CHAPTER 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.

1.1. Discrete-time population models

It seems appropriate to model such populations by discrete-time structured models in the form of the recursion (or difference equation),

$$x_n = F(x_{n-1}), \qquad n \in \mathbb{N}, \quad x_0 \in X_F. \tag{1.1}$$

The population structure is encoded in the closed subset $X_F \ni 0$ of a normed vector space X over $\mathbb{R}$, and $F(0) = 0$.

(See Definitions A.19 and A.13.)

The vector x_n describes the structural distribution of the population in year n while $F : X_F \to X_F$ formulates the rule how the structural distribution in a given year follows from the structural distribution of the previous year; the zero vector represents the extinction state of the population. The norm $\|x_n\|$ is some measure of the population size in year n. F is called the *(yearly) population turnover operator*. The recursive equation (1.1) is solved by

$$x_n = F^n(x_0), \quad n \in \mathbb{N}, \tag{1.2}$$

where F^n is the n fold composition of F with itself (nth iterate, nth power). We set $F^0(h_0) = h_0$. $\{F^n; n \in \mathbb{Z}_+\}$ is the *discrete semiflow* induced by F [**187**, **226**].

A fundamental question (Chapter 14) is as to whether the population dies out, $\|x_n\| \to 0$ as $n \to \infty$, or whether it persists uniformly weakly.

Definition 1.1. *The population* persists uniformly weakly *if the following holds for the solutions* (x_n) *of* (1.1)*:*

> *There is some* $\epsilon > 0$ *(independent of* (x_n)*) such that, if* $x_0 \neq 0$*, then* $\|x_n\| \geq \epsilon$ *for infinitely many* $n \in \mathbb{N}$*.*

In order to address this question, we assume that X_F is *a (positively) homogeneous subset* of X:

$$x \in X_F, \ \alpha \in \mathbb{R}_+ \implies \alpha x \in X_F. \tag{1.3}$$

Let X_B be the set of those $x \in X_F$ such that the directional derivative at 0 in the direction of x exists,

$$\lim_{\mathbb{R}_+ \ni b \to 0} \frac{1}{b} F(bx) = \partial F(0, x) =: B(x). \tag{1.4}$$

Since $0 \in X_F$ and $F(0) = 0$, $0 \in X_B$ and $B(0) = 0$. If $X_B = X_F$, $\partial F(0, \cdot)$ is called the *Gateaux derivative* of F at 0.

It is easy to see that $X_B \subseteq X_F$ is a homogeneous subset of X and the operator $B : X_B \to X$ is (positively) *homogeneous* (of degree one) (Theorem 14.1).

DEFINITION 1.2. *An operator $B : X_B \to X$, $X_B \subseteq X$, is* homogeneous *if X_B is a homogeneous subset of X and,*

$$x \in X_B, \alpha \in \mathbb{R}_+ \implies B(\alpha x) = \alpha B(x).$$

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* in a weak sense, and we will need B to be a first order approximation in a stronger sense (Section 14.2) 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 homogeneous operator $B : X_B \to X_B$ on a homogeneous subset X_B of X is defined as

$$\|B\| := \sup\big\{\|B(x)\|;\ x \in X_B,\ \|x\| \leq 1\big\}, \tag{1.5}$$

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

LEMMA 1.3. *Assume that there are $\delta > 0$ and $c > 0$ such $F : X_F \to X_F$ satisfies $\|F(x)\| \leq c\|x\|$ for all $x \in X_F$ with $\|x\| \leq \delta$ and $B(x) = \partial F(0, x)$, $x \in X_B$. Then the homogeneous operator $B : X_B \to X$ is bounded.*

1.2. The spectral radius of a bounded homogeneous operator

If $B : X_B \to X$, $X_B \subseteq X$, is a bounded homogeneous operator, then

$$\|B(x)\| \leq \|B\|\, \|x\|, \qquad x \in X_B. \tag{1.6}$$

If $B : X_B \to X_B$, this formula implies that the powers (iterates) $B^n : X_B \to X_B$ of a homogeneous bounded B are bounded homogenous operators and $\|B^n\| \leq \|B\|^n$ for all $n \in \mathbb{N}$.

The *spectral radius* of a bounded homogeneous $B : X_B \to X_B \subseteq X$ is defined by the *Gelfand* formula [**93**]

$$\mathbf{r}(B) = \inf_{n \in \mathbb{N}} \|B^n\|^{1/n} = \lim_{n \to \infty} \|B^n\|^{1/n}. \tag{1.7}$$

The last equality is shown in the same well-known way as for a bounded linear everywhere-defined map. See Chapter 5 for more information.

The name "spectral radius" is motivated by the following fact. Let B be a bounded linear map on X. If $X_\mathbb{C}$ is the complexification of X and $B_\mathbb{C}$ the extension of B to $X_\mathbb{C}$ (see Section 5.4), then

$$\mathbf{r}(B) = \sup\{|\lambda|; \lambda \in \sigma^\mathbb{C}(B)\}, \tag{1.8}$$

where $\sigma^\mathbb{C}(B) \subseteq \mathbb{C}$ denotes the spectrum of $B_\mathbb{C}$ [**93, 167**].

Equation (1.8) is partially preserved for bounded homogeneous B. Recall that, for linear bounded everywhere-defined B, eigenvalues are special elements of the spectrum of B.

If X_B is a homogeneous subset of X, then $0 \in X_B$. See (1.3). We use the notation

$$\dot{X}_B = X_B \setminus \{0\}, \qquad \dot{X}_F = X_F \setminus \{0\}. \tag{1.9}$$

For homogeneous $B : X_B \to X_B$, we call $\lambda \in (0, \infty)$ an *eigenvalue* of B and $v \in \dot{X}_B$ an *associated eigenvector* of B if $B(v) = \lambda v$.

PROPOSITION 1.4. *Let $B : X_B \to X_B$ be homogeneous and bounded, $\lambda \in (0, \infty)$, $v \in \dot{X}_B$ and $B(v) = \lambda v$.*

Then $\lambda \leq \mathbf{r}(B)$.

PROOF. Since B is homogeneous, we can assume that $\|v\| = 1$. By induction, $\lambda^n v = B^n(v)$ for all $n \in \mathbb{N}$. Since B^n is homogeneous and bounded, $\lambda^n \leq \|B^n\| \, \|v\| \leq \|B^n\|$ and $\lambda \leq \|B^n\|^{1/n}$ for all $n \in \mathbb{N}$. The assertion now follows from (1.7). □

The Gelfand formula for the spectral radius is used for restrictions of bounded positive linear operators to a cone by Bonsall [**27**] under the name "partial spectral radius" and somewhat later by Nussbaum [**167**] under the name "cone spectral radius." Mallet-Paret and Nussbaum [**156, 157**] use the Gelfand formula for homogeneous bounded operators on a cone under the name "Bonsall cone spectral radius." But since the Gelfand formula also makes sense on homogeneous sets (which concept includes the vector space), there seems to be good reason to simply say "spectral radius." While a much richer theory can be developed for order-preserving homogeneous operators on a cone, upper semicontinuity of the spectral radius (Section 1.4) can be shown for homogeneous operators in a normed vector space without any order under relatively mild conditions (Chapter 7).

If B has an interpretation as a basic population turnover operator, $\mathbf{r}(B)$ is called the *basic population turnover number* and is denoted by $\mathcal{T}_0$. $\mathcal{T}_0$ has also been called *inherent population growth rate* [**44**] or *(population) growth factor* [**150**].

1.3. Preview of extinction and persistence results

The following results which highlight the role of the basic turnover number $\mathcal{T}_0 = \mathbf{r}(B)$ as threshold parameter between population extinction and persistence hold under additional assumptions, which we do not mention here (Chapter 14). We first consider the subthreshold case $\mathcal{T}_0 < 1$.

THEOREM 1.5. *Let $F, B : X_F \to X_F$ and let B be homogeneous and bounded and B an appropriate first order approximation of F, $\mathcal{T}_0 = \mathbf{r}(B) < 1$. Then the extinction state 0 is locally asymptotically stable in the following sense:*

For each $\alpha \in (\mathcal{T}_0, 1)$, there exist some $\delta_0 > 0$ and $M \geq 1$ such that for all solutions (x_n) of (1.1) $\|x_n\| \leq M\alpha^n \|x\|$ for all $n \in \mathbb{N}$ and all $x_0 \in X_F$ with $\|x_0\| \leq \delta_0$.

See Theorem 14.13 for the precise formulation. We turn to the superthreshold case $\mathcal{T}_0 > 1$.

THEOREM 1.6. *Let $F, B : X_F \to X_F$ and B be bounded homogeneous and let B be an appropriate first order approximation of F, $\mathcal{T}_0 = \mathbf{r}(B) > 1$.*

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

There exists some $\epsilon > 0$ such that for all solutions (x_n) of (1.1) with $x_0 \in X_F$ and $x_0 \neq 0$ we have $\|x_n\| \geq \epsilon$ for infinitely many $n \in \mathbb{N}$.

See Theorem 14.27 for the precise formulation.

In the threshold case $\mathcal{T}_0 = 1$, stability of the extinction state or even extinction of the population can be shown, but the conditions are quite restrictive and technical. See Section 14.5 and Theorems 14.23 and 14.24.

For these results, whether in the subthreshold, threshold, or superthreshold case, it will be not enough to assume that X_F is a closed homogeneous subset of X; rather X_F needs to be a closed cone. Therefore, cones, wedges and ordered vector spaces are studied in Chapter 2. Special care is given to being clear about when completeness of X or X_F are really needed. See motivation ($\diamondsuit_3$) below. Also, not much can be done without assuming that B is order-preserving (Chapter 4).

The previous theorems are known if B can be extended to a bounded linear map on X and B is the Frechet derivative of F at 0 [**187**, **226**].

There are at least three motivations to consider the more general situation of a bounded homogeneous order-preserving operator.

($\diamondsuit_1$) The first motivation is mathematical: The Gateaux derivative at the zero vector, (1.4), is homogeneous but not linear, and homogeneous operators are not Frechet differentiable at 0 unless they are linear. Also see Section 14.1.

($\diamondsuit_2$) The second, biological, motivation are two-sex population models which often use homogeneous mating (or pair formation) functions (Section 4.5, [**83**, **106–109**, **115**, **117**, **118**, **130**, **161**, **202**] and the references therein).

Let $\varphi(f, m)$ be the amount of offspring produced by f females and m males via mating (ignoring competition for resources). Assume that

$$\varphi(\alpha f, \alpha m) = \alpha \varphi(f, m), \qquad f, m, \alpha \in \mathbb{R}_+.$$

This means that if both the numbers of females and males double (or triple), the number of mated pairs also doubles (or triples).

This type of mating functions leads to homogeneous first order approximations of the population turnover operator (Chapters 15, 17, and 18). Males and females may have different survival probabilities, the sex ratio at birth may not be one, the sexes may move differently in their habitat [**162**], fighting between males may spread diseases more readily [**11**] (to mention a few reasons while one would like to model females and males separately).

($\diamondsuit_3$) The third motivation are structural population distributions which are best described by measures μ on a metric space S (Chapters 3, 13 and 19) with $\mu(T)$ representing the number of individuals whose structural characteristic lies in the Borel subset T of S. So, the population state space of interest is the ordered vector space of real measures on the Borel σ-algebra of S, denoted by $\mathcal{M}(S)$, ordered by the cone of nonnegative measures $\mathcal{M}_+(S)$. The variation norm (Section 3.1) makes this vector space a Banach space but is too strong to provide the required compactness of the basic turnover operator B on $X_F = \mathcal{M}_+(S)$ in Theorem 1.6 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 (Section 3.2). Important linear basic turnover operators defined on all of X are compact and continuous on X_F, though they are not continuous on X (Chapters 13 and 19). As a trade off, the flat norm rarely makes

$X = \mathcal{M}(S)$ a Banach space and makes $\mathcal{M}_+(S)$ only complete if the metric space S can be chosen to be complete.

