DISCRETE-TIME DYNAMICS OF STRUCTURED POPULATIONS VIA FELLER KERNELS

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ABSTRACT. Feller kernels are a concise means to formalize individual structural transitions in a structured discrete-time population model. An iteroparous populations (in which generations overlap) is considered where different kernels model the structural transitions for neonates and for older individuals. Other Feller kernels are used to model competition between individuals. The spectral radius of a suitable Feller kernel is established as basic turnover number that acts as threshold between population extinction and population persistence. If the basic turnover number exceeds one, the population shows various degrees of persistence that depend on the irreducibility and other properties of the transition kernels.

1. Introduction. In a population dynamics context, a metric space $S$ can serve as state space of individual characteristics [4] and provide the structure of the population. 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. Individual state transitions, like moving from one location to another when the structure is given by physical space, or putting on weight when the structure is given by body mass, can be described by Feller kernels $P : \mathcal{B} \times S \to \mathbb{R}_+$ where $\mathcal{B}$ is the Borel $\sigma$-algebra on $S$ and $P(\cdot, s)$ is a finite non-negative measure on $\mathcal{B}$ for each $s \in S$.

Let $C_b(S)$ denote the Banach space of bounded continuous real-valued functions $f$ on $S$ with the supremum norm $\|f\|_\infty = \sup_{s \in S} |f(s)|$ and $C^b_+(S)$ the cone of nonnegative functions in $C^b(S)$. $C^b_+(S)$ denotes the latter set without the zero function.

The Feller property means that, if $f \in C^b(S)$,

$$(A_* f)(s) = \int_S f(t) P(dt, s), \quad s \in S,$$

provides a function $A_* f$ in $C^b(S)$. The Feller kernel $P$ can have a forward or a backward interpretation. If we model the year to year development of a population, the forward interpretation is that if $s \in S$ is an individual’s structural characteristic

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(location or weight, e.g.) this year, then \( P(T, s) \) is the probability that it will be still alive and its structural characteristic will lie in the set \( T \in \mathcal{B} \) next year. This suggests that \( P(S, s) \leq 1 \) for all \( s \in S \) but this restriction may not apply if we also include the structural distribution of the individual’s descendants.

The backward interpretation is that if \( s \in S \) is the individual’s structural characteristic this year, \( P(T, s) \) is the probability that its structural characteristic was in the set \( T \in \mathcal{B} \) last year. This suggests that \( P(S, s) = 1 \) for all \( s \in S \).

If we stick to the forward interpretation, Feller kernels become building blocks for turnover integral equations (discrete-time dynamics models for structured populations with integration over the metric space \( S \)) on the space of nonnegative Borel measures \([29, 30]\). If we use the backward interpretation, the turnover integral equations act on \( C^*_+ (S) \),

\[
f_n = F(f_{n-1}), \quad n \in \mathbb{N},
\]

with an integral operator \( F \) on \( C^*_+(S) \) and a given \( f_0 \in C^*_+(S) \). \( f_n \) is the structural distribution of the population in the \( n \)th year. We call \( F \) the (yearly) population turnover operator. For the interpretation of the qualitative behavior of \((f_n)\), it may matter when the yearly census of the population is taken \([19]\).

Equation (1.2) is solved by

\[
f_n = F^n(f_0), \quad n \in \mathbb{N},
\]

where \( F^n \) is the \( n \) fold composition of \( F \) with itself (\( n \)th iterate, \( n \)th power). \((F_n)\) is the discrete semiflow induced by the map \( F \) \([25, \text{Sec.1.2}]\).

Turnover integral equations on \( C^*_+(S) \), with density kernels with respect to some master measure rather than general Feller kernels, have been used mainly for spatially distributed populations. Traditionally, they are called integro-difference equations, though they may contain no visible difference operation. See \([14]\) and \([26, \text{Sec.3.4}]\) for some early contributions. An important application are propagation dynamics like spreading speeds and traveling waves (see \([16, 17, 32]\) and the literature mentioned there). Other questions concern stability and instability of the zero function, the extinction equilibrium (critical domain size), of interior equilibria and periodic solutions (see \([15, \text{Sec.5.4}], [18, 22, 23]\) and the literature cited there). Turnover integral equations for two-sex populations have also been considered \([13, 21]\) with the inclusion of Feller kernels being prepared for in \([27, \text{Sec.7.4}]\) and carried out in \([31]\).

If the population structure is not given by spatial distribution but by physiological characteristics like age, body size, maturity, also the name integral projection models is used (see \([8, 9, 10]\) and the references therein) because \( F \) gives a projection of next year’s structural distribution based on this year’s structural distribution (though \( F \) is not a projection in the functional analytic sense).

However the models or model equations are called, typically the Feller kernels that have been used are of the special form

\[
P(T, s) = \int_T k(t, s)\nu(dt), \quad s \in S, T \in \mathcal{B},
\]

with \( k \in C^*_+(S \times S) \) and a nonnegative measure \( \nu \) on \( \mathcal{B} \). Feller kernels are not only more general, but also allow for more succinct formulations. They present an exciting framework to be explored \([11, 27, 29, 30]\).

If \( S \) is an open subset of \( \mathbb{R}^n \) representing the habitat of a population, a natural master measure on \( S \) is induced by the Lebesgue measure, and a function \( f \in C^*_+(S) \)
can be interpreted as spatial density of the population by \( \int_T f(x)dx \) giving the number of individuals located in the Borel subset \( T \) of \( S \).

If \( S \) is an arbitrary metric space, there may be no natural master measure, and, while \( f \in C^b_+(S) \) is still supposed to somehow have the meaning of a structural distribution, it is difficult to pin it down in more concrete terms. Measures may still be of help though none measure rules over the others. If a measure \( \mu \) on \( S \) represents the food distribution on \( S \), \( \int_T f d\mu \) gives the food eaten by the population in the set \( T \in B \).

In its most general form, the turnover operator \( F \) in (1.2) is given in this paper by

\[
F(f)(s) = \int_S f(t) \kappa^j(dt, s), \quad f \in C^b_+(S), s \in S. \tag{1.4}
\]

Here \( \{\kappa^j; f \in C^b_+(S)\} \) is a family of Feller kernels (Section 3).

In its most specialized form, \( F \) is given by

\[
F(f)(s) = \sum_{j=1}^2 \int_S f(t) \tilde{g}_j(s, t, f(t)) P_j(dt, s), \quad f \in C^b_+(S), s \in S. \tag{1.5}
\]

Here, the Feller kernels \( P_j \) describe the spatial movement in the backward sense for adult individuals (\( j = 1 \)) and their offspring (\( j = 2 \)) as explained above, and \( \tilde{g}_j(s, t, f(t)) \) give the survival rates of adult individuals moving from \( t \) to \( s \) for \( j = 1 \) and the amount and survival of their offspring for \( j = 2 \) where \( \tilde{g}_j : S^2 \times R_+ \rightarrow R_+ \). See Section 7. The Sections 5 and 6 contain the transition from the most general to more and more specialized models. They apply to populations where individuals reproduce during a short season within the year and can do so several times during their life (iteroparity). We also assume that individuals have become adults one year after their birth. We take the census immediately before the reproductive season (pre-reproductive census [9]) so that the structural distribution \( f_n \) comprises adult individuals only.

Our analysis concentrates on the most fundamental question of population dynamics, namely under which conditions the population dies out and under which it persists. Here persistence is understood in a stronger sense than mere instability of the zero function, the extinction fixed point ([25, 30, 33] and the references therein).

Let \( \hat{C}^b_+ \) be \( C^b_+ \) without the zero function.

**Definition 1.1.** The population is *uniformly weakly persistent* if there exists some \( \epsilon > 0 \) with the following property:

For any \( f \in \hat{C}^b_+(S) \) and any \( m \in N \), there exists some \( n \in N \), \( n \geq m \), such that \( \|F^n(f)\|_{\infty} \geq \epsilon \).

In other words: \( \limsup_{n \to \infty} \|F^n(f)\|_{\infty} \geq \epsilon \) for all \( f \in \hat{C}^b_+(S) \).

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For all \( f \in \hat{C}^b_+(S) \), there exists some \( m = m_f \in N \) such that \( \|F^n(f)\|_{\infty} \geq \epsilon \) for all \( n \in N \) with \( n \geq m \).

In other words: \( \liminf_{n \to \infty} \|F^n(f)\|_{\infty} \geq \epsilon \) for all \( f \in \hat{C}^b_+(S) \).

Obviously, uniform persistence implies uniform weak persistence. In this context, to obtain uniform persistence rather than uniform weak persistence, we use the
concept of a uniform Feller kernel [30]: For any \( s \in S \),
\[
\sup_{T \in \mathcal{B}} |P(T, t) - P(T, s)| \to 0, \quad S \ni t \to s.
\] (1.6)

If \( S \) has an accumulation point, an example for a Feller kernel that is not a uniform Feller kernel is \( P(T, s) = \chi_T(s) = \delta_s(T) \), formed by the Dirac measures concentrated at \( s \in S \). Notice that the map \( A_* \) associated with this kernel by (1.1) is the identity map.

In the most general turnover integral equation, with turnover map (1.4), we will assume that all \( \kappa f \) are uniform Feller kernels (actually we assume even more, Assumption 3.18). In the most specialized integro-difference equation, with turnover map (1.5), we will assume that either both \( P_j \) are uniform Feller kernels (special case of Section 6) or that \( P_2 \) is a uniform Feller kernel and \( \tilde{g}_1 \) satisfies a rather stringent Lipschitz condition (Section 7).

In dynamical systems terms, the use of uniform Feller kernels gives the discrete semiflow induced by \( F \) via (1.3) a compact attractor of bounded sets [25, Sec.2.2.3].

In (1.4), let \( \kappa^o \) denote the Feller kernel \( \kappa^f \) when \( f \) is the zero function. In the special case (1.5),
\[
\kappa^o(T, s) = \sum_{j=1}^2 \int_T \tilde{g}_j(s, t, 0) P_j(dt, s), \quad s \in S, T \in \mathcal{B}.
\] (1.7)

Let \( A_* \) be the bounded linear map on \( C^b_b(S) \) associated with \( \kappa^o \) by (1.1) with \( \kappa^o \) replacing \( P \). Under suitable assumptions, \( A_* \) is a (lower, upper) first order approximation or even Frechet-derivative of the turnover operator \( F \), called the basic turnover operator. In view of the existing literature, it is expected that the spectral radius of \( A_* \), \( r(A_*) \), is the critical parameter that separates local stability of the extinction fixed point, the zero function (if \( r(A_*) < 1 \)), from uniform (weak) persistence of the population (if \( r(A_*) > 1 \)). \( r(A_*) \) can be described in terms of \( \kappa^o \) (Section 2) and will be denoted by \( r(\kappa^o) \) and can be interpreted as basic turnover number (called inherent population growth rate in [2]). The basic turnover number coincides with the basic reproduction number [5] (called inherent net reproduction number in [2, 3]) if the population is semelparous. For the relation between basic turnover number and basic reproduction number in iteroparous populations, see [29, Sec.3.3.], [30, Sec.2.4] or Section 3.3.

2. The basics on Feller kernels. By [29, Prop.6.3], if \( \kappa : \mathcal{B} \times S \to \mathbb{R}_+ \) 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, the bounded linear map \( A_* \) on \( C^b(S) \) given by
\[
(A_*f)(s) = \int_S f(t) \kappa(dt, s), \quad s \in S, f \in C^b(S)
\] (2.1)
can be extended to a map on \( M^b(S) \), the Banach space of bounded Borel measurable functions with the supremum norm.

Let \( \mathcal{M}(S) \) denote the vector space of finite measures \( \mu : \mathcal{B} \to \mathbb{R} \) and \( \mathcal{M}_+(S) \) the cone of nonnegative measures in \( \mathcal{M}(S) \). For each \( \mu \in \mathcal{M}(S) \), we can define
\[
\int_S \kappa(T, s) \mu(ds) = (A \mu)(T), \quad T \in \mathcal{B},
\] (2.2)
and obtain a measure $A\mu$ and a linear map $A$ on $M(S)$ and the duality relation
\[ \int_S (A_* f) \, d\mu = \int_S f \, d(A\mu), \quad f \in M^b(S), \quad \mu \in M(S). \]  
(2.3)

The linear operator $A$ on $M(S)$ is bounded with respect to the variation norm,
\[ \|A\| = \sup_{s \in S} \kappa(S,s) = \|A_*\|, \]  
(2.4)

but not necessarily bounded with respect to the flat norm [29, Sec.9,10].

