Persistent Discrete-Time Dynamics on Measures

Horst R. Thieme

Abstract A discrete-time structured population model is formulated by a *population turnover map* F on the cone of finite nonnegative Borel measures that maps the structural population distribution of a given year to the one of the next year. F has a first order approximation at the zero measure (the extinction fixed point), which is a positive linear operator on the ordered vector space of real measures and can be interpreted as a *basic population turnover operator*. A spectral radius can be defined by the usual Gelfand formula and can be interpreted as *basic population turnover number*. We continue our investigation (Thieme, H.R.: Discrete-time population dynamics on the state space of measures, Math. Biosci. Engin. 17:1168–1217 (2020). doi: 10.3934/mbe.2020061) in how far the spectral radius serves as a threshold parameter between population extinction and population persistence. Emphasis is on conditions for various forms of uniform population persistence if the basic population turnover number exceeds 1.

Keywords Extinction · Basic reproduction number · Feller kernel · Eigenfunctions · Flat norm (also known as dual bounded lipschitz norm)

1 Introduction

Many animal and plant populations have yearly cycles with reproduction occurring once a year during a relatively short period. They also carry population structures which may be due to spatial distribution, age or rank structure, or degree of maturity.

It seems appropriate to describe such populations by discrete-time structured models in the form of difference equations,

H. R. Thieme (✉)
School of Mathematical and Statistical Sciences, Arizona State University,
Tempe, AZ 85287-1804, USA
e-mail: hthieme@asu.edu
URL: https://asu.digication.com/horst-thieme/welcome/published

S. Baigent et al. (eds.), *Progress on Difference Equations and Discrete Dynamical Systems*, Springer Proceedings in Mathematics & Statistics 341,
https://doi.org/10.1007/978-3-030-60107-2_4

$$x_n = F(x_{n-1}), \qquad n \in \mathbb{N}, \quad x_0 \in X_+, \tag{1}$$

with the population structure being encoded in the closed subset $X_+ \ni 0$ of a normed vector space X over $\mathbb{R}$, $F(0) = 0$ [17, 20, 32]. The vector x_n describes the structural distribution of the population in year n while $F : X_+ \to X_+$ formulates the rule how the structural distribution in a given year follows from the structural distribution of the previous year. The norm $\|x_n\|$ is some measure of the population size in year n. F is called the *(yearly) population turnover operator*. The condition $F(0) = 0$ means that the population is closed: If there is no population this year, then there is no population next year. We use the notation

$$\dot{X}_+ = X_+ \setminus \{0\}. \tag{2}$$

Notice that (1) is solved by

$$x_n = F^n(x_0), \qquad n \in \mathbb{N}, \tag{3}$$

where F^n is the n-fold composition or iterate of the operator F and $\{F^n; n \in \mathbb{N}\}$ is the discrete semiflow on X_+ induced by the map F [26, Sect. 1.2].

Since this paper relies more heavily on dynamical systems theory than its prequel [32], we will rather use the iterates F^n than solutions of (1) to formulate our results.

A fundamental question is as to whether the population always dies out, $\|F^n(x_0)\| \to 0$ as $n \to \infty$ for all $x_0 \in X_+$, or whether it persists uniformly [26, 33]:

There is some $\epsilon > 0$ such that for all $x_0 \in \dot{X}_+$ there is some $N \in \mathbb{N}$ such that $\|F(x_0)\| \geq \epsilon$ for all $n \geq N$ (with ϵ not depending on x_0).

In addressing this question, we assume that X_+ is *a (positively) homogeneous subset* of X:

If $x \in X_+$ and $\alpha \in \mathbb{R}_+$, then $\alpha x \in X_+$.

We assume that F is directionally differentiable at $0 = F(0)$, i.e., that all directional differentials

$$B(x) = \partial F(0, x) = \lim_{\mathbb{R}_+ \ni b \to 0} \frac{1}{b} F(bx), \qquad x \in X_+, \tag{4}$$

exist. It is easy to see that the directional derivative $B : X_+ \to X_+$ at 0 is (positively) *homogeneous* (of degree one) [20, Theorem 3.1]:

If $x \in X_+$ and $\alpha \in \mathbb{R}_+$, then $B(\alpha x) = \alpha B(x)$.

Since we rarely consider homogeneity in a different sense, B with this property is simply called *homogeneous*. B is a *first order approximation of F at 0* in a weak sense, and we will need B to be a first order approximation in a stronger sense [20, Sect. 3] with which we do not want to burden the reader quite yet. We call B the *basic population turnover operator* because it approximates the turnover operator at low population densities.

The operator norm of a homogenous operator $B : X_+ \to X_+$ is defined as

$$\|B\| := \sup\{\|B(x)\|; x \in X_+, \|x\| \le 1\}, \tag{5}$$

and B is called *bounded* if this supremum exists.

Lemma 1 *Assume that there are $\delta > 0$ and $c > 0$ such that $F : X_+ \to X_+$ satisfies $\|F(x)\| \le c\|x\|$ for all $x \in X_+$ with $\|x\| \le \delta$. Then the directional derivative B of F at 0 is bounded and $\|B\| \le c$.*

1.1 The Spectral Radius of a Homogeneous Operator

Since B is homogeneous,

$$\|B(x)\| \le \|B\| \, \|x\|, \qquad x \in X_+, \tag{6}$$

provided that B is bounded. This formula implies that the powers (iterates) $B^n : X_+ \to X_+$ of a homogeneous bounded B are bounded and $\|B^n\| \le \|B\|^n$ for all $n \in \mathbb{N}$.

The *spectral radius* of a bounded homogeneous $B : X_+ \to X_+$ is defined by the *Gelfand* formula [13]

$$\mathbf{r}(B) = \inf_{n \in \mathbb{N}} \|B^n\|^{1/n} = \lim_{n \to \infty} \|B^n\|^{1/n}. \tag{7}$$

The last equality is shown in the same well-known way as for a bounded linear everywhere-defined map. See [20, 28, 31, 32] for more information.

For restrictions of bounded positive linear operators to a cone, the Gelfand formula for the spectral radius was used by Bonsall [4] under the name "partial spectral radius" and by Nussbaum [24] under the name "cone spectral radius." Mallet-Paret and Nussbaum [21, 22] used the Gelfand formula for homogeneous bounded operators on a cone under the name "Bonsall cone spectral radius". But since this formula also makes sense on homogeneous sets (which concept includes the vector space), we simply say "spectral radius".

If B has an interpretation as basic population turnover operator, then $\mathbf{r}(B)$ is called the *basic population turnover number* [17, 20, 32].

1.2 Preview of Extinction and Persistence Results

The following results, which highlight the role of the basic turnover number as threshold parameter between population extinction and persistence, hold under additional assumptions, all of which we do not mention here.

It will be not enough to assume that X_+ is a closed homogeneous subset of X; rather X_+ needs to be a closed cone.

A homogeneous subset X_+ of X is called a *cone* if it is also a convex subset of X and if $x = 0$ is the only vector in X such that x and $-x$ are both elements in X_+. A cone is called a closed cone if it is a closed subset of the normed vector space X.

Cones, wedges and ordered vector spaces are studied in this context in [20, 28, 32] to which we refer. Similarly, not much can be done without assuming that B is order-preserving i.e., for all $x, \tilde{x} \in X_+$,

$$x - \tilde{x} \in X_+ \implies B(x) - B(\tilde{x}) \in X_+. \tag{8}$$

- For the rest of this section, let X_+ be the closed cone of the normed vector space X.
- Further, let $B : X_+ \to X_+$ be homogeneous and order-preserving and let B be an appropriate first order approximation of F.

Theorem 1 *Let X_+ be a normal cone, $F, B : X_+ \to X_+$, $r = \mathbf{r}(B) < 1$. Then the extinction state 0 is locally asymptotically stable in the following sense:*

For each $\alpha \in (r, 1)$, there exist some $\delta_0 > 0$ and $M \geq 1$ such that $\|F^n(x)\| \leq M\alpha^n \|x\|$ for all $n \in \mathbb{N}$ and all $x \in X_+$ with $\|x\| \leq \delta_0$.

See [20, Theorem 4.2] for the precise formulation. A rigorously formulated application to a general population model in the state space of measures is given in Theorem 4.

Theorem 2 *Let $F, B : X_+ \to X_+$ and B be compact and continuous, $\mathbf{r}(B) > 1$.*

Then, under appropriate additional assumptions, the population persists uniformly weakly:

There exists some $\epsilon > 0$ such that for all $x \in \dot{X}_+$ and all $m \in \mathbb{N}$ there exists some $n \in \mathbb{N}$ with $n > m$ and that $\|F^n(x)\| \geq \epsilon$.

See [20, Theorem 5.2] for the precise formulation. A rigorously formulated application to a general population model in the state space of measures is given in Theorem 6 and to a more specific model for iteroparous populations in Theorem 25.

Theorem 3 *Let $F, B : X_+ \to X_+$ and B be compact and continuous, $\mathbf{r}(B) > 1$, and*

$$\limsup_{\|x\| \to \infty} \frac{\|F(x)\|}{\|x\|} < 1.$$

Then, under appropriate additional assumptions, the semiflow induced by F has a compact persistence attractor $\mathcal{A}_1 \subseteq X_+$:

(a) $\mathcal{A}_1$ *is a compact set,* $F(\mathcal{A}_1) = \mathcal{A}_1$*, and* $\inf_{x \in \mathcal{A}_1} \|x\| > 0$.

(b) $\mathcal{A}_1$ *attracts all compact subsets* K *of* X_+ *with* $\inf_{x \in K} \|x\| > 0$*:*
If K *is such a subset and* $\mathcal{U}$ *is an open set with* $\mathcal{A}_1 \subseteq \mathcal{U} \subseteq X_+$*, then there exists some* $N \in \mathbb{N}$ *such that* $F^n(\mathcal{K}) \subseteq \mathcal{U}$ *for all* $n \in \mathbb{N}$ *with* $n \geq N$.

Theorem 3 is a consequence of Theorem 2 and of the point-dissipativity Theorem 9 in Sect. 3 and is a special case of [26, Theorem 5.7] to which we refer for the precise assumptions. A rigorously formulated application to a general population model in the state space of measures is given in Theorem 22.

Corollary 1 *Let the assumptions of Theorem 3 be satisfied. Then there is some* $\epsilon_1 > 0$ *such that for any compact subset* $\mathcal{K}$ *of* X_+ *with* $\inf_{x \in \mathcal{K}} \|x\| > 0$ *there is some* $N \in \mathbb{N}$ *such that* $\|F^n(x)\| \geq \epsilon_1$ *for all* $x \in \mathcal{K}$ *and all* $n \in \mathbb{N}$ *with* $n \geq N$.

The theorems above are known if B can be extended to a bounded linear map on X and B is the Frechet derivative of F at 0 [7, 26, 33].

There are at least three motivations to consider the more general situation of a bounded homogenous order-preserving operator. The first is of mathematical nature, namely that the directional derivative is homogeneous but not necessarily linear and that homogenous operators are not Frechet differentiable at 0 unless they are linear [20, Sect. 3].

The second, biological, motivation are two-sex population models which often use homogeneous mating functions resulting in homogeneous first order approximations of the population turnover operator [18–20, 29–31].

The third motivation are structural population distributions which are best described by measures μ on a metric space S (see [1, 2, 32] and the references therein) which is the state space of individual characteristics [8]. A point in S gives an individual's characteristic, and the metric d describes how close the characteristics of two different individuals are to each other. If $\mu : \mathcal{B} \to \mathbb{R}_+$ is a measure on the σ-algebra $\mathcal{B}$ of Borel sets in S, $\mu(T)$ gives the number of individuals whose structural characteristic lies in the Borel subset T of S. This leads to choosing $X = \mathcal{M}(S)$ as population state space, the vector space of real finite Borel measures (or rather an appropriate closed subspace of it if S is not separable). Let $X_+ = \mathcal{M}_+(S)$ denote the cone of nonnegative measures and $\dot{X}_+ = \dot{\mathcal{M}}_+(S)$ be $\mathcal{M}_+(S)$ without the zero measure. The variation norm is too strong to provide the required compactness of the basic turnover operator B on X_+ in Theorem 2 even if B can be extended to a bounded linear operator on X. A suitable alternative is the flat norm aka dual bounded Lipschitz norm (see [14] and the references therein and Sect. 4). The flat norm has the trade off that important linear basic turnover operators defined on all of X are compact and continuous on X_+ but not bounded on X [32].

2 A General Framework for the State Space of Measures

In this paper, we will be guided by the third motivation, a population state space consisting of measures on a metric space S (Sect. 4).

2.1 Feller Kernels

Important building blocks for the turnover map F are Feller kernels $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ where $\mathcal{B}$ is the σ-algebra of Borel subsets of S ([32] and Sect. 5). In fact, the first order approximation of F at 0 mentioned before will be associated with a *Feller kernel*. As a first requirement,

- $\kappa(\cdot, s)$ is a nonnegative measure on $\mathcal{B}$ for each $s \in S$.

Then, for each $f \in C^b(S)$ (bounded continuous function), we can form the integrals

$$\int_S f(t)\kappa(dt, s) =: (A_* f)(s), \qquad s \in S. \tag{9}$$

As a second requirement,

- κ has the *Feller property*, i.e., definition (9) provides a continuous bounded function $A_* f$,

and a bounded linear map A_* on $C^b(S)$ is associated with κ.

Cf. [3, Sect. 19.3]. See Example 10.12 in [32].

$C^b(S)$, the vector space of bounded continuous real-valued functions, is a Banach space under the supremum norm and has $C^b_+(S)$, the subset of nonnegative functions in $C^b(S)$, as closed convex cone. $\dot{C}^b_+(S)$ denotes this cone without the zero function.

By [32, Proposition 6.3], if κ is a Feller kernel, $\kappa(U, \cdot)$ is a Borel measurable function on S for all open subsets U of S and thus for all Borel sets U in S. Consequently, A_* can be extended to $M^b(S)$ by (9), the Banach space of bounded Borel measurable functions with the supremum norm.

For each $\mu \in \mathcal{M}(S)$, we can define

$$\int_S \kappa(T, s)\mu(ds) = (A\mu)(T), \qquad T \in \mathcal{B}, \tag{10}$$

and obtain a measure $A\mu$ and a linear map on $\mathcal{M}(S)$ and the duality relation

$$\int_S (A_* f)\, d\mu = \int_S f\, d(A\mu), \qquad f \in M^b(S), \quad \mu \in \mathcal{M}(S). \tag{11}$$

The linear operator A on $\mathcal{M}(S)$ is bounded with respect to the variation norm,

$$\|A\| = \sup_{s\in S} \kappa(S, s) = \|A_*\|, \tag{12}$$

but not necessarily bounded with respect to the flat norm [32, Sect. 9, 10].

In some probabilistic applications, it is assumed that κ is also a Markov kernel, i.e., $\kappa(S, s) = 1$ for all $s \in S$. Then $\kappa(T, s)$ can be interpreted as the probability that an individual with characteristic $s \in S$ will have a characteristic within the set T after one year. This ignores that the individual may die during the year on the one hand or have offspring on the other hand.

So, we do not assume that κ is a Markov kernel, and $\kappa(T, s)$ is rather interpreted as follows: For an individual with characteristic feature $s \in S$, $\kappa(T, s)$ is the sum of the probability that, after one year, the individual is still alive and has its characteristic feature within the set T and of the amount of its surviving offspring that has also characteristic feature within the set T. For more on Feller kernels see Sect. 5.

Definition 1 A Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called a *uniform Feller kernel* if

$$\sup_{T\in\mathcal{B}} |\kappa(T, t) - \kappa(T, s)| \to 0, \qquad t \to s, \text{ for all } s \in S. \tag{13}$$

Equivalent characterizations of uniform Feller kernels are given in Proposition 9, in particular (13) implies the Feller property above. For more on uniform Feller kernels see Sect. 5.2.

2.1.1 Convolutions and Spectral Radius of Feller Kernels

The *convolution* of two Feller kernels $\kappa_j : \mathcal{B} \times S \to \mathbb{R}_+$, $j = 1, 2$, is defined by

$$(\kappa_1 \star \kappa_2)(T, s) = \int_S \kappa_1(T, t)\kappa_2(dt, s), \qquad T \in \mathcal{B}, s \in S. \tag{14}$$

$\kappa_1 \star \kappa_2$ is again a Feller kernel.