Theorems 1.5 and 1.6 highlight the importance of the spectral radius as threshold parameter separating population extinction and population persistence. Estimates, approximations, and equivalent characterizations of the spectral radius are therefore important (Chapters 5 and 6). This involves lower and upper Collatz–Wielandt numbers [**87**] and Collatz–Wielandt bounds and also Collatz–Wielandt spectral radii (Sections 5.5.1, 5.5.2, and 6.2).

Uniform weak versus uniform persistence. A stronger and more desirable concept than uniform weak persistence (Definition 1.1) is uniform persistence.

DEFINITION 1.7. *The population* persists uniformly *if the following holds for the solutions* (x_n) *of* (1.1)*:*

There is some $\epsilon > 0$ *(independent of* (x_n)*) such that, if* $x_0 \neq 0$*, then* $\|x_n\| \geq \epsilon$ *for all but finitely many* $n \in \mathbb{N}$*.*

It may be worth-while to write down the two definitions in formal logic.
Uniform persistence:

$$\exists \epsilon > 0 \; \forall x_0 \neq 0 \; \exists m \in \mathbb{N} \; \forall n \in \mathbb{N} \; \big(n \geq m \implies \|x_n\| \geq \epsilon\big).$$

Uniform weak persistence:

$$\exists \epsilon > 0 \; \forall x_0 \neq 0 \; \forall m \in \mathbb{N} \; \exists n \in \mathbb{N} \; \big(n \geq m \wedge \|x_n\| \geq \epsilon\big).$$

Verbally, in both concepts, there is some level $\epsilon > 0$ for the population size that does not depend on the initial state of the population.

If the population persists uniformly, after some time (which depends on the initial state of the population) the population size stays above the level ϵ.

If the population persists uniformly weakly, the population size may become arbitrarily small at times but always bounces back to or above the level ϵ.

If one is sufficiently familiar with the notions of limit superior and limit inferior of real functions or sequences (Appendix A.3.1)[**159**, Def.2.5], there is yet another way of formulating the concept of uniform weak and uniform persistence. Recall that if (x_n) is a solution of $x_n = F(x_{n-1}), n \in \mathbb{N}$, then $x_n = F^n(x_0)$ where F^n is the nth iterate or power of F.

- The population persists uniformly if there is some $\epsilon > 0$ such that, for all $x_0 \in \dot{X}_F$, $\liminf_{n\to\infty} \|F^n(x_0)\| \geq \epsilon$.
- The population persists uniformly weakly if there is some $\epsilon > 0$ such that, for all $x \in \dot{X}_F$, $\limsup_{n\to\infty} \|F^n(x_0)\| \geq \epsilon$.

See Exercise A.3.2. We will use the limsup liminf formulations in the rest of the book, e.g., Section 14.9. See also Appendix A.3.1.

Uniform persistence requires much stronger assumptions than uniform weak persistence. Compare Theorems 14.27 and 14.32. There are well-established routes [**92**], [**130**], Section 5 and Theorem 7.2, and [**187**], Sections 4.1 and 4.2, of getting from uniform weak to uniform persistence. These routes do not depend on whether the basic turnover operator B is a bounded homogeneous order preserving operator on X_F or whether it can be extended to a bounded linear positive map on all of X. Therefore, we mostly concentrate on uniform weak persistence (Section 14.9.1), but give a taste of uniform persistence in Section 14.9.2. As for the case studies, we work out uniform persistence for the less familiar case that the population state space is the cone of nonnegative real measures on a metric space.

We mention that there is also a direct route to uniform persistence ([**154**, **226**] and the references therein and in [**187**]).

1.4. Continuous dependence of the spectral radius on its operator

The threshold property of the spectral radius (between extinction and persistence of populations) outlined in Section 1.3 raises interest in the question whether the spectral radius of a bounded homogeneous operator B on X_B continuously depends on B. In other words: If the basic turnover operator is only slightly changed, does the same holds for the basic turnover number, $\mathcal{T}_0$? In mathematical formulation:

If (B_k) is a sequence of bounded homogeneous operators on X_B and $\|B_k - B\| \to 0$ as $k \to \infty$, then $\mathbf{r}(B_k) \to \mathbf{r}(B)$ as $k \to \infty$.

Here $\|\cdot\|$ is the operator norm for bounded homogeneous operators on X_B as defined in (1.5).

The definition of the spectral radius, (1.7), involves taking an infimum and upper semicontinuity of functions is preserved under taking infima (Lemma A.52). Thus, it is not surprising that upper semicontinuity of the spectral radius,

if (B_k) is any sequence of bounded homogeneous operators on X_B with $\|B_k - B\| \to 0$ as $k \to \infty$, then

$$\limsup_{k\to\infty} \mathbf{r}(B_k) \le \mathbf{r}(B),$$

can be proved under rather mild extra conditions (Theorem 7.1).

Conditions for lower semicontinuity,

if (B_k) is any sequence of bounded homogeneous operators on X_B with $\|B_k - B\| \to 0$ as $k \to \infty$, then

$$\liminf_{k\to\infty} \mathbf{r}(B_k) \ge \mathbf{r}(B),$$

are much harder to find (Chapter 10); actually lower semicontinuity may fail even if X_B is an additive homogeneous subset of the normed vector space X and the homogeneous B is compact, additive and continuous on X_B. See [**146**] and Section 10.4.

Instead of finding conditions for the lower semicontinuity of the spectral radius directly, we try to find them for the lower Collatz–Wielandt bound. The definition of the Collatz–Wielandt bound, (5.30), involves taking a supremum, an operation known to preserve lower semicontinuity of functions (Lemma A.53). Eventually, the upper semicontinuity of the spectral radius is combined with the lower semicontinuity of the lower CW bound, which requires some more conditions (see next section).

1.5. The spectral radius as (lower) eigenvalue

In Theorem 1.6, the link between the assumption $\mathbf{r}(B) > 1$ and the persistence statement is provided by $\mathbf{r}(B) =: \mathcal{T}_0$ to be an eigenvalue (or lower eigenvalue) of the homogeneous operator B associated with an eigenvector

$$v \in X_B, \quad \|v\| = 1, \quad B(v) = \mathcal{T}_0\, v,$$

(Chapter 9), or with a homogeneous eigenfunctional

$$\theta : X_B \to \mathbb{R}_+, \quad \theta(B(x)) = \mathcal{T}_0\, \theta(x), \quad x \in X_B,$$

(Chapter 11).

If $\theta : X_B \to \mathbb{R}_+$ is an eigenfunctional of B associated with $\mathcal{T}_0$, then, by induction,

$$\theta(B^n(x)) = \mathcal{T}_0^n \theta(x), \qquad x \in X_B.$$

Assume that $\theta(x) > 0$ is related to the size of a population with structural distribution $x \in X_B$ and that the basic turnover operator B were to coincide with the turnover operator F such that $\theta(B^n(x))$ were the population size after n years. Then the population would die out geometrically fast if $\mathcal{T}_0 < 1$ and would persist (in the form of geometric growth) if $\mathcal{T}_0 > 1$.

However, typically $B \neq F$, but these behaviors somewhat carry over to F (Section 1.3).

The existence of eigenvectors or homogeneous eigenfunctionals of B associated with $\mathcal{T}_0 = \mathbf{r}(B)$ occurs if B has sufficiently strong compactness properties (Section 9.1) or order boundedness properties ([**8**, **200**, **201**], Section 9.2, and Chapter 11) and/or the cone X_B has particular properties [**199**].

Some of the proofs rely on perturbation arguments similar to the ones used for bounded linear positive operators and on the monotonicity (Section 6.5) and the upper semicontinuity of the spectral radius (as a function of its operator) under reasonably general assumptions (Chapter 7).

As much as we can, we will avoid assuming that X_B is a complete subset of X (Definition A.27). The reason is that we want to consider population models in the cone $\mathcal{M}_+(S)$ of nonnegative measures with the flat norm, which is only complete if S is a complete metric space (see Section 1.3, ($\diamondsuit_3$) and Section 3.2.4). The flat norm is used to make the operator B compact (Sections 13.5 and A.1.8).

In turn, if there is an eigenvector of B associated with $\mathcal{T}_0 = \mathbf{r}(B)$, this helps to show that the spectral radius is also lower semicontinuous function of B by relating the spectral radius of B to the lower Collatz–Wielandt bound of B.

This is why the chapters on upper and lower semicontinuity (Chapters 7 and 10) of the spectral radius are separated by the chapter on eigenvectors (Chapter 9).

A tool that is very effective for the spectral analysis of bounded linear operators but works only partially for homogeneous operators are the resolvents which only work from one side (Chapter 8). This is enough to show that the spectral radius of an order-bounded homogeneous order-preserving operator is an eigenvalue associated with a positive bounded eigenfunctional (Chapter 11). However, this functional may not be continuous (Section 11.6).

1.6. Turnover versus reproduction number

While the basic turnover number $\mathcal{T}_0$, the spectral radius of the basic turnover operator B, is the threshold parameter between population extinction and persistence (Section 1.3), it may have little tangible biological interpretation except in special cases (Section 18.6). If $B = H + Q$ with bounded linear positive operators H and Q, $\mathbf{r}(Q) < 1$, the operator

$$H(\mathbb{I} - Q)^{-1} = H \sum_{n=0}^{\infty} Q^n \tag{1.10}$$

can be interpreted as *next generation operator* and its spectral radius, $\mathcal{R}_0$, as *basic reproduction number*. See Section 12.1. Under suitable assumptions (Section 12.2, [**50**, **150**], [**216**, Thm.5.1]), the basic turnover number $\mathcal{T}_0$ and the basic reproduction number $\mathcal{R}_0$ have the same threshold behavior: They are simultaneously strictly smaller than one, equal to one, or strictly larger than one. Typically, $\mathcal{R}_0$ has a more tangible biological interpretation than $\mathcal{T}_0$ and can sometimes be even explicitly expressed in terms of the model parameters [**12**, **50**, **128**, **150**]. Unfortunately, if H is an order-preserving continuous homogeneous operator, the relation between $\mathcal{T}_0$ and $\mathcal{R}_0$ seems to hold only under quite technical conditions [**207**]. An exception is the special case that H is a rank-one operator, $H(x) = \phi(x)u$, with u being a nonzero vector in cone and ϕ an order-preserving continuous homogeneous functional (Section 12.3, [**207**]). An application to a rank-structured population with mating can be found in Chapter 16.

1.7. Case studies in population dynamics

Theorems 1.5 and 1.6 are applied to a number of mathematical case studies. This includes the simplest possible discrete-time two-sex population model (Section 15.1) and a simple hybrid-time (periodically impulsive) population model with mating (Section 15.2).

As for structured populations, we first study a rank-structured population, with the state-space chosen as the sequence space ℓ^1_+ (Chapter 16). This is an example where we can derive a concrete basic reproduction number rather than the abstract basic turnover number as a threshold parameter to separate extinction from persistence (Chapter 12).

Later, we concentrate on spatial structure and consider a hybrid-time (periodically impulsive) model where females and males move by diffusion during the year and mate once a year during a very short mating season (Chapter 17). We also consider nonlocal spatial spread (where space can be interpreted in a very wide sense) for one-sex and two-sex populations (Chapters 18 and 19). Special consideration is given to the case where state transitions are modeled by Feller kernels (Section 13.3).

Let the structural characteristics of a population be represented by a metric space S. If the structure is given by spatial location, a point $s \in S$ is a location in the habitat S of the population. For a primer on metric spaces, see Appendix A.1.

Let $\mathcal{B}$ be the σ-algebra of Borel subsets of S (Section 3.2). A function $\kappa : \mathcal{B} \times S \to \mathbb{R}_+$ is called a *Feller kernel* if $\kappa(\cdot, s)$ is a finite measure on $\mathcal{B}$ for all $s \in S$ and $\int_S f(t)\kappa(dt, s)$ is a continuous function of $s \in S$ for all $f \in C^b(S)$, the space of bounded continuous real-valued functions on S. It follows that $\kappa(T, \cdot)$ is Borel measurable for each $T \in \mathcal{B}$.