2.1. **Convolutions and spectral radius of Feller kernels.** The convolution of two Feller kernels $\kappa_j : B \times S \to \mathbb{R}_+$, $j = 1, 2$, is defined by
\[ (\kappa_1 * \kappa_2)(T,s) = \int_S \kappa_1(T,t)\kappa_2(dt,s), \quad T \in B, s \in S. \]  
(2.5)

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

**Definition 2.1.** Let $\kappa : B \times S \to \mathbb{R}_+$ be a Feller kernel. We inductively define the multiple convolution kernels $\kappa^n$ by $\kappa^1 = \kappa$ and $\kappa^{n+1} = \kappa^n * \kappa$.

The spectral radius of the Feller kernel $\kappa$ is defined by
\[ r(\kappa) = \inf_{n \in \mathbb{N}} \left( \sup_{s \in S} \kappa^n(S,s) \right)^{1/n}. \]  
(2.6)

If $A_*$ is the map on $C^b(S)$ or on $M^b(S)$ induced by $\kappa$, then $A^n_*$ is induced by $\kappa^n$. This implies that
\[ r(\kappa) = r(A_*) = \inf_{n \in \mathbb{N}} \|A^n_*\|^{1/n} = \lim_{n \to \infty} \|A^n_*\|^{1/n} \]
by the Gelfand formula for the spectral radius of a bounded linear operator. So, in (2.6), $\inf$ can be replaced by $\lim$. See [29, Sec.9] for more details.

**Example 2.2.** Let the Feller kernel $\kappa$ have the form
\[ \kappa(T,s) = \mu(T)\gamma(s), \quad s \in S, T \in B, \]  
(2.7)

with some $\gamma \in \dot{C}^b_+(S)$ and some nonnegative finite measure $\mu$ on $B$. By induction,
\[ \kappa^n(T,s) = \mu(T)\left( \int_S \gamma \, d\mu \right)^{n-1} \gamma(s), \quad s \in S, T \in B, \]

and
\[ \sup_{s \in S} \kappa^n(S,s) = \mu(S)\left( \int_S \gamma \, d\mu \right)^{n-1} \sup S\gamma(S). \]

By (2.6), with $\inf_{n \in \mathbb{N}}$ being replaced by $\lim_{n \to \infty}$, $r(\kappa) = \int_S \gamma \, d\mu$.

We give two estimates for the spectral radius of a Feller kernel.

**Proposition 2.3.** Let $\kappa$ be a Feller kernel.

(a) Let $T_1, \ldots, T_m$ be pairwise disjoint nonempty sets in $B$ and
\[ \alpha_{jk} = \inf_{t \in T_j} \kappa(T_k,t), \quad j,k = 1, \ldots, m, \]
and assume that the matrix of size $m$ with coefficients $\alpha_{jk}$ has a spectral radius $r$.

Then $r(\kappa) \geq r$. 

(b) Let \( S \) be the union of pairwise disjoint nonempty sets \( T_1, \ldots, T_m \) in \( \mathcal{B} \) and
\[
\beta_{jk} = \sup_{t \in T_j} \kappa(T_k, t), \quad j, k = 1, \ldots, m,
\]
and assume that the matrix of size \( m \) with coefficients \( \beta_{jk} \) is irreducible and has a spectral radius \( r \).

Then \( r(\kappa) \leq r \).

See [29], Corollary 3.7, Theorem 3.8, and Section 11. For more estimates, see [29, Sec.9.2].

3. The general model with Feller kernels. Let \( S \) be a metric space with at least two elements. A function \( f \in C^b_{+}(S) \) represents the structural distribution of the population at the beginning of the year.

The year-to-year turnover map that determines how this year’s structural distribution is determined by the previous year’s structural distribution is given by
\[
F(f)(s) = \int_S f(t)\kappa^f(dt, s), \quad f \in C^b_{+}(S), \quad s \in S. \tag{3.1}
\]

We write \( \kappa^o \) if \( f \) is the zero function.

**Assumption 3.1.** For each \( f \in C^b_{+}(S) \), \( \kappa^f \) is a Feller kernel.

By the Feller property, we have the following result.

**Lemma 3.2.** Let Assumption 3.1 be satisfied. Then \( F \) maps \( C^b_{+}(S) \) into itself.

**Definition 3.3.** Let Assumption 3.1 be satisfied.

- The kernel family \( \{\kappa^f; f \in C^b_{+}(S)\} \) is called upper semicontinuous at the zero function if for any \( \epsilon \in (0, 1) \) there is some \( \delta > 0 \) such that
\[
\kappa^f(T, s) \leq (1 + \epsilon)\kappa^o(T, s), \quad T \in \mathcal{B}, s \in S,
\]
for all \( f \in C^b_{+}(S) \) with \( \|f\|_{\infty} \leq \delta \).

- The kernel family \( \{\kappa^f; f \in C^b_{+}(S)\} \) is called lower semicontinuous at the zero function if for any \( \epsilon \in (0, 1) \) there is some \( \delta > 0 \) such that
\[
\kappa^f(T, s) \geq (1 - \epsilon)\kappa^o(T, s), \quad T \in \mathcal{B}, s \in S,
\]
for all \( f \in C^b_{+}(S) \) with \( \|f\|_{\infty} \leq \delta \).

- The kernel family \( \{\kappa^f; f \in C^b_{+}(S)\} \) is called continuous at the zero function if for any \( \epsilon \in (0, 1) \) there is some \( \delta > 0 \) such that
\[
(1 - \epsilon)\kappa^o(T, s) \leq \kappa^f(T, s) \leq (1 + \epsilon)\kappa^o(T, s), \quad T \in \mathcal{B}, s \in S,
\]
for all \( f \in C^b_{+}(S) \) with \( \|f\|_{\infty} \leq \delta \).

3.1. Stability of the zero function in the subthreshold case. Recall the spectral radius \( r(\kappa^o) \) of the Feller kernel \( \kappa^o \) defined analogously to (2.6).

**Theorem 3.4.** Make Assumption 3.1. Let the kernel family \( \{\kappa^f; f \in C^b_{+}(S)\} \) be upper semicontinuous at the zero function and \( r = r(\kappa^o) < 1 \).

(a) Then 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,
\[
\|F^n(f)\|_{\infty} \leq M_\alpha\alpha^n\|f\|_{\infty}, \quad n \in \mathbb{N},
\]
if \( f \in C^b_{+}(S) \) with \( \|f\|_{\infty} \leq \delta_\alpha \).
3.2. Instability of the zero function in the superthreshold case.

Consider a subset \( \mathcal{N} \) given by

\[ \mathcal{N} = \{ \mu \in M_{+}(S) : \mu(S) > 0 \} \]

We can then extend this to a single measure \( \mu \in M_{+}(S) \) given by

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Remark 3.9. The assumption \( r(\kappa^o) > r(\kappa_1) \) implies part (a) of Theorem 3.8 without \( \kappa_1 \) necessarily being a tight kernel as well. In general, this assumption may not be easy to verify. In a population dynamics context, \( \kappa_1 \) is associated with survival, movement and individual development and \( \kappa_2 \) with reproduction. Since populations die out without reproduction, it is natural to assume that \( r(\kappa_1) \leq 1 \) or even \( r(\kappa_1) < 1 \). Then \( r(\kappa^o) > r(\kappa_1) \) follows from \( r(\kappa^o) > 1 \).

Theorem 3.10. Let Assumption 3.1 and the following assumptions be satisfied.

(a) The kernel family \( \{\kappa^j; \mu \in C^b_+(S)\} \) is lower semicontinuous at the zero function.

(b) \( \kappa^o = \kappa_1 + \kappa_2 \) with two Feller kernels \( \kappa_j \) of separable measures such that \( \kappa_2 \) is a tight kernel and \( r := r(\kappa^o) > r(\kappa_1) \) and \( r > 1 \).

(c) \( \kappa^o \) is top-irreducible.

Then the following two statements are equivalent:

(i) For all \( f \in \mathring{C}^b_+(S) \), there is some \( s \in S \) such that \( \kappa^j(\{f > 0\}, s) > 0 \).

(ii) There is some \( \delta_0 > 0 \) such for any \( f \in \mathring{C}^b_+(S) \) and any \( m \in \mathbb{N} \) there is some \( n \in \mathbb{N}, n \geq m \), with \( \|F^n(f)\|_{\infty} \geq \delta_0 \).

Proof. (i) is necessary for (ii). Suppose that (i) does not hold. Then there is some \( f \in \mathring{C}^b_+(S) \) such that \( \kappa^j(\{f > 0\}, s) = 0 \) for all \( s \in S \) and

\[
F(f)(s) = \int_{\{f > 0\}} f(t)\kappa^j(dt, s) \leq \|f\|_{\infty}\kappa^j(\{f > 0\}, s) = 0, \quad s \in S.
\]

Since \( F(0) = 0, F^n(f) = 0 \) for all \( n \in \mathbb{N} \), and (ii) is false.

Assume (i). We first show that \( F(f) \neq 0 \) for all \( f \in \mathring{C}^b_+(S) \). Let \( f \in \mathring{C}^b_+(S) \). By (i), there is some \( s \in S \) such that \( \kappa^j(\{f > 0\}, s) > 0 \). Since \( \{f > 0\} = \bigcup_{n \in \mathbb{N}} \{f \geq 1/n\} \) and the measure \( \kappa^j(\cdot, s) \) is continuous from below, there is some \( n \in \mathbb{N} \) such that \( \kappa^j(\{f \geq 1/n\}, s) > 0 \). For this \( s \),

\[
F(f)(s) \geq \int_{\{f \geq 1/n\}} f(t)\kappa^j(dt, s) \geq (1/n)\kappa^j(\{f \geq 1/n\}, s) > 0.
\]

\( \square \)
We apply [13, Thm.5.2] with $X = C^b(S)$, $Bf = \int_S f(t)\kappa^\circ(dt, \cdot)$ and $\theta(f) = \int_S f\,d\nu$ with the eigenmeasure $\nu$ from Theorem 3.8. By [30, Cor.6], $\theta(f) > 0$ for any $f \in X_+$. \hfill $\square$

**Corollary 3.11.** Let Assumption 3.1 be satisfied and assume the following:

(a) The kernel family $\{\kappa^\circ; \mu \in C^b(S)\}$ is lower semicontinuous at the zero function.

(b) $\kappa^\circ = \kappa_1 + \kappa_2$ with two Feller kernels $\kappa_j$ of separable measures such that $\kappa_2$ is a tight kernel and $r := r(\kappa^\circ) > r(\kappa_1)$ and $r > 1$.

(c) $\kappa^\circ$ is top-irreducible.

(d) For every $f \in C^b_+(S)$, there is some $\delta_f > 0$ such that

$$\kappa^\circ(T, s) \geq \delta_f \kappa^\circ(T, s), \quad s \in S, T \in \mathcal{B}.$$  

Then there is some $\delta_0 > 0$ such for any $f \in C^b(S)$ and any $m \in \mathbb{N}$ there is some $n \in \mathbb{N}, n \geq m$, with $\|F^n(f)\|_\infty \geq \delta_0$.

**Proof.** Define $\theta : C^b_+(S) \to \mathbb{R}_+$ by $\theta(f) = \int f\,d\nu$ with the eigenmeasure $\nu$ from Theorem 3.8. Let $f \in C^b_+(S)$. By (b),

$$\theta(F(f)) \geq \delta_f \int_S f(t)\kappa^\circ(dt, s) = \delta_f r(\kappa^\circ)\theta(f).$$

By (d) and [30, Cor.6], if $f \in C^b_+(S)$, $\theta(f) > 0$ and so $\theta(F(f)) > 0$ and $F(f) \neq 0$.

