Workshop on Transport in Supply Chains, Traffic and BIOLOGY

Horst R. Thieme, ASU

Physiologically structured populations and other systems with distributed parameters

joint work since 1982 with

Odo Diekmann, Mats Gyllenberg, Hans Metz, Henk Heijmans, Philippe Clément, Markus Kirkilionis, Haiyang Huang
individuals \( z \in Z \subseteq \mathbb{R}^n \) populations \( u \in M(Z) \) environment \( E \in \mathbb{R}^m \) 

\( Z \) open \( \cap \) closed \ B. measures \ vectors 

birth \quad growth \quad death 

\[ g(E, z) \quad \text{growth rate of an ind. at state } z \] 
\[ \text{in the environment } E \in \mathbb{R}^m \]

\[ \mu(E, z) \quad \text{mortality rate of an ind. at state } z \]

\[ \beta(E, z) \quad \text{per capita birth rate at state } z \]

\[ g : \mathbb{R}^m \times Z \to \mathbb{R}^n, \quad \mu, \beta : \mathbb{R}^m \times Z \to [0, \infty). \]

All individuals are born at same state \( z_b \in Z \).
Balance equation

\[ u(t, \Box) \quad \text{structural distrib. of pop. at time } t. \]
\[ C(t) \quad \text{population birth rate} \]
\[ E(t) \quad \text{environment at time } t \]

\[ \partial_t u + \nabla_z \cdot (ug(E, z)) \]
\[ = -\mu(E, z)u + \delta(z - z_b)C(t), \quad z \in Z, \]
\[ u(t, z)g(E(t), z) = 0, \quad z \in \partial Z \setminus \{z_b\}, \]

\[ C(t) = \int_Z \beta(E(t), z)u(t, z)dz. \]
\[ E(t) = \int_Z \eta(z)u(t, z)dz \]

Alternative

\[ E'(t) = f(E(t)) - \int_Z h(E(t), z)u(t, z)dz. \]
Assumptions

\( g(E, z), \mu(E, z), \beta(E, z), \eta(z) \) bounded.

\( g(E, z), \mu(E, z) \) Lipschitz in \( E \) and \( z \).

\( \beta(E, z) \) Lipschitz in \( E \), may have jumps for \( z \).

\( \eta(z) \) Lipschitz.

No sign conditions for \( g \).
weak formulation

\[ \phi \in C_0(Z) \cap C^1_b(Z) \]

\[
\frac{d}{dt} \int_Z \phi(z) u(t, z) dz = \int_Z \left[ g(E(t), z) \cdot \nabla \phi(z) - \mu(E(t), z) \phi(z) \right] u(t, z) dz \\
+ \int_Z \phi(z_b) \beta(E(t), z) u(t, z) dz
\]

\[
= \int_Z \left[ A(t) \phi + B(t) \phi \right] u(t, z) dz.
\]
Quasilinear Equation

Fix $E : [0, \infty) \to \mathbb{R}^m$.

Dynamics on the individual level

individual development (growth, maturation)

$G$ (non-auton.) dyn. system induced by ODE

$$z'(t) = g(E(t), z), \quad z(r) = z_0,$$

$$G(t, r, z_0 \mid E) := z(t).$$

dynamical system:

$$G(t, s, G(s, r, z_0)) = G(t, r, z_0), \quad r \leq s \leq t.$$

Lift the dyn. sys. from indiv. to pop. level:

$$G(t, r, z_0 \mid E) = G(t - r, 0, z_0 \mid E_r),$$

$$E_r(s) = E(r + s).$$
Incorporate death

\[ \mathcal{F}(t, r, z|E) \quad \text{prob. of being alive at time } t \]
under the condition that, at time \( r \), one was alive and at state \( z \).

\[
\mathcal{F}(t, r, z|E) = \exp \left( - \int_r^t \mu \left( E(s), G(s, r, z) \right) ds \right),
\]

\[
= \mathcal{F}(t - r, 0, z|E_r)
\]

\[
\partial_t \mathcal{F}(t, r, z) = -\mu \left( E(t), G(t, r, z) \right) \mathcal{F}(t, r, z)
\]
A functional-analytic approach
(Alternative: measure-theoretic)

Family of (growth and death) ops on \( C_0(Z) \):
\[
\left[ U_0(r, t) \phi \right](z) = \phi(G(t, r, z))F(t, r, z)
\]

\( U_0 \) is an evolutionary system on \( C_0(Z) \),
\[
U_0(r, s)U_0(s, t) = U_0(r, t), \quad r \leq s \leq t.
\]
\[
U_0(s, s)\phi = \phi.
\]

\[
U_0(t, r|E) = U_0(t - r, 0|E_r).
\]

\( \phi \in C_0(Z) \cap C^1_b(Z) \):
\[
\partial_t \left[ U_0(t, r) \phi \right](z) = F\nabla \phi(G) \cdot \partial_t G + \phi(G)\partial_t F
\]
\[
= F\nabla \phi(G) \cdot g(E(t), G) - \phi(G)\mu(E(t), G)F
\]
\[
= U_0(r, t) [g(E(t), \sqcup) \cdot \nabla \phi - \mu(E(t), \sqcup) \phi](z).
\]
\[
\frac{d}{dt}U_0(r, t)\phi = U_0(r, t)A(t)\phi,
\]
\[
[A(t)\phi](z) = g(E(t), z) \cdot \nabla \phi - \mu(E(t), z)\phi.
\]
Birth operators
\[
[B(t)\phi](z) = \phi(z_b)\beta(E(t), z).
\]