If $\kappa(S, s) \in [0, 1]$ for all $s \in S$, the Feller kernel has the following forward interpretation:

$\kappa(T, s)$ is the probability that an individual that is at location $s \in S$ at the beginning at the year is alive and located in the Borel set T at the end of the year. The forward interpretation is associated with a linear positive map on the space of real-valued Borel measures on S, $\mathcal{M}(S)$,

$$(A\mu)(T) = \int_S \kappa(T, s)\mu(ds), \qquad \mu \in \mathcal{M}(S), \quad T \in \mathcal{B}. \tag{1.11}$$

If $\mathcal{M}(S)$ is equipped with the variation norm, A is a bounded linear map. If $\mathcal{M}(S)$ is equipped with the flat norm, A map not be bounded, but its restriction A_+ to the cone $\mathcal{M}_+(S)$ of nonnegative Borel measures is bounded. See Chapter 13.

By definition, a Feller kernel also induces a map A_* on $C^b(S)$, the Banach space of bounded continuous real-valued functions on S, with the supremum norm,

$$(A_*f)(s) = \int_S f(t)\kappa(dt, s), \qquad f \in C^b(S), \quad s \in S. \tag{1.12}$$

The operators A and A_* are dual to each other,

$$\int_S f\, d(A\mu) = \int_S (A_*f)\, d\mu, \qquad f \in C^b(S), \quad \mu \in \mathcal{M}(S). \tag{1.13}$$

A and A_* have the same spectral radius $\mathcal{T}_0$ which we define to be the spectral radius of the Feller kernel κ, $\mathcal{T}_0 = \mathbf{r}(\kappa)$.

A_* is a bounded linear operator on $C^b(S)$ that maps $C^b_+(S)$ into itself, the closed cone of nonnegative bounded continuous functions. A_* can be extended to a bounded linear operator on $M^b(S)$, the Banach space of bounded measurable functions. This makes it possible to use Feller kernels to formulate density models for two-sex population models (Chapter 18) on $C^b_+(S)$ or $M^b_+(S)$. The basic turnover operator takes the form

$$(B\chi_T)(s) = \varphi\big(s, \kappa_1(T, s), \kappa_2(T, s)\big), \qquad s \in S, \quad T \in \mathcal{B}. \tag{1.14}$$

Here χ_T is the characteristic (indicator) function of the Borel subset T of S, $\chi_T(s) = 1$ if $s \in T$, and $\chi_T(s) = 0$ if $s \in S \setminus T$. For each $s \in S$, $\varphi(s, f, m)$ is the amount of offspring produced at location s by f females and m males ignoring competition for resources but not competition for mates. Cf. ($\diamondsuit_2$) in Section 1.3. As for dispersal, $\kappa_j(T, s)$ describes how females ($j = 1$), and males ($j = 2$) move from the set T to the point s. The expression in (1.14) relates the number of neonates (newborn individuals) at location s in the present year to the number of neonates in the set T in the previous year (again by ignoring competition or cooperation in using resources).

The class of these models intersects with integro-difference equations [**116**, **125**, **134**, **135**, **148**, **151**, **152**, **162**, **165**, **171**, **192**, **221**] and integral projection models [**74**, **78**, **79**, **89**]. To reduce the technicality of the presentation, only semelparous populations are considered, where individuals reproduce only once in their lifetime and, as far as population persistence goes, only uniform weak persistence is established (for uniform persistence see [**205**]). Unisex models for iteroparous populations, in which individuals reproduce several times during their lifespan, are considered in [**206**] where also uniform persistence is established. Differently from the state space $\mathcal{M}_+(S)$, the Feller kernel has no good biological interpretation for $C^b_+(S)$ but is still a handy mathematical tool. See Section 18.1.1.

It seems quite cumbersome to formulate two-sex population models on $\mathcal{M}_+(S)$ that can be analyzed by the methods developed in this monograph (see [**101**, Sec.6.4] and Section 19.5 for attempts); so mainly unisex population models are considered on the cone $\mathcal{M}_+(S)$ of the ordered vector space $\mathcal{M}(S)$ which will be endowed with either the variation norm or the flat norm (See ($\diamondsuit_3$) in Section 1.3 and Chapter 19). The models cover both semelparous and iteroparous populations, and both uniform weak and uniform persistence are established. A more general model framework is considered in [**204**].

For continuous-time population models on the space of measures we refer to [**72**] and the references therein. Following Section 1.5, we will look for and use an eigenfunction $f \in \dot{C}_+^b(S)$ and an eigenmeasure $\mu \in \dot{\mathcal{M}}_+(S)$ of the kernel κ, i.e., eigenvectors of A_* and A, respectively,

$$\mathcal{T}_0\, f(s) = \int_S f(t)\kappa(dt, s), \qquad s \in S,$$
$$\mathcal{T}_0\; \mu(T) = \int_S \kappa(T, s)\mu(ds), \qquad T \in \mathcal{B}.$$

1.8. Other aspects of population dynamics

In this monograph, we investigate the extinction and persistence of populations (in discrete-time models), but we do not explore the many ways in which the populations persist in the framework of discrete-time models (recursive equations): at stable equilibrium, in stable periodic or quasiperiodic oscillations or even chaotically, in competition or cooperation with other populations, or in adaptive evolution. See [**6, 7**] [**42**] – [**49**] [**53**] [**54**] [**58**] [**64**] [**65**] [**66**] [**67**] [**103**] [**104**] [**138**] [**160**] for a small sample of references. Other models do not only study the persistence of a population but also the persistence of a disease that afflicts it [**12, 80, 155, 176**]. We also do not investigate the effects of forcing [**89**].

Of course, there are many population models formulated in continuous time, some of them with homogeneous nonlinearities. For homogeneous differential equations, see [**35, 83, 84, 107–109, 115, 117, 120**] for time-autonomous and [**106, 219**] for periodically forced differential equations; see [**219**] (and the references therein) for periodically forced homogeneous partial differential equations. For continuous-time population models using the cone of nonnegative measures, see [**72**] and the references therein.

CHAPTER 14

Nonlinear dynamics

In this central chapter, the theory of homogeneous operators is connected to the question of extinction/persistence of structured populations in general discrete-time models. See Section 1.1.

14.1. Homogeneous maps as derivatives

Let us recall the following mathematical motivation to consider homogeneous operators (Section 1.1).

Let X and Y be normed vector spaces, X_F be a homogeneous subset of X and $F : X_F \to Y$, $F(0) = 0$. Let X_B be the set of those $x \in X_F$ such that the directional derivative at 0 in the direction of x exists,

$$\lim_{0<b\to 0} \frac{1}{b} F(bx) = \partial F(0, x) =: B(x). \tag{14.1}$$

Since $0 \in X_F$ and $F(0) = 0$, $0 \in X_B$ and $B(0) = 0$. If $X_B = X_F$, $\partial F(0, \cdot)$ is called the *Gateaux derivative* of F at 0.

THEOREM 14.1. *$X_B \subseteq X_F$ is a homogeneous subset of X and the operator $B : X_B \to Y$ is (positively)* homogeneous *(of degree one).*

PROOF. Let $x \in X_B$. Let $\alpha \in \mathbb{R}_+$. Obviously, if $\alpha = 0$, $\alpha x = 0 \in X_B$ and $B(\alpha x) = 0 = \alpha B(x)$.

So we assume $\alpha \in (0, \infty)$. Then

$$\frac{F(t[\alpha x])}{t} = \alpha \frac{F([t\alpha]x)}{t\alpha}, \qquad t \in (0, \infty).$$

As $t \to 0$, also $\alpha t \to 0$. Since $x \in X_B$, the directional derivative in direction αx exists and equals $\alpha \partial F(0, x)$. So $\alpha x \in X_B$ and

$$\partial F(0, \alpha x) = \alpha \partial F(0, x).$$ □

In turn, we want to explore in what sense homogeneous operators can serve as derivatives. Cf. [**130**].

14.2. (Lower and upper) order derivatives

Let X_+ be the closed order cone of an ordered normed vector space X.

A homogeneous $B : X_+ \to X_+$ is called an *order-derivative* of $F : X_+ \to X_+$ at $0 = F(0)$ if for any $\epsilon \in (0, 1)$ there is some $\delta > 0$ such that

$$(1 - \epsilon)B(x) \le F(x) \le (1 + \epsilon)B(x), \qquad x \in X_+, \quad \|x\| \le \delta. \tag{14.2}$$

A homogeneous $B : X_+ \to X_+$ is called a *lower order-derivative* of $F : X_+ \to X_+$ at $0 = F(0)$ if one part of (14.2) holds:

$$\text{For any } \epsilon \in (0,1) \text{ there is some } \delta > 0 \text{ such that} \\ F(x) \geq (1-\epsilon)B(x) \text{ for all } x \in X_+ \text{ with } \|x\| \leq \delta. \tag{14.3}$$

B is called an *upper order-derivative* of F at 0 if the other part of (14.2) holds:

$$\text{For any } \epsilon \in (0,1) \text{ there is some } \delta > 0 \text{ such that} \\ F(x) \leq (1+\epsilon)B(x) \text{ for all } x \in X_+ \text{ with } \|x\| \leq \delta. \tag{14.4}$$

PROPOSITION 14.2. *Let $F : X_+ \to X_+$, $F(0) = 0$, and let $B_1 : X_+ \to X_+$ be a lower order-derivative and $B_2 : X_+ \to X_+$ an upper order-derivative of F at 0. Then $B_1(x) \leq B_2(x)$ for all $x \in X_+$.*

PROOF. Let $\epsilon \in (0,1)$. Then there exist some $\delta > 0$ such that

$$(1-\epsilon)B_1(y) \leq F(y) \leq (1+\epsilon)B_2(y), \qquad y \in X_+, \quad \|y\| \leq \delta.$$

Let $x \in X_+$. Then there exists some $t > 0$ such that $\|tx\| < \delta$ and

$$(1-\epsilon)B_1(tx) \leq (1+\epsilon)B_2(tx).$$

Since B_1 and B_2 are homogeneous,

$$(1-\epsilon)B_1(x) \leq (1+\epsilon)B_2(x).$$

Since $\epsilon \in (0,1)$ has been arbitrary and X_+ is closed, $B_1(x) \leq B_2(x)$. □

COROLLARY 14.3. *Let $F : X_+ \to X_+$, $F(0) = 0$, and $B : X_+ \to X_+$ be an order-derivative of F at 0. Then B is uniquely determined.*

Chain rules hold for upper and lower order-derivatives under some extra assumptions.

PROPOSITION 14.4. *Let $F_i : X_+ \to X_+$ and $F_i(0) = 0$, $j = 1,2$. Let B_1 be a lower order-derivative of F_1 at 0 and B_2 be a lower order-derivative of F_2 at 0. Assume that F_1 is continuous at 0 and B_2 is order-preserving. Then $B_2 \circ B_1$ is a lower order-derivative of $F_2 \circ F_1$ at 0.*

PROOF. Let $\tilde{\epsilon} \in (0,1)$. Choose some $\epsilon \in (0,1)$ such that

$$(1-\epsilon)^2 \geq 1 - \tilde{\epsilon}. \tag{14.5}$$

Then there exist $\delta_i > 0$ such that

$$F_i(x) \geq (1-\epsilon)B_i(x), \qquad x \in X_+, \quad \|x\| \leq \delta_i, \quad i = 1,2. \tag{14.6}$$

Since F_1 is continuous at 0 and $F_1(0) = 0$, we can arrange that

$$\|F_1(x)\| \leq \delta_2, \qquad x \in X_+, \quad \|x\| \leq \delta_1 \tag{14.7}$$

(by making δ_1 smaller).

Let $x \in X_+$, $\|x\| \leq \delta_1$. By (14.6) and (14.7),

$$F_2(F_1(x)) \geq (1-\epsilon)B_2(F_1(x)).$$

Since B_2 is order-preserving and homogeneous, by (14.6) and (14.5),

$$\begin{aligned}(F_2 \circ F_1)(x) &\geq (1-\epsilon)B_2\big((1-\epsilon)B_1(x)\big) \\ &= (1-\epsilon)^2 B_2(B_1(x)) \geq (1-\tilde{\epsilon})(B_2 \circ B_1)(x).\end{aligned}$$ □

REMARK 14.5. An analogous chain rule holds for upper order-derivatives.

