Steady state problems in structured population dynamics

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Positive steady states of evolution equations with finite dimensional nonlinearities, *SIAM J. Math. Anal.*, **46** (2014), 1406-1426. *http://arxiv.org/abs/1402.6266*

On a strain-structured epidemic model, *preprint*.

Introduction to structured population dynamics

Motivation

Google returned (2013 May) 37.4m results in 0.25s for "structured population model".

Applications

Human demography, cancer modelling, marine ecosystems, mathematical epidemiology, insect populations, cell populations, ...

Our modelling work

Evolution in structured predator-prey systems, sealice dynamics in salmon farms, *Wolbachia* infection dynamics in arthropod species, superspreading in disease dynamics.

Modelling & Analysis

Discrete models: Leslie matrix models: Perron-Frobenius Theory.
Continuous models: Hyperbolic/parabolic PDE's: spectral theory of positive operators, semigroups of operators, fixed point results.

A simple example - 1-dimensional nonlinearity

Size-structured model with distributed states at birth

$$\frac{\partial}{\partial t}p(s,t) + \frac{\partial}{\partial s}\left(\gamma(s,P(t))p(s,t)\right) = -\mu(s,P(t))p(s,t) + \int_0^m \beta(s,y,P(t))p(y,t)\,\mathrm{d}y,$$

$$\gamma(0,P(t))p(0,t) = 0,$$

$$p(s,0) = p_0(s), \quad P(t) = \int_0^m p(s,t)\,\mathrm{d}s.$$

- μ - size-specific mortality rate
- β - fertility rate, y-parent size, s-offspring size
- γ - development/growth rate

Existence of positive steady states

For a fixed $P \in (0,\infty)$ we define the operator $\mathcal{B}_P$ as

$$\mathcal{B}_P\, u = -\frac{\partial}{\partial s}(\gamma(\cdot,P)u) - \mu(\cdot,P)u + \int_0^m \beta(\cdot,y,P)u(y)\,\mathrm{d}y,$$
$$\mathrm{Dom}(\mathcal{B}_P) = \left\{ u \in W^{1,1}(0,m) \,|\, u(0) = 0 \right\}.$$

p_* is a positive steady state, if $\mathcal{B}_{P_*} p_* = 0$ and $P_* = \int_0^m p_*(s)\,\mathrm{d}s$.

Show that there exists a P_* such that the operator $\mathcal{B}_{P_*}$ has eigenvalue (the spectral bound) 0 with a corresponding (unique) positive eigenvector. $\Rightarrow$ Estimates for the spectral bound using separable fertility functions.

JZF, D. M. Green, P. Hinow, Semigroup analysis of structured parasite populations, *Mathematical Modelling of Natural Phenomena*, **5** (2010), 94-114. `arxiv.org/abs/0812.1363`

General framework

Let $\mathcal{X}, \mathcal{Y}$ be Banach lattices, and consider:

$$\frac{du}{dt} = \mathcal{A}_{\mathbf{u}}\, u, \quad u(0) = u_0,$$

where for every $\mathbf{u} \in \mathcal{Y}$, $\mathcal{A}_{\mathbf{u}}$ is a linear operator with $D(\mathcal{A}_{\mathbf{u}}) \subseteq \mathcal{X}$. The relationship between $\mathbf{u} \in \mathcal{Y}$-parameter space, and $u \in \mathcal{X}$-state space, is determined by the environmental operator:

$$E : \mathcal{X} \to \mathcal{Y}, \quad E(u) = \mathbf{u}.$$

If the range of E is contained in $\mathbb{R}^n$ for some $n \in \mathbb{N}$ then we say that the problem incorporates a (finite) n-dimensional nonlinearity.

E is often a positive, linear, and bounded functional.