The claim now follows from Theorem 3.10. \hfill $\square$

### 3.3. The threshold condition.

In view of the results presented in this section, it is important whether $r(\kappa^\circ) < 1$ or $r(\kappa^\circ) > 1$. In Section 3.2 and 3.3, $\kappa^\circ = \kappa_1 + \kappa_2$ with two Feller kernels $\kappa_1$ and $\kappa_2$.

In an iteroparous population as we consider it in the next sections, the kernel $\kappa_1$ may be associated with adult survival and adult development and the kernel $\kappa_2$ with reproduction and first year development. If $r(\kappa_1) < 1$, $\kappa^\circ = \sum_{n=1}^{\infty} \kappa_2^n$ is a Feller kernel, and the Feller kernel

$$\kappa^\circ = \kappa_2 + \kappa_2 \ast \kappa^\infty_1 = \kappa_2 + \sum_{n=1}^{\infty} \kappa_2 \ast \kappa^*_1$$  

(3.2)

can be interpreted as next generation kernel and its spectral radius as basic [5] (or inherent net [2, 3]) reproduction number. We again like to think of $\kappa^\circ = \kappa_1 + \kappa_2$ as basic population turnover kernel and its spectral radius as basic turnover number; this spectral radius has also been called inherent population growth rate [2].

**Remark 3.12.** The following trichotomy holds if $r(\kappa_1) < 1$:

- $r(\kappa^\circ) > 1$ and $r(\kappa^\circ) > 1$

- $r(\kappa^\circ) = 1$ and $r(\kappa^\circ) = 1$

- $r(\kappa^\circ) < 1$ and $r(\kappa^\circ) < 1$.

See [29, Rem.3.14]. Notice that $\kappa_1$ and $\kappa_2$ have been reversed.

**Example 3.13.** In general, the spectral threshold condition may still be difficult to check. One special case is $\kappa_2(T, s) = \mu(T)\gamma(s)$ with a nonnegative finite measure
\( \mu \text{ and } \gamma \in C^b_+(S). \) Assume \( r(\kappa_1) < 1. \) Then
\[
\kappa^\circ(T, s) = \mu(T)\gamma^\infty(s), \quad \gamma^\infty(s) = \gamma(s) + \int_S \gamma(t)\kappa_1\infty(dt, s), \quad T \in \mathcal{B}, s \in S.
\]
By Example 2.2 and (3.2),
\[
r(\kappa^\circ) = \int_S \gamma^\infty d\mu = \int_S \gamma d\mu + \sum_{n=1}^\infty \int_S \left( \int_S \gamma(t)\kappa_1^n dt, s \right) \mu(ds).
\]

3.4. Compact attractor and uniform persistence.

**Assumption 3.14.** \( \{\kappa^f; f \in C^b_+(S)\} \) is a set of Feller kernels and \( \{\kappa^f(s, s); f \in C^b_+(S), s \in S\} \) is a bounded subset of \( \mathbb{R}. \)

**Lemma 3.15.** If Assumption 3.14 is satisfied, then \( F \) maps bounded subsets of \( C^b_+(S) \) into bounded subsets.

**Proof.** According to Assumption 3.14, choose some \( M > 0 \) such that \( \kappa^f(s, s) \leq M \) for all \( s \in S \) and \( f \in C^b_+(S). \) Then
\[
F(f)(s) \leq \|f\|_\infty M
\]
and
\[
\|F(f)\|_\infty \leq \|f\|_\infty M.
\]
This implies that \( F \) maps bounded subsets of \( C^b_+(S) \) into bounded subsets. \( \square \)

**Assumption 3.16.** There is some \( p \in (0, 1) \) and \( c \in (0, \infty) \) such that
\[
\kappa^f(\{f \geq c\}, s) \leq p, \quad s \in S, f \in C^b_+(S).
\]
Here \( \{f \geq c\} \) is a shorthand for \( \{t \in S; f(t) \geq c\}. \)

**Theorem 3.17.** Let the kernel family \( \{\kappa^f; f \in C^b_+(S)\} \) satisfy Assumptions 3.14 and 3.16.

Then, for any bounded subset \( B \) of \( C^b_+(S) \), there exists a bounded convex subset \( \hat{B} \) of \( C^b_+(S) \) such that \( F^n(B) \subseteq \hat{B} \) for all \( n \in \mathbb{N}. \)

Further, there exists a bounded convex subset \( B_0 \) of \( C^b_+(S) \) such that for each \( f \in C^b_+(S) \) there exists some \( m \in \mathbb{N} \) such that \( F^n(f) \in B_0 \) for all \( n \geq m. \)

If, in addition, \( F \) is continuous and some power (iterate) of \( F \) is compact, the semiflow induced by \( F \) has a compact attractor of bounded sets [25, Sec.2.2.3].

**Proof.** We apply [30, Thm.16] with \( \theta(f) = \|f\|_\infty \) for \( f \in C^b_+(S). \) By Lemma 3.15, \( F \) maps bounded subsets of \( C^b_+(S) \) to bounded subsets.

For all \( f \in C^b_+(S) \) and \( c > 0, \)
\[
F(f)(s) \leq \int_{\{f \geq c\}} f(t)\kappa^f(dt, s) + \int_{\{f < c\}} f(t)\kappa^f(dt, s)
\]
\[
\leq \|f\|_\infty \kappa^f(\{f \geq c\}, s) + c\kappa^f(S, s).
\]
According to Assumption 3.14, choose some \( M > 0 \) such that \( \kappa^f(s, s) \leq M \) for all \( s \in S \) and \( f \in C^b_+(S). \) Further choose \( c > 0 \) and \( p \in (0, 1) \) according to Assumption 3.16. Then
\[
\frac{\|F(f)\|_\infty}{\|f\|_\infty} \leq p + \frac{c}{\|f\|_\infty} M.
\]
Finally,
\[
\limsup_{\|f\|_\infty \to \infty} \frac{\|F(f)\|_\infty}{\|f\|_\infty} \leq p < 1.
\]
The assumptions of [30, Thm.16] are satisfied, which implies the assertion.  

**Assumption 3.18.** \( \{ \kappa^f : f \in C^b_+(S) \} \) is a family of Feller kernels such that, for any bounded subset \( Q \) of \( C^b_+(S) \) and any \( s \in S \),
\[
\sup_{f \in Q, t \in B} |\kappa^f(T, t) - \kappa^f(T, s)| \to 0 \quad \text{as} \quad S \ni t \to s.
\]

**Definition 3.19.** Let \( F \) be a set of functions \( f : S \to \mathbb{R} \) and \( s \in S \). \( F \) is called equicontinuous at \( s \) if for any \( \epsilon > 0 \) there exists some \( \delta > 0 \) such that \( |f(t) - f(s)| < \epsilon \) for all \( f \in F \) and all \( t \in S \) with \( d(t, s) < \delta \). \( F \) is called equicontinuous on \( S \) if it is equicontinuous at all \( s \in S \).

**Proposition 3.20.** Let \( \{ \kappa^f : f \in C^b_+(S) \} \) be a family of Feller kernels that satisfies Assumption 3.14 and Assumption 3.18 and let \( Q \) be a bounded subset of \( C^b_+(S) \). Then \( F(Q) \) is an equicontinuous bounded subset of \( C^b_+(S) \). If \( S \) is a compact metric space, \( F(Q) \) has compact closure.

**Proof.** Let \( h(t) = \sum_{i=1}^m \alpha_i \chi_{T_i} \) be a measurable function of finitely many values \( \alpha_1, \ldots, \alpha_m \), where \( T_i \in \mathcal{B} \) are pairwise disjoint. Then
\[
\left| \int_S h(t) \kappa^f(d\tilde{t}, t) - \int_S h(t) \kappa^f(d\tilde{t}, s) \right| \leq \|f\|_\infty \sum_{i=1}^m |\kappa^f(T_i, t) - \kappa^f(T_i, s)|.
\]
Since \( \kappa(\cdot, t) - \kappa(\cdot, s) \) is a real-valued measure and the \( T_i \) are pairwise disjoint,
\[
\left| \int_S h(t) \kappa^f(d\tilde{t}, t) - \int_S h(t) \kappa^f(d\tilde{t}, s) \right| \leq 2\|h\|_\infty \sup_{T \in \mathcal{B}} |\kappa^f(T, t) - \kappa^f(T, s)|. (3.3)
\]
If \( h \in M^b(S) \), \( h \) is the uniform limit of a sequence of such finitely-valued measurable functions and (3.3) holds for \( h \in M^b(S) \). This implies that, for all \( f \in C^b_+(S) \),
\[
|F(f)(t) - F(f)(s)| \leq 2\|f\|_\infty \sup_{T \in \mathcal{B}} |\kappa^f(T, t) - \kappa^f(T, s)|, \quad t, s \in S.
\]
Let \( Q \) be a bounded subset of \( C^b_+(S) \). Then there exists some \( c > 0 \) such that \( \|f\|_\infty \leq c \) for all \( f \in Q \) and
\[
|F(f)(t) - F(f)(s)| \leq 2c \sup_{T \in \mathcal{B}} |\kappa^f(T, t) - \kappa^f(T, s)|, \quad t, s \in S.
\]
By Assumption 3.18,
\[
\sup_{f \in Q} |F(f)(t) - F(f)(s)| \to 0, \quad t \to s, \quad \text{uniformly for} \quad f \in Q.
\]
This implies that \( F(Q) \) is an equicontinuous subset of \( C^b_+(S) \).

By Assumption 3.14 and Lemma 3.15, \( F(Q) \) is a bounded subset of \( C^b_+(S) \).

If \( S \) is a compact metric space, \( F(Q) \) has compact closure by the Arzela-Ascoli theorem.

**Assumption 3.21.** We assume:

(a) \( S \) is a separable metric space.

(b) If \( \{f_n\} \) is a bounded equicontinuous sequence in \( C^b_+(S) \) and \( f \in C^b_+(S) \) and \( f_n \to f \) as \( n \to \infty \) uniformly on every compact subset of \( S \), then
(i) \( \int_S f(t) \kappa^{f_n}(dt,s) \xrightarrow{n \to \infty} \int_S f(t) \kappa^f(dt,s) \) uniformly for \( s \in S \)

(ii) and \( \{ \kappa^{f_n}(\cdot,s); s \in S, n \in \mathbb{N} \} \) is tight.

**Proposition 3.22.** Let the family \( \{ \kappa^f; f \in C^b_+(S) \} \) of Feller kernels satisfy Assumption 3.14 and Assumption 3.21. Then the associated map \( F \) is continuous and maps bounded equicontinuous subsets of \( C^b_+(S) \) into subsets with compact closure.

**Proof.** To prove continuity of \( F \), we consider a sequence \((f_n)\) in \( C^b_+(S) \) and some \( f \in C^b_+(S) \) such that \( f_n \to f \) uniformly on \( S \) as \( n \to \infty \). Then \( \{ f_n; n \in \mathbb{N} \} \cup \{ f \} \) is compact in \( C^b_+(S) \) and thus equicontinuous. Then

\[
|F(f_n)(s) - F(f)(s)| \leq \int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) + \int_S |f(t)\kappa^{f_n}(dt,s) - f(t)\kappa^f(dt,s)|.
\]

By assumption,

\[
\limsup_{n \to \infty} \| F(f_n) - F(f) \|_{\infty} \leq \limsup_{n \to \infty} \| f_n - f \|_{\infty} \sup_{s \in S} \kappa^{f_n}(S,s) = 0.
\]

This finishes the proof of the continuity of \( F \).

Now let \( Q \) be an equicontinuous bounded subset of \( C^b_+(S) \). Let \( (f_n) \) be a sequence in \( Q \). It is sufficient to show that \( F(f_n) \) has a convergent subsequence in \( C^b_+(S) \).