LEMMA 14.6. *Let $F : X_+ \to X_+$ and $B : X_+ \to X_+$ be the order-derivative of F at $0 = F(0)$. Assume that X_+ is normal and B is bounded. Then*

$$\frac{\|F(x) - B(x)\|}{\|x\|} \to 0, \qquad \dot{X}_+ \ni x \to 0.$$

This means that B is kind of a Frechet derivative of F at 0, with the exception that it is not linear.

PROOF. Let $\epsilon > 0$. Choose $\delta > 0$ according to the definition of an order-derivative, (14.2). Let $x \in X_+$ and $\|x\| \le \delta$. Then

$$-\epsilon B(x) \le F(x) - B(x) \le \epsilon B(x).$$

Since X_+ is normal and B is homogeneous and bounded, by Corollary 2.52, there exists some $c > 0$ such that, for all $x \in X_+$, $\|x\| \le \delta$,

$$\|F(x) - B(x)\| \le c\|\epsilon B(x)\| \le c\epsilon \|B\|\|x\|.$$

This implies the assertion. □

A similar proof shows the following result.

LEMMA 14.7. *Let $F : X_+ \to X_+$ and $B : X_+ \to X_+$ be the order-derivative of F at $0 = F(0)$. Assume that X_+ is normal. Then*

$$B(x) = \lim_{t \to 0+} \frac{1}{t} F(tx), \qquad x \in X_+$$

This means that B is the Gateaux derivative of F at 0.

REMARK 14.8. If B is the order-derivative of F at $0 = F(0)$ and B is not additive on X_+, then F is not Frechet-differentiable at 0. The Frechet-derivative at 0, by definition, would be linear on X and equal the nonadditive Gateaux-derivative B on X_+.

14.3. Partial stability and persistence results

Let X be an ordered normed vector space with closed order cone X_+. Recall the definition of a normal point in Section 2.2.2 and the notation $\dot{X}_+ = X_+ \setminus \{0\}$.

14.3.1. A conditional stability and extinction result. Our first result gives conditions for the extinction of a population that has come too close to the extinction state in a specific order sense.

THEOREM 14.9. *Let X_+ be the closed cone of an ordered normed vector space. Let $F, B : X_+ \to X_+$ and let B be homogeneous and order-preserving.*

Let $v \in \dot{X}_+$ and $r \in (0, 1)$ such that $B(v) \le rv$.

Assume that B is an upper order-derivative of F at 0 in a v-modified way: For any $\eta > 0$, there exists some $\tilde{\delta} > 0$ such that

$$F(x) \le (1 + \eta)B(x) \qquad x \in X_+, \quad x \le \tilde{\delta} v. \tag{14.8}$$

Then, for each $\alpha \in (r, 1)$, there exists some $\delta_\alpha > 0$ such that the following holds for all $x \in X_+$ with $x \le \delta_\alpha v$:

(a) *$F^n(x) \le \alpha^n \delta_\alpha v$ for all $n \in \mathbb{N}$.*
(b) *$\|F^n(x)\| \le c_v \alpha^n \delta_\alpha \to 0$ as $n \to \infty$, for some $c_v \ge 1$ independent of n, if v is a normal point for X_+.*

(c) $\|F^n(x)\| \leq \alpha^n \delta_\alpha \|v\| \to 0$ *as* $n \to \infty$ *provided that the norm is order-preserving on* X_+.

In particular, the semiflow induced by F *is not uniformly weakly persistent (in the sense of Theorem* 1.6*).*

PROOF. Let $v \in \dot{X}_+$ and $r \in (0,1)$ such that $B(v) \leq rv$. Let $\alpha \in (r,1)$.

Choose $\eta > 0$ such that $(1+\eta)r = \alpha < 1$. Choose $\delta = \delta_\alpha > 0$ such that (14.8) holds.

Let $x \in X_+$, $x \leq \delta_\alpha v$.

By induction,

$$F^n(x) \leq \alpha^n \delta_\alpha v, \qquad n \in \mathbb{Z}_+. \tag{14.9}$$

Indeed, interpreting $F^0(x) = x$, this holds for $n = 0$. Assume that $n \in \mathbb{Z}_+$ and (14.9) holds for n.

Since $\alpha \leq 1$, by (14.8),

$$F^{n+1}(x) = F(F^n(x)) \leq (1+\eta)B(F^n(x)).$$

Since B is order-preserving,

$$F^{n+1}(x) \leq (1+\eta)B(\alpha^n \delta_\alpha v).$$

Since B is homogeneous, $\alpha \in (r,1)$ and $Bv \leq rv$,

$$F^{n+1}(x) \leq (1+\eta)\alpha^n \delta_\alpha B(v) \leq (1+\eta)\alpha^n \delta_\alpha rv \leq \alpha^{n+1}\delta_\alpha v.$$

By the induction principle, (14.9) holds and part (a) has been proved.

Part (b) and (c) follow from (a). □

We obtain the following result as a corollary.

THEOREM 14.10 ([**205**, Thm.4.1]). *Let* X_+ *be the closed cone of an ordered normed vector space. Let* $F, B : X_+ \to X_+$ *and let* B *be homogeneous and order-preserving.*

Assume that B *is an upper order-derivative of* F *at 0,* (14.4).

Let $v \in \dot{X}_+$ *be a normal point for* X_+ *and* $r \in (0,1)$ *such that* $B(v) \leq rv$.

Then, for each $\alpha \in (r,1)$*, there exists some* $\delta_\alpha > 0$ *such that the following holds for all* $x \in X_+$ *with* $x \leq \delta_\alpha v$:

(a) $F^n(x) \leq \alpha^n \delta_\alpha v$ *for all* $n \in \mathbb{N}$.

(b) $\|F^n(x)\| \leq c_v \alpha^n \delta_\alpha \to 0$ *as* $n \to \infty$*, for some* $c_v \geq 1$ *independent of* n.

(c) $\|F^n(x)\| \leq \alpha^n \delta_\alpha \|v\| \to 0$ *as* $n \to \infty$ *provided that the norm is order-preserving on* X_+.

In particular, the semiflow induced by F *is not uniformly weakly persistent (in the sense of Theorem* 1.6*).*

PROOF. Let v be a normal point for X_+ (Section 2.2.2). Then there exists some $c \geq 1$ such that $\|x\| \leq c$ for all $x \in X_+$ with $x \leq v$. Let B be an upper order-derivative of F at 0. Let $\epsilon > 0$. Then there exists some $\delta > 0$ such that

$$F(x) \leq (1+\epsilon)B(x), \qquad x \in X_+, \quad \|x\| \leq \delta.$$

Let $\tilde{\delta} = \delta/c$. Let $0 \leq x \leq \tilde{\delta} v$. Then $\|x\| \leq \tilde{\delta} c = \delta$ and $F(x) \leq (1+\epsilon)B(x)$.

This shows that B is an upper order-derivative of F in the sense of (14.8), and the assertion follows from Theorem 14.9. □

14.3.2. A conditional instability result. The second class of results gives conditions under which populations that are close to extinction can avoid extinction for at least for some time though it is not excluded that extinction finally occurs. These results can also been found in [**203**, Sec.8.1] but their presentation has been thoroughly edited in order to fit the larger framework of this book.

THEOREM 14.11. *Let $F, B : X_+ \to X_+$ and let B be homogeneous and order-preserving and a lower order-derivative of F at 0 as in* (14.3).

Let $r > 1$ and $\theta : X_+ \to \mathbb{R}_+$ be a homogeneous bounded order-preserving functional with

$$\theta(B(x)) \geq r\theta(x), \qquad x \in X_+. \tag{14.10}$$

Then there exists some $\delta_0 > 0$ such that

$$\sup_{n \in \mathbb{Z}_+} \|F^n(x)\| \geq \delta_0, \qquad x \in X_+, \quad \theta(x) > 0.$$

In particular, 0 is an unstable equilibrium of F.

PROOF. Choose some $\epsilon \in (0,1)$ such that $1 < (1-\epsilon)r =: s$. Since B is the lower order-derivative of F at 0, we can choose some $\delta > 0$ such that

$$F(x) \geq (1-\epsilon)B(x), \qquad x \in X_+, \quad \|x\| \leq \delta.$$

Suppose that the statement of the theorem is false. By contraposition, there exists some $x \in X_+$ such that

$$\theta(x) > 0, \qquad \sup_{n \in \mathbb{Z}_+} \|F^n(x)\| < \delta. \tag{14.11}$$

Since θ is bounded, this implies that $(\theta(F^n(x)))$ is a bounded sequence.

We will show by induction that

$$\theta(F^n(x)) \geq s^n \theta(x), \quad n \in \mathbb{Z}_+, \tag{14.12}$$

which is a contradiction because $s > 1$.

Statement (14.12) holds for $n = 0$. Let $n \in \mathbb{Z}_+$ and (14.12) hold for n. Since $\|F^n(x)\| \leq \delta$ by (14.11),

$$F^{n+1}(x) = F(F^n(x)) \geq (1-\epsilon)B(F^n(x)).$$

Since B and θ are order-preserving and homogeneous and θ satisfies (14.10),

$$\begin{aligned}\theta(F^{n+1}(x)) \geq& (1-\epsilon)\theta(B(F^n(x))) \geq (1-\epsilon)r\theta(F^n(x)) \\ \geq& s s^n \theta(x) = s^{n+1}\theta(x).\end{aligned}$$

□

Recall that, if $x, v \in X_+$, x is called v-positive provided that $x \geq \delta v$ for some $\delta > 0$. See Section 4.4.

COROLLARY 14.12. *Let $F, B : X_+ \to X_+$ and let B be an order-preserving lower order-derivative of F at 0. Let $r > 1$ and $v \in \dot{X}_+$ such that $B(v) \geq rv$.*

Then there exists some $\delta_0 > 0$ such that

$$\sup_{n \in \mathbb{Z}_+} \|F^n(x)\| \geq \delta_0$$

for all v-positive $x \in X_+$.

PROOF. We apply Theorem 14.11 with $\theta(x) = [x]_v$, $x \in X_+$. See Section 4.4. Notice that $\theta(x) > 0$ if and only if x is v-positive and use Remark 11.13. □

14.4. Local asymptotic stability of the extinction state in the subthreshold case

We establish one half of the threshold property of the basic turnover number $\mathcal{T}_0$ which is the spectral radius of the basic turnover operator, B, a homogeneous first order approximation of the turnover operator, F. See Sections 1.1 and 1.2. In the subthreshold case $\mathcal{T}_0 < 1$, populations the size of which falls under a certain level go extinct geometrically fast.

THEOREM 14.13. *Let X_+ be the normal closed cone of an ordered normed vector space. Let $F, B : X_+ \to X_+$ and let B be homogeneous, bounded and order-preserving, $\mathcal{T}_0 = \mathbf{r}(B) < 1$, and let B an upper order-derivative of F at 0,* (14.4).

Then F is locally asymptotically stable in the following sense:

For each $\alpha \in (\mathcal{T}_0, 1)$, 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 $\|x\| \leq \delta_0$.

The proof only relies on the definition of the spectral radius of the basic turnover operator B; existence of associated eigenvectors or eigenfunctionals is not needed.

PROOF. Since X_+ is normal, we can replace the original norm by an equivalent monotone norm (like the monotone companion norm, see Theorem 2.48). This does not affect $\mathcal{T}_0 = \mathbf{r}(B)$ given by (5.1).

Let $\alpha \in (\mathcal{T}_0, 1)$ Choose some s such that $\mathcal{T}_0 < s < \alpha$.