The steady state problem can be cast in the simple form:

$$\frac{\mathrm{d}u}{\mathrm{d}t} = 0 = \mathcal{A}_{\mathbf{u}}\, u, \quad u(0) = u_0, \quad E(u) = \mathbf{u}; \quad 0 \neq u \in \mathcal{X}_+.$$

Eigenvalue problem + Fixed point problem

General framework

Problems:

- Non-monotone spectral bound $s(\mathcal{A}_{\mathbf{u}})$ along positive rays of the parameter space.
- Semigroup generated by $\mathcal{A}_{\mathbf{u}}$ is not irreducible.
- "Difficult" infinite dimensional nonlinearity

Fixed point results for multivalued map:

Lower/upper hemi-continuity.
Require (essentially) convexity of the range of the set-valued map.

New fixed point result for multi-valued maps (at least in 2-dimensions).

Let $\Sigma = \{(x, y) \in \mathbb{R}^2_+ \,|\, x + y = 1\}$, S be any subset of $\mathbb{R}^2_+$ and $\pi : S \to \Sigma$ be the projection along positive rays. Note that $\pi^{-1} : \Sigma \multimap S$ is multivalued, in general.

Lemma

Let $S \subset \mathbb{R}^2_+$ be connected, such that $S \cap \{(0, y) \,|\, y \in (0, R)\} \neq \emptyset$, and $S \cap \{(x, 0) \,|\, x \in (0, R)\} \neq \emptyset$ for some $R > 0$. Let $G : S \to \Sigma$ be continuous. Then the multivalued map $H = \pi^{-1} \circ G : S \multimap S$ has at least one fixed point, i.e. there exists $s \in S$ such that $s \in \pi^{-1}(G(s))$.

Lemma

Let $f : \mathbb{R}_+^2 \to \mathbb{R}$ be a continuous function, and assume that $f(0,0) > 0$, and that there exists an $R > 0$ such that $f(x,y) < 0$ for $x^2 + y^2 > R^2$. Then the set

$$Z = \left\{ \mathbf{z} \in \mathbb{R}_+^2 \,|\, f(\mathbf{z}) = 0 \right\}$$

has a compact connected subset S, which intersects the sets

$$\{(0,y)\,|\, r \leq y \leq R\}, \text{ and } \{(x,0)\,|\, r \leq x \leq R\},$$

for some $r > 0$.

Our main result is the following:

Theorem

Assume that the linear operator $\mathcal{A}_{\mathbf{u}}$ *generates a positive irreducible and eventually compact semigroup of bounded linear operators for every* $\mathbf{u} \in \mathbb{R}^2_+$*, and that* $\mathbf{u_n} \to \mathbf{u}$ *implies* $\mathcal{A}_{\mathbf{u_n}} \to \mathcal{A}_{\mathbf{u}}$ *in the generalised sense. Moreover, assume that* $s(\mathcal{A}_{\mathbf{0}}) > 0$*, and there exists an* $R > 0$ *such that* $s(\mathcal{A}_{\mathbf{u}}) < 0$ *for* $||\mathbf{u}|| \geq R$*. Further assume that* E *is a strictly positive linear functional. Then the steady state problem has a solution.*

General results - a spectral result

de Pagter (1986), Compact irreducible operator is not quasi-nilpotent. Our general result:

Theorem

Let $\mathcal{X}$ be a normed vector lattice and K be a cone. Let $\mathcal{S}$ denote the unit sphere of $\mathcal{X}$ and let $C = Conv(\mathcal{S} \cap K)$, the convex hull of $\mathcal{S} \cap K$. Let $\mathcal{L}$ be a strictly K-positive bounded linear operator. If $\mathcal{L}(C)$ is relatively compact in $\mathcal{X}_0$, then $\mathcal{L}$ has a positive eigenvalue with a corresponding eigenvector from K.

Theorem

(Cauty, 2001) [Schauder's fixed point theorem]
Let V be a separated (i.e. Hausdorff) topological vector space. Let C be a non-empty convex subset of V and f a continuous function from C to C. If $f(C)$ is contained in a compact subset of C then f has a fixed point.