By a version of the Arzela-Ascoli theorem [20, Thm.8.5], after choosing a subsequence, there is some \( f \in C^b_+(S) \) such that \( f_n \to f \) pointwise on \( S \) and uniformly on every compact subset of \( S \) as \( n \to \infty \). By the triangle inequality,

\[
|F(f_n)(s) - F(f)(s)| \leq \int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) + \int_S |f(t)\kappa^{f_n}(dt,s) - f(t)\kappa^f(dt,s)|.
\]

By our assumptions, it is sufficient to show that

\[
\int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) \to 0, \quad n \to \infty,
\]

uniformly for \( s \in S \).

Let \( K \) be a compact subset of \( S \) and \( \| \hat{f} \|_{\infty} \leq c \) for all \( \hat{f} \in Q \). Then

\[
\int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) \leq 2c \kappa^{f_n}(S \setminus K, s) + \sup_{t \in K} |f_n(t) - f(t)| \kappa^{f_n}(S,s).
\]

Since \( f_n \to f \) uniformly on any compact subset \( K \) of \( S \),

\[
\limsup_{n \to \infty} \sup_{s \in S} \int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) \leq \limsup_{n \to \infty} 2c \kappa^{f_n}(S \setminus K, s).
\]

Let \( \epsilon > 0 \). By Assumption 3.21 (ii), there exists some compact subset \( K \) of \( S \) such that \( \kappa^{f_n}(S \setminus K, s) \leq \epsilon \) for all \( n \in \mathbb{N} \) and \( s \in S \). So

\[
\limsup_{n \to \infty} \sup_{s \in S} \int_S |f_n(t) - f(t)| \kappa^{f_n}(dt,s) \leq 2c \epsilon
\]

for any \( \epsilon > 0 \) which implies that this limit superior is zero. \( \square \)

**Theorem 3.23.** Let Assumption 3.14, 3.18, and 3.21 be satisfied.

(a) Then \( F \) is continuous and \( F^2 \) is a compact map.
(b) If also Assumption 3.16 is satisfied, the semiflow induced by $F$ has a compact attractor of bounded sets.

Proof. By Proposition 3.22, $F$ is continuous and maps bounded equicontinuous subsets of $C^b_+(S)$ into subsets with compact closure. By Proposition 3.20, $F$ maps bounded subsets of $C^b_+(S)$ into bounded equicontinuous subsets. So $F^2$ is compact. Part (b) follows from Theorem 3.17.

**Theorem 3.24.** Let Assumption 3.14, 3.16, 3.18, 3.21 and the following assumptions be satisfied.

(a) The kernel family $\{\kappa^f; \mu \in C^b_+(S)\}$ is lower semicontinuous at the zero function.

(b) $\kappa^o = \kappa_1 + \kappa_2$ with two Feller kernels $\kappa_j$ and such that $\kappa_2$ is a tight kernel and $r := r(\kappa^o) > 1 \geq r(\kappa_1)$.

(c) $\kappa^o$ is top-irreducible.

(d) For all $f \in C^b_+(S)$, there is some $s \in S$ such that $\kappa^f(\{f > 0\}, s) > 0$.

Then uniform persistence of the population holds in the following ways:

(i) There is some $\delta_0 > 0$ with the following property: For any $f \in C^b_+(S)$ there is some $n_f \in \mathbb{N}$ such that $\|F^n(f)\|_{\infty} \geq \delta_0$ for all $n \in \mathbb{N}$ with $n \geq n_f$.

(ii) If $\mu \in \mathcal{M}_+(S)$ with $\int_S f d\mu > 0$ for all $f \in C^b_+(S)$, then there exists some $\delta_\mu > 0$ with the following property:

For any $f \in C^b_+(S)$ there is some $N(\mu, f) \in \mathbb{N}$ such that $\int_S F^n(f) d\mu \geq \delta_\mu$ for all $n \in \mathbb{N}$ with $n \geq N(\mu, f)$.

**Remark 3.25.** Recall that, under the assumptions of Theorem 3.24, there is an eigenmeasure $\nu \in \mathcal{M}_+(S)$ with $r\nu(T) = \int_S \kappa^o(T, s)\nu(ds)$ which has the property $\int_S f d\nu > 0$ for all $f \in C^b_+(S)$ (Theorem 3.8 (a)).

Other measures that are strictly positive in this sense can be constructed using the separability of $S$. Choose any set $\{s_n; n \in \mathbb{N}\}$ which is dense in $S$ and define $\mu(T) = \sum_{n=1}^{\infty} 2^{-n} \chi_T(s_n)$.

Proof of Theorem 3.24. (i) We apply [25, Thm.4.5], where $X = C^b_+(S)$ and the metric is induced by the supremum norm and $\rho = \|\cdot\|_{\infty}$. By Theorem 3.10, the semiflow induced by $F$ is uniformly weakly $\rho$-persistent. $\dot{\mathbf{0}}$ in [25, Thm.4.5] is satisfied because $F$ is continuous by Theorem 3.23 (a). $\dot{\mathbf{1}}$ is satisfied because $F(0) = 0$.

(ii) Let $\mu \in \mathcal{M}_+(S)$ with $\int_S f d\mu > 0$ for all $f \in C^b_+(S)$. We apply [25, Thm.4.21] where $X = C^b_+(S)$ and the metric is induced by the supremum norm and $\rho = \|\cdot\|_{\infty}$ and $\check{\rho}(f) = \int_S f d\mu$. Both $\rho$ and $\check{\rho}$ are continuous. Assumption (i) and (ii) in [25, Thm.4.21] are satisfied by Theorem 3.23 (b) and the fact that $\rho(f) > 0$ implies $\check{\rho}(f) > 0$.

4. More on Feller kernels.

**Proposition 4.1.** Let $P: \mathcal{B} \times S \to \mathbb{R}_+$ be a Feller kernel and $g \in C^b_+(S^2)$.

Assume that for any $\epsilon > 0$ there exists some subset $K$ of $S$ such that $P(S \setminus K, s) < \epsilon$ for all $s \in S$ and $\{g(s, t); t \in K\}$ is equicontinuous on $S$.

Then $\tilde{\kappa}: \mathcal{B} \times S \to \mathbb{R}_+$, given by

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

(4.1)
is a Feller kernel. In particular, \( \tilde{\kappa}(S, \cdot) \in \mathcal{C}^b(S) \).

For the concept of equicontinuity see Definition 3.19.

Proof. Let \( f \in \mathcal{C}^b(S) \). Set \( h(s) = \int_S f(t)\tilde{\kappa}(dt, s), \) \( s \in S \). To check the Feller property for \( \tilde{\kappa} \) (see (1.1)), we show that \( h \in \mathcal{C}^b(S) \). By (4.1) and standard measure-theoretic arguments,

\[
h(s) = \int_S f(t)g(s,t)P(dt,s), \quad s \in S.
\]

Since \( g \) and \( f \) are bounded and \( P(S, \cdot) \) is bounded, \( h \) is bounded.

To demonstrate the continuity of \( h \) on \( S \), let \( s \in S \) and \( (s_n) \) a sequence in \( S \) with \( s_n \rightarrow s \) as \( n \rightarrow \infty \).

To show that \( h(s_n) \rightarrow h(s) \) as \( n \rightarrow \infty \), let \( \epsilon > 0 \). By assumption, there exists a subset \( K \) of \( S \) such that \( P(S \setminus K, s) \leq \epsilon \) for all \( s \in S \) and \( \{g(\cdot,t); t \in K\} \) is equicontinuous on \( S \).

By the triangle inequality,

\[
|h(s_n) - h(s)| \\
\leq \int_S |f(t)| |g(s_n, t) - g(s, t)| P(dt, s_n) \\
+ \left| \int_S f(t)g(s,t)P(dt,s_n) - \int_S f(t)g(s,t)P(dt,s) \right|.
\]

Since, for any \( s \in S \), \( f(t)g(s,t) \) is a continuous bounded function of \( t \in S \) and \( P \) is a Feller kernel, the second expression on the right hand side of this inequality converges to 0 as \( n \rightarrow \infty \) and

\[
\limsup_{n \rightarrow \infty} |h(s_n) - h(s)| \leq \limsup_{n \rightarrow \infty} \int_S |f(t)| |g(s_n, t) - g(s, t)| P(dt, s_n) \\
\leq 2 \sup_{s \in S} |f| \sup_{s \in S} |g| \epsilon + \sup_{s \in S} |f| \limsup_{n \rightarrow \infty} \sup_{t \in K} |g(s_n, t) - g(s, t)| P(S, s_n).
\]

Since \( \{g(\cdot,t); t \in K\} \) is equicontinuous on \( S \),

\[
\limsup_{n \rightarrow \infty} \sup_{t \in K} |g(s_n, t) - g(s, t)| = 0.
\]

This implies that

\[
\limsup_{n \rightarrow \infty} |h(s_n) - h(s)| \leq 2 \sup_{s \in S} |f| \sup_{s \in S} |g| \epsilon.
\]

Since this holds for any \( \epsilon > 0 \), \( |h(s_n) - h(s)| \rightarrow 0 \) as \( n \rightarrow \infty \). \( \square \)

**Corollary 4.2.** Let \( P : \mathcal{B} \times S \rightarrow \mathbb{R}_+ \) be a Feller kernel, \( g \in \mathcal{C}^b_+(S^2) \) and \( \{g(\cdot,t); t \in S\} \) be equicontinuous on \( S \). Then \( \tilde{\kappa} : \mathcal{B} \times S \rightarrow \mathbb{R}_+ \),

\[
\tilde{\kappa}(T, s) = \int_T g(s,t)P(dt,s), \quad s \in S, T \in \mathcal{B},
\]

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

**Proof.** The critical assumption in Proposition 4.1 is satisfied with \( K = S \). \( \square \)

**Corollary 4.3.** Let \( P : \mathcal{B} \times S \rightarrow \mathbb{R}_+ \) be a Feller kernel and \( g \in \mathcal{C}^b_+(S^2) \). Assume that for any \( \epsilon > 0 \) there exists a compact subset \( T \) of \( S \) such that \( g(s,t) < \epsilon \) for all \( s \in S \) and \( t \in S \setminus T \).

Proof. The critical assumption in Proposition 4.1 is satisfied with \( K = S \). \( \square \)
Then $\tilde{\kappa} : \mathcal{B} \times S \to \mathbb{R}_+$,

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

(4.3)
is a tight Feller kernel. In particular, $\tilde{\kappa}(S, \cdot) \in C^b(S)$.

**Proof.** We first show that $\{g(\cdot, t); t \in S\}$ is equicontinuous on $S$. Suppose not. Then there exist some $s_0 \in S$, some $\epsilon > 0$ and sequences $(s_n), (t_n)$ in $S$ such that $s_n \to s_0$ as $n \to \infty$ and

$$|g(s_n, t_n) - g(s_0, t_n)| \geq \epsilon, \quad n \in \mathbb{N}. \quad (4.4)$$

By our assumption for $g$, there is some compact subset of $T$ of $S$ such that $g(s, t) < \epsilon/2$ for all $s \in S$ and $t \in S \setminus T$. By the triangle inequality and (4.4), $t_n \to t$ for all $n \in \mathbb{N}$. Since $g$ is continuous, it is uniformly continuous on the compact subset $\{s_n; n \in \mathbb{Z}_+\} \times T$ of $S^2$, contradicting (4.4).

By Corollary 4.2, $\tilde{\kappa}$ is a Feller kernel.

To show that $\tilde{\kappa}$ is tight, let $\epsilon > 0$. By our assumption for $g$, there exists a compact subset $T$ of $S$ such that $g(s, t) < \epsilon$ for all $s \in S$ and all $t \in S \setminus T$. For all $s \in S$,

$$\tilde{\kappa}(S \setminus T, s) \leq \int_{S \setminus T} \epsilon P(dt, s) = \epsilon P(S \setminus T, s) \leq \epsilon P(S, s).$$

Since $P(S, \cdot)$ is bounded on $S$ and $\epsilon > 0$ has been arbitrary, $\tilde{\kappa}$ is tight. \qed

**Corollary 4.4.** Let $P : \mathcal{B} \times S \to \mathbb{R}_+$ be a tight Feller kernel and $g \in C^b(S^2)$. Then $\tilde{\kappa} : \mathcal{B} \times S \to \mathbb{R}_+$,

$$\tilde{\kappa}(T, s) = \int_T g(s, t)P(dt, s), \quad s, T \in \mathcal{B}, \quad (4.5)$$
is a tight Feller kernel. In particular, $\tilde{\kappa}(S, \cdot) \in C^b(S)$.

