0)$, in contradiction to our assumption. Hence $\lambda_0 < 0$ and all eigenvalues of $\mathcal{A}_0 + g'(0) = \mathcal{A}_0$ have strictly negative real parts. The assertion follows from Theorem 24. Recall $\tilde{w} = 0$. \square

2.11.2 Instability of the Extinction Equilibrium

Theorem 29. *Let the Assumptions 22 and 15 be satisfied. Assume that there is an element $v \in \ell_+^{11} \cap D(\mathcal{A}_0)$ such that $v \neq 0$ and $\mathcal{A}_0 v \geq 0$. Further assume that there is no element $v \in \ell_+^{11} \cap D(\mathcal{A}_0)$ such that $v \neq 0$ and $\mathcal{A}_0 v = 0$. Then the extinction equilibrium is unstable.*

Remark 5. Under the assumptions of Theorem 29, there exists an eigenvalue $\lambda_0 > 0$ of \mathcal{A}_0 which is associated with positive eigenvectors of \mathcal{A}_0 and \mathcal{A}_0^* .

Proof. We choose some $v \in \ell_+^{11}$, $v \neq 0$, such that $\mathcal{A}_0 v \geq 0$. For $\lambda > 0$, $(\lambda - \mathcal{A}_0)v \leq \lambda v$. For sufficiently large λ , $(\lambda - \mathcal{A}_0)^{-1}$ exists and is a bounded positive operator. We apply it to the previous inequality arbitrarily many times, $v \leq \lambda^n (\lambda - \mathcal{A}_0)^{-n} v$. This implies that the spectral radius of $\lambda(\lambda - \mathcal{A}_0)^{-1}$ is greater than or equal to 1. Hence the spectral bound of \mathcal{A}_0 , λ_0 , satisfies $\lambda_0 \in [0, \infty)$ [57, Cor. 3.6]. By Proposition 5, λ_0 is an eigenvalue of \mathcal{A}_0 associated with an eigenvector $v \in \ell_+^{11}$ of \mathcal{A}_0 and a positive eigenvector of \mathcal{A}_0^* . Since $\mathcal{A}_0 v \neq 0$ for all $v \in \ell_+^{11}$, $v \neq 0$, $\lambda_0 > 0$. So \mathcal{A}_0 has a positive eigenvalue and, by Theorem 28 (notice that $\mathcal{A} = \mathcal{A}_0$ because $w = \tilde{w} = 0$), the extinction equilibrium $(0, 0)$ is unstable. \square

2.11.3 Persistence of the Metapopulation

Since persistence is a stronger property than instability of the extinction equilibrium, it is not surprising that we uphold the assumptions of Theorem 29. Then the operator $\mathcal{A}_0 = B_0 + C$ has a positive eigenvalue which is associated with a positive eigenvector of \mathcal{A}_0^* . We need this eigenvector to be strictly positive in an appropriate sense. To this end we make irreducibility assumptions for the transition matrix (α_{jk}) .

Definition 1. The infinite matrix $(\alpha_{jk})_{j,k \in \mathbb{N}}$ is called *irreducible* if, for every $j, k \in \mathbb{N}$, $j \neq k$, there exist $n \in \mathbb{N}$ and $i_1, \dots, i_n \in \mathbb{N}$ such that $i_1 = k$, $i_n = j$ and $\alpha_{i_{l+1}, i_l} > 0$ for $l = 1, \dots, n-1$;

If $k_0 \in \mathbb{N}$, the finite matrix $(\alpha_{jk})_{j,k=1}^{k_0}$ is called *irreducible* if the analogous statement holds with the set \mathbb{N} be replaced by $\{0, \dots, k_0\}$.

A number $k_0 \in \mathbb{N}$ is called the *irreducibility bound* of the infinite matrix (α_{jk}) , if the matrix $(\alpha_{jk})_{j,k=0}^{k_0}$ is irreducible, $\alpha_{jk} = 0$ whenever $j > k_0$ and $k = 0, \dots, j-1$, and $\alpha_{kk} < 0$ for $k > k_0$.

Analogously the irreducibility of an infinite matrix $(\check{\alpha}_{jk})_{j,k \in \mathbb{Z}_+}$ or its irreducibility bound are defined.

Notice that the irreducibility together with the assumptions $\sum_{j=0}^{\infty} \alpha_{jk} \leq 0$, $\alpha_{jk} \geq 0$ for $j \neq k$, implies that $\alpha_{kk} < 0$ for all $k \in \mathbb{N}$. It is easy to see that the irreducibility bound (if there is one) is uniquely determined.

Assumption 30 Let one of the following be satisfied:

- (a) The infinite matrix $(\alpha_{jk})_{j,k \in \mathbb{N}}$ is irreducible and $\gamma_{j0} > 0$ for some $j \in \mathbb{N}$ and $\eta_k > 0$ for some $k \in \mathbb{N}$.
- or
- (b) The matrix $(\alpha_{jk})_{j,k \in \mathbb{N}}$ has the irreducibility bound k_0 , $\gamma_{j0} > 0$ for some $j \in \{1, \dots, k_0\}$ and $\eta_k > 0$ for some $k \in \{1, \dots, k_0\}$.

Proposition 6. Let Assumption 22, 15 and 30 be satisfied. Then the eigenvalue λ_0 of \mathcal{A}_0 in Proposition 5 is associated with a strictly positive eigenvector v^* of \mathcal{A}_0^* , $\langle \mathbf{x}, v^* \rangle > 0$ for all $\mathbf{x} \in \ell_+^{11}$, $\mathbf{x} \neq 0$.

Proof. Let us first assume (a) in the Assumption 30. The operator $\mathcal{A}_0 = B_0 + C$, with B_0 and C in (2.55) and x^*, z in Remark 4, is associated with the infinite matrix

$$(\beta_{jk})_{j,k=0}^{\infty} = \begin{pmatrix} -\xi & \eta_1 & \eta_2 & \cdots \\ \gamma_{10}N & \alpha_{11} & \alpha_{12} & \cdots \\ \gamma_{20}N & \alpha_{21} & \alpha_{22} & \cdots \\ \vdots & \vdots & \vdots & \vdots \end{pmatrix}. \quad (2.58)$$

By Assumption 30(a) this infinite matrix is irreducible and the semigroup T generated by \mathcal{A}_0 is strictly positive on ℓ_+^{11} , i.e., $[T(t)\mathbf{x}]_j > 0$ for every $t > 0$, $j \in \mathbb{Z}_+$, $\mathbf{x} \in \ell_+^{11}$, $\mathbf{x} \neq 0$. This implies that the eigenvector v^* of \mathcal{A}_0 associated with λ_0 is strictly positive, i.e. $\langle \mathbf{x}, v^* \rangle > 0$ for all $\mathbf{x} \in \ell_+^{11}$, $\mathbf{x} \neq 0$. Let us now assume (b) in the Assumption 30. v^* can be identified with a sequence $(y_j)_{j=0}^{\infty}$ with $y_j = \langle e_j, v^* \rangle \geq 0$ for all $j \in \mathbb{Z}_+$. Here e_j is the sequence which has 1 in the j^{th} term and only zeros otherwise. Suppose that $y_j = 0$ for $j = 0, \dots, k_0$. Let $k > k_0$ be the smallest natural number for which $y_k > 0$. Since $k > 1$, by the form of (2.58),

$$\langle e_k, \mathcal{A}^* v^* \rangle = \sum_{j=k}^{\infty} y_j \alpha_{jk}.$$

Since $\alpha_{jk} = 0$ for $j > k > k_0$ by Definition 1,

$$\langle e_k, \mathcal{A}^* v^* \rangle = \alpha_{kk} y_k.$$

But also $\langle e_k, \mathcal{A}^* v^* \rangle = \lambda_0 y_k$ which implies $0 < \lambda_0 = \alpha_{kk} \leq 0$, a contradiction. Hence $y_j > 0$ for at least one $j \in \{0, \dots, k_0\}$. Since the matrix $(\beta_{jk})_{j,k=0}^{k_0}$ is irreducible, $[T(t)\mathbf{x}]_j > 0$ for all $t > 0$, $j = 0, \dots, k_0$, $\mathbf{x} \in \ell_+^{11}$, $\mathbf{x} \neq 0$. Hence, for each $\mathbf{x} \in \ell_+^{11}$, $\mathbf{x} \neq 0$,

$$0 < \langle T(t)\mathbf{x}, v^* \rangle = e^{\lambda_0 t} \langle \mathbf{x}, v^* \rangle.$$

□

Theorem 31. *Let Assumptions 22, 15, and 30 be satisfied. Assume that there is an element $v \in \ell_+^{11}$, $v \neq 0$, such that $\mathcal{A}_0 v = (B_0 + C)v \geq 0$. Further assume that there is no element $v \in \ell_+^{11}$, $v \neq 0$, such that $(B_0 + C)v = 0$.*

Then the metapopulation is uniformly weakly persistent, i.e., there exists some $\epsilon_0 > 0$ such that

$$\limsup_{t \rightarrow \infty} \left(w(t) + \sum_{j=1}^{\infty} j x_j(t) \right) \geq \epsilon_0$$

for all solutions of (2.27) with $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$, $\check{w} + \sum_{j=1}^{\infty} j \check{x}_j > 0$.