Then there exists some $m \in \mathbb{N}$ such that

$$\|B^n\| < s^n, \qquad n \in \mathbb{N}, \quad n \geq m. \tag{14.13}$$

Further there exists some $c \geq 1$ such that

$$\|B^n\| \leq c, \qquad n = 1, \dots, m. \tag{14.14}$$

Choose $\eta > 0$ such that

$$\alpha = (1+\eta)s \tag{14.15}$$

and then, by (14.4), choose $\delta > 0$ such that $F(x) \leq (1+\eta)B(x)$ for all $x \in X_+$ with $\|x\| \leq \delta$. (Since we switched to an equivalent norm, the δ may not be the same as in the assumption of the theorem.) Choose $\delta_0 \in (0, \delta)$ such that

$$(1+\eta)^m c\delta_0 \leq \delta. \tag{14.16}$$

Let $x \in X_+$ and $\|x\| \leq \delta_0$. Then $F(x) \leq (1+\eta)B(x)$. Since the norm is monotone, by (4.2), (14.14), and (14.16),

$$\|F(x)\| \leq (1+\eta)\|B\| \, \|x\| \leq (1+\eta)c\delta_0 \leq \delta.$$

Since B is order-preserving and homogeneous,

$$F^2(x) \leq (1+\eta)B(F(x)) \leq (1+\eta)^2 B^2(x).$$

Since the norm is monotone, by (4.2), (14.14), and (14.16),

$$\|F^2(x)\| \leq (1+\eta)^2 \|B^2\| \|x\| \leq (1+\eta)^2 c\delta_0 \leq \delta.$$

Proceeding this way we obtain that

$$F^n(x) \leq (1+\eta)^n B^n(x), \qquad n = 1, \dots, m,$$

and

$$\|F^n(x)\| \leq (1+\eta)^n c\|x\| \leq (1+\eta)^n c\delta_0 \leq \delta, \qquad n = 1, \dots, m. \tag{14.17}$$

For $n = m + 1$,

$$F^n(x) \le (1+\eta)B(F^m(x)) \le (1+\eta)^n B^n(x).$$

Since the norm is monotone,

$$\|F^n(x)\| \le (1+\eta)^n \|B^n\| \|x\| \le (1+\eta)^n s^n \|x\| = \alpha^n \|x\| < \delta.$$

Now, by induction,

$$F^n(x) \le (1+\eta)^n B^n(x), \qquad n \ge m.$$

By (14.15) and (14.13),

$$\|F^n(x)\| \le \alpha^n \|x\|, \qquad n \ge m.$$

We combine this estimate with the one in (14.17) using (14.15) again and obtain the assertion. ☐

14.5. Local stability of the extinction state in the threshold case

In the threshold case $\mathcal{T}_0 = \mathbf{r}(B) = 1$, under appropriate assumptions (see Chapter 9), there exists some $u \in \dot{X}_+ = X_+ \setminus \{0\}$ such that $B(u) \le u$.

THEOREM 14.14. *Let X_+ be the normal closed cone of an ordered normed vector space X. Let $F, B : X_+ \to X_+$ and let B be homogeneous, bounded and order-preserving and $F(x) \le B(x)$ for all $x \in X_+$. Let $u \in \dot{X}_+$ such that $B(u) \le u$ and a power of B is uniformly u-bounded (Definition* 6.1*).*

Then there exists some $c > 0$ such that $\|F^n(x)\| \le c\|x\|$ for all $x \in X_+$ and $n \in \mathbb{N}$.

Instead of assuming that X_+ is normal, it is sufficient that u is a normal point for X_+. See Section 2.2.2. As it is well-known, $\mathbf{r}(B) = 1$ is not sufficient for this result even if B can be represented by a matrix.

PROOF. Since B is order-preserving, by induction, $F^n(x) \le B^n(x)$ for all $x \in X_+$. Since some power of B is uniformly u-bounded, there is some $m \in \mathbb{N}$ and $\tilde{c} > 0$ such that $B^m(x) \le \tilde{c}\|x\|u$ for all $x \in X_+$. Since B is order-preserving and homogeneous, for all $n \in \mathbb{Z}_+$,

$$F^{n+m}(x) \le B^n(B^m(x)) \le \tilde{c}\|x\|B^n(u) \le \tilde{c}\|x\|u, \qquad x \in X_+.$$

Since X_+ is normal (or u is a normal point for X_+), there exists some $\check{c} > 0$ such that

$$\|F^{n+m}(x)\| \le \check{c}\tilde{c}\|x\| \, \|u\|, \qquad n \in \mathbb{Z}_+, \quad x \in X_+.$$

For $n = 1, \dots, m$, $F^n(x) \le B^n(x)$ and

$$\|F^n(x)\| \le \check{c}\|B^n(x)\| \le \check{c}\|B^n\| \, \|x\|.$$ ☐

14.6. Point-dissipativity and compact attractors

For many aspects of nonlinear dynamics, it is useful if the semiflow induced by F (or otherwise) has a compact attractor of points [**187**, Sec.2.2].

$F : X_+ \to X_+$ is called *point dissipative* if there exists a bounded subset B of X such that $d(F^n(x), B) \to 0$ as $n \to \infty$ for all $x \in X_+$. Here, $d(y, B)$ denotes the distance from y to B in X.

Since X is a normed vector space, equivalently, F is point-dissipative if there exists some constant $c > 0$ such that

$$\limsup_{n\to\infty} \|F^n(x)\| \leq c, \qquad x \in X_+.$$

F is said to be *asymptotically smooth* if for every closed, bounded subset U of X_+ with $F(U) \subseteq U$ and for every sequence (n_i) in $\mathbb{Z}_+$, $n_i \to \infty$ as $i \to \infty$, and every sequence (u_i) in U, $(F^{n_i}(u_i))$ has a convergent subsequence.

Recall that a homogeneous functional $\theta : X_B \to \mathbb{R}_+$ on a homogeneous subset X_B of X is called *uniformly positive* if there exists some $\epsilon > 0$ such that $\theta(x) \geq \epsilon\|x\|$ for all $x \in X_B$. See Definition 5.37.

THEOREM 14.15. *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. Assume that*

$$\limsup_{\|x\|\to\infty} \frac{\theta(F(x))}{\theta(x)} < 1. \tag{14.18}$$

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 $\hat{B}$ of X_+ which absorbs all points in X_+: For each $x \in X_+$ there exists some $m \in \mathbb{N}$ such that $F^n(x) \in \hat{B}$ for all $n \geq m$. In particular, F is point-dissipative.

If, in addition, F is continuous and asymptotically smooth, the semiflow induced by F has a compact attractor of bounded sets [**187**, Sec.2.2.3].

PROOF. By (14.18) and the other properties of θ, there exists some $\xi \in (0, 1)$ and $R_1 > 0$ such that

$$\theta(F(x)) \leq \xi\theta(x), \qquad x \in X_+, \quad \theta(x) \geq R_1. \tag{14.19}$$

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

$$\theta(x) \leq R_2 \implies \theta(F(x)) \leq R_2. \tag{14.20}$$

If not, for any $n \in \mathbb{N}$, there exists some $x_n \in X_+$ such that

$$\theta(x_n) \leq n < \theta(F(x_n)). \tag{14.21}$$

Since F maps bounded sets in X_+ into bounded sets of X_+ and θ is bounded and uniformly positive, $\theta(x_n) \to \infty$ as $n \to \infty$. By (14.19) and (14.21), this leads to a contradiction for n large enough such that $\theta(x_n) \geq R_1$:

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

So (14.20) holds. Let $R_3 = \max\{R_1, R_2\}$. Let $R \geq R_3$ and $B_R^+ = \{x \in X_+; \theta(x) \leq R\}$. Since θ is convex and continuous, B_R^+ is convex and closed. Since θ is uniformly positive, B_R^+ is bounded. By (14.20), $F(B_R^+) \subseteq B_R^+$.

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 $\|x\| \leq R_3$, $\theta(F^n(x)) \leq R_3$ for all $n \in \mathbb{N}$.

If $\theta(x) > R_3$, by (14.19), $\theta(F^{n+1}(x)) \leq \xi\theta(F^n(x))$ as long as $\theta(F^n(x)) \geq R_3$. So $\theta(F^m(x)) \leq R_3$ for some $m = m_x \in \mathbb{N}$ and $\theta(F^n(x)) \leq R_3$ for all $n \geq m_x$.

In either case, $\limsup_{n\to\infty} \theta(F^n(x)) \leq R_3$.

Set $\hat{B} = B_{R_3}$ and $F^n(x) \in \hat{B}$ for all $n \geq m_x$.
Since θ is uniformly positive, there exists some $c > 0$ such that

$$\limsup_{n\to\infty} \|F^n(x)\| \leq c \qquad x \in X_+. \qquad \square$$

14.6.1. Normal cones.

THEOREM 14.16. *Let X_+ be the normal closed cone of an ordered normed vector space X. Let $F : X_+ \to X_+$ satisfy*

$$F(x) \leq Ax + G(x), \qquad x \in X_+, \tag{14.22}$$

with a continuous, subadditive, homogeneous map $A : X_+ \to X_+$ and continuous $G : X_+ \to X_+$ such that

$$\mathbf{r}(A) < 1, \qquad \frac{\|G(x)\|}{\|x\|} \to 0, \quad \|x\| \to \infty. \tag{14.23}$$

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, in addition, F is asymptotically smooth, the semiflow induced by F has a compact attractor of bounded sets [**187**, Sec.2.2.3].

This theorem follows by combining Theorem 14.15 with the subsequent result.

LEMMA 14.17. *Let X_+ be the normal closed cone of an ordered normed vector space X. Let $F : X_+ \to X_+$ satisfy*

$$F(x) \leq Ax + G(x), \qquad x \in X_+, \tag{14.24}$$

with a continuous, subadditive, homogeneous map $A : X_+ \to X_+$ and continuous $G : X_+ \to X_+$ such that

$$\mathbf{r}(A) < 1, \qquad \frac{\|G(x)\|}{\|x\|} \to 0, \quad \|x\| \to \infty. \tag{14.25}$$

Then there is some homogeneous, continuous, subadditive, uniformly positive, order-preserving functional $\theta : X_+ \to \mathbb{R}_+$ such that

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

PROOF. By Theorem 5.19, since X_+ is normal, there is some homogeneous, continuous, subadditive, order-preserving $\theta : X_+ \to X_+$ and some $r \in (\mathbf{r}(A), 1)$, $c > 0$ such that $\theta(Ax) \leq r\theta(x)$ and $\|x\| \leq \theta(x) \leq c\|x\|$ for all $x \in X_+$. By (14.25), $\theta(G(x))/\theta(x) \to 0$ as $\|x\| \to \infty$. Since θ is order-preserving and subadditive,

$$\frac{\theta(F(x))}{\theta(x)} \leq \frac{\theta(Ax + G(x))}{\theta(x)} \leq \frac{\theta(Ax)}{\theta(x)} + \frac{\theta(G(x))}{\theta(x)}.$$

So

$$\limsup_{\|x\|\to\infty} \frac{\theta(F(x))}{\theta(x)} \leq r < 1. \qquad \square$$

14.6.2. Variation of constants formula. Since some problems are better studied in ordered Banach spaces X with nonnormal cones X_+ [**167**], we add a point-dissipativity result [**128**, Thm.2.3] in which normality of the cone is replaced by G mapping bounded sets into bounded sets. More severely, we assume the equality $F(x) = Ax + G(x)$, $x \in X_+$, rather than an inequality (Theorem 14.16). By induction and the additivity of A, the sequence of iterates $(x_n = F(x_{n-1}))$ of $x_0 \in X_+$ satisfies

$$x_n = A^n x_0 + \sum_{k=1}^{n} A^{k-1} G(x_{n-k}), \qquad n \in \mathbb{N}. \tag{14.26}$$

THEOREM 14.18. *Let $F = A + G$ on X_+ with a bounded additive homogeneous operator A on X_+, $\mathbf{r}(A) < 1$. Assume that $G : X_+ \to X_+$ maps bounded subsets of X_+ into bounded subsets of X_+ and*

$$\frac{\|G(x)\|}{\|x\|} \to 0, \qquad \|x\| \to \infty. \tag{14.27}$$

Then the semiflow induced by F is point-dissipative and is bounded on bounded sets.