Definition 2 Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel. We inductively define the *multiple convolution kernels* $\kappa^{n\star}$ by $\kappa^{1\star} = \kappa$ and $\kappa^{(n+1)\star} = \kappa^{n\star} \star \kappa$.

The *spectral radius* of the Feller kernel κ is defined by

$$\mathbf{r}(\kappa) = \inf_{n\in\mathbb{N}} \Big(\sup_{s\in S} \kappa^{n\star}(S, s)\Big)^{1/n}. \tag{15}$$

If A_* is the map on $C^b(S)$ or on $M^b(S)$ induced by κ, then A_*^n is induced by $\kappa^{n\star}$. This implies that $\mathbf{r}(\kappa) = \mathbf{r}(A_*)$, and so, in (15), $\inf_{n\in\mathbb{N}}$ can be replaced by $\lim_{n\to\infty}$ because of (7). See [32, Sect. 9] for more details.

2.1.2 Irreducible Feller Kernels

Since a Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ induces the positive bounded linear map A_* on the Banach lattice $C^b(S)$ with the supremum norm, irreducibility of κ could be defined as irreducibility of A_* like in [25, III.8]. However, the following weaker irreducibility concept seems to be better tailored to a Feller kernel.

Definition 3 ([27]) A Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called *top-irreducible* (short for "topologically irreducible") if for any nonempty open subset U of S and for any $s \in S \setminus U$ there is some $n \in \mathbb{N}$ such that $\kappa^{n\star}(U, s) > 0$.

We will also use the following stronger concept.

Definition 4 A Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called *strongly top-irreducible* if for any nonempty open subset U of S and any nonempty compact subset K of S there exists some $n \in \mathbb{N}$ such that $\kappa^{n\star}(U, s) > 0$ for all $s \in K$.

For more on (strongly) irreducible Feller kernels see Sect. 5.3.

2.2 *Turnover Maps on the State Space of Measures*

We consider yearly turnover maps F of the following general form,

$$F(\mu)(T) = \int_S \kappa^\mu(T, s)\, \mu(ds), \qquad \mu \in \mathcal{M}_+(S), \qquad T \in \mathcal{B}, \tag{16}$$

where $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ is a family of Feller kernels $\kappa^\mu : \mathcal{B} \times S \to \mathbb{R}_+$.

The interpretation of κ^μ is as before except that individual survival, development and reproduction play out in the environment being effected by the structural distribution μ of the population.

If μ is the zero measure, we use the notation κ^o. Often, the operator A associated with κ^o by (10) will turn out to be the first order approximation of F at the zero measure.

Finally, we emphasize that, while individual survival, development, and reproduction are modeled stochastically through the family of Feller kernels, the population model is completely deterministic.

A more specific model for a semelparous population can be found in [32, Sect. 2 and 12] and for an iteroparous population in Sect. 7.

Assumption 5 For each $\mu \in \mathcal{M}_+(S)$, κ^μ is a Feller kernel and $\{\kappa^\mu(S, t);\ \mu \in \mathcal{M}_+(S), t \in S\}$ is a bounded subset of $\mathbb{R}$.

Standard measure-theoretic arguments imply the following result.

Proposition 1 *Let the Assumption 5 be satisfied. Then F maps $\mathcal{M}_+(S)$ into itself.*

Definition 6 The kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ is called *upper semicontinuous at the zero measure* if for any $\epsilon \in (0, 1)$ there is some $\delta > 0$ such that

$$\kappa^\mu(T, s) \le (1 + \epsilon)\kappa^o(T, s), \qquad T \in \mathcal{B}, s \in S,$$

for all $\mu \in \mathcal{M}_+(S)$ with $\mu(S) \le \delta$.

The kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ is called *lower semicontinuous at the zero measure* if for any $\epsilon \in (0, 1)$ there is some $\delta > 0$ such that

$$\kappa^\mu(T, s) \ge (1 - \epsilon)\kappa^o(T, s), \qquad T \in \mathcal{B}, s \in S,$$

for all $\mu \in \mathcal{M}_+(S)$ with $\mu(S) \le \delta$.

The kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ is called *continuous at the zero measure* if for any $\epsilon \in (0, 1)$ there is some $\delta > 0$ such that

$$(1 - \epsilon)\kappa^o(T, s) \le \kappa^\mu(T, s) \le (1 + \epsilon)\kappa^o(T, s), \qquad T \in \mathcal{B}, s \in S,$$

for all $\mu \in \mathcal{M}_+(S)$ with $\mu(S) \le \delta$.

In a preview of results, we will showcase the spectral radius of the basic turnover kernel κ^o as a crucial threshold parameter between local stability (in the subthreshold case $\mathbf{r}(\kappa^o) < 1$) and instability (in the superthreshold case $\mathbf{r}(\kappa^o) > 1$) of the extinction state represented by the zero measure; $\mathbf{r}(\kappa^o)$ is called the *basic population turnover number*. For a semelparous population, as it is considered in [32, Sect. 12], the *basic turnover number* coincides with the *basic reproduction number*.

2.3 Local (Global) Stability of the Zero Measure in the Subthreshold Case

For perspective, we cite the following result [32, Theorem 3.6].

Theorem 4 *Make Assumption 5 and let the kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ be upper semicontinuous at the zero measure.*
(a) If $r = \mathbf{r}(\kappa^o) < 1$, the zero measure (the extinction state) is locally asymptotically stable in the following sense:

For each $\alpha \in (r, 1)$, there exist some $\delta_\alpha > 0$ and $M_\alpha \ge 1$ such that,

$$F^n(\mu)(S) \le \alpha^n M_\alpha\, \mu(S), \qquad n \in \mathbb{N},$$

if $\mu \in \mathcal{M}_+(S)$ with $\mu(S) \le \delta_\alpha$.

(b) If $r = \mathbf{r}(\kappa^o) < 1$ and $\kappa^\mu(T, s) \le \kappa^o(T, s)$ for all $T \in \mathcal{B}$, $s \in S$, the zero measure is globally stable in the following sense:

For each $\alpha \in (r, 1)$*, there exists some* $M_\alpha \ge 1$ *such that*

$$F^n(\mu)(S) \le \alpha^n M_\alpha \, \mu(S), \qquad n \in \mathbb{N}, \quad \mu \in \mathcal{M}_+(S).$$

Recall that $F^n(\mu)(S)$ is the total population size in the nth year and $\mu(S)$ the population size at the beginning.

2.4 Instability of the Zero Measure in the Superthreshold Case

We consider the following concepts [10, 14, 16, 32].

Definition 7 Consider a subset $\mathcal{N}$ of $\mathcal{M}_+(S)$.

- $\mathcal{N}$ is called *tight* if for any $\epsilon > 0$ there exists a compact subset K of S such that $\mu(S \setminus K) < \epsilon$ for all $\mu \in \mathcal{N}$.
- A single measure $\mu \in \mathcal{M}_+(S)$ is called *tight*, and we write $\mu \in \mathcal{M}_+^t(S)$, if $\{\mu\}$ is tight.
- $\mathcal{N}$ is called *pre-tight* if for any $\epsilon > 0$ there exists a closed totally bounded subset T of S such that $\mu(S \setminus T) < \epsilon$ for all $\mu \in \mathcal{N}$.
- A single measure $\mu \in \mathcal{M}_+(S)$ is called *separable*, and we write $\mu \in \mathcal{M}_+^s(S)$, if there exists a countable subset T of S such that $\mu(S \setminus \bar{T}) = 0$.
- A single measure $\mu \in \mathcal{M}(S)$ is called *separable*, and we write $\mu \in \mathcal{M}^s(S)$, if its absolute value $|\mu|$ is separable.

By definition, a subset T of S is *totally bounded* if for any $\epsilon > 0$ there exists a finite subset K of T such that $T \subseteq \bigcup_{s \in K} U_\epsilon(s)$. Here $U_\epsilon(s) = \{t \in S; d(t, s) < \epsilon\}$ is the open neighborhood with center s and radius ϵ. $T \subseteq S$ is compact if and only if T is totally bounded and complete [3, Sect. 3.7].

If S is a compact metric space, $\mathcal{M}_+(S)$ is trivially tight. If S is a separable metric space, $\mathcal{M}_+(S) = \mathcal{M}_+^s(S)$.

Definition 8 A Feller kernel κ is called a *tight Feller kernel* if $\{\kappa(\cdot, s); s \in S\}$ is a tight set of measures.

A Feller kernel κ is called a *Feller kernel of separable measures* if all measures $\kappa(\cdot, s)$, $s \in S$, are separable.

The condition $\mathbf{r}(\kappa^o) < 1$ in Theorem 4 is almost sharp as seen from the next result ([32, Theorem 3.13] with switched roles of κ_1 and κ_2).

Theorem 5 *Make Assumption 5 and let the kernel family* $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ *be lower semicontinuous at the zero measure.*

Assume that $\kappa^o = \kappa_1 + \kappa_2$ *with two Feller kernels* κ_j *of separable measures and assume that* κ_2 *is a tight kernel and* $r := \mathbf{r}(\kappa^o) > 1 \ge \mathbf{r}(\kappa_1)$.

Then there exists some eigenmeasure $\nu \in \mathcal{M}_+^s(S)$, $\nu(S) = 1$, *such that*

$$r\nu(T) = \int_S \kappa^o(T, s)\nu(ds), \qquad T \in \mathcal{B}.$$

Further, the zero measure is unstable: There is some $\delta_0 > 0$ *such for any* ν*-positive* $\mu \in \mathcal{M}_+(S)$ *there is some* $n \in \mathbb{Z}_+$ *with* $F^n(\mu)(S) \geq \delta_0$.

A measure $\mu \in \mathcal{M}_+(S)$ is called ν-positive if there exists some $\delta > 0$ such that $\mu(T) \geq \delta\nu(T)$ for all $T \in \mathcal{B}$.

In an iteroparous population, as we will consider it in Sect. 7, the Feller kernel κ_1 may be associated with adult survival and adult development and the Feller kernel κ_2 with reproduction and first year development. If $\mathbf{r}(\kappa_1) < 1$, $\kappa_1^\infty = \sum_{n=1}^\infty \kappa_1^{n\star}$ is a Feller kernel, and the Feller kernel

$$\kappa_2 + \kappa_2 \star \kappa_1^\infty = \kappa_2 + \sum_{n=1}^\infty \kappa_2 \star \kappa_1^{n\star}$$

can be interpreted as *next generation kernel* and its spectral radius as *basic* [9] (or *inherent net* [5, 6]) *reproduction number*. We again like to think of $\kappa^o = \kappa_1 + \kappa_2$ as *basic population turnover kernel* and its spectral radius as *basic turnover number*; this spectral radius has also been called *inherent population growth rate* [6].

Remark 1 Let $\mathbf{r}(\kappa_1) < 1$. The following trichotomy holds:

- $\mathbf{r}(\kappa_2 + \kappa_2 \star \kappa_1^\infty) > 1$ and $\mathbf{r}(\kappa_1 + \kappa_2) > 1$
  or
- $\mathbf{r}(\kappa_2 + \kappa_2 \star \kappa_1^\infty) = 1$ and $\mathbf{r}(\kappa_1 + \kappa_2) = 1$
  or
- $\mathbf{r}(\kappa_2 + \kappa_2 \star \kappa_1^\infty) < 1$ and $\mathbf{r}(\kappa_1 + \kappa_2) < 1$.

See [32, Remark 3.14, Theorem 7.16], but notice that the roles of κ_1 and κ_2 have been switched.

2.5 Persistence of the Population in the Superthreshold Case

We now give a preview of this paper's main results in the general framework for the population state space of measures. The proofs can be found in Sect. 6.

Assumption 9 For each $\mu \in \mathcal{M}_+^s(S)$, κ^μ is a Feller kernel of separable measures and $\{\kappa^\mu(S, t); \mu \in \mathcal{M}_+^s(S), t \in S\}$ is a bounded subset of $\mathbb{R}$.

Assumption 10 For any $\mu \in \dot{\mathcal{M}}_+^s(S)$, $\kappa^\mu(S, s) > 0$ for all $s \in S$.

Recall that $\dot{\mathcal{M}}_+^s(S)$ is the set of nonnegative separable measures without the zero measure.

Theorem 6 *Assume Assumptions 9 and 10. Let the kernel family* $\{\kappa^\mu;\ \mu \in \mathcal{M}_+^s(S)\}$ *be lower semicontinuous at the zero measure.*

Assume that κ^o *is a top-irreducible Feller kernel and* $\kappa^o = \kappa_1 + \kappa_2$ *with two tight Feller kernels* κ_j*, where* κ_2 *is a uniform Feller kernel.*

Finally, assume $r = \mathbf{r}(\kappa^o) > 1 \ge \mathbf{r}(\kappa_1)$.

Then the semiflow induced by F *is uniformly weakly persistent: There exists some* $\delta > 0$ *such that* $\limsup_{n\to\infty} F^n(\mu)(S) \ge \delta$ *for all* $\mu \in \dot{\mathcal{M}}_+^s(S)$.

The next assumption looks rather technical, but is often satisfied; the technicality is the prize we pay for the generality of the framework. We will derive from it that F is continuous on $\mathcal{M}_+^s(S)$ with respect to the flat norm.

Assumption 11 If $\mu \in \mathcal{M}_+^s(S)$ and (μ_n) is a sequence in $\mathcal{M}_+^s(S)$ such that $\int_S f d\mu_n \to \int_S f d\mu_n$ for all $f \in C_+^b(S)$, then

$$\int_S h(t)\,\kappa^{\mu_n}(dt, s) \stackrel{n\to\infty}{\longrightarrow} \int_S h(t)\,\kappa^{\mu}(dt, s) \tag{17}$$

uniformly for s in every closed totally bounded subset of S, for all $h \in \mathcal{L}$,

$$\mathcal{L} = \Big\{h \in [0,1]^S;\ \forall t, \tilde{t} \in S:\ |h(t) - h(\tilde{t})| \le d(t, \tilde{t})\Big\}. \tag{18}$$

Assumption 12 If $\mathcal{N}$ is a bounded subset of $\mathcal{M}_+^s(S)$, then the set of measures $\{\kappa^\mu(\cdot, s);\ s \in S, \mu \in \mathcal{N}\}$ is tight and the set $\{\kappa^\mu(S, s);\ s \in S, \mu \in \mathcal{N}\}$ is bounded in $\mathbb{R}$.

This assumption will imply that F is compact on $\mathcal{M}_+^s(S)$ with respect to the flat norm.

Assumption 13 $\limsup_{\mu(S)\to\infty} \sup_{s\in S} \kappa^\mu(S, s) < 1.$

This assumption will allow us to use the abstract point-dissipativity result in the upcoming Sect. 3.

Theorem 7 *Make Assumptions 9, 10, 11, 12, 13 and let the kernel family* $\{\kappa^\mu;\ \mu \in \mathcal{M}_+^s(S)\}$ *be lower semicontinuous at the zero measure.*

Assume that κ^o *is a top-irreducible Feller kernel and* $\kappa^o = \kappa_1 + \kappa_2$ *with two tight Feller kernels* κ_j *where* κ_2 *is a uniform Feller kernel.*

Finally, assume $r = \mathbf{r}(\kappa^o) > 1 > \mathbf{r}(\kappa_1)$.

Then the semiflow induced by F *is uniformly persistent: There exists some* $\delta > 0$ *such that* $\liminf_{n\to\infty} F^n(\mu)(S) \ge \delta$ *for all* $\mu \in \dot{\mathcal{M}}_+^s(S)$.

To obtain uniform persistence in a stronger sense, we will assume the following.