**Proof.** $\tilde{\kappa}$ inherits tightness from $P$ via the boundedness of $g$.

We check the assumptions of Proposition 4.1. Let $\epsilon > 0$. Since $P$ is tight, there exists some compact subset of $S$ such that $P(S \setminus K, s) < \epsilon$ for all $s \in S$.

Suppose that $\{g(\cdot, t); t \in K\}$ is not equicontinuous on $S$. Then there exist some $s \in S$ and some $\delta > 0$ and sequences $(s_n)$ in $S$ and $(t_n)$ in $K$ such that $s_n \to s$ as $n \to \infty$ and $|g(s_n, t_n) - g(s, t_n)| > \epsilon$ for all $n \in \mathbb{N}$. Since $K$ is compact, $t_n \to t$ for some $t \in K$ as $n \to \infty$ after choosing subsequences. Since $g$ is continuous, $g(s_n, t_n) - g(s, t_n) \to 0$ as $n \to \infty$, a contradiction. \qed

Recall Definition 3.7.

**Lemma 4.5 ([30, Lem.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 (2.1). Then the following are equivalent:

(a) $\kappa$ 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 $f \in \tilde{C}^b_+(S)$, $S = \bigcup_{n \in \mathbb{Z}_+} \{A^*_n f > 0\} =: U(f)$.
(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 $\{s \in S; (A^*_n f)(s) > 0\}$. 

Remark 4.6. Let $\kappa : B \times S \to \mathbb{R}_+$ be a top-irreducible Feller kernel and not the zero kernel.

(a) If $S$ is not a singleton set, then $\kappa(S \setminus \{s\}, s) > 0$ for all $s \in S$.
(b) $\kappa(S, s) > 0$ for all $s \in S$.
(c) For any nonempty open subset $U$ of $S$, there is some $s \in S$ such that $\kappa(U, s) > 0$.

Proof. (a) 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 $\kappa$ is top-irreducible, by Lemma 4.5 (b), there exists some $\tilde{s} \in S \setminus T$ such that $\kappa(T, \tilde{s}) > 0$. Since $S \setminus T = \{s\}$, $\kappa(T, s) > 0$.

(b) By part (a), we only need to consider the case that $S$ is a singleton set in which the statement follows from $\kappa$ not being the zero kernel.

(c) If $U$ is a nonempty strict subset of $S$, this follows from Lemma 4.5 (b). If $U = S$, it follows from part (b). Recall that a metric space is not empty by definition.

5. A model for an iteroparous population. If the population is iteroparous, individuals reproduce several times during their life. If reproduction occurs during a short season in the year, neonates may develop differently from their parents during the rest of the year. We assume that neonates have turned into adults one year after their birth. Biologically, this is restrictive, but it seems better than modeling neonates in the same way as the rest of the population. The yearly population census is taken immediately before the reproductive season when every individuals present is an adult. Let $f_n \in C^b_+(S)$ be the structural distribution of the population in the $n$th year.

We consider the discrete-time integral equation

$$f_{n+1}(s) = \sum_{j=1}^{2} \int_S g_j(s, t, f_n) f_n(t) P_j(dt, s), \quad s \in S, n \in \mathbb{Z}_+.$$  \hspace{1cm} (5.1)

Here $P_j(T, s)$ is the probability that an individual that is at $s \in S$ at the end of the year and is older than one year was in $T$ at the beginning of the year. $g_1(s, t, f)$ is the fraction of individuals at $t$ at the beginning of the year with destination $s$ at the end of the year that actually make it there if the spatial density at the beginning of the year is $f$.

According to this interpretation,

$$g_1(s, t, f) \in [0, 1]$$  \hspace{1cm} (5.2)

is a natural assumption though we will not always make it.

$P_2(T, s)$ is the probability that an individual that is at $s \in S$ at the end of the year and is slightly younger than one year was born in $T$ at the beginning of the year. $g_2(s, t, f)$ is amount of offspring of individuals in $t$ at the beginning of the year that has $s \in S$ as the destination at the end of year and actually makes it there if the spatial density at the beginning of the year is $f$.

Here, $g_2 : S^2 \times C^b_+(S) \to \mathbb{R}_+$ and we write $g_j(s, t, o)$ if $f$ is the zero function.

Assumption 5.1. For $j = 1, 2$,

(a) $P_j$ are Feller kernels, $P_j(S, s) = 1$ for all $s \in S$.
(b) $g_j(\cdot, f) \in C^b_+(S^2)$ for all $f \in C^b_+(S)$.
F is of the form \((3.1)\) with

\[
\kappa^f = \kappa^f_1 + \kappa^f_2, \quad f \in C^b_c(S),
\]

\[
\kappa^f_j(T, s) = \int_T g_j(s, t, f)P_j(dt, s), \quad T \in \mathcal{B}, s \in S. \tag{5.3}
\]

We have

\[
\kappa^o = \kappa^o_1 + \kappa^o_2,
\]

\[
\kappa^o_j(T, s) = \int_T g_j(s, t, o)P_j(dt, s), \quad T \in \mathcal{B}, s \in S. \tag{5.4}
\]

Recall Definition 3.6.

**Assumption 5.2.** For \(j = 1, 2\), \(P_j\) is a tight Feller kernel or \(\{g_j(\cdot, t, f); t \in S\}\) is equicontinuous on \(S\) for all \(f \in C^b_c(S)\).

**Proposition 5.3.** The Assumptions 5.1 and 5.2 imply Assumption 3.1.

**Proof.** Apply Corollaries 4.2 and 4.4 to see that \(\kappa^f_j\) are Feller kernels for \(j = 1, 2\) and all \(f \in C^b_c(S)\). \(\square\)

**Theorem 5.4.** Let the Assumptions 5.1 and 5.2 be satisfied and \(r(\kappa^o) < 1\).

Let the functions \(g_j\) satisfy the follower upper continuity condition at the zero function:

For any \(\epsilon \in (0, 1)\) there is some \(\delta > 0\) such that

\[
g_j(s, t, f) \leq (1 + \epsilon)g_j(s, t, o), \quad \|f\|_{\infty} \leq \delta, s, t \in S.
\]

Then the statements (a) and (b) of Theorem 3.4 hold.

**Proof.** Continuity of the kernel family (5.3) at the zero function follows from the upper continuity condition for the functions \(g_j\) at the zero function \(\square\)

**Assumption 5.5.** We assume:

(a) \(P_2\) is a tight Feller kernel and \(P_1\) is a Feller kernel of separable measures.

(b) \(P_1\) is a tight Feller kernel, or \(\{g_1(\cdot, t, f); t \in S\}\) is equicontinuous for all \(f \in C^b_c(S)\).

(c) \(g_1(s, t, o) \leq 1\) for all \(s, t \in S\).

**Theorem 5.6.** Let the Assumptions 5.1 and 5.5 be satisfied and \(r(\kappa^o) > 1\).

Let the functions \(g_j\) satisfy the following lower continuity condition at the zero function:

For any \(\epsilon \in (0, 1)\) there is some \(\delta > 0\) such that

\[
(1 - \epsilon)g_j(s, t, o) \leq g_j(s, t, f), \quad \|f\|_{\infty} \leq \delta, s, t \in S.
\]

Then the statements (a) and (b) of Theorem 3.8 hold.

**Proof.** It follows from (5.4) and Assumption 5.1 (a) and Assumption 5.5 (c) that \(\kappa_1(S, s) \leq 1\) for all \(s \in S\) and so \(r(\kappa_1^o) \leq 1\). Further, \(\kappa_2^o\) is a tight Feller kernel by Corollary 4.4. The Assumptions 5.5 imply the Assumptions 5.2. The lower semicontinuity of the kernel family (5.3) follows from the lower continuity condition for \(g_j\) at the zero function. By Proposition 5.3, all assumptions of Theorem 3.8 are satisfied and (a) and (b) of its conclusions follow. \(\square\)
5.1. Uniform weak persistence. Recall Definition 3.7.

Assumption 5.7. The following is assumed for newborn individuals.
(a) For all $f \in \mathcal{C}_b^+(S)$, $g_2(s,t,f) > 0$ for all $s,t \in S$.
(b) $P_2$ is a top-irreducible tight Feller kernel.
(c) The functions $g_j$ satisfy the following lower continuity condition at the zero function:
   For any $\epsilon \in (0,1)$ there is some $\delta > 0$ such that
   $$(1 - \epsilon)g_j(s,t,o) \leq g_j(s,t,f), \quad \|f\|_\infty \leq \delta, s,t \in S.$$  

Proposition 5.8. If Assumption 5.1, 5.5 and 5.7 hold and $P_2$ is not the zero kernel, then $F(f) \neq 0$ for all $f \in \mathcal{C}_b^+(S)$, $\kappa^o$ is top-irreducible, and the kernel family (5.3) is lower semicontinuous at the zero function.

Proof. Let $f \in \mathcal{C}_b^+(S)$. Then $U = \{t \in S; f(t) > \|f\|_\infty/2\}$ is a non-empty open subset of $S$. Since Assumption 5.7 (b) holds and $P_2$ is not the zero kernel, there is some $s \in S$ such that $P_2(U,s) > 0$ by Remark 4.6 (c). For this $s$,

$$F(f)(s) \geq (\|f\|_\infty/2) \int_U g_2(s,t,f)P_2(dt,s). \tag{5.5}$$

By Assumption 5.7 (a), $g_2(s,t,f) > 0$ for all $s \in S$. Hence, $U = \bigcup_{n \in \mathbb{N}} U_n$ with

$$U_n = \{t \in U; g_2(s,t,f) > 2/n\}.$$

Since the $U_n$ form an increasing sequence of open subsets of $U$ and $P_2(\cdot, s)$ is continuous from below, $P(U,s) = \lim_{n \to \infty} P(U_n,s)$. Since $P(U,s) > 0$, there exists some $n \in \mathbb{N}$ such that $P(U_n,s) > 0$. By (5.5),

$$F(f)(s) \geq (\|f\|_\infty/2) \int_{U_n} g_2(s,t,f)P_2(dt,s) \geq (\|f\|_\infty/n)P_2(U_n,s) > 0.$$

The proof that $\kappa^o$ inherits top-irreducibility from $P_2$ is similar.

The lower semicontinuity of kernel family (5.3) follows from that of the functions $g_j$ (Assumption 5.7 (c)). \hfill \Box

Theorem 5.9. Let the Assumptions 5.1, 5.5 and 5.7 be satisfied and $r(\kappa^o) > 1$.

Then the population is uniformly weakly persistent: There is some $\delta_0 > 0$ such for any $f \in \mathcal{C}_b^+(S)$ and any $m \in \mathbb{N}$ there is some $n \in \mathbb{N}$, $n \geq m$, with $\|F^n(f)\|_\infty \geq \delta_0$.

Proof. It follows from (5.4), Assumption 5.1 (a) and Assumption 5.5 (c) that $\kappa_1(S,s) \leq 1$ for all $s \in S$ and so $r(\kappa^o_1) \leq 1$. Since $r(\kappa^o) > 1$, $P_2$ is not the zero kernel by (5.3). By Proposition 5.3, all assumptions of Theorem 3.10 are satisfied and its conclusion follows. By Proposition 5.8, statement (i) in Theorem 3.10 holds and so does the equivalent statement (ii), which is our persistence statement above. \hfill \Box

5.2. Compact attractor and uniform persistence.

Assumption 5.10. For $j = 1, 2$,

(a) $P_j$ is a tight uniform Feller kernel,
(b) $\{g_j(s,t,f); s,t \in S, f \in \mathcal{C}_b^+(S)\}$ is a bounded subset of $\mathbb{R}$.

Lemma 5.11. Assumption 5.1 and Assumption 5.10 imply Assumption 3.1 and Assumption 3.14. Further, $\{\kappa^j(\cdot, s); f \in \mathcal{C}_b^+(S), s \in S\}$ is a tight set of measures.
Proof. Since the $P_j$ are tight Feller kernels, Assumption 5.2 is satisfied and Assumption 3.1 holds by Proposition 5.3.