Example: Juvenile-adult model

JZF, T. Hagen, Asymptotic behaviour of size-structured populations via juvenile-adult interaction, *Discrete and Continuous Dynamical Systems - Series B*, **9** (2008), 249-266.

$$p_t(s,t) + (\gamma(s,J(t),A(t))\,p(s,t))_s = -\mu(s,J(t),A(t))\,p(s,t),$$

$$\gamma(0,J(t),A(t))p(0,t) = \int_l^m \beta(s,J(t),A(t))\,p(s,t)\,ds, \quad t>0,$$

We define the operator

$$\Psi_{(J,A)}\,p = -(\gamma(\cdot,J,A)p)_s - \mu(\cdot,J,A)p,$$
$$D\left(\Psi_{(J,A)}\right) = \{p\in W^{1,1}(0,m)\,|\,p(0) = B_{(J,A)}\,p\},$$

where

$$B_{(J,A)}\,p = \frac{1}{\gamma(0,J,A)}\int_l^m \beta(s,J,A)p(s)\,ds, \quad D(B_{(J,A)}) = L^1(l,m).$$

Example: Juvenile-adult model

$\Psi_{(J,A)}$ generates a positive and eventually compact semigroup for every $(J,A) \in \mathbb{R}^2_+$, which is irreducible if there exists an $\varepsilon > 0$ such that

$$\int_{m-\varepsilon}^{m} \beta(s,\cdot,\cdot)\,ds > 0.$$

The (positive linear) environmental operator E is defined as

$$E(p) = \left(\int_0^l p(s)\,ds, \int_l^m p(s)\,ds\right)^t.$$

The main Theorem implies that if β satisfies the irreducibility condition above, and there exist positive real numbers r, R such that $0 < r < R < \infty$ and $s(\Psi_{(J,A)}) > 0$ for $J + A \leq r$, and $s(\Psi_{(J,A)}) < 0$ for $J + A \geq R$ then the model admits a positive steady state.

Example: Juvenile-adult model - Remark

There is a one-to-one correspondence between positive steady states and pairs of positive numbers (J_*, A_*) satisfying

$$\frac{J_*}{A_*} = \frac{\displaystyle\int_0^l \exp\left\{-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\}\,ds}{\displaystyle\int_l^m \exp\left\{-\int_0^s \frac{\mu(r,J_*,A_*)+\gamma_s(r,J_*,A_*)}{\gamma(r,J_*,A_*)}\,dr\right\}\,ds},\ R(J_*,A_*)=1,$$

where

$$R(J,A) = \int_l^m \frac{\beta(s,J,A)}{\gamma(s,J,A)} \exp\left\{-\int_0^s \frac{\mu(r,J,A)}{\gamma(r,J,A)}\,dr\right\}\,ds.$$

Define a nonlinear multi-valued map, via the right hand-side of the first equation, on the positive quadrant, and apply Lemma 1 and Lemma 2, with the level set Z defined via $R(J_*,A_*)=1$. Then the conditions on R are the biologically relevant ones, i.e. that $R(0,0)>1$ and $R(J,A)<1$ for $J+A>\bar{R}$ for some $\bar{R}>0$.

Model with infinite dimensional nonlinearity

$$\begin{aligned} v_t(x,t) - \left(d(x)v_x(x,t)\right)_x &= -\varrho(x)v(x,t) \\ &\quad + S(t)\int_0^1 \beta(x,y)v(y,t)^{1+\gamma(y)}\,\mathrm{d}y, \end{aligned}$$

$$S'(t) = \int_0^1 \varrho(x)v(x,t)\,\mathrm{d}x - S(t)\int_0^1\int_0^1 \beta(x,y)v(y,t)^{1+\gamma(y)}\,\mathrm{d}y\,\mathrm{d}x,$$

$$v_x(0,t) = v_x(1,t) = 0, \quad v(x,0) = v_0(x),\ S(0) = S_0.$$

- ϱ - recovery rate
- β - individuals of strain y produce newly infected individuals of strain x
- γ - infectiousness of individuals of different strains
- d - changes of infectiousness due to random mutations inside the host