PROOF. By (14.26) and the triangle inequality,

$$\|x_n\| \le \|A^n\| \, \|x_0\| + \sum_{k=1}^{n} \|A^{k-1}\| \, \|G(x_{n-k})\|, \qquad n \in \mathbb{N}.$$

Let $\epsilon > 0$, to be chosen later. Since G maps bounded sets into bounded sets, by (14.27), there exists some $c_\epsilon > 0$ such that

$$\|G(x)\| \le c_\epsilon + \epsilon \|x\|, \qquad x \in X_+.$$

We substitute this inequality into the previous one,

$$\|x_n\| \le \|A^n\| \, \|x_0\| + \sum_{k=1}^{n} \|A^{k-1}\| \, c_\epsilon + \sum_{k=1}^{n} \|A^{k-1}\| \, \epsilon \, \|x_{n-k}\|, \qquad n \in \mathbb{N}. \tag{14.28}$$

For $m \in \mathbb{N}$, we define

$$\alpha_m = \sup_{n=0}^{m} \|x_n\|.$$

Since $\mathbf{r}(A) < 1$,

$$\sum_{k=1}^{\infty} \|A^{k-1}\| =: \zeta \tag{14.29}$$

converges. For all $m \in \mathbb{N}$, by (14.28),

$$\alpha_m \le \max_{n=0}^{m} \|A^n\| \, \|x_0\| + \zeta \, c_\epsilon + \epsilon \zeta \alpha_m.$$

Choose $\epsilon > 0$ such that

$$\epsilon \zeta \le 1/2. \tag{14.30}$$

Then, for all $m \in \mathbb{N}$,

$$\|x_m\| \le \alpha_m \le 2 \sup_{n=0}^{\infty} \|A^n\| \, \|x_0\| + 2\zeta \, c_\epsilon.$$

This shows that the semiflow induced by F is bounded on bounded sets.

We apply Fatou's lemma to (14.28) with the counting measure on ℕ. Then, for $\alpha^\infty = \limsup_{n\to\infty} \|x_n\|$,

$$\alpha^\infty \le \sum_{k=1}^\infty \|A^{k-1}\|(c_\epsilon + \epsilon\alpha^\infty).$$

We choose $\epsilon > 0$ as in (14.30),

$$\alpha^\infty \le 2\zeta\|c_\epsilon.$$

This shows that the semiflow induced by F is point-dissipative. □

14.6.3. Asymptotic smoothness. The previous results motivate us to look for conditions that make the semiflow induced by F asymptotically smooth.

THEOREM 14.19. *Let X_+ be the closed cone of an ordered Banach space X and $F : X_+ \to X_+$ and $F = A + G$ with a bounded linear positive map A on X, $\mathbf{r}(A) < 1$, and a compact continuous map $G : X_+ \to X_+$. Then the semiflow induced by F is asymptotically smooth.*

The semiflow has a compact attractor of bounded sets if, in addition,

$$\|G(x)\|/\|x\| \to 0 \text{ as } \|x\| \to \infty$$

and if X_+ is normal or G maps bounded sets into bounded sets.

PROOF. By induction, $F^n = A^n + K_n$ with compact continuous maps $K_n : X_+ \to X_+$. We apply [**187**, Thm.2.46]. Let C be a bounded subset of X_+. Then diam $A^n(C) \le \|A^n\|$ diam $(C) \to 0$, $n \to \infty$. Further, $K_n(C)$ has compact closure. So the semiflow induced by F is asymptotically smooth.

The last statement follows from Theorem 14.16 or from Theorem 14.18. □

14.6.4. Weak point-dissipativity. A possible road to point-dissipativity consists in showing weak point-dissipatitivity first.

DEFINITION 14.20. *Let X be a normed vector space and $F : X_F \to X_F$ be an operator on a subset X_F of X.*

Recall that F is point-dissipative *if there exists some $c > 0$ such that*

$$\limsup_{n\to\infty} \|F^n(x)\| < c \quad \text{for all } x \in X_F.$$

F is called weakly point-dissipative *if there exists some $c > 0$ such that*

$$\liminf_{n\to\infty} \|F^n(x)\| < c \quad \text{for all } x \in X_F.$$

THEOREM 14.21. *Let X be a normed vector space and $F : X_F \to X_F$ be a compact operator on a closed subset X_F of X such that $\|F(x)\|$ is a continuous function of $x \in X_F$.*

Assume that F is weakly point-dissipative. Then F is point-dissipative and, if F is also continuous, the semiflow induced by F has a compact attractor of points.

PROOF. Suppose that F is weakly point-dissipative but not dissipative. Then there exists some $c > 0$ such that

$$\liminf_{n\to\infty} \|F^n(x)\| < c \qquad x \in X_F, \tag{14.31}$$

and sequences (x_k) and (c_k) in X_F and $(0,\infty)$ such that

$$\limsup_{n\to\infty} \|F^n(x_k)\| > c_k, \quad k \in \mathbb{N}, \quad c_k \overset{k\to\infty}{\longrightarrow} \infty. \tag{14.32}$$

Then there exist sequences (r_k), (s_k), (t_k) in $\mathbb{N}$ such that $r_k \to \infty$ and

$$
\begin{aligned}
&\|F^{r_k}(x_k)\| \le c+1,\\
&\|F^{r_k+s_k}(x_k)\| \ge c_k,\\
&\|F^{r_k+s}(x_k)\| \ge c+1, \quad s=1,\dots,s_k+t_k,\\
&\|F^{r_k+s_k+t_k+1}(x_k)\| < c+1.
\end{aligned}
\tag{14.33}
$$

We set $y_k = F^{r_k}(x_k)$. Then

$$
\begin{aligned}
&\|y_k\| \le c+1,\\
&\|F^{s_k}(y_k)\| \ge c_k,\\
&\|F^{s}(y_k)\| \ge c+1, \quad s=1,\dots,s_k+t_k,\\
&\|F^{s_k+t_k+1}(y_k)\| \le c+1.
\end{aligned}
\tag{14.34}
$$

Since F is compact, after choosing subsequences, $F(y_k) \to x$ for $k \to \infty$ with some $x \in X_F$. Since $\|F(z)\|$ is a continuous function of $z \in X_F$, $\|F^n(y_k)\| \to \|F^{n-1}(x)\|$ for all $n \in \mathbb{N}$.

We claim that $s_k \to \infty$ as $k \to \infty$.

If not, there exists a constant subsequence (s_{k_j}) with $s_{k_j} = m \in \mathbb{N}$ for all $j \in \mathbb{N}$ and $c_{k_j} \le \|F^{s_{k_j}}(y_{k_j})\| \to \|F^m(x)\|$, a contradiction.

Let $s \in \mathbb{N}$. Since $s_k \to \infty$, $s_k > s$ for all but finitely many $k \in \mathbb{N}$. So $\|F^s(y_k)\| \ge c+1$ for all but finitely many $k \in \mathbb{N}$ and thus $\|F^{s-1}(x)\| \ge c+1$. This contradicts (14.31).

This proves that F is dissipative. Since F is compact, F is asymptotically smooth and the induced semiflow has a compact attractor of point by [**187**, Thm.2.28]. □

14.7. Population extinction

We derive conditions that imply that $F^n(x) \to 0$ as $n \to \infty$ for all $x \in X_+$. The first result, for the subthreshold case $\mathcal{T}_0 = \mathbf{r}(B) < 1$, is proved by using the definition of the spectral radius, (1.7) .

THEOREM 14.22. *Let X_+ be the normal closed cone of an ordered normed vector space. Let $F, B : X_+ \to X_+$ and let B be homogeneous, bounded and order-preserving , $\mathbf{r}(B) < 1$, and $F(x) \le B(x)$ for all $x \in X_+$.*

Then $F^n(x) \to 0$ as $n \to \infty$ uniformly for x in bounded subsets of X_+.

PROOF. By induction, since B is order-preserving, $F^n(x) \le B^n(x)$ for all $n \in \mathbb{N}$ and $x \in X_+$. Since X_+ is a normal closed cone, there is some $c > 0$ such that $\|F^n(x)\| \le c\|B^n(x)\| \le c\|B^n\|\,\|x\|$ for all $x \in X_+$ and $n \in \mathbb{N}$. Since $\mathbf{r}(B) < 1$, $\|B^n\| \to 0$ as $n \to \infty$ by (1.7) and the assertion follows. □

The next extinction results deal with the threshold case that the basic turnover number equals 1, $\mathcal{T}_0 = \mathbf{r}(B) = 1$. It is useful if $\mathcal{T}_0 = 1$ is an eigenvalue of B associated with a homogeneous upper eigenfunctional; see Theorem 14.23(b) and see Chapter 11 for scenarios where this is the case.

THEOREM 14.23. *Let X_+ be the normal closed cone of an ordered normed vector space. Let $F, B : X_+ \to X_+$ and let B be homogeneous, bounded and order-preserving, $\mathcal{T}_0 = \mathbf{r}(B) = 1$, and $F(x) \le B(x)$ for all $x \in X_+$.*

Further, by assumption, for any $\delta > 0$ there is some $\epsilon \in (0,1)$ such that $F(x) \le \epsilon B(x)$ for all $x \in X_+$ with $\|x\| \ge \delta$ and $\|F(x)\| \ge \delta$.

(a) *Then $\liminf_{n\to\infty} \|F^n(x)\| \to 0$ for all $x \in X_+$.*

(b) *If there exists a bounded homogeneous order-preserving eigenfunctional $\theta : X_+ \to \mathbb{R}_+$ of B, $\theta(B(x)) \le \theta(x)$ for all $x \in X_+$, then $\theta(F_n(x)) \to 0$ as $n \to \infty$.*

If, in addition, $\theta(x) > 0$ for all $x \in \dot{X}_+$ and θ is continuous and the semiflow induced by F is asymptotically smooth and point-dissipative, then $\|F_n(x)\| \to 0$ as $n \to \infty$, $x \in X_+$.

Proof. (a) Suppose that $x \in X_+$ and $\liminf_{n\to\infty} \|F^n(x)\| > \delta > 0$.

Then there is some $m \in \mathbb{N}$ such that $\|F^n(x)\| > \delta$ for all $n \ge m$. Choose $\epsilon \in (0,1)$ according to our assumption.

We claim that $F^{n+m}(x) \le \epsilon^n B^n(F^m(x))$ for all $n \in \mathbb{Z}_+$.

This holds for $n = 0$. Suppose that $n \in \mathbb{Z}_+$ and the claim holds for n.

$$F^{n+1+m}(x) = F(F^{n+m}(x)) \le \epsilon B(F^{n+m}(x))$$

because both $\|F(F^{n+m}(x))\| \ge \delta$ and $\|(F^{n+m}(x))\| \ge \delta$. Since B is order-preserving,

$$F^{n+1+m}(x) \le \epsilon B \epsilon^n B^n(F^m(x)).$$

This concludes our induction proof.

Since X_+ is normal, there exists some $c > 0$ such that

$$\|F^{n+m}(x)\| \le c\|\epsilon B\|^n \|F^m(x)\|.$$

Since $\mathbf{r}(\epsilon B) = \epsilon \mathbf{r}(B) < 1$, $\|F^{n+m}(x)\| \to 0$ as $n \to \infty$, a contradiction.

This finishes the proof of part (a).

(b) Let $\theta : X_+ \to \mathbb{R}_+$ be a bounded homogeneous order-preserving eigenfunctional of B, $\theta \circ B(x) \le \theta(x)$ for all $x \in X$, and let $x \in X_+$. Then $(\theta(F^n(x))$ is a decreasing sequence,

$$\theta(F^{n+1}(x)) \le \theta(B(F^n(x))) = \theta(F^n(x)), \qquad n \in \mathbb{N}.$$

Since θ is bounded, $\liminf_{n\to\infty} \theta(F^n(x)) = 0$ and thus $\theta(F^n(x)) \to 0$ as $n \to \infty$.

Let, in addition, F be point-dissipative and asymptotically smooth. Then, for each $x \in X_+$, there exists a nonempty compact invariant ω-limit set $\omega(x)$ which attracts $(F^n(x))$ [**187**, Thm.2.28]. For each $y \in \omega(x)$, since θ is continuous, $\theta(y) = 0$ and so $y = 0$. This implies $F^n(x) \to 0$ as $n \to \infty$. □

Alternatively, it is useful if $\mathcal{T}_0 = 1$ is an eigenvalue associated with an (upper) eigenvector of B, see Theorem 14.24 and Chapter 9 for scenarios where this is the case.