Proof. By Remark 5, \mathcal{A}_0 has an eigenvalue $\lambda_0 > 0$. We first show that the operators \mathcal{A}_ϵ also have positive eigenvalues provided that $\epsilon > 0$ is small enough. Let λ be a resolvent value of B_0 . Then

$$\lambda - \mathcal{A}_\epsilon = [\mathbb{I} + \epsilon(\lambda - B_0)^{-1} - (1 - \epsilon)C(\lambda - B_0)^{-1}](\lambda - B_0).$$

If $\lambda > 0$ is chosen large enough,

$$\|\epsilon(\lambda - B_0)^{-1} - (1 - \epsilon)C(\lambda - B_0)^{-1}\| < 1$$

for all $\epsilon \in [0, 1]$ and the operator in $[\]$ has a bounded inverse. Thus $\lambda - \mathcal{A}_\epsilon$ has a bounded inverse and

$$\begin{aligned} (\lambda - \mathcal{A}_\epsilon)^{-1} &= (\lambda - B_0)^{-1} [\mathbb{I} + \epsilon(\lambda - B_0)^{-1} - (1 - \epsilon)C(\lambda - B_0)^{-1}]^{-1} \\ &\xrightarrow{\epsilon \rightarrow 0} (\lambda - B_0)^{-1} [\mathbb{I} - C(\lambda - B_0)^{-1}]^{-1} = (\lambda - \mathcal{A}_0)^{-1}. \end{aligned}$$

As $\lambda_0 > 0$ is an eigenvalue of \mathcal{A}_0 and an isolated point of the spectrum of \mathcal{A}_0 by Proposition 5, we can choose $\epsilon > 0$ so small that $\lambda_\epsilon > 0$ for the spectral bound λ_ϵ of \mathcal{A}_ϵ [32, Chap. 4, Theorem 2.25 and Sect. 3.5]. Then Propositions 5 and 6 hold for \mathcal{A}_ϵ and λ_ϵ rather than \mathcal{A}_0 and λ_0 . Once $\epsilon > 0$ has been chosen, by Lemma 7 there exists some $\epsilon_0 > 0$ such that $g_\epsilon(\mathbf{x}) := \epsilon \mathbf{x} + \epsilon C \mathbf{x} + g(\mathbf{x}) \geq 0$ for all $\mathbf{x} \in \ell_+^{11}$, $\|\mathbf{x}\|_1 \leq \epsilon_0$. Assume that there exists a non-negative solution $w, (x_j)_{j=0}^\infty$ of (2.27) with $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$, $\check{w} + \sum_{j=1}^{\infty} j \check{x}_j > 0$ and

$$\limsup_{t \rightarrow \infty} \left(w(t) + \sum_{j=1}^{\infty} j x_j(t) \right) < \epsilon_0.$$

If we set $x(t) = (x_j(t))_{j=1}^{\infty}$, w and x satisfy (2.33). Then $\mathbf{x} = (w, x)$ in ℓ_+^{11} with $\mathbf{x}(0) \neq 0$ and $\limsup_{t \rightarrow \infty} \|\mathbf{x}(t)\|_1 < \epsilon_0$. By Propositions 5 and 6, $\lambda_\epsilon = s(\mathcal{A}_\epsilon)$ is an eigenvalue of \mathcal{A}_ϵ and there exists $v_\epsilon^* \in X_+^*$, $X = \ell^{11}$, such that $\langle x, v_\epsilon^* \rangle > 0$ for all $x \in \ell_+^{11}$, $x \neq 0$. By making a time shift forward and using the semiflow property, we can assume that $\langle \mathbf{x}(t), v_\epsilon^* \rangle > 0$ and $\|\mathbf{x}(t)\|_1 \leq \epsilon_0$ for all $t \geq 0$. Then, for all $t \geq 0$,

$$\mathbf{x}(t) = \mathbf{x}(0) + \mathcal{A}_\epsilon \int_0^t \mathbf{x}(s) ds + \int_0^t g_\epsilon(\mathbf{x}(s)) ds \geq \mathbf{x}(0) + \mathcal{A}_\epsilon \int_0^t \mathbf{x}(s) ds.$$

Let $\hat{\mathbf{x}}(\lambda)$ denote the Laplace transform of \mathbf{x} ,

$$\hat{\mathbf{x}}(\lambda) = \int_0^\infty e^{-\lambda t} \mathbf{x}(t) dt.$$

We take the Laplace transform of the equation above,

$$\hat{\mathbf{x}}(\lambda) \geq \frac{1}{\lambda} \mathbf{x}(0) + \frac{1}{\lambda} \mathcal{A}_\epsilon \hat{\mathbf{x}}(\lambda).$$

We multiply by λ and apply the functional v_ϵ^* ,

$$\lambda \langle \hat{\mathbf{x}}(\lambda), v_\epsilon^* \rangle \geq \langle \mathbf{x}(0), v_\epsilon^* \rangle + \lambda_\epsilon \langle \hat{\mathbf{x}}(\lambda), v_\epsilon^* \rangle.$$

For $\lambda = \lambda_\epsilon$ we obtain the contradiction, $0 \geq \langle \mathbf{x}(0), v_\epsilon^* \rangle > 0$. \square

If the solution semiflow has a compact attract, a stronger persistence results can be obtained.

Theorem 32. *Let the Assumptions 15, 17, 20, 22, and 30 be satisfied.*

Assume that there is an element $v \in \ell_+^{11}$, $v \neq 0$, such that $(B_0 + C)v \geq 0$. Further assume that there is no element $v \in \ell_+^{11}$, $v \neq 0$, such that $(B_0 + C)v = 0$.

Then the metapopulation is uniformly strongly persistent in the following sense: Under Assumption 30(a), for every $j \in \mathbb{Z}_+$, there exists some $\epsilon_j > 0$ such that

$$\liminf_{t \rightarrow \infty} w(t) \geq \epsilon_0, \quad \liminf_{t \rightarrow \infty} x_j(t) \geq \epsilon_j \quad \forall j \in \mathbb{N}$$

for all integral solutions of (2.27) with $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$, $\check{w} + \sum_{j=1}^{\infty} j \check{x}_j > 0$. Under Assumption 30(b), such a result holds for w and x_1, \dots, x_{k_0} .