Existence of the endemic steady state for $\gamma \equiv 0$

Theorem

Assume that $\gamma \equiv 0$, $\varrho \not\equiv 0$, and $\int_0^1 \beta(x,y)\,\mathrm{d}y > 0$ for every $x \in [0,1]$. Then there exists a unique value S_* of the susceptible population size such that for any infected population size $V_* > 0$ there is a unique steady state (v_*, S_*), with $V_* = \int_0^1 v_*(x)\,\mathrm{d}x$.

Proof For every $R \in \mathbb{R}_+$ we define the following linear operator

$$\Psi_R\, v = \left(d(\cdot)v'\right)' - \varrho(\cdot)v + R\int_0^1 \beta(\cdot,y)v(y)\,\mathrm{d}y,$$
$$\mathrm{D}\left(\Psi_R\right) = \left\{v \in W^{2,1}(0,1) \,|\, v'(0) = v'(1) = 0\right\}.$$

$(v_*, S_*) \in \mathcal{X}^\alpha$ is a positive steady state if and only if $s(\Psi_R) = 0$ for some $R > 0$, $v_* \in \mathrm{Ker}(\Psi_R)$, and $S_* = R$.

1-d parameter space, monotone nonlinearity!

Existence of the endemic steady state for $\gamma \equiv 1$

Theorem

Assume that $\gamma \equiv 1$ holds, $\varrho \not\equiv 0$, and that β is strictly positive. Then for every $S_* > 0$ the model admits a strictly positive (endemic) steady state of the form (v_*, S_*).

Proof We consider the parameter set

$$C = \{0 \leq u \in W^{1,1}(0,1) \,|\, 0 < ||u||_{W^{1,1}(0,1)} \leq 1\}.$$

For every $(u, R) \in C \times \mathbb{R}_+$ we define the following linear operators:

$$\Psi^1 v = \left(d(\cdot)v'\right)' - \varrho(\cdot)v,$$

$$\Psi^2_{(u,R)} v = R \int_0^1 \beta(\cdot, y)v(y)u(y)^{\gamma(y)} \,\mathrm{d}y, \quad \Psi_{(u,R)} = \Psi^1 + \Psi^2_{(u,R)},$$

$$\mathrm{D}\left(\Psi^1\right) = \left\{v \in W^{2,1}(0,1) \,|\, v'(0) = v'(1) = 0\right\} = \mathrm{D}\left(\Psi_{(u,R)}\right).$$

Existence of the endemic steady state for $\gamma \equiv 1$

For every $R \in \mathbb{R}_+$ we define

$$\Phi_R \; : \underbrace{c}_{\in C} \to \underbrace{u_*}_{\in K_c \cap S_R} \to \underbrace{v_{u_*}}_{W^{2,1}(0,1)\cap C}, \qquad (1)$$

where

$$S_R = \{0 < u \in W_+^{1,1}(0,1) \,|\, s(\Psi_{(u,R)}) = 0\}.$$

The maps Φ_R are continuous because the projection along rays is continuous on C and the function $u_* \to v_{u_*}$ is also continuous.
Difficulties:

- Prove for every R a uniform lower bound for the spectral bound $s(\Psi_{(u,R)})$ for $u \in C$. Only possible for $1 \leq \gamma \leq \Gamma < \infty$!
- To prove that the set of eigenvectors $\Phi_R(C)$ is a bounded set in $W^{2,1}(0,1)$. Only possible for $\gamma \leq 1$!

References

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Acknowledgements

- my collaborator: Àngel Calsina
- Edinburgh Mathematical Society
- Spanish government project DGI MTM2011-27739-C04-02
- The Carnegie Trust
- University of Stirling

Thank you for your attention!