Theorem 14.24. *Let X_+ be the normal closed cone of an ordered normed vector space. Let $F, B : X_+ \to X_+$ and let B be homogeneous, bounded and order-preserving, $\mathbf{r}(B) = 1$, and $F(x) \le B(x)$ for all $x \in X_+$.*

Further, by assumption, for any $\delta > 0$ there is some $\epsilon \in (0,1)$ such that $F(x) \le \epsilon B(x)$ for all $x \in X_+$ with $\|x\| \ge \delta$.

Finally, assume that there is some $v \in \dot{X}_+$ such that $B(v) \le v$ and that some power of B is uniformly v-bounded (Definition 6.1).

Then $\|F^n(x)\| \to 0$ as $n \to \infty$.

Proof. Let $m \in \mathbb{N}$ such that B^m is uniformly v-bounded (Definition 6.1). We define the functional $\theta : X_+ \to \mathbb{R}_+$ by

$$\theta(x) = \|B^m(x)\|_v, \qquad x \in X_+. \tag{14.35}$$

Then θ is homogeneous, order-preserving and bounded. By (2.32), for $x \in X_+$, $B^m(x) \le \theta(x)v$. Since B is homogeneous and order-preserving,

$$B(B^m(x)) \le \theta(x)B(v) \le \theta(x)v.$$

By (2.26), $\|B^m(B(x))\|_v \le \theta(x)$ and, by (14.35), $\theta(B(x)) \le \theta(x)$. By Theorem 14.23, $\|B^m(F^n(x))\|_v \to 0$ as $n \to \infty$. Since $F(y) \le B(y)$ for all $y \in X_+$, $\|F^{m+n}(x)\|_v \to 0$ as $n \to \infty$. Since X_+ is normal, $\|F^n(x)\| \to 0$ as $n \to \infty$ by Lemma 2.69 (b). □

Alternative proof. By Theorem 14.23,

$$\liminf_{n\to\infty} \|F^n(x)\| = 0, \qquad x \in X_+.$$

By Theorem 14.14, there exists some $c > 0$ such that $\|F^n(y)\| \le c\|y\|$ for all $y \in X_+$, $n \in \mathbb{Z}_+$.

Let $x \in X_+$ and $\epsilon > 0$. Then there exists some $m \in \mathbb{N}$ such that $\|F^m(x)\| \le \epsilon/c$. For all $n \ge m$,

$$\|F^n(x)\| = \|F^{n-m}F^m(x)\| \le c\|F^m(x)\| \le \epsilon.$$ □

14.8. Nonzero fixed points

One way of showing that populations the dynamics of which are governed by the turnover operator F do not always go extinct consists in establishing the existence of a nonzero fixed point $F(x) = x$ (persistence at equilibrium). For a more condensed presentation see [**203**, Sec.8.3].

Theorem 14.25. *Let X_+ be the closed cone of an ordered normed vector space X and $F : \dot{X}_+ \to X_+$ be continuous and compact. Assume that there are some homogeneous subadditive functional $\theta : X_+ \to \mathbb{R}_+$ and some order-preserving lower order-derivative $B : X_+ \to X_+$ of F at 0 with the following properties:*

(i) *θ is uniformly positive and continuous.*

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

(iii) *There is some $v \in \dot{X}_+$ and $r > 1$ such that $B(v) \ge rv$.*

Then there exists some $x \in \dot{X}_+$ such that $F(x) = x$.

We emphasize that X_+ does not need to be complete. Recall that θ is uniformly positive if there is some $\zeta \in (0,1)$ such that $\theta(x) \ge \zeta\|x\|$ for all $x \in X_+$. The concept of a lower order-derivative can be found in Section 14.2. Recall the notation $\dot{X}_+ = X_+ \setminus \{0\}$.

We use the well-established idea [**135**, Sec.2.2] [**177**, Sec.3] [**211**, Thm.3.6]. of considering perturbed operators F_λ, $\lambda > 0$, with $F_\lambda(x) \to F(x)$ for $\lambda \to 0$, $x \in X_+$. The F_λ inherit continuity and compactness from F and have fixed points x_λ by a fixed point theorem by Tychonoff which does not require completeness [**55**, Thm.10.1]. Because of the perturbation, $0 \ne x_\lambda \in X_+$. Because of the compactness of F, there exists a sequence (λ_n) in $(0,1)$ with $\lambda_n \to 0$ and $x_{\lambda_n} \to x$ for some fixed point $F(x) = x \in X_+$. Condition (iii) is used to show that $x \ne 0$.

PROOF. For $\lambda \in (0,1)$, we define $F_\lambda : X_+ \to X_+$ by

$$F_\lambda(x) = F(x + \lambda v) + \lambda v, \qquad x \in X_+, \tag{14.36}$$

where v is chosen according to assumption (iii). We claim:

($\diamondsuit$) There exists some $R > 0$ such that $\theta(F_\lambda(x)) \le R$ for all $\lambda \in (0,1]$ and all $x \in X_+$ with $\theta(x) \le R$.

Suppose that ($\diamondsuit$) does not hold. Then, for any $n \in \mathbb{N}$, there exist some $x_n \in X_+$ and $\lambda_n \in (0,1]$ such that $\theta(x_n) \le n$ and $\theta(F_{\lambda_n}(x_n)) \ge n$.

So, for all $n \in \mathbb{N}$, since θ is subadditive and homogeneous,

$$n \le \theta\big(F(x_n + \lambda_n v) + \lambda_n v\big) \le \theta(F(x_n + \lambda_n v)) + \theta(v).$$

Since F is compact on $\dot{X}_+$ and θ bounded, (x_n) is unbounded. After choosing subsequences, $\|x_n\| \to \infty$ as $n \to \infty$. By assumption (ii), there exists some $\alpha \in (0,1)$ and $\beta > 0$ such that

$$\theta(F(x)) \le \alpha\theta(x), \qquad x \in X_+, \quad \|x\| \ge \beta.$$

So, for large enough n,

$$n \le \alpha\theta(x_n + \lambda_n v) + \theta(v) \le \alpha n + 2\theta(v),$$

a contradiction because $\alpha \in (0,1)$.

So, we have shown that ($\diamondsuit$) holds which can be rephrased as follows:

There is some $R > 0$ such that, for any $\lambda \in (0,1]$, F_λ maps the set $\{x \in X_+; \theta(x) \le R\}$ into itself. This set is bounded because θ is uniformly positive by assumption (i). It is convex and closed because θ is subadditive, homogeneous and continuous. Since F_λ is compact and continuous on X_+, by Tychonov's fixed point theorem [**55**, Thm.10.1], there exists some $x_\lambda \in X_+$ with

$$F_\lambda(x_\lambda) = x_\lambda, \qquad \theta(x_\lambda) \le R, \quad \lambda \in (0,1]. \tag{14.37}$$

Now, choose a sequence (λ_n) in $(0,1]$ such that $\lambda_n \to 0$ for $n \to \infty$. Since θ is uniformly positive by assumption (i) and since (14.36) holds, there exists a bounded sequence (x_n) in X_+such that

$$F(x_n + \lambda_n v) + \lambda_n v = x_n, \qquad n \in \mathbb{N}. \tag{14.38}$$

We choose $\epsilon \in (0,1)$ such that $(1-\epsilon)r > 1$ with the number r from assumption (iii). Since B is a lower order-derivative of F, by (14.3) we choose $\delta > 0$ such that $F(x) \ge (1-\epsilon)B(x)$ for all $x \in \dot{X}_+$ with $\|x\| \le 2\delta$.

We claim that

$$\liminf_{n\to\infty} \|x_n\| \ge \delta. \tag{14.39}$$

Suppose not. Then, for some large $n \in \mathbb{N}$, $\|x_n\| \le \delta$ and $\lambda_n\|v\| \le \delta$ and so $\|x_n + \lambda_n v\| \le 2\delta$ and by (14.38),

$$x_n \ge (1-\epsilon)B(x_n + \lambda_n v) + \lambda_n v.$$

Since $v \in X_+$ and B is order-preserving, $x_n \ge (1-\epsilon)B(x_n)$. Since B is homogeneous and order-preserving, by induction,

$$x_n \ge (1-\epsilon)^k B^k(x_n), \qquad k \in \mathbb{N}.$$

We also have that $x_n \ge \lambda_n v$ and $B(v) \ge rv$. Since B is order-preserving and homogeneous,

$$x_n \ge (1-\epsilon)^k B^k(\lambda_n v) \ge [(1-\epsilon)r]^k \lambda_n v, \qquad k \in \mathbb{N}.$$

Since X_+ is a closed cone and $(1-\epsilon)r > 1$, this implies that $v = 0$, a contradiction.

This proves (14.39). Since F is compact on $\dot{X}_+$ and the sequence $(x_n + \lambda_n v)$ in $\dot{X}_+$ is bounded by (14.38) and $\lambda_n \to 0$, $F(x_n + \lambda_n v) \to y \in X_+$ after choosing a subsequence. By (14.38) and (14.39), $x_n \to y$ as $n \to \infty$ with $y \in X_+$ and $\delta \le \|y\|$. Since F is continuous on $\dot{X}_+$, $F(y) = y$ by (14.38). □

By Corollary 9.11, Theorem 14.25 has the following consequence for the superthreshold case $\mathcal{T}_0 > 1$. Since we want to apply this result to the cone of nonnegative Borel measures with the flat norm (Theorem 19.18), we emphasize again that X_+ does not need to be complete.

COROLLARY 14.26. *Let X_+ be the closed cone of an ordered normed vector space X and $F : \dot{X}_+ \to X_+$ be continuous and compact,*

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

Further assume that there is some lower order-derivative $B : X_+ \to X_+$ of F at 0 that is order-preserving, compact and continuous and $\mathcal{T}_0 = \mathbf{r}(B) > 1$.

Then there exists some $x \in \dot{X}_+$ such that $F(x) = x$.

14.9. Population persistence

The results in this section are related to the other half of the threshold property of the basic turnover number $\mathcal{T}_0$ which is the spectral radius of the basic turnover operator, B, a homogeneous first order approximation of the turnover operator, F. See Sections 1.1 and 1.2. If $\mathcal{T}_0 > 1$, populations persist in a certain sense under suitable extra conditions. See Section 1.2.

14.9.1. Uniform weak persistence. As before, let X_+ be the closed order cone of an ordered normed vector space X and $\dot{X}_+ = X_+ \setminus \{0\}$. Recall the definitions of a normal cone (Section 2.2.1) and of a serially complete cone (Section 2.1.2).

THEOREM 14.27. *Let X_+ be a serially complete normal closed cone and $u \in \dot{X}_+$. Let $F, B : X_+ \to X_+$ and B be bounded homogeneous and order-preserving and B a lower order-derivative of F at 0 (Section* 14.2*). Assume $\mathcal{T}_0 = \mathbf{r}(B) > 1$.*

Let the following properties be satisfied.

(a) $F(\dot{X}_+) \subseteq \dot{X}_+$.
(b) *A power of B is uniformly u-bounded (Definition* 6.1*).*
(c) *B is pointwise u-positive (Definition* 11.3*).*

Then the population is uniformly weakly persistent: There exists some $\delta > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \ge \delta$ for all $x \in \dot{X}_+$.

The subsequent results, which are of their own interest, prepare the proof of this theorem, which is at the end of this section. Eventually, they need to be combined with Theorem 11.14, which provides a homogeneous eigenfunctional of B associated with $\mathcal{T}_0 = \mathbf{r}(B)$.

The presentation loosely follows [**130**].

PROPOSITION 14.28. *Let $F, B : X_+ \to X_+$ and B be homogeneous and order-preserving and a lower order-derivative of F at 0 (Section* 14.2*). Let $\theta : X_+ \to \mathbb{R}_+$ be homogeneous, bounded, and order-preserving, and $\rho : X_+ \to \mathbb{R}_+$.*

Let the following properties be satisfied.