By Assumption 5.10 (b), there exists some $M > 0$ such that $g_j(s,t,f) \leq M$ for $J = 1, 2$, all $s,t \in S$ and all $f \in C^b_k(S)$. Then

$$\kappa_J(S,s) = \sum_{j=1}^{2} \int_S g(s,t,f)P_j(dt,s) \leq \sum_{j=1}^{2} M_j P_j(S,s) \leq M_1 + M_2.$$ 

The last inequality follows from Assumption 5.1 (a).

Let $c > 0$. Since $P_1$ and $P_2$ are tight Feller kernel by Assumption 5.10 (a), there exist compact subsets $K_1$ and $K_2$ of $S$ such that

$$P_j(S \setminus K_j,s) < \frac{c}{2M}, \quad j = 1, 2, \quad s \in S.$$ 

Set $K = K_1 \cup K_2$. Then $K$ is a compact subset of $S$ and, by (5.3),

$$\kappa_J(S, K, s) \leq M \sum_{j=1}^{2} P_j(S \setminus K_j, s) < c, \quad s \in S, f \in C^b_k(S). \quad \square$$

**Assumption 5.12.** For any bounded subset $Q$ of $C^b_k(S)$ and any compact subset $K$ of $S$ and any $s_0 \in S$, $|g_j(s, t, f) - g_j(s_0, t, f)| \to 0$ as $s \to s_0$ uniformly for $t \in K$ and $f \in Q$.

**Lemma 5.13.** Let the Assumptions 5.1, 5.10 and 5.12 be satisfied.

Then the kernel family $\{\kappa_J; f \in C^b_k(S)\}$ given by (5.3) satisfies Assumption 5.18. In particular, $\kappa_J$ is a uniform Feller kernel for any $f \in C^b_k(S)$, and $F(Q)$ is a bounded equicontinuous subset of $C^b_k(S)$ for any bounded subset of $Q$ of $C^b_k(S)$.

Proof. Let $Q$ be a bounded subset of $C^b_k(S)$ and $(s_n)$ be a sequence in $S$ and $s \in S$ and $s_n \to s$ as $n \to \infty$. In the following we suppress the index $j$ except for $\kappa_J$. For all $t \in B$,

$$|\kappa_J(T, s_n) - \kappa_J(T, s)|
\leq \left| \int_S \chi_T(t) g(s_n, t, f) |P(dt, s_n) - P(dt, s)| \right|
+ \int_T |g(s_n, t, f) - g(s, t, f)| P(dt, s)
\leq 2 \sup_{t \in S} g(s_n, t, f) \sup_{t \in B} |P(T, s_n) - P(T, s)|
+ \int_S |g(s_n, t, f) - g(s, t, f)| P(dt, s).$$

By assumption, there exists some $c > 0$ such that $g(\tilde{s}, t, f) \leq c$ for all $\tilde{s}, t \in S$ and $f \in Q$. For any compact subset $K$ of $S$,

$$\sup_{T \in B} |\kappa_J(T, s_n) - \kappa_J(T, s)|
\leq 2c \sup_{T \in B} |P(T, s_n) - P(T, s)| + 2c P(s, S \setminus K)
+ \int_K |g(s_n, t, f) - g(s, t, f)| P(dt, s).$$
Since $P$ is a uniform Feller kernel,
\[
\limsup_{n \to \infty} \sup_{T \in B, f \in Q} |\kappa^f_j(T, s_n) - \kappa^f_j(T, s)|
\leq 2cP(s, S \setminus K) + \sup_{f \in Q, t \in K} |g(s_n, t, f) - g(s, t, f)| P(S, s).
\]

By Assumption 5.12 and Assumption 5.1, for any compact subset $K$ of $S$,
\[
\limsup_{n \to \infty} \sup_{T \in B, f \in Q} |\kappa^f_j(T, s_n) - \kappa^f_j(T, s)| \leq 2cP(s, S \setminus K).
\]

Since $P$ is a tight kernel,
\[
\limsup_{n \to \infty} \sup_{T \in B, f \in Q} |\kappa^f_j(T, s_n) - \kappa^f_j(T, s)| = 0.
\]

Assumption 3.18 now follows from $\kappa^f = \kappa^f_1 + \kappa^f_2$ and the triangle inequality.

Assumption 3.14 also follows by Lemma 5.11.

By Proposition 3.20, $F(Q)$ is a bounded equicontinuous subset of $\mathcal{C}_+(S)$ for any bounded subset $Q$ of $\mathcal{C}_+(S)$.

**Assumption 5.14.** There exist $p_1, p_2 > 0$ and $c \in (0, \infty)$ such that $p_1 + p_2 < 1$ and
\[
g_j(s, t, f) \leq p_j, \quad s, t \in S, f \in \mathcal{C}_+(S), f(t) \geq c.
\]

**Lemma 5.15.** Let Assumption 5.1 and Assumption 5.14 be satisfied. Then Assumption 5.16 is satisfied.

**Proof.** Choose $p_1, p_2, c$ according to Assumption 5.14. Then, for all $s \in S$ and $f \in \mathcal{C}_+(S)$,
\[
\kappa^f(\{ f \geq c \}, s) = \sum_{j=1}^{2} \int_{S} g_j(s, t, f) \chi_{\{ f \geq c \}}(t) P_j(dt, s) 
\leq p_1 P_j(s, s) + p_2 P_j(s, s) \leq p_1 + p_1 < 1.
\]

The last inequality follows from Assumption 5.1 (a). \hfill \Box

**Assumption 5.16.** $S$ is separable and,

if $(f_n)$ is a bounded sequence in $\mathcal{C}_+(S)$ and $f \in \mathcal{C}_+(S)$ and $f_n \to f$ uniformly on every compact subset of $S$, then, for every compact subset $K$ of $S$,
\[
g_j(s, t, f_n) \to g_j(s, t, f) \text{ as } n \to \infty \text{ uniformly for } s \in S \text{ and } t \in K, j = 1, 2.
\]

**Proposition 5.17.** Let Assumption 5.1, Assumption 5.10, and Assumption 5.16 be satisfied. Then Assumption 3.21 holds. In particular, the turnover map $F$ is continuous and maps equicontinuous bounded subsets of $\mathcal{C}_+(S)$ into subsets with compact closure.

**Proof.** $\{ \kappa^f(\cdot, s); f \in \mathcal{C}_+(S), s \in S \}$ is a tight set of measures by Lemma 5.11.

Let $(f_n)$ be a sequence in $\mathcal{C}_+(S)$ and $f \in \mathcal{C}_+(S)$ such that $f_n \to f$ uniformly on every compact subset of $S$. By Assumption 5.10, there exists some $M > 0$ such that $g_j(s, t, f) \leq M$ for $j = 1, 2$, all $s, t \in S$ and all $f \in \mathcal{C}_+(S)$. For all $n \in \mathbb{N}$,
\[
L_n(s) := \left| \int_S f(t) \kappa^{f_n} (dt, s) - \int_S f(t) \kappa^f (dt, s) \right| 
\leq \sum_{j=1}^{2} \left| \int_S f(t) (g_j(s, t, f_n) - g_j(s, t, f)) \right| P_j(dt, s).
\]
Let $K_j$ be compact subsets of $S$, $j = 1, 2$. Then this can be estimated by
\[
L_n(s) \leq 2 \sum_{j=1}^{2} \|f\|_{\infty} M_j P_j(S \setminus K_j, s) + \sum_{j=1}^{2} \|f\|_{\infty} \int_{K_j} |g_j(s, t, f_n) - g_j(s, t, f)| P_j(dt, s)
\]
By Assumption 5.16,
\[
\limsup_{n \to \infty} \sup_{s \in S} L_n(s) \leq 2 \sum_{j=1}^{2} \|f\|_{\infty} M_j \epsilon.
\]

Let $\epsilon > 0$. Since $P_j$ are tight Feller kernels for $j = 1, 2$, we can choose compact subsets $K_j$ of $S$ such that $P_j(S \setminus K_j, s) \leq \epsilon$ for $j = 1, 2$ and $s \in S$. So
\[
\limsup_{n \to \infty} \sup_{s \in S} L_n(s) = 0 \quad \text{and} \quad \int_{S} f(t) \kappa^{f_n}(dt, s) \to \int_{S} f(t) \kappa^f(dt, s), \quad n \to \infty,
\]
uniformly for $s \in S$.

**Theorem 5.18.** Let Assumption 5.1, 5.10, 5.12, 5.14 and 5.16 be satisfied. Then the semiflow induced by $F$ and the kernel family (5.3) has a compact attractor of bounded sets.

**Proof.** We check the assumptions of Theorem 3.23.

Assumption 3.1 and 3.14 are satisfied by Proposition 5.3 and Lemma 5.11.

Assumption 3.18 is satisfied by Lemma 5.13. and Assumption 3.21 is satisfied by Proposition 5.17. □

**Theorem 5.19.** Let Assumption 5.1, 5.7, 5.10, 5.12, 5.14 and 5.16 be satisfied. Assume that $g_1(s, t, o) \leq 1$ for all $s, t \in S$ and $r(\kappa^o) > 1$.

Then the population persists uniformly in the sense of Theorem 3.24.

**Proof.** The assumptions of Theorem 5.18 and of Theorem 5.9 are satisfied. These two theorems imply uniform persistence in a similar way as in the proof of Theorem 3.24. □

**Remark 5.20.** For biological justification of $g_1(s, t, 0) \leq 1$ see (5.2). Mathematically, together with $P_1(S, s) = 1$, it implies that $r(\kappa_1) \leq 1 < r(\kappa^o)$. See Remark 3.9.

6. **A special model for an iteroparous species.** We consider a special case of (5.1) where, for $j = 1, 2$,
\[
g_j(s, t, f) = \hat{g}_j(s, t, f_j(t)) \quad \text{and} \quad f_j(t) = f(t) + \int_{S} f(u) \hat{\kappa}_j(du, t), \quad s, t \in S, \quad f \in C^b(S),
\]
with $\hat{g}_j : S^2 \times \mathbb{R}_+ \to \mathbb{R}_+$ and Feller kernels $\hat{\kappa}_j : \mathcal{B} \times S \to \mathbb{R}_+.$
More generally at first look, one could consider \( f_j(t) = \alpha_j f(t) + \int_S f(u) \tilde{\kappa}_j(du, t) \) with \( \alpha_j > 0 \), but \( \alpha_j \) can be absorbed into \( \tilde{g}_j \) and \( \tilde{\kappa}_j \).

The threshold kernel \( \kappa^\alpha \) takes the form

\[
\kappa^\alpha(T, s) = \sum_{j=1}^2 \int_T \tilde{g}_j(s, t, 0) P(dt, s), \quad T \in \mathcal{B}, s \in S. \tag{6.2}
\]

**Assumption 6.1.** For \( j = 1, 2 \),

\( \tilde{g}_j : S^2 \times \mathbb{R}_+ \to \mathbb{R}_+ \) and \( P_j, \tilde{\kappa}_j : \mathcal{B} \times S \to \mathbb{R}_+ : 
\)

(a) \( P_j \) are tight Feller kernels, \( P_j(S, s) = 1 \) for all \( s \in S \).

(b) \( \tilde{g}_j \) is continuous.

(c) \( \tilde{\kappa}_j \) are Feller kernels.

**Lemma 6.2.** If Assumption 6.1 is satisfied, so are Assumptions 5.1 and 5.2.

**Proof.** To check Assumption 5.1 (b), let \( f \in C^b_+ (S) \). Since \( \tilde{\kappa}_j \) is a Feller kernel, \( f_j \in C^b_+ (S) \) and \( g_j \) is a continuous function of \((s, t) \in S^2 \) as composition of continuous functions where \( f_j \) and \( g_j \) are as in (6.1).