Proof. We define $\rho : \mathbb{R}_+ \times \ell_+^{11} \rightarrow \mathbb{R}_+$ by $\rho(w, x) = w + \sum_{j=1}^{\infty} j x_j$, $x = (x_j)_{j=0}^{\infty}$. By Theorem 31, the semiflow induced by the solutions of (2.27) is uniformly weakly ρ -persistent in the language of [58, A.5] and has a compact attractor by Theorem 21. We apply [58, Theorem A.34]. In order to show the

persistence result for x_j , fix $j \in \mathbb{N}$ for (a) and $j \in \{1, \dots, k_0\}$ for (b) and define $\tilde{\rho}(x) = x_j$, $x = (x_j)_{j=0}^\infty$. In order to show the persistence result for w define $\tilde{\rho}$ by $\tilde{\rho}(w, x) = w$. Let Φ be the semiflow induced by the solutions of (2.28), $\Phi_t(\tilde{w}, \tilde{x}) = (w(t), x(t))$ with $w, x = (x_j)_{j=0}^\infty$ satisfying (2.28). A total orbit $(w(t), x(t))$ of Φ is defined for all $t \in \mathbb{R}$ and satisfies $(w(t), x(t)) = \Phi_{t-r}(w(r), x(r))$ for all $t, r \in \mathbb{R}$, $t \geq r$. This is equivalent to

$$\begin{aligned} w' &= \sum_{k=1}^{\infty} \eta_k x_k - w \sum_{k=0}^{\infty} \sigma_k x_k - \delta w \quad \text{on } \mathbb{R}, \\ x_j(t) - x_j(r) &= \sum_{k=0}^{\infty} \alpha_{jk} \int_r^t x_k(s) ds + \sum_{k=0}^{\infty} \gamma_{jk} \int_r^t w(s) x_k(s) ds, \\ j &\in \mathbb{Z}_+, r, t \in \mathbb{R}, t > r. \end{aligned} \quad (2.59)$$

Cf. (2.28). The assumptions of [58, Theorem A.34] are satisfied by the following Lemma. \square

Lemma 8. *Let the assumptions of Theorem 32 be satisfied. Let $w(t), x(t) = (x_j(t))_{j=0}^\infty$ be a non-negative solution of (2.59) which exists on \mathbb{R} such that $w(t) + \|x(t)\|_1 \leq c$ for all $t \in \mathbb{R}$ with some constant $c > 0$ and $\|x(t)\| = N$ for all $t \in \mathbb{R}$.*

Then $w(t) > 0$ and $x_j(t) > 0$ for all $t \in \mathbb{R}$ and all $j \in \mathbb{N}$, whenever $w(t) + \sum_{k=1}^\infty k x_k(t) > 0$ for all $t \in \mathbb{R}$.

Proof. By (2.59), integrating the equation for w , for $t > r$,

$$\begin{aligned} w(t) &= w(r) \frac{\phi(t)}{\phi(r)} + \int_r^t \sum_{k=1}^{\infty} \eta_k x_k(s) \frac{\phi(t)}{\phi(s)} ds, \\ \phi(t) &= \exp\left(\int_0^t \left[\sum_{k=0}^{\infty} \sigma_k x_k(s) - \delta\right] ds\right) > 0, \\ x_j(t) &= x_j(r) \frac{\phi_j(t)}{\phi_j(r)} + \int_r^t \sum_{k \neq j, k=1}^{\infty} [\alpha_{jk} + \gamma_{jk} w(s)] x_k(s) \frac{\phi_j(t)}{\phi_j(s)} ds, \\ \phi_j(t) &= \exp\left(\int_0^t [\alpha_{jj} + \gamma_{jj} w(s)] ds\right) > 0. \end{aligned} \quad (2.60)$$

The irreducibility assumptions are now combined with the following kind of arguments.

Case 1: Suppose that $x_k(r) > 0$ for some r , $k \in \mathbb{N}$. By (2.60), $x_k(t) \geq x_k(r) \frac{\phi_j(t)}{\phi_j(r)} > 0$ for all $t \geq r$. Now let $j \in \mathbb{N}$, $\alpha_{jk} > 0$. By (2.60),

$$x_j(t) \geq \int_r^t \alpha_{jk} x_k(s) \frac{\phi_j(t)}{\phi_j(s)} ds > 0 \quad \forall t > r.$$

If we combine this argument with the respective irreducibility properties of the matrix $(\alpha_{jk})_{j,k \in \mathbb{N}}$ we obtain that $x_j(t) > 0$ for $t > r$ and $j \in \mathbb{N}$ or $j = 1, \dots, k_0$ respectively.

By Assumption 30, there exists some $k \in \mathbb{N}$ such that $\eta_k > 0$. Then

$$w(t) \geq \int_r^t \eta_k x_k(s) \frac{\phi(t)}{\phi(s)} ds > 0 \quad \forall t > r.$$

Case 2: Now assume that $w(r) > 0$ for some $r \in \mathbb{R}$. By (2.60), $w(t) > 0$ for all $t > r$. Since $\sum_{k=0}^{\infty} x_k(r) = N$ there are two cases, $x_0(r) > 0$ or $x_k(r) > 0$ for some $k \in \mathbb{N}$. If the second is the case, the considerations for case 1 imply that $x_j(t) > 0$ for all $t > r$ and all $j \in \mathbb{N}$ or $j = 1, \dots, k_0$ respectively. So let us assume that $x_0(r) > 0$. Then $x_0(t) > 0$ for all $t \geq r$. By Assumption 30, there exists some $j \in \mathbb{N}$ (or $j \in \{1, \dots, k_0\}$) such that $\gamma_{j0} > 0$. By (2.60),

$$x_j(t) \geq \int_r^t \gamma_{j0} w(s) x_0(s) \frac{\phi_j(t)}{\phi_j(s)} ds > 0 \quad \forall t > r.$$

By Case 1, $x_j(t) > 0$ for all $t > r$, $j \in \mathbb{N}$. \square

We conclude this section by emphasizing that there is a distinct threshold condition (though we can only express it in abstract terms) which separates local stability of the extinction equilibrium on the one hand from existence of a persistence equilibrium and (weak or strong) persistence of the metapopulation on the other hand.

Theorem 33. *Let the Assumptions 15 and 22 be satisfied. Let z , x^* , ξ and the operator \tilde{A} be as in Remark 4. Then the following hold:*

- (a) *Let $\xi > -\langle \tilde{A}^{-1}z, x^* \rangle$. Then the extinction equilibrium is locally asymptotically stable.*
- (b) *Let $\xi < -\langle \tilde{A}^{-1}z, x^* \rangle$. Then the extinction equilibrium is unstable and there exists a persistence equilibrium. If in addition, Assumption 30 holds, the metapopulation is uniformly weakly persistent in the sense of Theorem 31. If we also add Assumptions 17 and 20, then the metapopulation is uniformly strongly persistent in the sense of Theorem 32.*

Proof. (a) We apply Theorem 28. Suppose that the assumptions of this theorem are not satisfied. Then there exists an element $v \in \ell_+^{11} \cap D(\mathcal{A}_0)$, $v \neq 0$, such that $\mathcal{A}_0 v \geq 0$. By definition of \mathcal{A}_0 in (2.57) and by (2.55), $v = (w, x)$ with $w \geq 0$, $x \in \tilde{\ell}_+^{11}$, with

$$0 \leq -\xi w + \langle x, x^* \rangle, \quad 0 \leq \tilde{A}x + wz. \quad (2.61)$$

By Proposition 3, $-\tilde{A}^{-1}$ exist and is a positive bounded linear operator. We apply it to the second inequality in (2.61), $x \leq -w\tilde{A}^{-1}z$. If $w = 0$, $x \in -\tilde{\ell}_+^{11}$ and so $x = 0$ and $v = 0$. Since $v \neq 0$, $w > 0$. We substitute $x \leq -w\tilde{A}^{-1}z$ in

the first inequality in (2.61), $0 \leq -\xi w - w \langle \tilde{A}^{-1} z, x^* \rangle$. We divide by $w > 0$ and obtain a contradiction to the assumption $\xi > -\langle \tilde{A}^{-1} z, x^* \rangle$. So the assumptions of Theorem 28 are satisfied and the local asymptotic stability of the extinction equilibrium follows.