Assumption 14 If $\mathcal{N}$ is a tight bounded subset of $\mathcal{M}_+(S)$, then there exists a strongly top-irreducible Feller kernel $\tilde{\kappa}$ such that

$$\kappa^\mu(T, s) \geq \tilde{\kappa}(T, s), \qquad T \in \mathcal{B}, s \in S, \mu \in \mathcal{N}.$$

Theorem 8 *Make Assumptions 9, 10, 11, 12, 13, 14 and let the kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+^s(S)\}$ be lower semicontinuous at the zero measure.*

Assume that κ^o is a strongly top-irreducible Feller kernel and $\kappa^o = \kappa_1 + \kappa_2$ with two tight Feller kernels κ_j, where κ_2 is a uniform Feller kernel. Finally, assume $r = \mathbf{r}(\kappa^o) > 1 \geq \mathbf{r}(\kappa_1)$.

Then the semiflow induced by F is uniformly persistent in the following sense: For each $f \in \dot{C}_+^b(S)$, there exists some $\epsilon_f > 0$ with the following property:

If $\mathcal{N}$ is a bounded tight subset of $\mathcal{M}_+^s(S)$ with $\inf_{\mu \in \mathcal{N}} \mu(S) > 0$, there exists some $N \in \mathbb{N}$ such that

$$\int_S f \, d\, F^n(\mu) \geq \epsilon_f \quad \textit{for all } \mu \in \mathcal{N} \textit{ and all } n \in \mathbb{N} \textit{ with } n > N.$$

3 An Abstract Point-Dissipativity Result

The next abstract result will be used in proving Theorem 8.

Theorem 9 *Let X_+ be the closed cone of an ordered normed vector space X. Let $F : X_+ \to X_+$ map bounded subsets of X_+ into bounded subsets of X_+. Let $\theta : X_+ \to \mathbb{R}_+$ be homogeneous, subadditive, continuous and uniformly positive (there is some $\epsilon > 0$ such that $\epsilon \|x\| \leq \theta(x)$ for all $x \in X_+$). Assume that*

$$\limsup_{\|x\| \to \infty} \frac{\theta(F(x))}{\theta(x)} < 1. \tag{19}$$

Then, for any bounded subset B of X_+, there exists a bounded convex subset $\tilde{B}$ of X_+ such that $F^n(B) \subseteq \tilde{B}$ for all $n \in \mathbb{N}$. Further, there exists a bounded convex subset B_0 of X_+ such that for each $x \in X_+$ there exists some $m \in \mathbb{N}$ such that $F^n(x) \in B_0$ for all $n \geq m$. If F is continuous and compact, the semiflow induced by F has a compact attractor of bounded sets [26, Sect. 2.2.3].

Proof Cf. [26, L.7.1]. By (19) and the other properties of θ, there exists some $\xi \in (0, 1)$ and $R_1 > 0$ such that

$$\theta(F(x)) \leq \xi \theta(x), \qquad x \in X_+, \theta(x) \geq R_1. \tag{20}$$

We claim that there exists some $R_2 > 0$ such that, for all $x \in X_+$,

$$\theta(x) \leq R_2 \implies \theta(F(x)) \leq R_2. \tag{21}$$

If not, for any $n \in \mathbb{N}$, there exists some $x_n \in X_+$ such that $\theta(x_n) \le n < \theta(F(x_n))$. Since F maps bounded sets in X_+ into bounded sets of X_+ and θ is bounded, $\theta(x_n) \to \infty$ as $n \to \infty$. This leads to a contradiction for n large enough such that $\theta(x_n) \ge R_1$:

$$n < \theta(F(x_n)) \le \xi\theta(x_n) < n.$$

Let $R_3 = \max\{R_1, R_2\}$. Let $R \ge R_3$ and $B_R^+ = \{x \in X_+; \theta(x) \le R\}$. Since θ is convex and continuous, B_R^+ is convex and closed. Since θ is uniformly positive, B_R^+ is bounded. By (21), $F(B_R^+) \subseteq B_R^+$. Let B be a bounded subset of X_+. Then there exists some $R > R_3$ such that $B \subseteq B_R^+$ and $F^n(B) \subseteq B_R^+$ for all $n \in \mathbb{N}$. Let $x \in X_+$. If $\|x\| \le R_3$, $\limsup_{n\to\infty} \theta(F^n(x)) \le R_3$. If $\theta(x) > R_3$, by (20), $\theta(F^{n+1}(x)) \le \xi\theta(F^n(x))$ as long as $\theta(F^n(x)) \ge R_3$. So $\theta(F^n(x)) \le R_3$ for some $m \in \mathbb{N}$ and $\limsup_{n\to\infty} \theta(F^n(x)) \le R_3$ as well. Since θ is uniformly positive, there exists some $c > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \le c$ for all $x \in X_+$.

In the language of [26, Definition 2.25], we have shown that the semiflow induced by F is point-dissipative and eventually bounded on every bounded set. If F is also continuous and the semiflow is asymptotically smooth (in particular if F is compact). then the semiflow has a compact attractor of bounded set by [26, Theorem 2.30]. □

4 The Ordered Vector Space of Real Measures

Let S be a nonempty set, $\mathcal{B}$ a σ-algebra on S, and $\mathcal{M}(S)$ denote the set of real measures on $\mathcal{B}$.

$\mathcal{M}(S)$ becomes a real vector space by the definitions $(\mu + \nu)(T) = \mu(T) + \nu(T)$ and $(\alpha\mu)(T) = \alpha\mu(T)$ where $T \in \mathcal{B}$ and $\alpha \in \mathbb{R}$ and $\mu, \nu \in \mathcal{M}(S)$.

$\mathcal{M}(S)$ contains the cone of all nonnegative measures, $\mathcal{M}_+(S)$ (a convex homogeneous set). $\mathcal{M}(S)$ is an order-complete vector lattice: Each subset $\mathcal{N}$ of $\mathcal{M}(S)$ which has an lower (upper) bound has an infimum (supremum).

The absolute value $|\mu|$ of a measure (in this context also called the variation of the measure) is given by

$$\begin{aligned} |\mu|(T) &= \sup\{\mu(U) - \mu(T \setminus U); \mathcal{B} \ni U \subseteq T\} \\ &= \sup\{|\mu(U)| + |\mu(T \setminus U)|; \mathcal{B} \ni U \subseteq T\} = \sup\Big\{\sum_{j=1}^{n} |\mu(T_j)|\Big\}, \end{aligned} \tag{22}$$

where the supremum is taken over all $n \in \mathbb{N}$ and subsets $\{T_1, \dots, T_n\}$ of $\mathcal{B}$ such that T is its disjoint union [3, Corollary 10.54 and Theorem 10.56].

4.1 Measures Under the Variation Norm and the Flat Norm

The *variation norm* (also called *total variation*) on $\mathcal{M}(S)$ is defined by

$$\|\mu\|_\sharp = |\mu|(S), \qquad \mu \in \mathcal{M}(S), \tag{23}$$

where $|\mu|$ is the absolute value of μ defined by (22).

If $\mu \in \mathcal{M}_+(S)$, $\|\mu\|_\sharp = \mu(S)$. So the variation norm is additive and order-preserving on $\mathcal{M}_+(S)$, and $\mathcal{M}_+(S)$ is a normal cone. The variation norm makes $\mathcal{M}(S)$ a Banach lattice; in particular, $\mathcal{M}_+(S)$ is a non-flat generating cone: Every real-valued measure μ can be written as the difference of its positive and negative variation, $\mu = \mu_+ - \mu_-$, and $\|\mu_\pm\|_\sharp \le \|\mu\|_\sharp$.

The variation norm is equivalent to the supremum norm

$$\|\mu\|_\infty = \sup_{T\in\mathcal{B}} |\mu(T)|, \qquad \mu \in \mathcal{M}(S), \tag{24}$$

and the two norms are equal on $\mathcal{M}_+(S)$.

Let (S, d) be a metric space. $\mathcal{B}$ now denotes the *Borel* σ-algebra of S which is the smallest σ-algebra that contains all open and closed sets. The sets in the Borel σ-algebra are called *Borel sets*. In a metric space, the Borel σ-algebra is also the smallest σ-algebra for which all (bounded) continuous functions are continuous [11, Theorem 7.1.1]. This second σ-algebra is often [11] but not always [3] called the *Baire-*σ-algebra.

The following is a summary of results needed later. For more details, we refer to [14]. Many of the results can already been found in [10, 11]. See also [15, 16].

For perspective, we present the following result for the variation norm.

Theorem 10 *For all* $\mu \in \mathcal{M}(S)$,

$$\|\mu\|_\sharp = |\mu|(S) = \sup\Big\{\Big|\int_S f d\mu\Big|;\ f \in C^b(S), \|f\|_\infty \le 1\Big\}.$$

Proof By [12, IV.6.2], $\mu \mapsto \theta$ with $\theta(f) = \int_S f d\mu$, $f \in C^b(S)$, is an isometric isomorphism between the Banach space of regular additive set functions with the variation norm and the dual space of $C^b(S)$. The assertion now follows because every real measure on $\mathcal{B}$ is regular [3, Theorem 12.5]. □

We introduce the following functional on $\mathcal{M}(S)$,

$$\begin{aligned} \|\mu\|_\flat &= \sup_{f\in\mathcal{L}} \Big|\int_S f d\mu\Big|, \\ \mathcal{L} &= \Big\{f \in [0,1]^S;\ \forall_{x,y\in S}\, |f(x) - f(y)| \le d(x,y)\Big\}. \end{aligned} \tag{25}$$

Recall that M^S denotes the set of functions from S to a set M. $\|\cdot\|_\flat$ is a norm on $\mathcal{M}(S)$ [14], which we call the *flat norm*, and

$$\|\mu\|_\flat \le \|\mu\|_\sharp, \qquad \mu \in \mathcal{M}(S). \tag{26}$$

In the literature, definitions different from (25) are used that lead to equivalent norms. For instance, $[0,1]^S$ is replaced by $[-1,1]^S$. Also different names are used for the flat norm or its equivalent definitions. For details see [14].

All the definitions have in common that

$$\|\mu\|_\flat = \mu(S) = \|\mu\|_\sharp, \qquad \mu \in \mathcal{M}_+(S). \tag{27}$$

This implies that the flat norm is additive and order-preserving on $\mathcal{M}_+(S)$.

In the following, all topological notions concerning $\mathcal{M}(S)$ and $\mathcal{M}_+(S)$ are meant with respect to the flat norm unless it is explicitly said otherwise.

Theorem 11 *$\mathcal{M}_+(S)$ is a generating, normal, closed cone.*

Lemma 2 *For $x \in S$, let δ_x denote the Dirac measure at x. Then $1 = \|\delta_x\|_\flat$ and, for $y, x \in S$,*

$$\|\delta_x - \delta_y\|_\flat = \min\{1, d(x,y)\}.$$

Corollary 2 ([16]) *If S is not uniformly discrete (i.e., its metric is not equivalent to the discrete metric), then the ordered normed vector space $\mathcal{M}(S)$ is not complete.*

4.1.1 Convergence in $\mathcal{M}_+(S)$

Definition 15 Let $\mathcal{F}$ be a set of functions $f : S \to \mathbb{R}$ and $s \in S$. $\mathcal{F}$ is called *equicontinuous* at s if for any $\epsilon > 0$ there exists some $\delta > 0$ such that $|f(t) - f(s)| < \epsilon$ for all $f \in \mathcal{F}$ and all $t \in S$ with $d(t,s) < \delta$. $\mathcal{F}$ is called equicontinuous on S if it is equicontinuous at all $s \in S$.

$\mathcal{F}$ is called *uniformly equicontinuous* on $\tilde{S} \subseteq S$ if for any $\epsilon > 0$ there is some $\delta > 0$ such that $|f(t) - f(s)| < \epsilon$ for all $f \in \mathcal{F}$ and all $s, t \in \tilde{S}$ with $d(t,s) < \delta$.

$\mathcal{F}$ is called *equibounded* if there exists some $c > 0$ such that $|f(s)| \le c$ for all $s \in S$ and all $f \in \mathcal{F}$.

The following is proved in [32, Proposition 6.10].

Proposition 2 *Let $\mathcal{F}$ be an equicontinuous and equibounded family of functions $f : S \to \mathbb{R}_+$ and $\mu \in \mathcal{M}(S)$ and (μ_n) be a sequence in $\mathcal{M}_+(S)$ such that $\|\mu_n - \mu\|_\flat \to 0$ as $n \to \infty$. Then $\int_S f d\mu_n \to \int_S f d\mu$ as $n \to \infty$ uniformly for $f \in \mathcal{F}$.*

Recall the definition of a (pre-)tight set of measures (Definition 7).

To show that pre-tightness does not change under topologically equivalent metrics, we note the following.

Proposition 3 *$\mu \in \mathcal{M}_+(S)$ is separable if and only if it is pre-tight.*

Proposition 4 *The closure of a tight set of nonnegative measures is tight. The closure of a pre-tight set of nonnegative measures is pre-tight.*

The closure of a set of separable nonnegative measures consists of separable measures.

Proof The first two statements follow from [14, Theorem 4.10d]. The third statement holds because a countable union of countable sets is countable.

Corollary 3 *$\mathcal{M}_+^s(S)$ is a closed cone of $\mathcal{M}(S)$.*

Here is the characterization of convergence.

Theorem 12 *Let (μ_n) in $\mathcal{M}_+(S)$ and $\mu \in \mathcal{M}_+^s(S)$. Equivalent are*

(i) $\|\mu_n - \mu\|_\flat \to 0$,
(ii) $\int_S f\, d(\mu_n - \mu) \to 0$ *for all continuous functions $f \in C^b(S)$,*
(iii) $\int_S f\, d(\mu_n - \mu) \to 0$ *for all Lipschitz continuous functions $f : S \to [0, 1]$.*

4.1.2 Compactness and Completeness in $\mathcal{M}_+(S)$

Theorem 13 *Let (μ_n) be a tight sequence in $\mathcal{M}_+(S)$ such that $(\mu_n(S))$ is bounded. Then (μ_n) has a converging subsequence (with the limit measure being tight as well).*

Proposition 5 *Let $\mathcal{N} \subseteq \mathcal{M}_+^s(S)$ be a totally bounded set of pre-tight measures. Then $\mathcal{N}$ is pre-tight and, if S is complete, tight.*

Theorem 14 ([16, Theorem 3.8]) *$\mathcal{M}_+^s(S)$ is complete if and only if S is complete.*

5 More on Feller Kernels

Let S be metrizable topological space and $\mathcal{B}$ and the respective Borel σ-algebra.

Definition 16 A function $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called a *Feller kernel* if

$\kappa(\cdot, s) \in \mathcal{M}_+(S)$ for all $s \in S$ and if κ has the *Feller property*
$\int_S f(y)\kappa(dy, \cdot) \in C^b(S)$ for any $f \in C^b(S)$.

A Feller kernel κ is called a *Feller kernel of separable measures* if

$\kappa(\cdot, s) \in \mathcal{M}_+^s(S)$ for all $s \in \tilde{S}$.

Cf. [3, Sect. 19.3] and Sect. 2.1. For examples and details see [32]. Recall that every Feller kernel induces maps $A : \mathcal{M}(S) \to \mathcal{M}(S)$ and $A_* : M^b(S) \to M^b(S)$ with $M^b(S)$ denoting the Banach space of bounded measurable functions with the supremum norm. See (10) and (9). Since κ is a Feller kernel, A_* maps $C^b(S)$ to $C^b(S)$.

The next result is part of [32, Theorem 10.4].

Theorem 15 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel of separable measures. Then the following hold:*

(a) A maps $\mathcal{M}^s_+(S)$ into $\mathcal{M}^s_+(S)$, and $A : \mathcal{M}^s_+(S) \to \mathcal{M}^s_+(S)$ is continuous with respect to the flat norm.
(b) A maps $\mathcal{M}^s(S)$ into $\mathcal{M}^s(S)$.

Remark 2 Let κ be a Feller kernel of separable measures and A^s denote the restriction of A from $\mathcal{M}^s(S)$ to $\mathcal{M}^s(S)$ and A^s_+ the restriction of A from $\mathcal{M}^s_+(S)$ to $\mathcal{M}^s_+(S)$. Since the Dirac measures are separable, we still have for the operator norms that $\|A^s\| = \|A^s_+\| = \sup_{s \in S} \kappa(S, s)$, (see 12). By (15),

$$\mathbf{r}(A^s) = \mathbf{r}(A) = \mathbf{r}(A^s_+) = \mathbf{r}(\kappa).$$

Remark 3 The map A induced by a Feller kernel via (10) is continuous from $\mathcal{M}_+(S)$ to $\mathcal{M}_+(S)$ with respect to the variation norms even without the Feller type property. But it seems difficult to come up with conditions for A to be compact with respect to the variation norm.