Assumption 5.2 follows from Assumption 6.1 (a). \qed

**Theorem 6.3.** Let Assumption 6.1 be satisfied and \( r(\kappa^\alpha) < 1 \).

Let \( \tilde{g}_j \) satisfy the following upper continuity property:

For any \( \epsilon \in (0, 1) \), there is some \( \delta > 0 \) such that

\[
\tilde{g}_j(s, t, q) \leq (1 + \epsilon)\tilde{g}_j(s, t, 0), \quad s, t \in S, \quad 0 \leq q \leq \delta.
\]

Then the statements (a) and (b) of Theorem 3.4 hold.

**Proof.** Combine Lemma 6.2 and Theorem 5.4. \qed

**Assumption 6.4.** We assume:

(a) For all \( q \in \mathbb{R}_+ \), \( \tilde{g}_2(s, t, q) > 0 \) for all \( s, t \in S \).

(b) \( P_2 \) is top-irreducible.

(c) \( \tilde{g}_1(s, t, 0) \leq 1 \) for all \( s, t \in S \).

(d) The functions \( \tilde{g}_j \) satisfy the following lower semi-continuity condition:

For any \( \epsilon \in (0, 1) \) there exists some \( \delta > 0 \) such that

\[
(1 - \epsilon)\tilde{g}_j(s, t, 0) \leq \tilde{g}_j(s, t, q), \quad s, t \in S, \quad 0 \leq q \leq \delta.
\]

**Lemma 6.5.** If Assumption 6.4 is satisfied, so are Assumption 5.5 and 5.7.

**Theorem 6.6.** Let Assumption 6.1 and 6.4 be satisfied and \( r(\kappa^\alpha) > 1 \).

Then the population is uniformly weakly persistent in the sense of Theorem 5.9.

**Assumption 6.7.** For \( j = 1, 2 \),

(a) \( P_j \) is a tight uniform Feller kernel,

(b) \( \tilde{g}_j \) is bounded on \( S^2 \times \mathbb{R}_+ \).

**Lemma 6.8.** Let Assumption 6.1 and 6.7 be satisfied. Then Assumption 5.10 is satisfied.

**Lemma 6.9.** Let Assumption 6.1 be satisfied. Then Assumption 5.12 holds.

**Proof.** Let \( Q \) be a bounded subset of \( C^b_+ (S) \). Then there exists some \( c \in (0, \infty) \) such that \( f(t) + \int_S f(u) \tilde{\kappa}_j(du, t) \leq c \) for all \( t \in S, f \in Q, j = 1, 2 \). By (6.1),

\[
\sup_{f \in Q} |g_j(s, t, f) - g_j(s_0, t, f)| \leq \sup_{q \in [0, c]} |\tilde{g}_j(s, t, q) - \tilde{g}_j(s_0, t, q)|.
\]
Suppose that there is some compact set $T$ of $S$ such that $\sup_{q \in [0,c]} |\tilde{g}_j(s,t,q) - \tilde{g}_j(s_0,t,q)|$ does not tend to 0 uniformly for $t \in T$ as $s \to s_0$. Then there exist some $\epsilon > 0$ and sequences $(s_n)_{n \in \mathbb{N}}$ and $(t_n)_{n \in \mathbb{N}}$ in $T$ and $(q_n)$ in $[0,c]$ such that $s_n \to s_0$ as $n \to \infty$ and

$$\left|\tilde{g}_j(s_n,t_n,q_n) - \tilde{g}_j(s_0,t_n,q_n)\right| \geq \epsilon, \quad n \in \mathbb{N}.$$  

Since $\tilde{g}_j$ is continuous by Assumption 6.1 (b), it is uniformly continuous on the compact set $\{s_n : n \in \mathbb{Z}_+\} \times T \times [0,c]$, which yields a contradiction.

**Assumption 6.10.** There exist $p_1, p_2 > 0$ and $c \in (0, \infty)$ such that $p_1 + p_2 < 1$ and, for $j = 1, 2$,

$$\tilde{g}_j(s,t,q) \leq p_j, \quad s, t, q \in S, q \geq c.$$

**Lemma 6.11.** If Assumption 6.1 and 6.10 are satisfied, so is Assumption 5.14.

**Proof.** Let $f \in C^b_+(S)$ and $s, t \in S$ and $f(t) \geq c$. Then $f(t) + \int_S f(u)\tilde{\kappa}_j(du,t) \geq c$ and the conclusion is straightforward from (6.1).

**Assumption 6.12.** $S$ is separable and, for $j = 1, 2$,

(a) $\tilde{\kappa}_j$ is a tight Feller kernel,

(b) $\{\tilde{g}_j(s, \cdot) : s \in S\}$ is a family of equicontinuous functions on $S \times \mathbb{R}_+$.

**Lemma 6.13.** If Assumption 6.1 and 6.12 are satisfied, so is Assumption 5.16. In particular, $F(Q)$ has compact closure for any bounded equicontinuous subset of $C^b_+(S)$.

**Proof.** Let $(f_n)$ be a bounded sequence in $C^b_+(S)$ and $f \in C^b_+(S)$ and $f_n \to f$ as $n \to \infty$ uniformly on every compact subset of $S$.

Define $f_j$ as in (6.1) and

$$f_{j,n}(t) = f_n(t) + \int_S f_n(u)\tilde{\kappa}_j(du,t), \quad t \in S, n \in \mathbb{N}. \quad (6.3)$$

We first show that $f_{j,n} \to f_j$ as $n \to \infty$ uniformly on every compact subset of $S$. Let $K$ be a compact subset of $S$. By the triangle inequality, for all $t \in S$,

$$\left|f_{j,n}(t) - f_j(t)\right| \leq \left|f_n(t) - f(t)\right| + \int_{S \setminus K} |f_n(u) - f(u)|\tilde{\kappa}_j(du,t)$$

$$+ \int_K |f_n(u) - f(u)|\tilde{\kappa}_j(du,t).$$

For all $t \in S$,

$$\left|f_{j,n}(t) - f_j(t)\right| \leq \left|f_n(t) - f(t)\right| + \left(\|f_n\|_{\infty} + \|f\|_{\infty}\right)\tilde{\kappa}_j(S \setminus K, t)$$

$$+ \sup_{u \in K} |f_n(u) - f(u)|\tilde{\kappa}_j(S, t).$$

Let $T$ be also a compact subset of $S$. Then

$$\sup_{t \in T} \left|f_{j,n}(t) - f_j(t)\right| \leq \sup_{t \in T} \left|f_n(t) - f(t)\right|$$

$$+ \left(\|f_n\|_{\infty} + \|f\|_{\infty}\right)\sup_{t \in T} \tilde{\kappa}_j(S \setminus K, t)$$

$$+ \sup_{u \in K} \left|f_n(u) - f(u)\right|\sup_{t \in T} \tilde{\kappa}_j(S, t).$$

Since $f_n \to f$ as $n \to \infty$ uniformly on $K$ and $T$,

$$\limsup_{n \to \infty} \sup_{t \in T} \left|f_{j,n}(t) - f_j(t)\right| \leq \left(\sup_{n \in \mathbb{N}} \|f_n\|_{\infty} + \|f\|_{\infty}\right)\sup_{t \in T} \tilde{\kappa}_j(S \setminus K, t)$$
for any compact subset $K$ of $S$. Let $\epsilon > 0$. Since $\kappa_j$ is a tight Feller kernel, there exists some compact subset $K$ of $S$ such that $\kappa_j(S \setminus K, t) \leq \epsilon$ for all $t \in S$. Thus
\[
\limsup_{n \to \infty} \sup_{t \in T} |f_{j,n}(t) - f_j(t)| \leq (\sup_{n \in \mathbb{N}} \|f_{n}\|_{\infty} + \|f\|_{\infty}) \epsilon.
\]
Since this holds for any $\epsilon > 0$, this expression is 0 and $f_{j,n} \to f_j$ as $n \to \infty$ uniformly on every compact subset of $S$.

Now
\[
|g_j(s,t,f_{n}) - g_j(s,t,f)| = |\tilde{g}_j(s,t,f_{j,n}(t)) - \tilde{g}_j(s,t,f_j(t))|.
\]
Assume that there is a compact subset $K$ of $S$ such that $g_j(s,t,f_{n}) - g_j(s,t,f)$ does not converge to 0 as $n \to \infty$ uniformly for $s \in S$ and $t \in K$. Then there exists some $\epsilon > 0$ such that, after choosing a subsequence of $(f_n)$, there exist sequences $(s_n)$ in $S$ and $(t_n)$ in $K$ such that
\[
\epsilon \leq |\tilde{g}_j(s_n,t_n,f_{j,n}(t_n)) - \tilde{g}_j(s_n,t_n,f_j(t_n))|, \quad n \in \mathbb{N}.
\]
Since $K$ is compact, after choosing subsequences again, $t_n \to t$ as $n \to \infty$ for some $t \in K$. Since $f_{j,n} \to f_j$ uniformly on $K$, $f_{j,n}(t_n) \to f_j(t_n)$ and $f_j(t_n) \to f_j(t)$ as $n \to \infty$. Since $\{\tilde{g}_j(s,\cdot); s \in S\}$ is an equicontinuous family of functions on $S \times \mathbb{R}_+$, $|\tilde{g}_j(s_n,t_n,f_{j,n}(t_n)) - \tilde{g}_j(s_n,t_n,f_j(t_n))| \to 0$ as $n \to \infty$, a contradiction.

**Theorem 6.14.** Let Assumption 6.1, 6.7, 6.10 and 6.12 be satisfied.

Then the semiflow induced by $F$ via the kernel family (5.3) with (6.1) has a compact attractor of bounded sets.

**Remark 6.15.** Assumption 6.1 (c) is not needed for this theorem.

**Proof.** Combine Theorem 5.18 with Lemma 6.2, 6.8, 6.11, and 6.13.

**Theorem 6.16.** Let Assumption 6.1, 6.4, 6.7, 6.10 and 6.12 be satisfied.

Then the population persists uniformly in the sense of Theorem 3.24.

**Proof.** Combine Theorem 5.19 with Lemma 6.2, 6.5, 6.8, 6.11, and 6.13.

7. Uniform persistence if only one kernel is a uniform Feller kernel. In special cases, it is not necessary for uniform persistence that both Feller kernels are uniform Feller kernels.

For simplicity we look at the case were nonlinear feedback is completely local, $\kappa_j = 0$, $j = 1, 2$, in (6.1). It is convenient to write the turnover map as
\[
F(f)(s) = \left\{ \begin{array}{c}
\sum_{j=1}^{2} \int_{S} h_j(s,t,f(t)) P_j(dt,s) \quad f \in C^b_+(S) \\
h_j(s,t,q) = \tilde{g}_j(s,t,q)q, \quad q \in \mathbb{R}_+
\end{array} \right\} \quad s \in S.
\]

The threshold kernel takes the form
\[
\kappa^\omega(T,s) = \sum_{j=1}^{2} \int_{T} \tilde{g}_j(s,t,0) P_j(dt,s), \quad s \in S, T \in \mathcal{B}.
\]

As for Theorem 6.3 and 6.6, this is just a special case. As for uniform persistence, we want to assume that only $P_2$ is a uniform Feller kernel and replace the uniform Feller property of $P_1$ by Lipschitz conditions for $h_j$ with a particularly stringent one for $h_1$.

**Assumption 7.1.** $S$ is a separable metric space.

(a) Both $P_j$ are tight Feller kernels, $P_j(S,s) = 1$ for all $s \in S$. 