(b) The existence of a persistence equilibrium has already been established in Theorem 27 (a). (Notice that Assumption 23 is only needed for the instability statements in Theorem 27 (a).) Similarly as in (a), we show that existence of an element $v \in \ell_+^{11}$, $v \neq 0$, $\mathcal{A}_0 v = (B_0 + C)v = 0$, leads to $\xi = -\langle \tilde{A}^{-1} z, x^* \rangle$ which is ruled out by assuming $\xi < -\langle \tilde{A}^{-1} z, x^* \rangle$. Set $x = -\tilde{A}^{-1} z$ and $w = 1$. Then $0 = \tilde{A}x + wz$ and $0 \leq -\xi w + \langle x, x^* \rangle$ which translates into $(B_0 + C)v \geq 0$ for $v = (w, x)$ by (2.55). The respective assumptions of Theorems 29, 31 and 32 are satisfied and uniform weak or uniform strong persistence follow. \square

2.12 Application to Special Metapopulation Models

In [38], we consider the following metapopulation model,

$$\begin{cases} w' = \sum_{n=1}^{\infty} (1 - q_n) \beta_n x_n(t) - \left[\delta + \sum_{n=0}^{\infty} \sigma_n x_n(t) \right] w, \\ x'_0(t) = \mu_1 x_1(t) + \sum_{n=1}^{\infty} \kappa_n x_n(t) - \sigma_0 w(t) x_0(t), \\ x'_n(t) = [q_{n-1} \beta_{n-1} + \sigma_{n-1} w(t)] x_{n-1}(t) + \mu_{n+1} x_{n+1}(t) \\ \quad - [q_n \beta_n + \sigma_n w(t) + \mu_n + \kappa_n] x_n(t), \\ \quad n = 1, 2, \dots \end{cases} \quad (2.62)$$

β_n and μ_n are the birth and death rates in local populations of size n , q_n is the probability that a juvenile stays on its birth patch if the local population size is n , κ_n is the rate at which a local population of size n is completely wiped out, and σ_n the rate at which an average migrating individual settles on a patch with local population size n . Migrating individuals are assumed to not reproduce, their per capita death rate is δ .

In comparison to (2.27), we identify

$$\begin{cases} \alpha_{k+1,k} = q_k \beta_k, & k \in \mathbb{N}, \\ \alpha_{k-1,k} = \mu_k, & k \in \mathbb{N}, \\ \alpha_{kk} = -(q_k \beta_k + \mu_k + \kappa_k), & k \in \mathbb{N}, \\ \alpha_{0k} = \kappa_k, & k \in \mathbb{N}, \\ \alpha_{k0} = 0, & k \in \mathbb{Z}_+, \\ \alpha_{jk} = 0, & |j - k| > 1, \end{cases} \quad (2.63)$$

and

$$\begin{cases} \gamma_{k+1,k} = \sigma_k, & k \in \mathbb{Z}_+, \\ \gamma_{k,k} = -\sigma_k, & k \in \mathbb{Z}_+, \\ \gamma_{jk} = 0, & j, k \in \mathbb{Z}_+ \text{ otherwise} \end{cases} \quad (2.64)$$

and $\eta_k = (1 - q_k)\beta_k$. Then

$$\sum_{j=0}^{\infty} \alpha_{jk} = 0, \quad k = 0, 1, \dots$$

For $k \in \mathbb{N}$,

$$\begin{aligned} \sum_{j=1}^{\infty} j\alpha_{jk} &= (k+1)q_k\beta_k + (k-1)\mu_k - k(q_k\beta_k + \mu_k + \kappa_k) \\ &= q_k\beta_k - \mu_k - k\kappa_k, \\ \eta_k + \sum_{j=1}^{\infty} j\alpha_{jk} &= \beta_k - \mu_k - k\kappa_k. \end{aligned}$$

For $k = 0$, $\sum_{j=1}^{\infty} j\alpha_{j0} = 0$. For $k \in \mathbb{Z}_+$,

$$\sum_{j=0}^{\infty} \gamma_{jk} = 0, \quad \sum_{j=1}^{\infty} j\gamma_{jk} = \sigma_k, \quad \sum_{j=1}^{\infty} j|\gamma_{jk}| \leq 2(1+k)\sigma_k.$$

Assumption 34 (a) $\beta_n, \kappa_n \geq 0$, $\mu_n > 0$ for all $n \in \mathbb{N}$.

(b) $0 \leq q_n \leq 1$ for all $n \in \mathbb{N}$.

(c) $\sigma_n \geq 0$ for all $n \in \mathbb{Z}_+$, $\sup_{n=0}^{\infty} \sigma_n < \infty$.

Theorem 35. *Let the Assumption 34 be satisfied. Further, if $\epsilon > 0$ is chosen small enough, let $\sup_{n=1}^{\infty} \frac{(1+\epsilon)\beta_n - \mu_n}{n} < \infty$. Then, for every $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$, there exists a unique integral solution of on $[0, \infty)$. Further $\|x(t)\| \leq \|\check{x}\|$ for all $t \geq 0$.*

Theorem 36. *Let the assumptions of Theorem 35 be satisfied. Further assume that there exist constants $c_4, \epsilon_4 > 0$ such that $\beta_n - \mu_n - n\kappa_n \leq c_4 - \epsilon_4 n$ for all $n \in \mathbb{N}$. Then*

$$w(t) + \sum_{j=1}^{\infty} jx_j(t) \leq \left(\check{w} + \sum_{j=1}^{\infty} j\check{x}_j \right) e^{-\epsilon_4 t} + \frac{c_4 \|\check{x}\|}{\epsilon_4}$$

for all solutions (w, x) of (2.62) with initial data $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$. Further $\|x(t)\| \leq \|\check{x}\|$ for all $t \geq 0$.

We apply Theorem 21.

Theorem 37. *In addition to the Assumption 34 assume that*

$$\inf_{n=1}^{\infty} \frac{\mu_n}{n} > 0, \quad \limsup_{n \rightarrow \infty} \frac{\beta_n}{\mu_n} < 1, \quad \text{and} \quad \sup_{n=1}^{\infty} \frac{\kappa_n}{n} < \infty.$$

Then the semiflow induced by the solutions of (2.62) on $\mathbb{R}_+ \times \ell_+^{11}$ has a compact attractor for bounded sets.

2.12.1 Scenarios of Extinction

The population goes extinct without emigration from the patches or colonization of empty patches.

Theorem 38. *Let the Assumptions of Theorem 37 be satisfied. If $q_k = 1$ for all $k \in \mathbb{N}$ (i.e. there is no patch emigration) or if $\sigma_0 = 0$ (empty patches are not colonized), the total population size, $w(t) + \sum_{j=1}^{\infty} jx_j(t)$, is integrable on $[0, \infty)$ and converges to 0 as $t \rightarrow \infty$.*

Proof. This follows from Corollary 2, $\gamma_{00} = -\sigma_0$, and $\eta_k = (1 - q_k)\beta_k$. \square

The population also goes extinct if on every patch the birth rate is smaller than the death rate.

Corollary 4. *Let the assumptions of Theorem 35 be satisfied. Assume that there exists some $\epsilon > 0$ such that $\beta_k - \mu_k - k\kappa_k \leq -\epsilon k$ for all $k \in \mathbb{N}$. Then the total population size, $w(t) + \sum_{j=1}^{\infty} jx_j(t)$, converges to 0 as time tends to infinity.*

Proof. The assumptions of Theorem 36 are satisfied with $c_4 = 0$. \square

2.12.2 Persistence

We assume that the metapopulation is not subject to catastrophes, $\kappa_n = 0$, and introduce the following number which can be interpreted as the basic reproduction ratio of the metapopulation [38],

$$\mathcal{R}_0 = \frac{\sigma_0 N}{\sigma_0 N + \delta} \left(\sum_{j=1}^{\infty} (1 - q_j) \frac{\beta_j}{\mu_j} \prod_{k=1}^{j-1} \frac{q_k \beta_k}{\mu_k} \right). \quad (2.65)$$

Theorem 39. *Let $\sigma_0 > 0$, $\kappa_n = 0$ for all $n \in \mathbb{N}$ and $\inf_{n=1}^{\infty} \frac{\mu_n}{n} > 0$, $\limsup_{n \rightarrow \infty} \frac{\beta_n}{\mu_n} < 1$. Then the following hold:*

- (a) *Let $\mathcal{R}_0 < 1$. Then the extinction equilibrium is locally asymptotically stable.*
- (b) *Let $\mathcal{R}_0 > 1$. Then there exists a persistence equilibrium.*
- (c) *Let $\mathcal{R}_0 > 1$ and one of the following be satisfied:*