5.1 Tight Feller Kernels

Definition 17 A Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called a *tight Feller kernel* if the set of measures $\{\kappa(\cdot, x); x \in S\}$ is tight.

A Feller kernel κ is called a *pre-tight Feller kernel* if set of measures $\{\kappa(\cdot, x); x \in S\}$ is pre-tight.

See [32, Sect. 10] for the proofs of the following and other results and for examples.

Proposition 6 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a tight Feller kernel. Then A is continuous and compact from $\mathcal{M}_+(S)$ to $\mathcal{M}_+(S)$ with respect to the flat norm and maps $\mathcal{M}_+(S)$ into $\mathcal{M}^t_+(S)$.*

Proposition 7 *Let $P : \mathcal{B} \times S \to \mathbb{R}_+$ be a tight Feller kernel and $g \in C^b_+(S \times S)$. Then $\tilde{\kappa} : \mathcal{B} \times S \to \mathbb{R}_+$,*

$$\tilde{\kappa}(T, s) = \int_T g(s, t) P(dt, s), \qquad s \in S, T \in \mathcal{B}, \tag{28}$$

is a tight Feller kernel. In particular, $\tilde{\kappa}(S, \cdot) \in C^b(S)$.

5.2 Uniform Feller Kernels

We start from the observation that tight Feller kernels are related to compactness in $C^b(S)$. Recall the concepts of equicontinuity and equiboundedness, Definition 15.

Proposition 8 *Let κ be a tight Feller kernel and Q be an equicontinuous bounded subset of $C^b(S)$. Let A_* be the map on $C^b(S)$ induced by κ via (9). Then $A_*(Q)$ has compact closure in in $C^b(S)$.*

Proof Let (g_n) be a sequence in Q. Since κ is tight, there exists a sequence (K_j) of compact subsets of S such that

$$\sup_{s\in S} \kappa(S \setminus K_j, s) \to 0, \qquad j \to \infty. \tag{29}$$

Set $\tilde S = \bigcup_{j\in\mathbb{N}} K_j$. Then $\tilde S$ is separable. By a version of the Arzela-Ascoli theorem [23, Theorem 8.5], there exists a subsequence (g_{n_i}) and some $g \in C^b(\tilde S)$ such that $g_{n_i} \to g$ pointwise on $\tilde S$ and uniformly on each K_j. Set $h_n = A_* g_n$ and $h(s) = \int_{\tilde S} g(t)\kappa(dt, s)$, $s \in S$. Then $h_n \in C^b(S)$ and $h \in M^b(S)$. For each $s \in S$ and $j, i \in \mathbb{N}$,

$$|h_{n_i}(s) - h(s)| \le \int_{S\setminus K_j} |g_{n_i}(t)|\kappa(dt, s) + \int_{K_j} |g_{n_i}(t) - g(t)|\kappa(dt, s) + \int_{\tilde S\setminus K_j} |g(t)|\kappa(dt, s).$$

By our various assumptions, there is some $c > 0$ such that, for all $i, j \in \mathbb{N}$,

$$\|h_{n_i} - h\|_\infty \le 2c \sup_{s\in S} \kappa(S \setminus K_j, s) + c \sup_{t\in K_j} |g_{n_i}(t) - g(t)|.$$

For all $j \in \mathbb{N}$, since $g_{n_i} \to g$ as $i \to \infty$ uniformly on K_j,

$$\limsup_{i\to\infty} \|h_{n_i} - h\|_\infty \le 2c\kappa(S \setminus K_j).$$

By (29), we can take the limit as $i \to \infty$,

$$\limsup_{i\to\infty} \|h_{n_i} - h\|_\infty = 0.$$

This shows $A_*(Q)$ is a compact subset of $C^b(S)$. Since all h_n are continuous, h is continuous as well. □

The preceding result motivates us to look for Feller kernels that are related to equicontinuous sets of functions.

Proposition 9 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel and A the induced linear map on $\mathcal{M}(S)$ and A_* the induced linear map on $M^b(S)$ via (10) and (9), respectively.*

Then the following are equivalent:

(a) $\sup_{T\in\mathcal{B}} |\kappa(T, t) - \kappa(T, s)| \to 0, \qquad t \to s,$ *for all $s \in S$.*

(b) *If Q is a bounded subset of $M^b(S)$, then $A_*(Q)$ is an equicontinuous and equibounded subset of $C^b(S)$.*
(c) *If Q is a bounded subset of $C^b(S)$, then $A_*(Q)$ is an equicontinuous and equibounded subset of $C^b(S)$.*
(d) *A is continuous from $\mathcal{M}_+(S)$ with the flat norm to $\mathcal{M}_+(S)$ with the variation norm.*

Proof Assume (a). Let $f(t) = \sum_{i=1}^m \alpha_i \chi_{T_i}$ be a measurable function of finitely many values $\alpha_1, \dots, \alpha_m$, where $T_i \in \mathcal{B}$ are pairwise disjoint. Then

$$\big|A_* f)(t) - A_*(f)(s)\big| \le \|f\|_\infty \sum_{i=1}^m \big|\kappa(T_i, t) - \kappa(T_i, s)\big|.$$

Since $\kappa(\cdot, t) - \kappa(\cdot, s)$ is a real-valued measure and the T_i are pairwise disjoint,

$$\big|A_* f)(t) - A_*(f)(s)\big| \le 2\|f\|_\infty \sup_{T\in\mathcal{B}} \big|\kappa(T, t) - \kappa(T, s)\big|. \tag{30}$$

If $f \in M^b(S)$, f is the uniform limit of a sequence of such finitely-valued measurable functions and (30) holds for $f \in M^b(S)$. This implies that A_* maps $M^b(S)$ into $C^b(S)$. Let Q be a bounded subset of $M^b(S)$. Then $A_*(Q)$ is a bounded subset of $C^b(S)$ and an equicontinuous subset by (a) and (30), and (b) follows.

Obviously, (b) implies (c).

Assume (c). Let (μ_n) be a sequence in $\mathcal{M}_+(S)$ and $\mu \in \mathcal{M}_+(S)$ such that $\|\mu_n - \mu\|_\flat \to 0$ as $n \to \infty$. By (c), $\{A_* f;\ f \in C^b(S), 0 \le f \le 1\}$ is a uniformly equicontinuous and equibounded family of functions from S to $\mathbb{R}_+$. By Proposition 2, $\int_S (A_* f) d\mu_n \to \int_S (A_* f) d\mu$ as $n \to \infty$ uniformly for $f \in C^b(S)$ with $0 \le f \le 1$. Let $f \in C^b(S)$ with $\|f\|_\infty \le 1$. Then $f = f_+ - f_-$ with $0 \le f_\pm \le 1$. So $\int_S (A_* f) d\mu_n \to \int_S (A_* f) d\mu$ uniformly for $f \in C^b(S)$ with $\|f\|_\infty \le 1$. By the duality between A_* and A, (11), $\int_S f d(A\mu_n) \to \int_S f d(A\mu)$ as $n \to \infty$ uniformly for $f \in C^b(S)$ with $\|f\|_\infty \le 1$. Assertion (d) now follows from Theorem 10.

Assume (d). As $t \to s$, $\|\delta_t - \delta_s\|_\flat \to 0$ by Lemma 2 and, by (d), $A\delta_t \to A\delta_s$ in variation norm and $\sup_{T\in\mathcal{B}} |\kappa(T, t) - \kappa(T, s)| \to 0$ by (10).

Definition 18 A Feller kernel $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called a *uniform Feller kernel* if it satisfies property (a) of Proposition 9.

Corollary 4 *If κ is a Feller kernel and the map $A_* : C^b(S) \to C^b(S)$ associated with κ is compact, then κ is a uniform Feller kernel.*

Corollary 5 *Let κ_1 be a Feller kernel on S and κ_2 a uniform Feller kernel on S. Then $\kappa_1 \star \kappa_2$ is a uniform Feller kernel on S.*

Proof Let A_i be the linear maps on $\mathcal{M}_+(S)$ induced by κ_i via (10). By Proposition 9, A_2 continuously maps $\mathcal{M}_+(S)$ with the flat norm into $\mathcal{M}_+(S)$ with the variation norm, while A_1 is a bounded liner map on $\mathcal{M}(S)$ with the variation norm. So $A_1 A_2$

continuously maps $\mathcal{M}_+(S)$ with the flat norm into $\mathcal{M}_+(S)$ with the variation norm. Since $A_1 A_2$ is induced by $\kappa_1 \star \kappa_2$ [32, L.9.2], $\kappa_1 \star \kappa_2$ is a uniform Feller kernel by Proposition 9.

Proposition 10 *Let κ be a uniform Feller kernel. Let $g : S \times S \to \mathbb{R}$ be bounded and $g(s, \cdot)$ be Borel measurable and $g(\cdot, s)$ be continuous on S for every $s \in S$.*

Let $\tilde{\kappa} : \mathcal{B} \times S \to \mathbb{R}$ be given by

$$\tilde{\kappa}(T, s) = \int_T g(s, t)\kappa(dt, s), \qquad s \in S, \quad T \in \mathcal{B}.$$

Then $\tilde{\kappa}$ is a uniform Feller kernel.

Proof Let $s \in S$. Since $g(s, \cdot)$ is Borel measurable and bounded and $\kappa(\cdot, s)$ is a finite non-negative measure, $\tilde{\kappa}(\cdot, s)$ is a finite non-negative measure.

Let (s_n) be a sequence in S and $s \in S$ and $s_n \to s$. Then

$$\begin{aligned}
&\Big| \int_T g(s_n, t)\kappa(dt, s_n) - \int_T g(s, t)\kappa(dt, s)\Big| \\
\le &\Big| \int_T g(s_n, t)\kappa(dt, s_n) - \int_T g(s_n, t)\kappa(dt, s)\Big| \\
&+ \Big| \int_T g(s_n, t)\kappa(dt, s) - \int_T g(s, t)\kappa(dt, s)\Big| \\
\le &\, 2 \sup |g| \sup_{\tilde{T} \in \mathcal{B}} \big|\kappa(\tilde{T}, s_n) - \kappa(\tilde{T}, s)\big| + \int_S |g(s_n, t) - g(s, t)|\kappa(dt, s).
\end{aligned}$$

The last integral converges to 0 as $n \to \infty$ by Lebesgue's dominated convergence theorem because $|g(s_n, t) - g(s, t)| \to 0$ as $n \to \infty$ pointwise in $t \in S$ and $|g(s_n, t) - g(s, t)| \le 2 \sup g(S \times S)$ for all $n \in \mathbb{N}$.

Notice that the last expression in the inequality converges to 0 as $n \to \infty$ uniformly for $T \in \mathcal{B}$. □

This trivially provides examples for uniform Feller kernels.

Example 1 Let $\nu \in \mathcal{M}_+(S)$ and $g : S \times S \to \mathbb{R}$ be bounded and $g(s, \cdot)$ be Borel measurable and $g(\cdot, s)$ continuous on S for every $s \in S$.

Let $\kappa : \mathcal{B} \times S \to \mathbb{R}$ be given by

$$\kappa(T, s) = \int_T g(s, t)\nu(dt), \qquad s \in S, T \in \mathcal{B}.$$

Then κ is a uniform Feller kernel.

The class of Feller kernels provided this way can be quite comprehensive.

Example 2 Let S be a separable metric space and $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a uniform Feller kernel.

Choose a countable dense subset $\{s_n; n \in \mathbb{N}\}$ in S.
Define $\nu \in \mathcal{M}_+(S)$.

$$\nu(T) = \sum_{n=1} 2^{-n} \kappa(T, s_n), \qquad T \in \mathcal{B}.$$

Let $T \in \mathcal{B}$ and $\nu(T) = 0$. Then $\kappa(T, s_n) = 0$ for all $n \in \mathbb{N}$. Since $\{s_n; n \in \mathbb{N}\}$ is dense in S and κ is a uniform Feller kernel, $\kappa(T, s) = 0$ for all $s \in S$. By the Radon-Nikodym theorem, for any $s \in S$, there exists a Borel measurable function $g(s, \cdot)$ such that

$$\kappa(T, s) = \int_T g(s, t)\nu(dt), \qquad s \in \mathcal{B}. \tag{31}$$

Since κ is a uniform Feller kernel,

$$\int_S |g(s, t) - g(\tilde{s}, t)|\nu(dt) \to 0, \qquad s \to \tilde{s}. \tag{32}$$

Conversely, any kernel of the form (31) satisfying (32) is a uniform Feller kernel.

Theorem 16 *Let κ_1 be a tight Feller kernel and κ_2 a uniform Feller kernel. Then*

$$(A_{1*} f)(s) = \int_S f(t)\kappa_1(dt, s), \qquad s \in S,\ f \in M^b(S),$$

defines a bounded positive linear map A_{1*} from $M^b(S)$ to $M^b(S)$ and from $C^b(S)$ to $C^b(S)$, and

$$(A_{2*} f)(s) = \int_S f(t)\kappa_2(dt, s), \qquad s \in S,\ f \in M^b(S),$$

is a bounded positive linear map A_{2*} from $M^b(S)$ to $C^b(S)$ such that $A_{1*}A_{2*}$ is compact from $M^b(S)$ to $C^b(S)$.

Proof Combine Propositions 8 and 9.

Theorem 17 *Let κ_2 be a uniform Feller kernel that is tight. Let κ_1 be a tight Feller kernel and $\kappa = \kappa_1 + \kappa_2$. Assume that $\mathbf{r}(\kappa) > \mathbf{r}(\kappa_1)$. Then there exists some $f \in \dot{C}_+^b(S)$ such that $\mathbf{r}(\kappa) f(s) = \int_S f(t)\kappa(dt, s)$ for all $s \in S$.*

Proof Let A_{*j} be the operators on $C^b(S)$ associated with κ_j. By Theorem 16, $A_{*1}A_{*2}$ and A_{*2}^2 are compact on $C^b(S)$. The assertion now follows from [32, Theorem 7.17].

5.3 *Irreducible and Colonization Kernels*

Recall the definition of a (strongly) top-irreducible Feller kernel (Sect. 2.1.2).

Lemma 3 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel and A_* be the bounded linear map on $C^b(S)$ induced by (9). Then the following are equivalent:*

(a) κ is top-irreducible.
(b) For any nonempty open strict subset U of S there exists some $s \in S \setminus U$ such that $\kappa(U, s) > 0$.
(c) For any $f \in \dot{C}^b_+(S)$, $S = \bigcup_{n\in\mathbb{Z}_+}\{A^n_* f > 0\} =: U(f)$.
(d) For any Lipschitz continuous $f : S \to \mathbb{R}_+$ that is not identically equal to 0, $S = \bigcup_{n\in\mathbb{Z}_+}\{A^n_* f > 0\} =: U(f)$.

Here, $\{A^n_* f > 0\}$ is a shorthand for $\{s \in S; (A^n_* f)(s) > 0\}$.

Proof (a)⇒(b): Suppose that (b) does not hold: Then there exists some nonempty open strict subset U of S such that $\kappa(U, s) = 0$ for all $s \in S \setminus U$. Since $\kappa(S, \cdot)$ is bounded, there exists some $c > 0$ such that $\kappa(U, s) \le c\chi_U(s)$ for all $s \in S$. Then

$$\kappa^{*2}(U, s) = \int_S \kappa(U, t)\kappa(dt, s) \le \int_S c\chi_U(s)\kappa(dt, s) = c\kappa(U, s) \le c^2\chi_U(s).$$

By induction, $\kappa^{n*}(U, s) \le c^n\chi_U(s)$ for all $s \in S$ and all $n \in \mathbb{N}$. So (a) does not hold.