(a) *If $x \in X_+$ and $\rho(x) > 0$, then $\theta(F^n(x)) > 0$ for infinitely many $n \in \mathbb{N}$.*

(b) *There exists some $r > 1$ such that $\theta(B(x)) \geq r\theta(x)$ for all $x \in X_+$.*

Then the extinction state $0 \in X_+$ is uniformly weakly ρ-repelling for the semiflow induced by F: There exists some $\delta > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \geq \delta$ for all $x \in X_+$ with $\rho(x) > 0$.

Notice that assumption (b) in Proposition 14.28 and Theorem 14.29 implies that $\mathcal{T}_0 = \mathbf{r}(B) > 1$ (Section 5.6).

In turn, additional general assumptions under which $\mathcal{T}_0 = \mathbf{r}(B) > 1$ implies assumption (b) can be found in Chapter 11 and in [**130**, Sec.7].

Further assumptions tailored to specific ordered normed vector spaces are presented in Section 13.5 and 13.6.

Proof. Choose some $r > 1$ according to (b) and some $\epsilon \in (0, 1)$ such that

$$1 < r(1-\epsilon) =: s. \tag{14.40}$$

Since B is a lower order-derivative of F at 0, we can choose $\delta > 0$ according to (14.3):

$$F(x) \geq (1-\delta)B(x), \qquad x \in X_+, \quad \|x\| \leq \delta. \tag{14.41}$$

Suppose that the extinction state is not uniformly weakly ρ-repelling: There exists some $x \in X_+$ such that

$$\rho(x) > 0 \text{ and } \limsup_{n\to\infty} \|F^n(x)\| < \delta.$$

By (a), after a shift in time, we can assume that $x \in X_+$ and

$$\theta(x) > 0, \qquad \|F^n(x)\| < \delta, \quad n \in \mathbb{Z}_+. \tag{14.42}$$

Set $x_n = F^n(x)$ for $n \in \mathbb{Z}_+$. Then

$$x_{n+1} = F(x_n), \quad n \in \mathbb{Z}_+, \qquad x_0 = x. \tag{14.43}$$

By (14.42), $\|x_n\| \leq \delta$ for all $n \in \mathbb{N}$, and the sequence $(\theta(x_n))$ is bounded because θ is bounded. We claim that

$$x_n \geq (1-\epsilon)^n B^n(x), \qquad n \in \mathbb{Z}_+. \tag{14.44}$$

This trivially holds for $n = 0$. Assume it holds for n. By (14.43) and (14.41), since B is order-preserving,

$$x_{n+1} = F(x_n) \geq (1-\epsilon)B(x_n) \geq (1-\epsilon)B((1-\epsilon)^n B^n(x_0)).$$

Since B is homogeneous, $x_{n+1} \geq (1-\epsilon)^{n+1}B^{n+1}(x_0)$. So, (14.44) holds by the induction principle.

By (14.44), since θ is order-preserving and homogeneous,

$$\theta(x_n) \geq (1-\epsilon)^n \theta(B^n(x)). \tag{14.45}$$

We claim that, for all $n \in \mathbb{Z}_+$,

$$\theta(B^n(x)) \geq r^n \theta(x). \tag{14.46}$$

This is trivially true for $n = 0$. Assume it holds for some arbitrary $n \in \mathbb{Z}_+$. Then, by (b), since θ is homogeneous and order-preserving,

$$\theta(B^{n+1}(x)) = \theta(B(B^n(x))) \geq r\theta(B^n(x)) \geq r\theta(r^n x) = r^{n+1}\theta(x).$$

We combine (14.44) and (14.46) and obtain that $\theta(x_n) \geq (1-\epsilon)^n r^n \theta(x) = s^n \theta(x)$.

Since $s > 1$ by (14.40) and $\theta(x) > 0$ by (14.42), this implies that $\theta(x_n) \to \infty$. Since we have established above that $(\theta(x_n))$ is bounded, we have arrived at a contradiction. □

The following result implies that the origin is unstable.

THEOREM 14.29. *Let $F, B : X_+ \to X_+$ and B be homogeneous and order-preserving and B a lower order-derivative of F at 0 (Section 14.2),*

(a) $F(\dot{X}_+) \subseteq \dot{X}_+$.

Further, assume that there is some bounded homogeneous $\theta : X_+ \to \mathbb{R}_+$ that is order-preserving and satisfies the following properties:

(b) *There exists some $r > 1$ such that $\theta(B(x)) \geq r\theta(x)$ for all $x \in X_+$.*

(c) *For any $x \in \dot{X}_+$, there exists some $n \in \mathbb{Z}_+$ such that $\theta(F^n(x)) > 0$.*

Then the semiflow induced by F is uniformly weakly norm-persistent: There exists some $\delta > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \geq \delta$ for all $x \in \dot{X}_+$.

Since $F(0) = 0$, assumption (a) is necessary for uniform weak persistence.

This theorem is used in the proof of Theorem 18.14 and Theorem 19.10.

PROOF. We apply Proposition 14.28 with $\rho(x) = \|x\|$.

It is sufficient to show assumption (a) of Proposition 14.28 is satisfied.

Suppose that there is $x \in X_+$ with $\rho(x) > 0$ and that the set $\{n \in \mathbb{N}; \theta(F^n(x)) > 0\}$ is finite.

Then there exists some $m \in \mathbb{N}$ such that $\theta(F^n(x)) = 0$ for all $n \in \mathbb{N}$, $n \geq m$. By assumption (a), $F^m(x) \in \dot{X}_+$. By assumption (c), there exists some $k \in \mathbb{N}$ such that $\theta(F^k(F^m(x))) > 0$. So $\theta(F^{m+k}(x)) > 0$, a contradiction.

All assumptions of Proposition 14.28 are satisfied and the assertion follows. □

The following result is different from Proposition 14.28 in so far as the norm is replaced by ρ.

THEOREM 14.30. *Let $F, B : X_+ \to X_+$ and B be homogeneous and order-preserving and a lower order-derivative of F at 0. Let $\theta : X_+ \to \mathbb{R}_+$ be homogeneous, bounded, and order-preserving, and $\rho : X_+ \to \mathbb{R}_+$. Let the following properties be satisfied.*

(a) *If $x \in X_+$ and $\rho(x) > 0$, then $\theta(F^n(x)) > 0$ for infinitely many $n \in \mathbb{N}$.*

(b) *There exists some $r > 1$ such that $\theta(B(x)) \geq r\theta(x)$ for all $x \in X_+$.*

(c) *For any $\epsilon > 0$ there exists some $\delta > 0$ such that*

$$\sup_{n\in\mathbb{N}} \rho(F^n(x)) \leq \delta \implies \limsup_{n\to\infty} \|F^n(x)\| \leq \epsilon.$$

Then the semiflow induced by F is uniformly weakly ρ-persistent: There is some $\delta > 0$ such that $\limsup_{n\to\infty} \rho(F^n(x)) \geq \delta$ for all $x \in X_+$ with $\rho(x) > 0$.

PROOF. By assumptions (a) and (b), all assumptions of Proposition 14.28 are satisfied. So, there exists some $\epsilon > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \geq \epsilon$ for all $x \in X_+$ with $\rho(x) > 0$.

According to (c), choose some $\delta > 0$ such that $\limsup_{n\to\infty} \|F^n(x)\| \leq \epsilon/2$ if $x \in X_+$ and $\sup_{n\in\mathbb{N}} \rho(F^n(x)) \leq \delta$.

Suppose that $x \in X_+$, $\rho(x) > 0$ and $\limsup_{n\to\infty} \rho(F^n(x)) < \delta$. Then there exists some $m \in \mathbb{N}$ such that

$$\delta > \sup_{n\ge m} \rho(F^n(x)) = \sup_{n\in\mathbb{Z}_+} \rho(F^n(F^m(x)).$$

So

$$\epsilon/2 \ge \limsup_{n\to\infty} \|F^n(F^m(x))\| = \limsup_{n\to\infty} \|F^n(x)\|,$$

a contradiction. □

The following is an example for condition (c) in Theorem 14.30 to hold.

REMARK 14.31. Let X_+ be normal and $w \in X_+$ such that $F(x) \le \rho(x)w + A(x)$ for all $x \in X_+$ with $A : X_+ \to X_+$ homogeneous, subadditive and $\sum_{j=0}^\infty \|A^j(w)\| < \infty$ and $A^n(x) \to 0$ as $n \to \infty$ for all $x \in X_+$.

Then there exists some $c > 0$ such that

$$\limsup_{n\to\infty} \|F^n(x)\| \le c \sum_{j=0}^\infty \|A^j(w)\| \limsup_{n\to\infty} \rho(F^n(x)).$$

PROOF. Let $x \in X_+$ and $x_n = F^n(x)$ for all $n \in \mathbb{Z}_+$. By induction, since A is subadditive and homogeneous,

$$x_n \le \sum_{j=0}^{n-1} \rho(x_{n-1-j})A^j(w) + A^n(x), \quad n \in \mathbb{N}.$$

Since X_+ is normal, there exists some $c > 0$ such that

$$\|x_n\| \le c \sum_{j=0}^{n-1} \rho(x_{n-1-j})\|A^j(w)\| + \|A^n(x)\|.$$

Now apply Fatou's lemma with the counting measure. □

PROOF OF THEOREM 14.27. We apply Theorem 14.29. By Theorem 11.14, there exists some homogeneous, order-preserving bounded eigenfunctional $\theta : X_+ \to \mathbb{R}_+$ such that $\theta(B(x)) = \mathcal{T}_0\,\theta(x)$ for all $x \in X_+$. So assumption (b) of Theorem 14.29 is satisfied.

Since a power of B is uniformly u-bounded, $\theta(u) > 0$. Since B is pointwise u-positive, $\theta(x) > 0$ for all $x \in \dot{X}_+$. See Remark 11.4. By assumption (a), $\theta(B^n(x)) > 0$ for all $n \in \mathbb{N}$ and $x \in \dot{X}_+$. So assumption (c) of Theorem 14.29 is satisfied.

All assumptions of Theorem 14.29 are satisfied, and it implies our assertion. □

14.9.2. Uniform persistence. There are many assumptions that lead from uniform weak to uniform population persistence. They can be obtained by combining the previous results in various ways guided by [**187**, Sec.4.1,4.2]. We choose one set of assumptions that may be stronger than needed but can be stated as succinctly as possible.

THEOREM 14.32. *Let X_+ be a serially complete normal closed cone and $u \in \dot{X}_+$. Let $F, B : X_+ \to X_+$ and let B be bounded homogeneous and order-preserving and let B a lower order-derivative of F at 0 (Section* 14.2*). Assume $\mathcal{T}_0 = \mathbf{r}(B) > 1$.*

Let the following properties be satisfied.

(a) *$F(0) = 0$ and $F(\dot{X}_+) \subseteq \dot{X}_+$.*
(b) *A power of B is uniformly u-bounded (Definition* 6.1*).*

(c) *B is pointwise u-positive (Definition* 11.3*).*

(d) *F is point-dissipative and asymptotically smooth (Section* 14.6*).*

Then the population is uniformly persistent: There exists some $\epsilon > 0$ such that $\liminf_{n\to\infty} \|F^n(x)\| \geq \epsilon$ for all $x \in \dot{X}_+$.

The proof combines Theorem 14.29 with [**187**, Thm.4.5].

Proof. By Theorem 14.29, the population is uniformly weak persistence; in the language of [**187**, Thm.4.5] uniformly ρ-persistent with $\rho = \|\cdot\|$.

We apply [**187**, Thm.4.5].

Since F (more precisely, the semiflow induced by F) is asymptotically smooth and point-dissipative, there exists a compact attractor of points [**187**, Thm.2.28]: There exists a nonempty compact subset Y of X_+ such that $d(F^n(x), Y) \to 0$ as $n \to \infty$ for all $x \in X_+$. Here $d(y, Y)$ is the distance from y to Y. This is condition $\tilde{\clubsuit}_2$ in [**187**, Thm.2.28]. Condition $\tilde{\clubsuit}_1$ follows from $F(0) = 0$ and $F(\dot{X}_+) \subseteq \dot{X}_+$.

By [**187**, Thm.4.5], the semiflow induced by F is uniformly ρ-persistent with $\rho = \|\cdot\|$, and the assertion has been proved. $\square$

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