(c₁) $q_j \beta_j > 0$ for all $j \in \mathbb{N}$ and $(1 - q_k) \beta_k > 0$ for some $k \in \mathbb{N}$,

or

(c₂) *There exists some $k_0 \in \mathbb{N}$ such that $q_j \beta_j > 0$ for $j = 1, \dots, k_0 - 1$, $q_j \beta_j = 0$ for all $j \geq k_0$, and that $(1 - q_j) \beta_j > 0$ for some $j \in \{1, \dots, k_0\}$.*

Under (c₁), for every $j \in \mathbb{Z}_+$, there exists some $\epsilon_j > 0$ such that

$$\liminf_{t \rightarrow \infty} w(t) \geq \epsilon_0, \quad \liminf_{t \rightarrow \infty} x_j(t) \geq \epsilon_j \quad \forall j \in \mathbb{N}$$

for all solutions of (2.62) with $\check{w} \geq 0$, $\check{x} \in \ell_+^{11}$, $\check{w} + \sum_{j=1}^{\infty} j\check{x}_j > 0$. Under Assumption (c₂), such a result holds for w and x_1, \dots, x_{k_0} .

Proof. We apply Theorem 33. Let $x = -\tilde{A}^{-1}z$. Then $\sum_{k=1}^{\infty} \alpha_{jk}x_k + z_j = 0$ for $j \in \mathbb{N}$ where $x \in D(\tilde{A})$. By Remark 4, $z_j = \gamma_{j0}N$. So $z_1 = N\sigma_0$ and $z_j = 0$ for $j \geq 2$ by (31). By (2.63),

$$\begin{aligned} \mu_2x_2 - q_1\beta_1x_1 &= \mu_1x_1 - \sigma_0N, \\ \mu_{j+1}x_{j+1} - q_j\beta_jx_j &= \mu_jx_j - q_{j-1}\beta_{j-1}x_{j-1}, \quad j \geq 2. \end{aligned} \quad (2.66)$$

Since $x \in D(\tilde{A})$, $\sum_{j=1}^{\infty} |\alpha_{jj}|x_j < \infty$ and (2.63) implies that the series $\sum_{j=1}^{\infty} \mu_jx_j$ and $\sum_{j=1}^{\infty} q_j\beta_jx_j$ converge. So we can add the second equality in (2.66) from j to infinity and obtain that $x_j = \frac{q_{j-1}\beta_{j-1}}{\mu_j}x_{j-1}$ for $j \geq 2$. The first equation in (2.66) implies $\mu_1x_1 = \sigma_0N$. This recursive equation is solved by

$$x_j = \prod_{l=1}^{j-1} \frac{q_l\beta_l}{\mu_l} \frac{\sigma_0N}{\mu_j}. \quad (2.67)$$

with the understanding that $\prod_{j=1}^0 = 1$. By Remark 4, $\langle x, x^* \rangle = \sum_{j=1}^{\infty} \eta_jx_j$ with $\eta_j = (1 - q_j)\beta_j$, $\xi = N\sigma_0 - \delta$. This implies that $\xi + \langle \tilde{A}^{-1}z, x^* \rangle$ has the same sign as $1 - \mathcal{R}_0$. \square

We refer to [38] for existence of multiple persistence equilibria, the special case of obligatory juvenile emigration, and a bang-bang principle of persistence-optimal emigration.

2.13 Special Host-Macroparasite Models and Existence of Solutions

Let x_n denote the number of hosts with n parasites and w the average number of free-living parasites,

$$\begin{cases} w' = \sum_{n=1}^{\infty} (1 - q_n)\beta_nx_n - \left[\delta + \sum_{n=0}^{\infty} \sigma_nx_n \right] w, \\ x'_0 = \sum_{n=0}^{\infty} \gamma_n(x)x_n + \mu_1x_1 + \sum_{n=1}^{\infty} \kappa_nx_n - \sigma_0wx_0 - \nu_0x_0, \\ x'_n = [q_{n-1}\beta_{n-1} + \sigma_{n-1}w]x_{n-1} + \mu_{n+1}x_{n+1} \\ \quad - [q_n\beta_n + \sigma_nw + \mu_n + \kappa_n + \nu_n]x_n, \\ \quad n = 1, 2, \dots \end{cases} \quad (2.68)$$

2.13.1 Explanation of Parameters

In a host with n parasites, parasites die at a rate $\mu_n \geq 0$ and are born at a rate $\beta_n \geq 0$. With probability $q_n \in [0, 1]$, newborn parasites stay within the birth host.

Hosts with n parasites are found and entered by an average free-living parasite at a per capita rate σ_n . They look for treatment and are completely delivered of their parasite load at a per capita rate $\kappa_n \geq 0$. Hosts with n parasites die at a per capita rate $\nu_n \geq 0$ and give birth at a per capita rate γ_n . To be specific, we choose a Ricker type per capita reproduction function,

$$\gamma_n(x) = \tilde{\gamma}_n \exp\left(-\sum_{k=0}^{\infty} \eta_{nk} x_k\right)$$

with $\tilde{\gamma}_n, \eta_{nk} \geq 0$. Notice that no vertical transmission has been assumed, i.e., newborn hosts have no parasites.

2.13.2 Unique Existence of Solutions

To fit the host-parasite model into the general framework we identify

$$\begin{cases} \alpha_{k+1,k} = q_k \beta_k, & k \in \mathbb{N}, \\ \alpha_{k-1,k} = \mu_k, & k = 2, 3, \dots, \\ \alpha_{01} = \mu_1 + \kappa_1, & \\ \alpha_{0k} = \kappa_k, & k = 2, 3, \dots, \\ \alpha_{kk} = -(q_k \beta_k + \mu_k + \kappa_k + \nu_k), & k \in \mathbb{N}, \\ \alpha_{00} = -\nu_0, & \\ \alpha_{jk} = 0, & \text{otherwise,} \end{cases} \quad (2.69)$$

$$\begin{aligned} f(w, x) &= \sum_{n=1}^{\infty} (1 - q_n) \beta_n x_n - \left[\delta + \sum_{n=0}^{\infty} \sigma_n x_n \right] w, \\ g_0(w, x) &= \sum_{n=0}^{\infty} \gamma_n(x) x_n - \sigma_0 w x_0, \\ g_j(w, x) &= w(\sigma_{j-1} x_{j-1} - \sigma_j x_j), \quad j \in \mathbb{N}. \end{aligned} \quad (2.70)$$

We calculate

$$\sum_{j=0}^{\infty} \alpha_{jk} = -\nu_k, \quad k = 0, 1, \dots$$

For $k \in \mathbb{N}$,

$$\begin{aligned} \sum_{j=1}^{\infty} j \alpha_{jk} &= (k+1) q_k \beta_k + (k-1) \mu_k - k(q_k \beta_k + \mu_k + \kappa_k + \nu_k) \\ &= q_k \beta_k - \mu_k - k(\kappa_k + \nu_k). \end{aligned}$$

For $k = 0$, $\sum_{j=1}^{\infty} j \alpha_{j0} = 0$. For $k \in \mathbb{Z}$,

$$\sum_{j=0}^{\infty} g_j(w, x) = \sum_{k=1}^{\infty} \gamma_k(x) x_k \quad \text{and} \quad \sum_{j=1}^{\infty} j g_j(w, x) = w \sum_{k=0}^{\infty} \sigma_k x_k.$$

Theorem 40. *Let the Assumptions 34 be satisfied and $\nu_k, \delta \geq 0$. Then, for all $\check{w} \in \mathbb{R}_+$ and $\check{x} \in \ell_+^{11}$, there exists a unique solution w, x on $[0, \infty)$ of (2.22).*

Per capita host mortality rates that depend on host density and parasite burden would realistically not lead to a bounded perturbation, but require a different approach.