(b)⇒(c): Since κ is a Feller kernel, the functions $A^n_* f$ in part (c) are continuous and $U(f)$ is open as union of open sets. Since f is not the zero function and $A^0_* f = f$, $U(f)$ is nonempty. Suppose $U(f) \ne S$. By (b), there exists some $s \in S \setminus U(f)$ such that $\kappa(U(f), s) > 0$. Since the measure $\kappa(\cdot, s)$ is continuous from below, there is some $n \in \mathbb{N}$ such that $\kappa\big(\{A^n_* f > 0\}, s\big) > 0$. This implies that $(A^{n+1}_* f)(s) > 0$ and $s \in U(f)$, a contradiction.

(c)⇒(d): obvious.

(d)⇒(a): Let U be a nonempty open subset of S. Choose some $t_0 \in U$. Then there exists some Lipschitz continuous $f : S \to [0, 1]$ such that $f(t_0) = 1$, $f(t) \le \chi_U(t)$ for all $t \in S$ [14, L.2.1]. By (d), for any $s \in S$, there is some $n \in \mathbb{Z}_+$ such that $0 < (A^n_* f)(s)$. Let $s \in S \setminus U$. Then $(A^0_* f)(s) = f(s) \le \chi_U(s) = 0$ and $0 < (A^n_* f)(s)$ for some $n \in \mathbb{N}$. Since A^n_* is induced by κ^{n*},

$$0 < (A^n_* f)(s) \le \int_S \chi_U(t)\kappa^{n*}(dt, s) \le \kappa^{n*}(U, s).$$

So (a) holds.

Remark 4 Assume that S is not a singleton set. If $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is a top-irreducible Feller kernel, then $\kappa(S \setminus \{s\}, s) > 0$ for all $s \in S$.

Proof Let $s \in S$ and $T = S \setminus \{s\}$. Since S is not a singleton set, T is a nonempty open subset of S. Since κ is top-irreducible, by Lemma 3(b), there exists some $\tilde{s} \in S \setminus T$ such that $\kappa(T, \tilde{s}) > 0$. Since $S \setminus T = \{s\}$, $\kappa(T, s) > 0$.

Theorem 18 *Let κ be a top-irreducible Feller kernel, A_* the associated linear bounded map on $C^b(S)$, $r > 0$. Let $f \in \dot{C}^b_+(S)$ be an eigenfunction $rf = A_* f$. Then $f(s) > 0$ for all $s \in S$.*

Proof For all $n \in \mathbb{N}$, $f = r^{-n} A_*^n f$ and so $f(s) > 0$ for all $s \in S$ by Lemma 3(c).

Theorem 19 *Let κ be a top-irreducible Feller kernel. Then, for any $\mu \in \dot{\mathcal{M}}_+(S)$ and $f \in \dot{C}^b_+(S)$, there is some $n \in \mathbb{Z}_+$ such that $\int_S f\, d(A^n \mu) = \int_S A_*^n f\, d\mu > 0$.*

Proof Let $\mu \in \dot{\mathcal{M}}_+(S)$ and $f \in \dot{C}^b_+(S)$. By Lemma 3(c),

$$S = \bigcup_{n \in \mathbb{Z}_+} S_n(f), \qquad S_n(f) = \big\{A_*^n f > 0\big\}.$$

The last is a shorthand for $\big\{s \in S, (A_*^n f)(s) > 0\big\}$. Analogous shorthands will be used in the following.

Since μ is continuous from below and $\mu(S) > 0$, there exists some $m \in \mathbb{N}$ such that $0 < \mu\big(\bigcup_{n=0}^m S_n(f)\big)$. Since $\bigcup_{n=0}^m S_n(f) = \big\{\sum_{n=0}^m A_*^n f > 0\big\}$, there is some $k \in \mathbb{N}$ such that $\mu\big(T_{mk}(f)\big) > 0$, $T_{mk}(f) = \big\{\sum_{n=0}^m A_*^n f > 1/k\big\}$. Now

$$\sum_{n=0}^m \int_S f\, d\,(A^n \mu) = \int_S \sum_{n=0}^m (A_*^n f)\, d\mu$$
$$\geq \int_{T_{mk}(f)} \Big(\sum_{n=0}^m A_*^n f\Big) d\mu \geq (1/k)\mu\big(T_{mk}(f)\big) > 0.$$

So there is some $n \in \mathbb{Z}_+$ such that $\int_S f\, d(A^n \mu) = \int_S A_*^n f\, d\mu > 0$.

Corollary 6 *Let κ be a top-irreducible Feller kernel, A the associated linear map on $\mathcal{M}_+(S)$, $r > 0$. Let $\mu \in \dot{\mathcal{M}}_+(S)$ be an eigenmeasure $r\mu = A\mu$. Then $\int_S f d\mu > 0$ for any $f \in \dot{C}^b_+(S)$.*

Proof For all $n \in \mathbb{N}$, $\mu = r^{-n} A^n \mu$ and the assertion follows from Theorem 19.

Proposition 11 *Let κ be a top-irreducible Feller kernel and let $\mathcal{N}$ be a tight subset of $\mathcal{M}_+(S)$ with $\inf_{\mu \in \mathcal{N}} \mu(S) > 0$. Then, for any $f \in \dot{C}^b_+(S)$, there exist some $m \in \mathbb{N}$ and $\delta > 0$ such that*

$$\sum_{n=0}^m \int_S A_*^n f\, d\mu \geq \delta, \qquad \mu \in \mathcal{N}.$$

Proof Let $\eta = (1/2) \inf_{\mu \in \mathcal{N}} \mu(S)$. Then $\eta > 0$. Since $\mathcal{N}$ is tight, there exists some compact subset K of S such that $\mu(S \setminus K) \leq \eta$ for all $\mu \in \mathcal{N}$ and so

$$\mu(K) \geq \eta, \qquad \mu \in \mathcal{N}. \tag{33}$$

Let $f \in C_+^b(S)$, $f \neq 0$. Since κ is top-irreducible, $S = \bigcup_{n \in \mathbb{Z}_+} S_n(f)$ with open sets $S_n(f) = \{A_*^n f > 0\}$ by Lemma 3(c). Since K is compact, there exists some $m \in \mathbb{N}$ such that $K \subseteq \bigcup_{n=0}^m S_n(f)$. So there exists some $\tilde{\delta} > 0$ such that

$$\sum_{n=0}^m (A_*^n f)(s) \geq \tilde{\delta}, \qquad s \in K.$$

For all $\mu \in \mathcal{N}$, by (33),

$$\sum_{n=0}^m \int_S A_*^n f \, d\mu \geq \int_K \Big(\sum_{n=0}^m A_*^n f \Big) \, d\mu \geq \tilde{\delta}\mu(K) \geq \tilde{\delta}\eta > 0.$$

5.3.1 Strongly Top-Irreducible Feller Kernels.

Recall the definition of a strongly top-irreducible Feller kernel (Definition 4).

Lemma 4 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel and A_* be the associated bounded linear map on $C^b(S)$. Then the following are equivalent:*

(a) κ is strongly top-irreducible.
(b) For any $f \in \dot{C}_+^b(S)$ and any nonempty compact subset K of S there exists some $n \in \mathbb{Z}_+$ such that $(A_*^n f)(s) > 0$ for all $s \in K$.
(c) For any Lipschitz continuous $f : S \to \mathbb{R}_+$ that is not identically equal to 0 and any nonempty compact subset K of S, there exists some $n \in \mathbb{Z}_+$ such that $(A_*^n f)(s) > 0$ for all $s \in K$.

Proof (a) $\Rightarrow$ (b):

Let $f \in \dot{C}_+^b(S)$ and K be a compact subset of S. Then $U = \{t \in S; f(t) > \|f\|_\infty/2\}$ is a nonempty open subset of S. Since κ is strongly top-irreducible, there exists some $n \in \mathbb{N}$ such that, for all $s \in K$.

$$0 < \kappa^{n\star}(U, s) \leq \int_U \frac{2f(t)}{\|f\|_\infty} \kappa^{n\star}(dt, s) \leq \frac{2}{\|f\|_\infty} (A_*^n f)(s).$$

Obviously (b) implies (c).

(c) $\Rightarrow$ (a) follows similarly as in Lemma 3(d) $\Rightarrow$ (a).

Proposition 12 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel with the following property for any $f \in \dot{C}_+^b(S)$:*

For all $s \in S$ there exists some neighborhood $U_s \subseteq S$ of s and some $n_s \in \mathbb{N}$ such that $\int_S f(t)\kappa^{n\star}(dt, \tilde{s}) > 0$ for all $n \in \mathbb{N}$, $n \geq n_s$, and all $\tilde{s} \in U_s$.

Then κ is a strongly top-irreducible Feller kernel.

Proof The neighborhoods U_s can be chosen as open sets containing s. Let K be a nonempty compact subset of S. Then $K \subseteq \bigcup_{s\in S} U_s$ and there exists a finite subset $\tilde S$ of S such that $K \subseteq \bigcup_{s\in \tilde S} U_s$. Set $m = \max_{s\in\tilde S} n_s$. Then $m \in \mathbb{N}$ and

$$\int_S f(t)\kappa^{m\star}(dt, \tilde s) > 0, \qquad \tilde s \in K.$$

By Lemma 4, κ is strongly top-irreducible. □

A similar proof as for Proposition 11 yields the following result.

Proposition 13 *Let κ be a strongly top-irreducible Feller kernel and let $\mathcal{N}$ be a tight subset of $\mathcal{M}_+(S)$ with $\inf_{\mu\in\mathcal{N}} \mu(S) > 0$. Then, for any $f \in \dot C_+^b(S)$, there exist some $n \in \mathbb{N}$ and $\delta > 0$ such that*

$$\int_S A_*^n f \, d\mu \ge \delta, \qquad \mu \in \mathcal{N}.$$

Proposition 14 *Let $P : \mathcal{B} \times \tilde S \to \mathbb{R}_+$ be a Feller kernel, $g \in C_+^b(S \times S)$, and $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be defined by*

$$\kappa(T, s) = \int_T g(s, t) P(dt, s), \qquad s \in S, T \in \mathcal{B}. \tag{34}$$

Assume that κ is also a Feller kernel and that $g(s, t) > 0$ for all $s, t \in S$.

(a) P is top-irreducible if and only if κ is top-irreducible.
(b) P is strongly top-irreducible if and only if κ is strongly top-irreducible.

Proof For $f_0 \in \dot C_+^b(S)$, set $U_n = \{f_n > 0\}$ and $V_n = \{h_n > 0\}$ where $f_{n+1} = \int_S f_n(t) P(dt, \cdot)$ and $h_{n+1} = \int_S h_n(t)\kappa(dt, \cdot)$ for all $n \in \mathbb{N}$. Let $U(f_0)$ and $V(f_0)$ be the respective unions over $n \in \mathbb{N}$.

For any $f \in \dot C_+^b(S)$ and $s \in S$, we have the equivalence of the following two statements:

(i) $\int_S f(t)P(dt, s) > 0$,

(ii) $P\big(\{f > 0\}, s\big) > 0$.

An analogous equivalence holds for κ replacing P.

Since g is strictly positive on S^2, statement (ii) for P is equivalent to the statement (ii) for κ replacing P.

With this observation, it follows by induction that $U_n = V_n$ for all $n \in \mathbb{N}$ such that $U(f) = V(f)$. So $S = U(f)$ if and only if $S = V(f)$.

The equivalence in (a) follows from Lemma 3(c).

The equivalence in (b) follows from Lemma 4(b).

In these lemmata, $U_n = \{A_*^n f > 0\}$ if A_* is induced by P and $V_n = \{A_*^n f > 0\}$ if A_* is induced by κ.

5.3.2 Colonization Kernels.

The following example of strongly top-irreducible kernels seems particularly suited for spatially structured populations, but less for populations with other structures.

Definition 19 Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel. κ is called a *colonization kernel* if for any $s \in S$ there is an open subset $U \ni s$ of S such that $\kappa(V, s) > 0$ for all nonempty open subsets V of U.

Proposition 15 *Let S be connected and κ be a colonization Feller kernel. Then, for any $f \in \dot{C}_+^b(S)$, $S = \bigcup_{n \in \mathbb{Z}_+} S_n(f)$ where $S_n(f) = \{A_*^n f > 0\}$ form an increasing sequence of open sets, and κ is strongly top-irreducible.*

Here A_* is the operator defined in (9).

Proof Let $f \in \dot{C}_+^b(S)$ and define $S_n(f)$ as above.

Since $A_*^n f$ is continuous, the sets $S_n(f)$ form a sequence of open subsets of S. We claim that this sequence is increasing with respect to the subset relation. It is sufficient to show that $S_0(f) \subseteq S_1(f)$ because $S_{n+1}(f) = S_1(A_*^n(f))$. Let $s \in S$ and $f(s) > 0$. Since κ is a colonization kernel, there is an open subset $U \ni s$ of S such that $\kappa(V, s) > 0$ for all nonempty open subsets V of U. Set $V = \{t \in U;\ f(t) > f(s)/2\}$. Then V an open subset of U and $s \in V$; so

$$(A_* f)(s) \geq \int_V f(t)\kappa(dt, s) \geq \frac{f(s)}{2}\kappa(V, s) > 0.$$

This implies $S_0(f) \subseteq S_1(f)$.

Set $S(f) = \bigcup_{n \in \mathbb{N}} S_n(f)$. $S(f)$ is open as union of open sets. To show that $S(f)$ is closed, let $s \in S$ be a limit point of $S(f)$. Since κ is a colonization kernel, there is an open subset $U \ni s$ of S such that $\kappa(V, s) > 0$ for all nonempty open subsets V of U. Since s is a limit point of $S(f)$, $U \cap S(f) \neq \emptyset$ and $U \cap S_n(f) \neq \emptyset$ for some $n \in \mathbb{Z}_+$. Since $S_n(f) = \bigcup_{m \in \mathbb{N}} \{A_*^n f > 1/m\}$, there exists a nonempty open subset V of U and some $m \in \mathbb{N}$ such that $(A_*^n f)(t) > 1/m$ for all $t \in V$. For all $x \in U$,

$$(A_*^{n+1} f)(s) \geq \int_V (A_*^n f)(t)\kappa(dt, s) \geq (1/m)\kappa(V, s) > 0.$$

So $s \in S_{n+1}(f) \subseteq S(f)$. Since $S(f)$ is open and closed in the connected set S, $S = S(f)$.

Let K be a compact subset of S. Then there exists some $n \in \mathbb{N}$ such that $K \subseteq \bigcup_{j=1}^n S_j(f)$. Since the $S_n(f)$ form an increasing sequence of sets, $K \subseteq S_n(f)$, i.e., $(A_*^n f)(s) > 0$ for all $s \in K$. So, κ is strongly top-irreducible by Lemma 4.

Lemma 5 *Let $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ be a tight colonization Feller kernel and $g : S \times S \to (0, \infty)$ be continuous and bounded. Then $\tilde{\kappa} : \mathcal{B} \times S \to \mathbb{R}_+$ defined by*

$$\tilde{\kappa}(T, s) = \int_T g(s, t)\kappa(dt, s), \qquad T \in \mathcal{B}, s \in S,$$

is also a tight colonization Feller kernel.

Proof By Proposition 7, $\tilde{\kappa}$ is a tight Feller kernel.

Let $s \in S$. Since κ is a colonization kernel, there is some open subset $U \ni s$ of S such that $\kappa(V, s) > 0$ for all nonempty open subsets V of U. Since g is strictly positive and continuous, $V = \bigcup_{n\in\mathbb{N}} V_n$ with open subsets $V_n = \{t \in V; g(s,t) > 1/n\}$ of V. For all $n \in \mathbb{N}$,

$$\tilde{\kappa}(V, s) \geq \int_{V_n} g(s,t)\kappa(dt, s) \geq (1/n)\kappa(V_n, s).$$

Since $\kappa(\cdot, s)$ is continuous from below, $\kappa(V_n, s) \to \kappa(V, s) > 0$ as $n \to \infty$ and $\tilde{\kappa}(V, s) > 0$.

6 Proofs for the General Framework for The state Space of Measures. Tight Bounded Persistence Attractors

Recall that we consider yearly turnover maps F of the following form,

$$F(\mu)(T) = \int_S \kappa^\mu(T, s)\ \mu(ds), \qquad \mu \in \mathcal{M}_+^s(S), \qquad T \in \mathcal{B},$$

where $\{\kappa^\mu; \mu \in \mathcal{M}_+^s(S)\}$ is a set of Feller kernels $\kappa^\mu : \mathcal{B} \times S \to \mathbb{R}_+$.