(b) $P_2$ is a uniform Feller kernel.
(c) Lipschitz conditions for $h_j$: For any $c \in (0, \infty)$ and $j = 1, 2,$
\[ |h_j(s, t, q) - h_j(s, t, \tilde{q})| \leq \Lambda_j(c)|q - \tilde{q}|, \quad s, t \in S, \quad q, \tilde{q} \in [0, c], \]
\[ \Lambda_1(c) \in (0, 1), \Lambda_2(c) \in (0, \infty). \]
(d) $\tilde{g}_j$ is continuous and bounded on $S^2 \times \mathbb{R}$.
(e) For $j = 1, 2$, $\{\tilde{g}_j(s, \cdot); s \in S\}$ is a set of equicontinuous functions on $S \times \mathbb{R}_+.$
(f) $\tilde{g}_2(s, t, q) > 0$ for all $s, t \in S, q \in \mathbb{R}_+.$

Lemma 7.2. Let Assumption 7.1 be satisfied. Then
\[ F^n(f) = G_n(f) + H_n(f), \quad n \in \mathbb{N} \quad f \in C_b^1(S), \]
with maps $G_n$ on $C_b^1(S)$ and $H_n$ from $C_b^1(S)$ to $C_b(S)$ such that, for all bounded subsets $Q$ of $C_b^1(S)$ with $F(Q) \subseteq Q$, $G_n(Q)$ is an equicontinuous subset of $C_b^1(S)$, $G_n(Q) \subseteq [0, 2c]^S$ and there is some $\Lambda_1 = \Lambda_1(Q) \in (0, 1)$ with
\[ \|H_n(f)\|_\infty \leq \Lambda_1^n(Q)\|f\|_\infty, \quad f \in Q, n \in \mathbb{N}. \]

Proof: The maps $G_n$ and $H_n$ are constructed inductively.

Let $Q \subseteq C_b^1(S)$ with $F(Q) \subseteq Q$. Choose some $c \in [0, \infty)$ such that $Q \subseteq [0, c]^S$. Then $F^n(Q) \subseteq [0, c]^S$ for all $n \in \mathbb{N}$. Choose $\Lambda_1 = \Lambda_1(Q) = \Lambda_1(2c) \in (0, 1)$ according to Assumption 7.1 (c).

For $n = 1$,
\[ G_1(f)(s) = \int_S h_2(s, t, f(t)) P_2(dt, s), \]
\[ H_1(f)(s) = \int_S h_1(s, t, f(t)) P_1(dt, s). \]

Since $h_1(s, t, 0) = 0$, by Assumption 7.1 (a) and (c),
\[ |H_1(f)(s)| \leq \Lambda_1(2c)P_1(S, s)\|f\|_\infty = \Lambda_1(2c)\|f\|_\infty, \quad f \in Q. \]

For a bounded subset $Q$ of $C_b^1(S)$, $G_1(Q)$ is equicontinuous because of Assumption 7.1 (b) and (d). See Lemma 6.9 and the proofs of Proposition 3.20 and Lemma 5.13.

Now let $n \in \mathbb{N}$ and assume that $F^n = G_n + H_n$ with the desired properties. Since $0 \leq G_n(f) = F^n(f) - H_n(f),$
\[ G_n(f)(s) \leq F^n(f)(s) + |H_n(f)(s)| \leq c + c = 2c, \quad f \in Q. \quad (7.2) \]

By (7.1),
\[ F^{n+1}(f)(s) = \sum_{j=1}^2 \int_S h_j(s, t, F^n(f)(t)) P_j(dt, s) = G_{n+1}(f)(s) + H_{n+1}(f)(s) \]
with
\[ G_{n+1}(f) = \hat{G}_{n+1}(f) + \hat{G}_{n+1}(f), \]
\[ \hat{G}_{n+1}(f)(s) = \int_S h_2(s, t, F^n(f)(t)) P_2(dt, s), \]
\[ \hat{G}_{n+1}(f)(s) = \int_S h_1(s, t, G_n(f)(t)) P_1(dt, s). \]
and
\[ H_{n+1}(f)(s) = \int_S \left( h_1(s, t, F^n(f)(t)) - h_1(s, t, G_n(f)(t)) \right) P_1(dt, s). \]
By Assumption 7.1(c),
\[ |H_{n+1}(f)(s)| \leq \int_S \Lambda_1(c)|H_n(f)(t)| P_1(dt, s) \leq \Lambda_1(2c)\Lambda_1(2c)^n\|f\|_\infty = \Lambda_1(2c)^{n+1}\|f\|_\infty. \]

Let \( Q \) be bounded subset of \( C^b_+(S) \). \( \hat{G}_{n+1}(Q) \) is equicontinuous because \( F^n(Q) \subseteq [0,c]^S \) is bounded and Assumption 7.1 (b) and (d) hold. See Lemma 6.9 and the proofs of Proposition 3.20 and Lemma 5.13.

\( \hat{G}_{n+1}(Q) \) is equicontinuous because it has compact closure. The latter follows from the equicontinuity and boundedness of \( G_n(Q) \), \( G_n(Q) \subseteq [0,2c]^S \) and \( P_1 \) being a tight Feller kernel by Assumption 7.1 (a). See the proofs of Proposition 3.22, Lemma 6.13, and Proposition 5.17.

**Proposition 7.3.** Let Assumption 7.1 be satisfied. Then
\[ F^n(f) = \Theta_n(f) + \Psi_n(f), \quad n \in \mathbb{N}, n \geq 2, \quad f \in C^b_+(S), \]
with maps \( \Theta_n \) on \( C^b_+(S) \) and \( \Psi_n \) from \( C^b_+(S) \) to \( C^b(S) \) such that, for all bounded closed subsets \( Q \) of \( C^b_+(S) \) with \( F(Q) \subseteq Q \), \( \Theta_n(Q) \) is a subset of \( C^b_+(S) \) with compact closure and there exist \( \Lambda_1 \in (0, 1) \) and \( \Lambda_2 \in (0, \infty) \) such that
\[ \|\Psi_n(f)\|_\infty \leq (\Lambda_1 + \Lambda_2)\Lambda_1^{-1}\|f\|_\infty, \quad n \in \mathbb{N}, f \in Q. \]

**Proof.** Let \( n \in \mathbb{N} \). By Lemma 7.2,
\[ F^{n+1}(f)(s) = \sum_{j=1}^2 \int_S h_j(s, t, F^n(f)(t)) P_j(dt, s), \]
\[ F^n(f) = G_n(f)(t) + H_n(f)(t), \]
with \( G_n \) and \( H_n \) having the properties mentioned there. This can be rewritten as
\[ F^{n+1}(f)(s) = \Theta_{n+1}(f)(s) + \Psi_{n+1}(f)(t) \]
with
\[ \Theta_{n+1}(f)(t) = \sum_{j=1}^2 \int_S h_j(s, t, G_n(f)(t)) P_j(dt, s) \]
and
\[ \Psi_{n+1}(f)(s) = \sum_{j=1}^2 \int_S \left( h_j(s, t, F^n(f)(t)) - h_j(s, t, G_n(f)(t)) \right) P_j(dt, s). \]

Let \( Q \) be a bounded closed subset of \( C^b_+(S) \) with \( F(Q) \subseteq Q \) and \( c > 0 \) such that \( Q \subseteq [0,c]^S \). Then \( F^n(f) \in [0,c]^S \) and \( G_n(f) \in [0,2c]^S \) for all \( n \in \mathbb{N} \) and all \( f \in Q \) with the second following from Lemma 7.2. By Assumption 7.1 (c) and Lemma 7.2 and its proof,
\[ \Psi_{n+1}(f)(s) \leq \sum_{j=1}^2 \int_S \Lambda_j(c)H_n(f)(t) P_j(dt, s) \leq (\Lambda_1(2c) + \Lambda_2(2c))\Lambda_1^{-1}(2c)\|f\|_\infty. \]
\( \Theta_{n+1}(Q) \) has compact closure because \( G_n(Q) \) is equicontinuous and contained in \([0,2c]^2\) by Lemma 7.2 and the \( P_j \) are tight Feller kernels. See the proofs of Proposition 3.22, Proposition 5.17 and Lemma 6.13. \( \square \)

**Proposition 7.4.** Let Assumption 7.1 be satisfied. Then the semiflow induced by \( F \) is asymptotically smooth. If Assumption 6.10 is satisfied, the semiflow induced by \( F \) has a compact attractor of bounded sets.

See [25, Def.2.25] and [25, Def.2.9].

**Proof.** This result does not directly follow from [25, Thm.2.46] because \( \Psi_n \) does not map \( C^b_+(S) \) into itself but only into \( C^b(S) \). The proof still works though. \( \square \)

**Theorem 7.5.** Let Assumption 6.4, 6.10 and Assumption 7.1 be satisfied. Further assume that for any \( \epsilon > 0 \) there is some \( \delta > 0 \) such that

\[
(1 - \epsilon)\tilde{g}_j(s, t, 0) \leq \tilde{g}_j(s, t, q), \quad s, t \in S, \quad 0 \leq q < \delta.
\]

If \( r(\kappa^o) > 1 \), the population is uniformly persistent in the sense of Theorem 3.24.

**Proof.** Assumption 7.1 implies Assumption 6.1. By Theorem 6.6, the population is uniformly weakly persistent in the sense of Theorem 5.9. By Proposition 7.4, the semiflow induced by \( F \) has a compact attractor of bounded sets. Uniform persistence in the sense of Theorem 3.24 follows in the same way as in its proof. \( \square \)

8. **Discussion.**

8.1. **Timing of the census.** In interpreting the persistence results for iteroparous populations, it is important to keep in mind when the census of the population is done: just before the yearly reproduction season which is assumed to be short (pre-reproductive census [9]). With our assumptions, the persistence results may not hold if the census were done after the reproduction season (post-reproductive census [9]). The initial population could consist of adults only, without any neonates. In a spatially distributed population, the initial spatial distribution could interact with the adult migration kernel \( P_1 \) in such a way that the population were extinct after one year, \( P_1([f_0 > 0], s) = 0 \) for all \( s \in S \).

For pre-reproductive census, Assumption 5.7 (a) makes sure that there are newborn individuals after the reproductive season while the irreducibility of the Feller kernel for neonates in Assumption 5.7 (b) guarantees that the neonates of successive generations make it to every part of the habitat \( S \).

For other ways in which the timing of the census is important see [19].

8.2. **Use of uniform Feller kernels.** In order to obtain uniform rather than uniform weak persistence, we have assumed that some Feller kernels are uniform Feller kernels. For instance, in Section 6, we have assumed that both \( P_1 \) and \( P_2 \) are uniform Feller kernels and the metric space \( S \) is separable.

Choose a sequence \( (s_\ell) \) in \( S \) that is dense in \( S \) and a convergent series \( \sum_{\ell=1}^{\infty} \alpha_\ell \) of nonnegative terms and set

\[
\mu(T) = \sum_{\ell=1}^{\infty} \alpha_\ell (P_1(T, s_\ell) + P_2(T, s_\ell)), \quad T \in \mathcal{B}.
\]

(8.1)
Since $P_1$ and $P_2$ are uniform Feller kernels, $\mu(T) = 0$ implies $P_1(T, s) = 0 = P_2(T, s)$ for all $s \in S$. By the Radon-Nykodym Theorem, for any $s \in S$,

$$P_j(T, s) = \int_T \psi_j, s(t)\mu(dt)$$

with appropriate $\mu$-integrable functions $\psi_j, s$. It does not seem to be clear though, which properties $\psi_j, s(t)$ has as a function of $(t, s) \in S^2$. Still, one could take this as a motivation to study the integro-difference equation in the form

$$f_{n+1}(s) = \int_S g(s, t, f_n(t))\mu(dt), \quad n \in \mathbb{Z}_+, s \in S.$$ 

In the special case of Section 7, this would be an integro-difference equation of Urysohn type,

$$f_{n+1}(s) = \int_S h(s, t, f_n(t))\mu(dt), \quad n \in \mathbb{Z}_+, s \in S.$$ 

Here are some reasons to stick with the approach chosen in this paper.

(a) The uniform Feller property is not needed for uniform weak persistence.

(b) From a modeling point of view, the measure $\mu$ in (8.1) is rather arbitrary, depending on the sequence $(s_n)$ and the weights $(\alpha_n)$, and lacks interpretation.

(c) In Section 7, alternative assumptions allow that only $P_2$ is a uniform Feller kernel while $P_1$ is just a Feller kernel.

(d) In (6.1),

$$g_j(s, t, f) = \tilde{g}_j(s, t, f(t) + \int_S f(u)\tilde{\kappa}_j(du, t)),$$

with Feller kernels $\tilde{\kappa}_j$ that do not need to be uniform Feller kernels offers an attractive general way to model nonlocal competition or cooperation. So why not stay in the Feller kernel framework altogether?

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