2.14 Application to Prion Proliferation

We focus on model (2.2) and leave the models (2.4) and (2.5) for future work. We assume that the coefficients b_{jk} , σ_j , and κ_j are all non-negative and the parameters δ and Λ are positive. While the infinite matrices (α_{jk}) have been sparse (basically tri-diagonal with an additional full first row) in the special metapopulation model in Sect. 2.12 and the host-macroparasite model in Sect. 2.13, the matrix (α_{jk}) in (2.3) has a full array above the diagonal. The coefficients α_{jk} in (2.3) satisfy Assumption 1(a) (modified for the missing x_0 -equation). By (2.3), for $k \geq 2$,

$$\sum_{j=1}^{\infty} \alpha_{jk} = \kappa_k + \sum_{j=1}^{k-1} (b_{jk} + b_{k-j,k}) - \kappa_k - \sum_{i=1}^{k-1} b_{ik} = \sum_{j=1}^{k-1} b_{k-j,k}.$$

We substitute $k - j = i$,

$$\sum_{j=0}^{\infty} \alpha_{jk} = \sum_{i=1}^{k-1} b_{ik}. \quad (2.71)$$

Assumption 1(b) is satisfied if we assume

$$\sup_{k=1}^{\infty} \sum_{i=1}^{k-1} b_{ik} < \infty. \quad (2.72)$$

We cannot determine from the literature whether or not such an assumption is biologically reasonable. It seems to be mainly for mathematical reasons that the coefficients $b_{jk} = b$ are assumed to be constant in [45, App. A] because it allows a moment closure which transforms the infinite system to three ordinary differential equations which can be completely analyzed [47]. In this special case $\sum_{i=1}^{k-1} b_{ik} = b(k-1)$ and Assumption 1(b) is not satisfied. As for part (c),

$$\sum_{j=1}^{\infty} j \alpha_{jk} = \sum_{j=1}^{k-1} j (b_{jk} + b_{k-j,k}) - k \kappa_k - k \sum_{i=1}^{k-1} b_{ik}.$$

Again we substitute $i = j - k$,

$$\sum_{j=0}^{\infty} j \alpha_{jk} = -k \kappa_k + \sum_{j=1}^{k-1} j b_{jk} + \sum_{i=1}^{k-1} (k-i) b_{ik} - k \sum_{i=1}^{k-1} b_{ik} = -k \kappa_k. \quad (2.73)$$

This shows that Assumption 1(c) also follows from (2.72). Let $\tilde{\ell}_1 = \{x = (x_j)_{j=1}^\infty; \|x\|^\sim < \infty\}$ with $\|x\|^\sim = \sum_{j=1}^\infty |x_j|$. Then Theorem 2 and Lemma 2 hold mutandis mutatis under (2.72).

Since the state space of the non-linear equations involves $\tilde{\ell}_+^{11}$ rather than $\tilde{\ell}_+^1$, $\tilde{\ell}^{11} = \{x = (x_j)_{j=1}^\infty; \|x\|_1^\sim < \infty\}$ with $\|x\|_m^\sim = \sum_{j=1}^\infty j^m |x_j|$, it is sufficient, though, that the infinite matrix (α_{jk}) is associated with a positive C_0 -semigroup on $\tilde{\ell}^{11}$ which follows from (2.73) by the same construction as in [39] or in [59]. In order to get a handle on the generator in a analogous fashion as in Lemma 1, we investigate

$$\sum_{j=1}^\infty j^2 \alpha_{jk} = \sum_{j=1}^{k-1} j^2 (b_{jk} + b_{k-j,k}) - k^2 \kappa_k - k^2 \sum_{i=1}^{k-1} b_{ik}.$$

With the usual substitution $j = k - i$,

$$\begin{aligned} \sum_{j=1}^\infty j^2 \alpha_{jk} &= \sum_{j=1}^{k-1} j^2 b_{jk} + \sum_{i=1}^{k-1} (k-i)^2 b_{ik} - k^2 \kappa_k - k^2 \sum_{i=1}^{k-1} b_{ik} \\ &= -2 \sum_{j=1}^{k-1} j(k-j) b_{jk} - k^2 \kappa_k. \end{aligned}$$

If we do not want to impose (2.72), we can alternatively add the following boundedness and positivity assumptions.

Assumption 41 (a) $\sup_{k=2}^\infty \max_{j=1}^{k-1} b_{jk} < \infty$ and $\sup_{j=1}^\infty \frac{\kappa_j}{j} < \infty$.

(b) $\inf_{j=1}^\infty \kappa_j > 0$ or $\inf_{k=2}^\infty \frac{1}{k} \min_{j=1}^{k-1} b_{jk} > 0$.

It follows from these assumptions that there exist constants $c_0, c_1, \epsilon > 0$ such that

$$\sum_{j=1}^\infty j^2 \alpha_{jk} \leq c_0 - \epsilon k^2 - \epsilon k |\alpha_{kk}| \quad \forall k \in \mathbb{Z}_+.$$

The same proofs as in [39] or [59] provide the following result.

Lemma 9. *Let the Assumption 41 be satisfied. Then the operator \check{A}_1 on $\tilde{\ell}^{11}$ defined by*

$$\begin{aligned} \check{A}_1 x &= \left(\sum_{k=1}^\infty \alpha_{jk} x_k \right)_{j=1}^\infty, \quad x = (x_k)_{k=1}^\infty, \\ D(\check{A}_1) &= \left\{ x \in \tilde{\ell}^{11}; \sum_{k=1}^\infty k |\alpha_{kk}| |x_k| < \infty \right\} \end{aligned}$$

is closable and its closure generates a positive contraction C_0 -semigroup \tilde{S} on $\tilde{\ell}^{11}$. \tilde{S} leaves $\tilde{\ell}^{12} = \{x = (x_j); \|x\|_2^\sim < \infty\}$ invariant.

We set

$$\begin{aligned} f(t, w, x) &= \Lambda - w \sum_{k=1}^{\infty} \sigma_k x_k - \delta w, \\ g_j(t, w, x) &= w(\sigma_{j-1} x_{j-1} - \sigma_j x_j). \end{aligned}$$

Then the Assumption 4 are satisfied. Further

$$\begin{aligned} \sum_{j=1}^{\infty} g_j(t, w, x) &= 0, \\ \sum_{j=1}^{\infty} j g_j(t, w, x) &\leq w \sum_{j=1}^{\infty} \sigma_j x_j, \\ f(t, w, x) + \sum_{j=1}^{\infty} j g_j(t, w, x) &\leq \Lambda. \end{aligned}$$

By (2.73), by similar proofs as in Theorems 5 and 7, we obtain that solutions with non-negative initial data are defined and non-negative for all $t \geq 0$ and satisfy

$$\left. \begin{aligned} w(t) &\leq w(0)e^{-\delta t} + \frac{\Lambda}{\delta}(1 - e^{-\delta t}) \\ w(t) + \sum_{j=1}^{\infty} j x_j(t) &\leq w(0) + \sum_{j=1}^{\infty} j x_j(0) + \Lambda t \end{aligned} \right\} \quad \forall t \geq 0.$$

If $\inf_{j=1}^{\infty} \kappa_j > 0$, then

$$\limsup_{t \rightarrow \infty} \left(w(t) + \sum_{j=1}^{\infty} j x_j(t) \right) \leq \frac{\Lambda}{\zeta}, \quad \zeta = \min \left\{ \delta, \inf_{j=1}^{\infty} \kappa_j \right\} > 0.$$

If we additionally assume that the polymerization rates (σ_j) are bounded, a similar procedure as in Sect. 2.7 shows that the semiflow on $\mathbb{R}_+ \times \tilde{\ell}_+^{11}$ associated with system (2.2) has a compact attractor for bounded sets. If $\inf_{j=1}^{\infty} \kappa_j = 0$ but

$\inf_{k=2}^{\infty} \frac{1}{k} \min_{j=1}^{k-1} b_{jk} > 0$, we conjecture that the semiflow has a compact attractor for bounded sets if it is restricted to the positive cone of the invariant subspace $\mathbb{R} \times \tilde{\ell}^{12}$ with the stronger norm $(w, x) = |w| + \sum_{j=1}^{\infty} j^2 |x_j|^2$.