If μ is the zero measure, we use the notation κ^o.

Proposition 16 *Let the Assumption 9 be satisfied. Then F maps $\mathcal{M}_+^s(S)$ into itself.*

Proof Theorem 15(a).

Lemma 6 *Let $(\tilde{f}_n)$ be a bounded sequence in $C^b(S)$ and (μ_n) be a bounded pre-tight sequence in $\mathcal{M}_+(S)$. Then*

$$\int_S \tilde{f}_n d\mu_n \stackrel{n\to\infty}{\longrightarrow} 0 \qquad \textit{if} \quad \tilde{f}_n \stackrel{n\to\infty}{\longrightarrow} 0$$

uniformly on every totally bounded subset of S.

Proof Let $\epsilon > 0$. Since $\{\mu_n; n \in \mathbb{N}\}$ is pre-tight, there exists a closed totally bounded subset T of S such that $\mu_n(S \setminus T) < \epsilon$ for all $n \in \mathbb{N}$. For all $n \in \mathbb{N}$,

$$\begin{aligned}\Big|\int_S \tilde{f}_n d\mu_n\Big| &\leq \int_T |\tilde{f}_n| d\mu_n + \int_{S\setminus T} |\tilde{f}_n| d\mu_n \\ &\leq \sup_T |\tilde{f}_n| \sup_{k\in\mathbb{N}} \mu_k(S) + \sup_{k\in\mathbb{N}} \sup_S |\tilde{f}_k|\ \mu_n(S \setminus T).\end{aligned}$$

Since $\tilde{f}_n \to 0$ uniformly on T, the last but one expression converges to 0 as $n \to \infty$ and

$$\limsup_{n\to\infty} \Big| \int_S \tilde{f}_n d\mu_n \Big| \le \sup_{k\in\mathbb{N}} \sup_S |\tilde{f}_k| \, \epsilon.$$

Since this holds for arbitrary $\epsilon > 0$, the limit superior is zero and we have proved the assertion.

Proposition 17 *Let the family of Feller kernels* $\{\kappa^\mu); \mu \in \mathcal{M}_+^s(S)\}$ *satisfy the Assumptions 9 and 11. Then* $F : \mathcal{M}_+^s(S) \to \mathcal{M}_+^s(S)$ *is continuous with respect to the flat norm.*

Proof Let $\mu \in \mathcal{M}_+^s(S)$ and (μ_n) be a sequence in $\mathcal{M}_+^s(S)$ such that $\|\mu_n - \mu\|_\flat \to 0$. By Theorem 12,

$$\int_S \tilde{f} d\mu_n \to \int_S \tilde{f} d\mu, \qquad \tilde{f} \in C_+^b(S). \tag{35}$$

Then $\{\mu_n; n \in \mathbb{N}\}$ is a compact subset of $\mathcal{M}_+(S)$ with respect to the flat norm and pre-tight by Proposition 5 and a bounded subset of $\mathcal{M}_+(S)$.

Let $f \in \mathcal{F}$. By (16),

$$\Big| \int_S f \, dF(\mu_n) - \int_S f \, dF(\mu) \Big| = \Big| \int_S f_n d\mu_n - \int_S \tilde{f} d\mu \Big| \tag{36}$$

with

$$f_n(s) = \int_S f(t)\kappa^{\mu_n}(dt, s), \qquad \tilde{f}(s) = \int_S f(t)\kappa^{\mu}(dt, s).$$

By Theorem 12, it is sufficient that the expression on the right hand side of (36) converges to 0 as $n \to \infty$.

By the triangle inequality and (36),

$$\Big| \int_S f \, dF(\mu_n) - \int_S f \, dF(\mu) \Big| \le \Big| \int_S (f_n - \tilde{f}) d\mu_n \Big| + \Big| \int_S \tilde{f} d\mu_n - \int_S \tilde{f} d\mu \Big|.$$

Since κ^μ is a Feller kernel, $\tilde{f} \in C_+^b(S)$ and the second term on the right hand side of the last inequality converges to 0 as $n \to \infty$ by (35). As for the first term, by Assumption 11, for any closed totally bounded subset T of S

$$f_n(s) - \tilde{f}(s) \to 0, \qquad n \to \infty, \text{ uniformly for } s \in T. \tag{37}$$

Further, by Assumption 9, $(f_n - \tilde{f})$ is a bounded sequence in $C^b(S)$. Now the first term of the last inequality converges to 0 by Lemma 6.

Proposition 18 *Under the Assumptions 9 and 12, the yearly population turnover map* $F : \mathcal{M}_+^s(S) \to \mathcal{M}_+^s(S)$ *is compact; for any bounded subset* $\mathcal{N}$ *of* $\mathcal{M}_+^s(S)$, $F(\mathcal{N})$ *is a tight bounded subset of* $\mathcal{M}_+^s(S)$.

Proof Let $\mathcal{N}$ be a bounded subset of $\mathcal{M}_+^s(S)$. For any set $T \in \mathcal{B}$ and $\mu \in \mathcal{N}$,

$$F(\mu)(S \setminus T) = \int_S \kappa^\mu(S \setminus T, s)\,\mu(ds) \le \sup_{s \in S}\,\kappa^\mu(S \setminus T, s)\,\mu(S). \tag{38}$$

For $T = \emptyset$, we obtain that $\{F(\mu)(S); \mu \in \mathcal{N}\}$ is bounded in $\mathbb{R}$ by Assumption 12.

Let $\epsilon > 0$. By Assumption 12, there exists some compact set T in S such that

$$\kappa^\mu(S \setminus T, s) \le \epsilon\Big(1 + \sup_{\mu \in \mathcal{N}} \mu(S)\Big)^{-1}, \qquad s \in S.$$

By (38), $F(\mu)(S \setminus T) \le \epsilon$ for all $\mu \in \mathcal{N}$. By Definition 7, $F(\mathcal{N})$ is a tight subset of $\mathcal{M}_+^s(S)$.

By Theorem 13, $F(\mathcal{N})$ has compact closure in $\mathcal{M}_+^s(S)$.

Proposition 19 *Let the Assumptions 9 and 13 be satisfied. Then*

$$\limsup_{\mu(S) \to \infty} \frac{F(\mu)(S)}{\mu(S)} < 1.$$

Proof For all $\mu \in \mathcal{M}_+^s(S)$,

$$\mathcal{F}(\mu)(S) = \int_S \kappa^\mu(S, s)\,\mu(ds) \le \sup_{s \in S} \kappa^\mu(S, s)\,\mu(S).$$

This implies the assertion.

Theorem 20 *Let the Assumptions 9, 11, 12, and 13 be satisfied.*

Then the semiflow induced by F has a compact attractor of bounded sets.

Proof We apply Theorem 9. By Assumption 13 and Proposition 19, inequality (19) is satisfied with $\theta(\mu) = \mu(S)$. F is continuous by Proposition 17 and compact and thus asymptotically smooth by Proposition 18. All assumptions of Theorem 9 are satisfied which implies that the semiflow induced by F has a compact attractor of bounded sets. □

Let us spell out what Theorem 20 means [26, Chap. 2].

Remark 5 Under the assumptions of Theorem 20, there exists a subset $\mathcal{K}$ of $\mathcal{M}_+^s(S)$ which is tight, compact with respect to the flat norm, and satisfies $F(\mathcal{K}) = \mathcal{K}$. Further, if $\mathcal{N}$ is a bounded subset of $\mathcal{M}_+^s(S)$ and $\mathcal{U}$ an open set in $\mathcal{M}_+^s(S)$ with respect to the flat norm with $\mathcal{K} \subseteq U$, there exists some $N \in \mathbb{N}$ such that $F^n(\mathcal{N}) \subseteq \mathcal{U}$ for all $n \in \mathbb{N}$ with $n \ge N$.

The tightness of $\mathcal{K}$ follows from Proposition 18 and $F(\mathcal{K}) = \mathcal{K}$.

Proposition 20 *Under the Assumptions 9 and 10, F maps $\dot{\mathcal{M}}_+^s(S)$ into itself.*

Proof Let $\mu \in \dot{\mathcal{M}}_+(S)$. Then $\mu(S) > 0$. By Assumption 10, $S = \bigcup_{j\in\mathbb{N}} T_j$ with

$$T_j = \{s \in S; \kappa^\mu(S, s) \ge 1/j\}.$$

Notice that $T_j \subseteq T_{j+1}$ for all $j \in \mathbb{N}$. Since μ is continuous from below, $0 < \mu(S) = \lim_{j\to\infty} \mu(T_j)$. So, for some $j \in \mathbb{N}$, $\mu(T_j) > 0$ and

$$F(\mu)(S) \ge \int_{T_j} \kappa^\mu(S, s)\mu(ds) \ge (1/j)\mu(T_j) > 0$$

and $F(\mu) \in \dot{\mathcal{M}}^s_+(S)$. □

The following result implies that the extinction state is unstable.

Theorem 21 *Make Assumptions 9 and 10 and let the kernel family* $\{\kappa^\mu; \mu \in \mathcal{M}^s_+(S)\}$ *be lower semicontinuous at the zero measure.*

Further assume that there exists some $r > 0$ *and* $f \in C^b_+(S)$ *such that* $f(s) > 0$ *for all* $s \in S$ *and*

$$\int_S f(t)\kappa^o(dt, s) \ge rf(s), \qquad s \in S.$$

Then the semiflow induced by F *is uniformly weakly persistent: There exists some* $\delta > 0$ *such that* $\limsup_{n\to\infty} F^n(\mu)(S) \ge \delta$ *for all* $\mu \in \dot{\mathcal{M}}^s_+(S)$.

Proof We apply [20, Theorem 5.2] with

$$(B\mu)(T) = \int_S \kappa^o(T, s)\mu(ds)$$

and

$$\theta(\mu) = \int_S f d\mu, \qquad \mu \in \mathcal{M}^s_+(S).$$

The assumptions (a) and (b) are satisfied by Assumption 10 and the strict positivity of f. Assumption (c) follows from the lower semicontinuity of the kernel family. □

Proof of Theorem 6. We apply Theorem 21. By Theorem 17, there is some $f \in \dot{C}^b_+(S)$ such that

$$\int_S f(t)\kappa^o(dt, s) = rf(s), \qquad s \in S,$$

$r = \mathbf{r}(\kappa^o)$. f is strictly positive by Corollary 18. □

Proof of Theorem 7. We combine [26, Theorem 4.5], Theorems 20 and 6.

6.1 Compact Persistence Attractor

Theorem 22 *Make Assumptions 9, 10, 11, 12, 13, 14 and let the kernel family* $\{\kappa^\mu; \mu \in \mathcal{M}_+^s(S)\}$ *be lower semicontinuous at the zero measure.*

Assume that κ^o *is a strongly top-irreducible Feller kernel and* $\kappa^o = \kappa_1 + \kappa_2$ *with two tight Feller kernels* κ_j*, where* κ_2 *is a uniform Feller kernel. Finally, assume* $r = \mathbf{r}(\kappa^o) > 1 \ge \mathbf{r}(\kappa_1)$.

Then the semiflow induced by F *has a compact connected persistence attractor* $\mathcal{A}_1$*:*

(a) $\mathcal{A}_1$ *is a compact set with respect to the flat norm,* $F(\mathcal{A}_1) = \mathcal{A}_1$*, and* $\mathcal{A}_1$ *is a tight set of measures.*
(b) $\mathcal{A}_1$ *attracts all subsets* $\mathcal{N}$ *of* $\mathcal{M}_+^s(S)$ *with* $\inf_{\mu\in\mathcal{N}} \mu(S) > 0$ *that are compact with respect to the flat norm or are bounded and tight: If* $\mathcal{N}$ *is such a subset and* $\mathcal{U}$ *is an open set in* $\mathcal{M}_+^s(S)$ *with respect to the flat norm,* $\mathcal{A}_1 \subseteq \mathcal{U}$*, then there exists some* $N \in \mathbb{N}$ *such that* $F^n(\mathcal{N}) \subseteq \mathcal{U}$ *for all* $n \in \mathbb{N}$ *with* $n \ge \mathbb{N}$.
(c) For any $f \in \dot{C}_+^b(S)$*, there exists some* $\epsilon_f > 0$ *such that* $\int_S f d\mu \ge \epsilon_f$ *for all* $\mu \in \mathcal{A}_1$.
(d) $\mathcal{A}_1$ *is connected with respect to the flat norm. In particular, for any* $f \in \dot{C}_+^b(S)$*,* $\left\{ \int_S f d\mu; \mu \in \mathcal{A}_1 \right\}$ *is a compact interval (possibly a singleton set) contained in* $(0, \infty)$.

Proof We apply [26, Sect. 5.2] with $X = \mathcal{M}_+^s(S)$ and $\rho(\mu) = \mu(S)$ for $\mu \in \mathcal{M}_+^s(S)$. Since $F(0) = 0$ and $F(X \setminus \{0\}) \subseteq X \setminus \{0\}$ by Proposition 20, the set $X_0 := \big\{\mu \in X; \forall n \in \mathbb{Z}_+ : F^n(\mu) = 0\big\} = \{0\}$.

By Theorem 6, the semiflow $\{F^n; n \in \mathbb{Z}_+\}$ is uniformly weakly ρ-persistent.

The statements (a) and (b) follow from [26, Theorem 5.7](b) as does

$$\delta := \inf_{\mu\in\mathcal{A}_1} \mu(S) > 0. \tag{39}$$

(c) By Assumption 14, there exists a strongly top-irreducible Feller kernel $\tilde{\kappa}$ such that

$$\kappa^\nu(T, s) \ge \tilde{\kappa}(T, s), \qquad T \in \mathcal{B}, s \in S, \nu \in \mathcal{A}_1.$$

Let $\tilde{A}_*$ be the map on $C^b(S)$ associated with $\tilde{\kappa}$. For any $f \in C_+^b(S)$, $\mu \in \mathcal{A}_1$,

$$\begin{aligned}\int_S f \, d\, F(\mu) = \int_S \Big(\int_S f(t)\kappa^\mu(dt, s)\Big)\mu(ds) \\ \ge \int_S \Big(\int_S f(t)\tilde{\kappa}(dt, s)\Big)\mu(ds) = \int_S (\tilde{A}_* f) \, d\,\mu.\end{aligned}$$

By induction, for any $f \in C_+^b(S)$,

$$\int_S f \, dF^k(\mu) \ge \int_S (\tilde{A}_*^k f) \, d\,\mu, \qquad k \in \mathbb{N}, \mu \in \mathcal{A}_1. \tag{40}$$

Now let $f \in \dot{C}_+^b(S)$. By Proposition 13 since $\tilde{\kappa}$ is a strongly top-irreducible Feller kernel, there exists some $n \in \mathbb{N}$ and $\epsilon_f > 0$ such that

$$\epsilon_f \le \int_S (\tilde{A}_*^n f)\, d\mu \le \int_S f\, dF^n(\mu), \qquad \mu \in \mathcal{A}_1.$$

Since $F^n(\mathcal{A}_1) = \mathcal{A}_1$, this implies that $\int_S f\, d\nu \ge \epsilon_f > 0$ for all $\nu \in \mathcal{A}_1$.

(d) Connectedness from $\mathcal{A}_1$ follows from [26, Proposition 5.9] because ρ with $\rho(\mu) = \mu(S)$ is concave, actually additive on $\mathcal{M}_+^s(S)$. By Theorem 12, for any $f \in C^b(S)$, the map $\phi_f : \mathcal{M}_+^s(S) \to [0, \infty)$, $\phi_f(\mu) = \int_S f d\mu$, is continuous under the flat norm. Since continuous images of compact (connected) sets are compact (connected), $\phi_f(\mathcal{A}_1)$ is compact and connected and, by (c), a subset of $(0, \infty)$ if $f \in \dot{C}_+^b(S)$. □

Proof of Theorem 8. Let $\mathcal{A}_1$ be the persistence attractor from Theorem 22 and $f \in \dot{C}_+^b(S)$. Then there exists some $\epsilon_f > 0$ such that $\int_S f d\mu > \epsilon_f$ for all $\mu \in \mathcal{A}_1$. Set $\mathcal{U} = \{\nu \in \mathcal{M}_+^s(S); \int_S f d\nu > \epsilon_f\}$. By Theorem 12, $\mathcal{U}$ is an open set in $\mathcal{M}_+^s(S)$ with respect to the flat norm and $\mathcal{A}_1 \subseteq \mathcal{U} \subseteq \mathcal{M}_+^s(S)$. The statement now follows from Theorem 22(b) and (c). □

7 A More Specific Model for an Iteroparous Population

We consider a structured population the dynamics of which are governed by the processes of birth, death, and structural development, with the last being spatial movement to be specific.

We assume that each year has one very short reproductive season. We count the years in such a way that the census period is just before the reproductive season. At the end of the year, juveniles born at the beginning of the year have matured enough that they are reproductive as well and are counted as adults. This means that each year, at the very beginning of the year, just before the reproductive season, all individuals are adults. Differently from the model for a semelparous population considered in [32], individuals can reproduce several times during their life-time.

Births and deaths can be affected by competition for resources. Consider a typical adult individual at location $t \in S$. Let $q_1(s,t)$ denote the competitive effect it has on an adult located at $s \in S$ and $q_2(s,t)$ denote the competitive effect it has on a neonate located at $s \in S$. Here $q_j : S^2 \to \mathbb{R}_+$. If $\mu \in \mathcal{M}_+(S)$ is the distribution of adult individuals at the beginning of the year and $s \in S$,

$$(Q_1\mu)(s) = \int_S q_1(s,t)\mu(dt) \tag{41}$$

is the competition level exerted by μ on an adult that has been at s at the beginning of the year. while

$$(Q_2\mu)(s) = \int_S q_2(s,t)\mu(dt) \tag{42}$$

is the competition level exerted by μ on a juvenile born at s.

Further, let $g_1(s,q)$ be the probability of an adult located at $s \in S$ at the beginning of the year to survive competition till the end of the year when the competition level at s is $q \in \mathbb{R}_+$, $g_1 : S \times \mathbb{R}_+ \to [0,1]$.

Let $g_2 : S \times \mathbb{R}_+ \to \mathbb{R}_+$ be the effective per capita birth function, i.e., $g_2(s,q)$ is the per capita amount of offspring that is produced at $s \in S$ by an adult located at s and that survives competition till the end of the year when the competition level at s is $q \in \mathbb{R}_+$.

We assume that the migration patterns of neonates and adults are possibly different.

Let $P_1(T,s)$ be the probability that an adult staying at $s \in S$ at the beginning of the year does not die from noncompetitive causes till the end of the year and is located at some point in the set T at the end of the year.

Similarly, let $P_2(T,s)$ be the probability that a neonate born at $s \in S$ at the beginning of the year does not die from noncompetitive causes till the end of the year and is located at some point in the set T at the end of the year.

If the measure ν represents the spatial distribution of neonates shortly after the reproductive season at the beginning of the year,

$$(A_2\nu)(T) = \int_S P_2(T,s)\nu(ds), \qquad T \in \mathcal{B}, \tag{43}$$

provides the resulting number of adults that, at the end of the year, have not died from noncompetitive causes and are located within the set T.

A similar formula holds for the relation between the spatial distribution of adults at the beginning of the year and the resulting distribution of survivors at the end of the year.

In combination, the turnover kernel for a population with spatial distribution $\mu \in \mathcal{M}_+(S)$ is

$$\left.\begin{aligned} \kappa^\mu(T,s) &= \kappa_1^\mu(T,s) + \kappa_2^\mu(T,s) \\ \kappa_j^\mu(T,s) &= P_j(T,s)\; g_j\big(s,(Q_j\mu)(s)\big) \end{aligned}\right\} \qquad T \in \mathcal{B}, s \in S, \tag{44}$$

and $Q_j\mu$ from (41) and (42). Notice that

$$\kappa_j^o(T,s) = P_j(T,s)\; g_j(s,0), \qquad T \in \mathcal{B}, s \in S, \tag{45}$$

Assumption 20 For the per capita survival and reproduction rate functions g_1 and g_2,

(g1) $g_j : S \times \mathbb{R}_+ \to \mathbb{R}_+$ is continuous and bounded, $j = 1,2$; $g_1(s,q) \le 1$ for all $s \in S, q \in \mathbb{R}_+$.

(g2) $g_j(s,0) > 0$ for all $s \in S$ and $\dfrac{g_j(s,u)}{g_j(s,0)} \to 1$ as $u \to 0$ uniformly for $s \in S$.

For the competitive influence functions q_1 and q_2,

(q1) $q_j : S^2 \to \mathbb{R}_+$ is continuous and bounded.

For the survival/migration kernels P_1 and P_2,

(P1) $P_j : \mathcal{B} \times S \to \mathbb{R}_+$ is a Feller kernel (Definition 16) of separable measures.
(P2) $0 \le P_j(S,s) \le 1$ for all $s \in S$.

Here S^2 and $S \times \mathbb{R}_+$ are equipped with the respective product topologies.

Lemma 7 *Let the Assumptions 20 be satisfied and $j = 1, 2$. Then, for any $\mu \in \mathcal{M}_+(S)$, $Q_j\mu$ is continuous on S and $g_j\big(s, (Q_j\mu)(s)\big)$ is a continuous function of $s \in S$.*

For each $\mu \in \mathcal{M}_+(S)$, the kernels κ_j^μ, $j = 1, 2$, and κ^μ are Feller kernels of separable measures, and the Assumptions 5 are satisfied for κ_j^μ and $\kappa^\mu = \kappa_1^\mu + \kappa_2^\mu$.

Further, the kernel families $\{\kappa_j^\mu; \mu \in \mathcal{M}_+(S)\}$, $j = 1, 2$, and $\{\kappa^\mu; \mu \in \mathcal{M}_+(S)\}$ are continuous at the zero measure.

Moreover, $\kappa_1^\mu(S,s) \le 1$ for all $\mu \in \mathcal{M}_+^s(S)$ and all $s \in S$ and $\mathbf{r}(\kappa_1^o) \le 1$.

Finally, if the kernel P_2 is tight, so is the kernel κ_2^o.

Proof Let $\mu \in \mathcal{M}_+(S)$. Then

$$(Q_j\mu)(s) = \int_S q_j(s,t)\mu(dt)$$

is a continuous function of s by Lebesgue's theorem of dominated convergence because q_j is continuous and bounded by Assumption 20. By the same assumption, $g_j\big(s, (Q_j\mu)(s)\big)$ is a continuous function of $s \in S$ as composition of continuous functions.

Let $f \in C_+^b(S)$. Then

$$\int_S f(t)\kappa_j^\mu(dt,s) = h_j(s)\, g_j\big(s, (Q_j\mu)(s)\big),$$
$$h_j(s) = \int_S f(t)P_j(dt,s),$$

$h_j \in C^b(S)$ because P_j is a Feller kernel. As product of continuous functions, $\int_S f(t)\kappa_j^\mu(dt,s)$ is a continuous function of $s \in S$.

This implies that κ_j^μ is a Feller kernel and so is κ^μ.

Further, $\kappa_j^\mu(S,s) \le P_j(S,s) \sup g_j(S \times \mathbb{R}_+) \le \sup g_j(S \times \mathbb{R}_+)$ is a bounded function of $s \in S$ and $\kappa_1^\mu(S,s) \le 1$ by Assumption 20.

The separability of $\kappa_j^\mu(\cdot, s)$ is inherited from the separability of $P_j(\cdot, s)$.

The continuity of the kernel families at the zero measure follows from Assumption 20 (g2) and (44) and (45).

κ_2 inherits tightness from P_2 via the boundedness of g_2. □

The subsequent stability result follows from Theorem 4 [32, Theorem 3.6].

Theorem 23 *Let the Assumptions 20 be satisfied and* $r = \mathbf{r}(\kappa^o) < 1$.

(a) The extinction state is locally asymptotically stable in the following sense: For each $\alpha \in (r, 1)$, *there exist some* $\delta_\alpha > 0$ *and* $M_\alpha \geq 1$ *such that,*

$$F^n(\mu)(S) \leq \alpha^n M_\alpha \, \mu(S), \qquad n \in \mathbb{N},$$

if $\mu \in \mathcal{M}_+(S)$ *with* $\mu(S) \leq \delta_\alpha$.

(b) If $g_j(s, q) \leq g_j(s, 0)$ *for all* $s \in S$, $q \in \mathbb{R}_+$, $j = 1, 2$, *the extinction state is globally stable in the following sense: For each* $\alpha \in (r, 1)$, *there exists some* $M_\alpha \geq 1$ *such that*

$$F^n(\mu)(S) \leq \alpha^n M_\alpha \, \mu(S), \qquad n \in \mathbb{N}, \quad \mu \in \mathcal{M}_+(S).$$

The subsequent instability result follows from Theorem 5 and from Lemma 7 and shows that the assumption $\mathbf{r}(\kappa^o) < 1$ in Theorem 23 is almost sharp.

Theorem 24 *Let the Assumptions 20 be satisfied and* P_2 *be a tight Feller kernel. Let* $r = \mathbf{r}(\kappa^o) > 1$.

Then there exists some eigenmeasure $\nu \in \mathcal{M}_+^s(S)$, $\nu(S) = 1$, *such that*

$$r\nu(T) = \int_S \kappa^o(T, s)\nu(ds), \qquad T \in \mathcal{B}.$$

Further, the zero measure is unstable: There is some $\delta_0 > 0$ *such that for any* ν-*positive* $\mu \in \mathcal{M}_+(S)$ *there is some* $n \in \mathbb{Z}_+$ *with* $F^n(\mu)(S) \geq \delta_0$.

Recall that $\mu \in \mathcal{M}_+(S)$ is ν-positive if there exists some $\delta > 0$ such that $\mu(T) \geq \delta\nu(T)$ for all $T \in \mathcal{B}$.

Proposition 21 *Let Assumption 20 be satisfied. Assume that* P_1 *and* P_2 *are tight Feller kernels. Then, for any* $\mu \in \mathcal{M}_+(S)$, κ_1^μ, κ_2^μ *and* κ^μ *are tight Feller kernels. Further, the sets of measures*

$$\{\kappa_j^\mu(\cdot, s); s \in S, \mu \in \mathcal{M}_+(S)\}, \quad j = 1, 2, \quad \text{and } \{\kappa^\mu(\cdot, s); s \in S, \mu \in \mathcal{M}_+(S)\}$$

are tight and the sets

$$\{\kappa_j^\mu(S, s); s \in S, \mu \in \mathcal{M}_+(S)\}, \quad j = 1, 2, \ \text{and } \{\kappa^\mu(S, s); s \in S, \mu \in \mathcal{M}_+(S)\}$$

are bounded in $\mathbb{R}$. *In particular, Assumption 12 is satisfied.*

Proof $\kappa_1^\mu, \kappa_2^\mu$ and κ^μ are tight Feller kernels by Proposition 7 and Lemma 7.

Since the functions g_j are bounded, there exists some $c > 0$ such that $g_j\big(s, (Q_j\mu)(s)\big) \le c$ for all $s \in S$ and $\mu \in \mathcal{M}_+(S)$, $j = 1, 2$. For any $T \in \mathcal{B}$,

$$\kappa_j^\mu(S \setminus T, s) \le \kappa^\mu(S \setminus T, s) \le c\big(P_1(S \setminus T, s) + P_2(S \setminus T, s)\big).$$

Since P_j are Feller kernels, the right hand side has a common upper bound for $s \in S, T \in \mathcal{B}$. This implies the boundedness of the various sets in $\mathbb{R}$ in the assertion of the Proposition. Let $\epsilon > 0$. For $j = 1, 2$, since the P_j are tight kernels, there exist compact sets $T_j \in \mathcal{B}$ such that $P_j(S \setminus T_j, s) \le \epsilon/(2c)$. Set $T = T_1 \cup T_2$. Then T is compact and, for all $\mu \in \mathcal{M}_+(S)$, $s \in S$,

$$\kappa_j^\mu(S \setminus T, s) \le \kappa^\mu(S \setminus T, s) \le c\big(P_1(S \setminus T_1, s) + P_2(S \setminus T_2, s)\big) \le \epsilon.$$

Proposition 22 *Let Assumption 20 be satisfied. If $P := P_1 + P_2$ is a (strongly) top-irreducible kernel, so is κ^o.*

Proof Set $h(s) = \min\{g_1(s, 0), g_2(s, 0)\}$, $s \in S$. Then $h \in C_+^b(S)$ and, by Assumption 20, $h(s) > 0$ for all $s \in S$.

By (44),

$$\kappa^o(T, s) \ge P(T, s)h(s) =: \tilde{\kappa}(T, s), \qquad T \in \mathcal{B}, s \in S.$$

Since P is a (strongly) top-irreducible kernel and h is strictly positive, $\tilde{\kappa}$ is a (strongly) top-irreducible kernel by Proposition 14 and so is κ^o as one sees from Definition 19. □

In view of these results, we collect the following set of assumptions.

Assumption 21 • P_1 and P_2 are tight Feller kernels.
• $g_j(s, q) > 0$ for $j = 1, 2$ and all $s \in S$ and $q \in \mathbb{R}_+$.

Lemma 8 *Assume that $g_j(s, q) > 0$ for all $s \in S$, $q \in \mathbb{R}_+$. Let $\mathcal{N}$ be a bounded subset of $\mathcal{M}_+(S)$ and $P = P_1 + P_2$ be a strongly top-irreducible kernel. Then there exists a strongly top-irreducible kernel $\tilde{\kappa}$ such that $\kappa^\mu(T, s) \ge \tilde{\kappa}(T, s)$ for all $T \in \mathcal{B}$, $s \in S$ and $\mu \in \mathcal{N}$.*

In particular, Assumption 14 is satisfied.

Proof Let $\mathcal{N}$ be a bounded subset of $\mathcal{M}_+(S)$. Since q_j is bounded, by (41) and (42) there exists some $c \in (0, \infty)$ such that $(Q_j\mu)(s) \le c$ for $j = 1, 2$, $s \in S$, and $\mu \in \mathcal{N}$. Set

$$h_j(s) = \inf_{0 \le q \le c} g_j(s, q), \quad s \in S, \qquad j = 1, 2.$$

Since g_j is continuous and $g_j(s, q) > 0$ for all $s \in S, q \in \mathbb{R}_+, h_j(s) > 0$ for all $s \in S$. To show that h_j is continuous, let $s \in S$ and (s_ℓ) be a sequence in S such that $s_\ell \to s$ as $\ell \to \infty$. Then $T = \{s_\ell; \ell \in \mathbb{N}\} \cup \{s\}$ is a compact subset of S and $T \times [0, c]$ is a compact subset of $S \times \mathbb{R}$ and g_j is uniformly continuous on $T \times [0, c]$. This implies that $g_j(s_\ell, q) \to g_j(s, q)$ as $\ell \to \infty$ uniformly for $q \in [0, c]$ and so $h_j(s_\ell) \to h_j(s)$ for $\ell \to \infty$. Finally set $h(s) = \min\{h_1(s), h_2(s)\}$. Then $h \in C_+^b(S)$ and $h(s) > 0$ for all $s \in S$.

By (44),

$$\kappa^\mu(T, s) \geq P(T, s)h(s) =: \tilde{\kappa}(T, s).$$

Since P is a strongly top-irreducible kernel and h is strictly positive, $\tilde{\kappa}$ is a strongly top-irreducible kernel by Proposition 14. In particular, for each $\mu \in \mathcal{M}_+(S)$, $\kappa^\mu(S, s) \geq \tilde{\kappa}(S, s) > 0$ for all $s \in S$.

Theorem 25 *Let the Assumptions 20 and 21 be satisfied, P_2 be a uniform Feller kernel, $P_1 + P_2$ be top-irreducible and $r = \mathbf{r}(\kappa^o) > 1$.*

Then there exists some strictly positive eigenfunction $f \in \dot{C}_+^b(S)$ with $\int_S f(t)\kappa^o(dt, s) = rf(s)$ for all $s \in S$.