A. Non-Differentiability of the Simple Death Process Semigroup

We prove formulas (2.19) and (2.20) which imply that the semigroups S on ℓ and S_1 on ℓ^{11} associated with the simple birth process are not differentiable

at any $t \in (0, \ln 2]$. Recall that we have chosen $\bar{t} = \ln 2$ such that $e^{-\bar{t}} = 1/2$. By (2.17) and (2.18),

$$\begin{aligned} \left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\| &= 2 \sum_{j=0}^{2n} \binom{2n}{j} 2^{-2n} |n-j| \\ &= 2 \sum_{j=0}^{n-1} \binom{2n}{j} 2^{-2n} (n-j) + 2 \sum_{j=n+1}^{2n} \binom{2n}{j} 2^{-2n} (j-n). \end{aligned}$$

We substitute $j = 2n - k$ in the last sum and use $\binom{2n}{k} = \binom{2n}{2n-k}$,

$$\left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\| = 4 \sum_{j=0}^{n-1} \binom{2n}{j} 2^{-2n} (n-j). \quad (2.74)$$

By the binomial theorem,

$$2^{2n} = \sum_{j=0}^{2n} \binom{2n}{j} = 2 \sum_{j=0}^{n-1} \binom{2n}{j} + \binom{2n}{n}. \quad (2.75)$$

By rearranging the binomial coefficients,

$$\sum_{j=0}^{n-1} \binom{2n}{j} j = 2n \sum_{j=1}^{n-1} \binom{2n-1}{j-1} = 2n \sum_{j=0}^{n-2} \binom{2n-1}{j}. \quad (2.76)$$

Again by the binomial theorem,

$$2^{2n-1} = \sum_{j=0}^{2n-1} \binom{2n-1}{j} = \sum_{j=0}^{n-2} \binom{2n-1}{j} + \sum_{j=n-1}^{2n-1} \binom{2n-1}{j}.$$

In the second sum we substitute $j = 2n - 1 - k$. Then

$$\begin{aligned} 2^{2n-1} &= \sum_{j=0}^{n-2} \binom{2n-1}{j} + \sum_{k=0}^n \binom{2n-1}{2n-1-k} \\ &= 2 \sum_{j=0}^{n-2} \binom{2n-1}{j} + \binom{2n-1}{n} + \binom{2n-1}{n-1}. \end{aligned}$$

We combine this formula with (2.76),

$$\sum_{j=0}^{n-1} \binom{2n}{j} j = n \left(2^{2n-1} - \binom{2n}{n} \right).$$

We combine this last formula with (2.75),

$$2 \sum_{j=0}^{n-1} \binom{2n}{j} (n-j) = n \left(2^{2n} - \binom{2n}{n} \right) - 2n \left(2^{2n-1} - \binom{2n}{n} \right) = n \binom{2n}{n}.$$

By (2.74), we obtain the equation in (2.19). One checks by induction that

$$\binom{2n}{n} 2^{-2n} = \frac{(1 - \frac{1}{2}) \cdots (n - \frac{1}{2})}{1 \cdots n}.$$

(Cf. [17, II.(12.5)] and [17, II.(4.1)].) By (2.19), for $n \geq 2$,

$$\left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\| = \frac{(1 + \frac{1}{2}) \cdots (n - 1 + \frac{1}{2})}{1 \cdots (n-1)} = \prod_{j=1}^{n-1} \frac{j + \frac{1}{2}}{j} = \prod_{j=1}^{n-1} \left(1 + \frac{1}{2j} \right).$$

We take the logarithm,

$$\begin{aligned} \ln \left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\| &= \sum_{j=1}^{n-1} \ln \left(1 + \frac{1}{2j} \right) \\ &\geq \int_1^{n-1} \ln \left(1 + \frac{1}{2x} \right) dx = \frac{1}{2} \int_2^{2(n-1)} \ln \left(1 + \frac{1}{y} \right) dy \\ &\geq \frac{1}{2} \int_2^{2(n-1)} \left(\frac{1}{y} - \frac{1}{2y^2} \right) dy \geq \frac{1}{2} (\ln 2(n-1) - \ln 2 - 1) \\ &= \frac{1}{2} (\ln(n-1) - 1). \end{aligned}$$

We exponentiate this estimate and obtain (2.20). As for the inequality in (2.19),

$$\begin{aligned} &\left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\|_1 - \left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\| \\ &= \sum_{j=1}^{\infty} j \left| \frac{d}{dt} [S(\bar{t}) e^{[2n]}]_j \right| = 2 \sum_{j=1}^{2n} \binom{2n}{j} 2^{-2n} j |n-j| \\ &= 2 \sum_{j=1}^{n-1} \binom{2n}{j} 2^{-2n} j (n-j) + 2 \sum_{j=n+1}^{2n} \binom{2n}{j} 2^{-2n} j (j-n) \\ &= 2 \sum_{j=1}^{n-1} \binom{2n}{j} 2^{-2n} j (n-j) + 2 \sum_{k=0}^{n-1} \binom{2n}{2n-k} 2^{-2n} (2n-k)(n-k) \\ &= 2^{1-2n} 2n^2 + 4n \sum_{j=1}^{n-1} \binom{2n}{j} 2^{-2n} (n-j). \end{aligned}$$

Here we have used that $\binom{2n}{2n-k} = \binom{2n}{k}$. By (2.74),

$$\left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\|_1 = 2^{-2n} 2n^2 + (n+1) \left\| \frac{d}{dt} S(\bar{t}) e^{[2n]} \right\|.$$

This implies the inequality in (2.19).

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References

1. L.J.S. ALLEN, *An Introduction to Stochastic Processes with Applications to Biology*, Pearson Education, Upper Saddle River 2003
2. F. ARRIGONI, Deterministic approximation of a stochastic metapopulation model, *Adv. Appl. Prob.* **35** (2003) 691–720
3. J.M. AYERBE TOLEDANO, T. DOMINGUEZ BENAVIDES, and G. LÓPEZ ACEDO, *Measures of Noncompactness in Metric Fixed Point Theory*, Birkhäuser, Basel 1997
4. J. BANASIAK and L. ARLOTTI, *Perturbations of Positive Semigroups with Applications*, Springer, London 2006
5. A.D. BARBOUR and A. PUGLIESE, Asymptotic behaviour of a metapopulation model, *Ann. Appl. Prob.* **15** (2005) 1306–1338
6. E. BORN and K. DIETZ, Parasite population dynamics within a dynamic host population. *Prob. Theor. Rel. Fields* **83** (1989) 67–85
7. R. CASAGRANDE and M. GATTO, A persistence criterion for metapopulations, *Theor. Pop. Biol.* **61** (2002) 115–125
8. S.-N. CHOW and J.K. HALE, *Methods of Bifurcation Theory*, Springer, New York 1982
9. PH. CLÉMENT, H.J.A.M. HEIJMANS, S. ANGENT, C.J. VAN DUIN, and B. DE PAGTER, *One-Parameter Semigroups*, North-Holland, Amsterdam 1987
10. M.D. CLINCHY, D.T. HAYDON, and A.T. SMITH, Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? *Am. Nat.* **159** (2002) 351–362
11. E.A. CODDINGTON and N. LEVINSON, *Theory of Ordinary Differential Equations*, McGraw-Hill, New York 1955
12. W. DESCH and W. SCHAPPACHER, Linearized stability for nonlinear semigroups, *Differential Equations in Banach Spaces* (A. Favini, E. Obrecht, eds.) 61–73, LNIM 1223, Springer, Berlin Heidelberg New York 1986
13. K. DIETZ, Overall population patterns in the transmission cycle of infectious disease agents, *Population Biology of Infectious Diseases* (R.M. Anderson, R.M. May, eds.), 87–102, Life Sciences Report **25**, Springer, Berlin Heidelberg New York 1982
14. K.-J. ENGEL and R. NAGEL, *One-Parameter Semigroups for Linear Evolution Equations*, Springer, Berlin Heidelberg New York 2000
15. H. ENGLER, J. PRÜSS, and G.F. WEBB, Analysis of a model for the dynamics of prions II, *J. Math. Anal. Appl.* **324** (2006) 98–117