Further, the semiflow generated by F is uniformly weakly persistent: There exists some $\delta > 0$ such that $\limsup_{n\to\infty} F^n(\mu)(S) \geq \delta$ for all $\mu \in \dot{\mathcal{M}}_+^s(S)$.

Proof By Proposition 10, κ_2^o is a uniform Feller kernel. By Proposition 7, κ_j^o is a tight Feller kernel, $j = 1, 2$. By Proposition 22, κ^o is a top-irreducible Feller kernel. By Lemma 7, the kernel family $\{\kappa^\mu; \mu \in \mathcal{M}_+^s(S)\}$ is lower semicontinuous at the zero measure.

Assumption 9 is satisfied by Proposition 21, and Assumption 10 is satisfied by Lemma 8. By Lemma 7, $\mathbf{r}(\kappa_1^o) \leq 1$. Apply Theorem 6. □

Recall Definition 15.

Assumption 22 (a) For any closed totally bounded subset T of S, $\{q_j(s, \cdot); s \in T\}$ is equicontinuous on S, $j = 1, 2$.

(b) For any closed totally bounded subset T of S, $\{g_j(s, \cdot); s \in T\}$ is uniformly equicontinuous on bounded subsets of $\mathbb{R}$, $j = 1, 2$.

Lemma 9 *Assumption 22 is satisfied if S be completely metrizable, and Assumption 20 holds.*

Proof Let T be a closed totally bounded subset of S and let S be completely metrizable. Then T is compact.

(b) Let $c > 0$. Then the set $T \times [0, c]$ is compact. Since g_j is continuous on $S \times \mathbb{R}_+$, g_j is uniformly continuous on $T \times [0, c]$. This implies (b).

(a) Suppose that Assumption 22(a) is false for $j = 1$ or $j = 2$. Then there is some $\tilde{s} \in S$ such that $\{q_j(s, \cdot); s \in T\}$ is not equicontinuous at $\tilde{s}$.

Then there exists some $\epsilon > 0$ and a sequence (s_n) in T and a sequence $(\tilde{s}_n)$ in S such that $\tilde{s}_n \to \tilde{s}$ as $n \to \infty$ and

$$|q_j(s_n, \tilde{s}_n) - q_j(s_n, \tilde{s})| > \epsilon, \qquad n \in \mathbb{N}.$$

Since $T \times \big(\{\tilde{s}_n; n \in \mathbb{N}\} \cup \{\tilde{s}\}\big)$ is a compact subset of S^2, q_j is uniformly continuous on this set, a contradiction.

Lemma 10 *Let the Assumptions 20 and 22(a) be satisfied. Further let* $\mu \in \mathcal{M}_+^s(S)$ *and* (μ_n) *be a sequence in* $\mathcal{M}_+^s(S)$*,* $\|\mu_n - \mu\|_\flat \to 0$ *as* $n \to \infty$*.*

Then, for $j = 1, 2$*,* $(Q_j\mu_n)(s) \to (Q_j\mu)(s)$ *as* $n \to \infty$ *uniformly for* s *in any closed totally bounded subset of* S*. Further* $Q_j\mu_n$ *and* $Q_j\mu$ *are bounded functions.*

Proof The convergence statement follows from Proposition 2 and (41) and (42). The boundedness statements are immediate.

Lemma 11 *Let the Assumptions 20 and 22(b) be satisfied. Let* T *be a closed totally bounded subset of* S *and* $f_n : T \to \mathbb{R}_+$*,* $n \in \mathbb{N}$*, and* $f : T \to \mathbb{R}_+$ *be bounded functions such that* $f_n \to f$ *uniformly on* T*. Then* $g_j\big(s, f_n(s)\big) \to g_j\big(s, f(s)\big)$ *as* $n \to \infty$ *uniformly for* $s \in T$*.*

Proof There exists some $c \in (0, \infty)$ such that $f_n(s), f(s) \le c$ for all $n \in \mathbb{N}$, $s \in T$. Since $\{g_j(s, \cdot); s \in T\}$ is uniformly equicontinuous on $[0, c]$, the assertion follows.

Proposition 23 *Let the Assumptions 20 and 22 be satisfied. Then Assumption 11 is satisfied for* κ_j^μ*,* $j = 1, 2$ *and* κ^μ*.*

Proof It is sufficient to show the claim for κ_1^μ. Let (μ_n) be a sequence in $\mathcal{M}_+^s(S)$ and $\mu \in \mathcal{M}_+^s(S)$ such that $\int_S f d\mu_n \to \int_S f d\mu$ as $n \to \infty$ for all $f \in C_+^b(S)$. Then $\|\mu_n - \mu\|_\flat \to 0$ as $n \to \infty$ by Theorem 12.

Let $h \in C_+^b(S)$. For $s \in S$,

$$\begin{aligned}&\int_S h(t)\kappa_1^{\mu_n}(dt, s) - \int_S h(t)\kappa_1^\mu(dt, s)\\ &= \int_S h(t)P_1(dt, s)\big[g_1\big(s, (Q_1\mu_n)(s)\big) - g_1\big(s, (Q_1\mu)(s)\big)\big].\end{aligned}$$

Since $\int_S h(t)P_1(dt, s) \le \sup h(S)$, it is sufficient to show that

$$g_1\big(s, (Q_1\mu_n)(s)\big) \to g_1\big(s, (Q_1\mu)(s)\big), \qquad n \to \infty$$

uniformly on every closed totally bounded subset T of S. But this follows by combining Lemmas 10 and 11.

Assumption 23 $\sup_{s\in S, q\ge 0} P_1(S, s)g_1(s, q) < 1; \qquad \inf_{s,t\in S} q_2(s, t) > 0;$

$$g_2(s, q) \to 0 \text{ as } q \to \infty, \text{ uniformly for } s \in S.$$

From the interpretation of g_1 as probability of surviving competition, it is suggestive that $0 \le g_1(s, q) \le 1$ (Assumption 20 g1). So, together with $P_1(S, s) \le 1$, the first of the assumptions is not really drastic. The second assumption means that competitive influence on somebody else's reproduction reaches everywhere in the habitat. The third assumption means that fertility drops very low if resources are very low due to large competition.

Proposition 24 *Under the Assumptions 23,*

$$\sup_{\mu\in\mathcal{M}_+^s(S)} \sup_{s\in S} \kappa_1^\mu(S,s) < 1, \qquad \sup_{s\in S} \kappa_2^\mu(S,s) \to 0 \text{ as } \mu(S)\to\infty,$$

and Assumption 13 is satisfied. Further $\mathbf{r}(\kappa_1^o) < 1$.

Proof Recall that

$$\kappa_1^\mu(S,s) = P_1(S,s) g_1\big(s, (Q_1\mu)(s)\big) \le P_1(S,s) \sup_{q\in\mathbb{R}_+} g_1(s,q),$$

which implies the first assertion. Further

$$(Q_2\mu)(s) \ge \inf_{s,t\in S} q_2(s,t)\, \mu(S) \overset{\mu(S)\to\infty}{\longrightarrow} \infty$$

uniformly for $s \in S$, and so

$$\kappa_2^\mu(S,s) = P_2(S,s) g_2\big(s, (Q_\mu)(s)\big) \to 0, \qquad \mu(S)\to\infty,$$

uniformly for $s \in S$. We combine,

$$\begin{aligned}\limsup_{\mu(S)\to\infty} \sup_{s\in S} \kappa^\mu(S,s) \le & \sup_{\mu\in\mathcal{M}_+^s(S),\, s\in S} \kappa_1^\mu(S,s) + \limsup_{\mu(S)\to\infty} \sup_{s\in S} \kappa_2^\mu(S,s) \\ = & \sup_{\mu\in\mathcal{M}_+^s(S),\, s\in S} \kappa_1^\mu(S,s) < 1.\end{aligned}$$

Theorem 26 *Let the Assumptions 20, 22 and 23 be satisfied. Assume that P_1 and P_2 are tight Feller kernels and* $\mathbf{r}(\kappa^o) > 1$.

Then there exists a fixed point $F(\mu) = \mu \in \dot{\mathcal{M}}_+^s(S)$.

Proof We apply [32, Theorem 3.19]. Its assumptions are satisfied by Lemma 7, Propositions 21, 23 and 24.

Theorem 27 *Let the Assumptions 20, 21, 22 and 23 be satisfied. Assume that P_2 is a uniform Feller kernel, $P_1 + P_2$ is top-irreducible and* $\mathbf{r}(\kappa^o) > 1$.

Then the population is uniformly persistent in the following sense: There exists some $\epsilon_0 > 0$ such that $\liminf_{n\to\infty} F^n(\mu)(S) \ge \epsilon_0$ for all $\mu \in \dot{M}_+^s(S)$.

Proof We apply Theorem 7. Its assumptions are satisfied by Lemma 7, Propositions 21, 23, 24. □

Theorem 28 *Let the Assumptions 20, 21, 22 and 23 be satisfied. Assume that P_2 is a uniform Feller kernel, $P_1 + P_2$ is strongly top-irreducible and* $\mathbf{r}(\kappa^o) > 1$.

Then the semiflow induced by F is uniformly persistent in the following sense: For each $f \in \dot{C}_+^b(S)$, there exists some $\epsilon_f > 0$ with the following property:

If $\mathcal{N}$ is a compact (or bounded tight) subset of $\mathcal{M}_+^s(S)$ with $\inf_{\mu \in \mathcal{N}} \mu(S) > 0$, *there exists some $N \in \mathbb{N}$ such that*

$$\int_S f \, dF^n(\mu) \geq \epsilon_f \quad \textit{for all } \mu \in \mathcal{N} \textit{ and all } n \in \mathbb{N} \textit{ with } n > N.$$

Proof We apply Theorem 8. Its assumptions are satisfied by Lemma 7, Propositions 21, 23, 24, Lemma 8. □

Acknowledgements The author thanks Azmy Ackleh for useful hints and Odo Diekmann and Eugenia Franco for helpful suggestions.

References

1. Ackleh, A.S., Colombo, R.M., Goatin, P., Hille, S.C., Muntean, A. (guest editors): Mathematical modeling with measures. Math. Biosci. Eng. **17**(special issue) (2020)
2. Ackleh, A.S., Colombo, R.M., Hille, S.C., Muntean, A. (guest editors): Modeling with measures. Math. Biosci. Eng. **12**(special issue) (2015)
3. Aliprantis, C.D., Border, K.C.: Infinite Dimensional Analysis. A Hitchhiker's Guide, 3rd edn. Springer, Berlin (1999, 2006)
4. Bonsall, F.F.: Linear operators in complete positive cones. Proc. Lond. Math. Soc. **8**, 53–75 (1958)
5. Cushing, J.M., Zhou, Y.: The net reproductive value and stability in matrix population models. Nat. Res. Mod. **8**, 297–333 (1994)
6. Cushing, J.M.: On the relationship between r and R_0 and its role in the bifurcation of stable equilibria of Darwinian matrix models. J. Biol. Dyn. **5**, 277–297 (2011)
7. Desch, W., Schappacher, W.: Linearized stability for nonlinear semigroups. In: Favini, A., Obrecht, E. (eds.) Differential Equations in Banach Spaces. Lecture Notes in Mathematics, vol. 1223, pp. 61–67. Springer, Berlin (1986)
8. Diekmann, O., Gyllenberg, M., Metz, J.A.J., Thieme, H.R.: The 'cumulative' formulation of (physiologically) structured population models. In: Clément, Ph., Lumer, G. (eds.) Evolution Equations, Control Theory, and Biomathematics, pp. 145–154. Dekker, Marcel (1994)
9. Diekmann, O., Heesterbeek, J.A.P., Metz, J.A.J.: On the definition and the computation of the basic reproduction number R_0 in models for infectious diseases in heterogeneous populations. J. Math. Biol. **28**, 365–382 (1990)
10. Dudley, R.M.: Convergence of Baire measures. Stud. Math. **27**, 251–268 (1966). (Correction to "Convergence of Baire measures". Stud. Math. **51**, 275 (1974))
11. Dudley, R.M.: Real Analysis and Probability, 2nd edn. Cambridge University Press, Cambridge (2002)
12. Dunford, N., Schwartz, J.T.: Linear Operators. Part I. General Theory, John Wiley, Classics Library Edition, New York (1988)
13. Gel'fand, I.M.: Normierte Ringe. Mat Sbornik NS **9**, 3–24 (1941)
14. Gwiazda, P., Marciniak-Czochra, A., Thieme, H.R.: Measures under the flat norm as ordered normed vector space. Positivity **22**, 105–138 (2018). (Correction. Positivity **22**, 139–140 (2018))
15. Hille, S.C., Worm, D.T.H.: Continuity properties of Markov semigroups and their restrictions to invariant L^1 spaces. Semigroup Forum **79**, 575–600 (2009)
16. Hille, S.C., Worm, D.T.H.: Embedding of semigroups of Lipschitz maps into positive linear semigroups on ordered Banach spaces generated by measures. Integral Equ. Oper. Theory **63**, 351–371 (2009)

17. Jin, W., Smith, H.L., Thieme, H.R.: Persistence versus extinction for a class of discrete-time structured population models. J. Math. Biol. **72**, 821–850 (2016)
18. Jin, W., Smith, H.L., Thieme, H.R.: Persistence and critical domain size for diffusing populations with two sexes and short reproductive season. J. Dyn. Differ. Eqn. **28**, 689–705 (2016)
19. Jin, W., Thieme, H.R.: Persistence and extinction of diffusing populations with two sexes and short reproductive season. Discret. Contin. Dyn. Syst. B **19**, 3209–3218 (2014)
20. Jin, W., Thieme, H.R.: An extinction/persistence threshold for sexually reproducing populations: the cone spectral radius. Discret. Contin. Dyn. Syst. B **21**, 447–470 (2016)
21. Mallet-Paret, J., Nussbaum, R.D.: Eigenvalues for a class of homogeneous cone maps arising from max-plus operators. Disc. Cont. Dyn. Syst. A **8**, 519–562
22. Mallet-Paret, J., Nussbaum, R.D.: Generalizing the Krein-Rutman theorem, measures of noncompactness and the fixed point index. J. Fixed Point Theory Appl. **7**, 103–143 (2010)
23. McDonald, J.N., Weiss, N.A.: A Course in Real Analysis. Academic Press, San Diego (1999)
24. Nussbaum, R.D.: Eigenvectors of nonlinear positive operators and the linear Krein-Rutman theorem. In: Fadell, E., Fournier, G. (eds.) Fixed Point Theory, pp. 309–331. Springer, Berlin (1981)
25. Schaefer, H.H.: Banach Lattices and Positive Operators. Springer, Berlin (1974)
26. Smith, H.L., Thieme, H.R.: Dynamical Systems and Population Persistence. American Mathmetical Society, Providence (2011)
27. Shurenkov, V.M.: On the relationship between spectral radii and Perron Roots. Chalmers University of Technology and Göteborg University (preprint)
28. Thieme, H.R.: Spectral radii and Collatz-Wielandt numbers for homogeneous order-preserving maps and the monotone companion norm. In: de Jeu, M., de Pagter, B., van Gaans, O., Veraar, M. (eds.) Ordered Structures and Applications. Trends in Mathematics, pp. 415–467. Birkhäuser/Springer, Cham (2016)
29. Thieme, H.R.: Eigenfunctionals of homogeneous order-preserving maps with applications to sexually reproducing populations. J. Dyn. Differ. Eqn. **28**, 1115–1144 (2016)
30. Thieme, H.R.: Eigenvectors of homogeneous order-bounded order-preserving maps. Discret. Contin. Dyn. Syst. B **22**, 1073–1097 (2017)
31. Thieme, H.R.: From homogeneous eigenvalue problems to two-sex population dynamics. J. Math. Biol. **75**, 783–804 (2017)
32. Thieme, H.R.: Discrete-time population dynamics on the state space of measures. Math. Biosci. Eng. **17**, 1168–1217 (2020). https://doi.org/10.3934/mbe.2020061
33. Zhao, X.-Q.: Dynamical Systems in Population Biology. Springer, New York (2003)