16. W. FELLER, On the integro-differential equations of purely discontinuous Markoff processes, *Trans. AMS* **48** (1940) 488–515, Errata *ibid.*, **58** (1945) 474
17. W. FELLER, *An Introduction to Probability Theory and Its Applications*, Vol. I, 3rd edition, Wiley, New York 1968
18. W. FELLER, *An Introduction to Probability Theory and Its Applications*, Vol. II, Wiley, New York 1965
19. Z. FENG, L. RONG, and R.K. SWIHART, Dynamics of an age-structured metapopulation model, *Nat. Res. Mod.* **18** (2005) 415–440
20. M. GILPIN and I. HANSKI, eds., *Metapopulation Dynamics. Empirical and Theoretical Investigations*, Academic Press, New York 1991
21. M.L. GREER, L. PUJO-MENJOUET, and G.F. WEBB, A mathematical analysis of the dynamics of prion proliferation, *J. Theor. Biol.* **242** (2006) 598–606
22. M.L. GREER, P. VAN DEN DRIESSCHE, L. WANG, and G.F. WEBB, Effects of general incidence and polymer joining on nucleated polymerization in a prion disease model, *SIAM J. Appl. Math.* **68**(1) (2007) 154–170
23. M. GYLLENBERG and I. HANSKI, Single species metapopulation dynamics: a structured model, *Theor. Pop. Biol.* **42** (1992) 35–61
24. K.P. HADELER and K. DIETZ, An integral equation for helminthic infections: global existence of solutions, *Recent Trends in Mathematics, Reinhardtsbrunn 1982* (H. Kurke, J. Mecke, H. Triebel, R. Thiele, eds.) 153–163, Teubner, Leipzig 1982
25. K.P. HADELER and K. DIETZ, Population dynamics of killing parasites which reproduce in the host, *J. Math. Biol.* **21** (1984) 45–65
26. J.K. HALE, *Asymptotic Behavior of Dissipative Systems*. AMS, Providence 1988
27. J.K. HALE and P. WALTMAN, Persistence in infinite-dimensional systems, *SIAM J. Math. Anal.* **20** (1989) 388–395
28. I. HANSKI and M.E. GILPIN, eds., *Metapopulation Biology: Ecology, Genetics, and Evolution*, Academic Press, San Diego 1996
29. E. HILLE and R.S. PHILLIPS, *Functional Analysis and Semi-Groups*, AMS, Providence 1957
30. T. KATO, On the semi-groups generated by Kolmogoroff's differential equations, *J. Math. Soc. Japan* **6** (1954) 12–15
31. A.N. KOLMOGOROV, Über die analytischen Methoden der Wahrscheinlichkeitrechnung, *Math. Annalen* **104** (1931) 415–458
32. T. KATO, *Perturbation Theory for Linear Operators*, Springer, Berlin Heidelberg New York 1976
33. V.A. KOSTIZIN, Symbiose, parasitisme et évolution (étude mathématique), Herman, Paris 1934, translated in *The Golden Age of Theoretical Ecology* (F. Scudo, J. Ziegler, eds.), 369–408, Lecture Notes in Biomathematics **22**, Springer, Berlin Heidelberg New York 1978
34. M. KRETZSCHMAR, A renewal equation with a birth-death process as a model for parasitic infections, *J. Math. Biol.* **27** (1989) 191–221
35. P. LAURENÇOT and C. WALKER, Well-posedness for a model of prion proliferation dynamics, *J. Evol. Eqn.* **7** (2007) 241–264
36. R. LEVINS, Some demographic and genetic consequences of environmental heterogeneity for biological control, *Bull. Entom. Soc. Am.* **15** (1969) 237–240

37. R. LEVINS, Extinction, *Some Mathematical Questions in Biology* (M.L. Gerstenhaber, ed.) 75–107, Lectures on Mathematics in the Life Sciences 2, AMS 1970
38. M. MARTCHEVA and H.R. THIEME, A metapopulation model with discrete patch-size structure, *Nat. Res. Mod.* **18** (2005), 379–413
39. M. MARTCHEVA, H.R. THIEME, and T. DHIRASAKDANON, Kolmogorov’s differential equations and positive semigroups on first moment sequence spaces, *J. Math. Biol.* **53** (2006) 642–671
40. R.H. MARTIN, *Nonlinear Operators and Differential Equations in Banach Spaces*, Wiley, New York 1976
41. J. MASEL, V.A.A. JANSEN, and M.A. NOWAK, Quantifying the kinetic parameters of prion replication, *Biophys. Chem.* **77** (1999) 139–152
42. J.A.J. METZ and M. GYLLENBERG, How should we define fitness in structured metapopulation models? Including an application to the calculation of evolutionary stable dispersal strategies, *Proc. R. Soc. Lond. B* **268** (2001) 499–508
43. A. MOILANEN, A.T. SMITH, and I. HANSKI, Long term dynamics in a metapopulation of the American pika, *Am. Nat.* **152** (1998) 530–542
44. J. NAGY, *Evolutionary Attracting Dispersal Strategies in Vertebrate Metapopulations*, Ph.D. Thesis, Arizona State University, Tempe 1996
45. M.A. NOWAK, D.C. KRAKAUER, A. KLUG, and R.M. MAY, Prion infection dynamics, *Integr Biol* **1** (1998) 3–15
46. A. PAZY, *Semigroups of Linear Operators and Applications to Partial Differential Equations*, Springer, Berlin Heidelberg New York 1982
47. J. PRÜSS, L. PUJO-MENJOUET, G.F. WEBB, and R. ZACHER, Analysis of a model for the dynamics of prions, *Discr. Cont. Dyn. Syst. B* **6** (2006) 215–225
48. A. PUGLIESE, Coexistence of macroparasites without direct interactions, *Theor. Pop. Biol.* **57** (2000) 145–165
49. A. PUGLIESE, Virulence evolution in macro-parasites, *Mathematical Approaches for Emerging and Reemerging Infectious Diseases* (C. Castillo-Chavez, S. Blower, P. van den Driessche, D. Kirschner, A.-A. Yakubo, eds.) 193–213, Springer, Berlin Heidelberg New York 2002
50. G.E.H. REUTER, Denumerable Markov processes and the associated contraction semigroups on ℓ , *Acta Mathematica* **97** (1957), 1–46
51. G.E.H. REUTER and W. LEDERMANN, On the differential equations for the transition probabilities of Markov processes with enumerable many states, *Proc. Camb. Phil. Soc.* **49** (1953) 247–262
52. G.R. SELL and Y. YOU, *Dynamics of Evolutionary Equations*, Springer, Berlin Heidelberg New York 2002
53. G. SIMONETT and C. WALKER, On the solvability of a mathematical model for prion proliferation, *J. Math. Anal. Appl.* **324** (2006) 580–603
54. A.T. SMITH and M.E. GILPIN: Spatially correlated dynamics in a pika metapopulation, [28], 407–428
55. H.R. THIEME, Semiflows generated by Lipschitz perturbations of non-densely defined operators, *Differential Integral Equations* **3** (1990) 1035–1066
56. H.R. THIEME, Persistence under relaxed point-dissipativity (with applications to an epidemic model), *SIAM J. Math. Anal.* **24** (1993) 407–435
57. H.R. THIEME, Remarks on resolvent positive operators and their perturbation, *Disc. Cont. Dyn. Sys.* **4** (1998) 73–90
58. H.R. THIEME, *Mathematics in Population Biology*, Princeton University Press, Princeton 2003

59. H.R. THIEME and J. VOIGT, Stochastic semigroups: their construction by perturbation and approximation, *Positivity IV – Theory and Applications* (M.R. Weber, J. Voigt, eds.), 135–146, Technical University of Dresden, Dresden 2006
60. J. VOIGT, On substochastic C_0 -semigroups and their generators, *Transp. Theory Stat. Phys.* **16** (1987) 453–466
61. C. WALKER, Prion proliferation with unbounded polymerization rates, *Electron. J. Diff. Equations*, Conference **15** (2007) 387–397
62. X.-Q. ZHAO, *Dynamical Systems in Population Biology*, Springer, Berlin Heidelberg New York 2003

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