Find an evolutionary system \( U \) on \( C_0(Z) \),
\[
U(r, t) = U_0(r, t) + \int_r^t U(r, s)B(s)U_0(s, t)ds.
\]
Then
\[
\frac{d}{dt}U(r, t)\phi = U_0(r, t)A(t)\phi + U(r, t)B(t)\phi
\]
\[
+ \int_r^t U(r, s)B(s)U_0(s, t)A(t)\phi ds
\]
\[
= U(r, t)[A(t) + B(t)]\phi.
\]

\( X \) the dual space of \( C_0(Z) \), \( X = \mathcal{M}(Z) \). Set
\[
\langle \phi, U^*(t, r)x \rangle = \langle U(r, t)\phi, x \rangle, \quad x \in X.
\]
\[
\frac{d}{dt} \langle \phi, U^*(t, r)x \rangle = \langle U(r, t) [A(t) + B(t)] \phi, x \rangle = \langle [A(t) + B(t)] \phi, U^*(t, r)x \rangle.
\]

\[
V(r, t) = U(r, t)B(t), \quad V_0(r, t)B(t).
\]

\[
V(r, t) = V_0(r, t) + \int_r^t V(r, s)V_0(s, t)ds
\]

\[
U(r, t) = U_0(r, t) + \int_r^t V(r, s)U_0(s, t)ds.
\]

Problem: \( V_0(r, t)\phi \notin C_0(Z) \)
\[ W(r, t) = \int_r^t V(r, s)ds, \]

\[ W_0(r, t) = \int_r^t V_0(r, s)ds. \]

\( W_0 \) is a step response family for \( U_0 \),

\[ W_0(r, t) : C_0(Z) \to C_0(Z) \]

\[ U_0(r, s)W_0(s, t) = W_0(r, t) - W_0(r, s). \]

Stieltjes integral equation for \( W \)

\[ W(r, t) = W_0(r, t) + \int_r^t W(r, ds)W_0(s, t). \]

Solve for \( W \) and set

\[ U(r, t) = U_0(r, t) + \int_r^t W(r, ds)U_0(s, t). \]

\( W \) is a step response family for \( U \)

and \( U \) is an evolutionary system.
Feedback

Fixed point problem for $E$:

$$E(t) = KU^*(t, 0|E)x,$$
$$K \in \mathcal{L}(X, \mathbb{R}^m).$$

Write $E^x$ for the solution. Set

$$\Phi(t, x) = U^*(t, 0|E^x)x, \quad x \in X.$$ 

$\Phi$ is a dynamical system. Recall

$$U_0(r, t|E) = U_0(0, t - r|E_r)$$
$$E_r(s) = E(r + s)$$
$$W_0(r, t|E) = W_0(0, t - r|E_r)$$

This properties are inherited by $W$ and $U$, and by $U^*$. 
\[ E_r^x(t) = E^x(t + r) = KU^*(t + r, 0|E^x) x \]

\[ = KU^*(t + r, r|E^x) U^*(r, 0|E^x) x \]

\[ = KU^*(t, 0|E_r^x) \Phi(r, x). \]

\[ E_r^x = E^y, \quad y = \Phi(r, x). \]

\[ \Phi(t + r, x) = U^*(t + r, 0|E^x) x \]

\[ = U^*(t + r, r|E^x) U^*(r, 0|E^x) x \]

\[ = U^*(t, 0|E_r^x) \Phi(r, x) = U^*(t, 0|E^y)y \]

\[ = \Phi(t, y) = \Phi(t, \Phi(r, x)). \]
Equilibria

\[ x = U^*(t, 0|E)x, \quad E = KU^*(t, 0|E)x = Kx \]

\[ x = U^*(t, 0|Kx)x. \]

Set

\[ S(t) = U(0, t|Kx), \quad S_0 = \cdots \]

\[ T(t) = W(0, t|Kx), \quad T_0 = \cdots \]

\[ S(t) = S_0(t) + \int_0^t T(ds)S(t-s) \]

\[ T(t) = T_0(t) + \int_0^t T(ds)T_0(t-s) \]

Laplace transforms

\[ \hat{T}(\lambda) = \int_0^\infty e^{-\lambda s} T(s) ds \]

\[ \hat{S}(\lambda) = \hat{S}_0(\lambda) + \lambda \hat{T}(\lambda) \hat{S}_0(\lambda) \]

\[ = (I - \lambda \hat{T}_0(\lambda))^{-1} \hat{S}_0(\lambda). \]

Fixed point equation for equilibrium

\[ x = [\hat{S}_0(\lambda|Kx)]^*(I - \lambda \hat{T}_0(\lambda|Kx))^{-1}x \]
More about the time-dependent fixed point problem

\[ \mathcal{E} = \left\{ E : [0, T] \to \mathbb{R}^m ; E \text{ cont. } , \| E(t) \| \leq M \right\} \]

where \( M > 0 \). Metric induced by

\[ \| E \|_\lambda = \sup_{0 \leq t \leq T} e^{-\lambda t} \| E(t) \|. \]

Boundedness conditions

There exist \( \xi : [0, \infty) \to [0, \infty) \) s.t., for all \( E \in C([0, T], \mathbb{R}^m) \),

\[ \| KU^*(t, r|E) \| \leq \xi(t) \]
semi-variation:

\[ \text{Var}(W_0, [r, t]) = \sup \left\| \sum_{j=1}^{k} \left[ W_0(r, s_j) - W_0(r, s_{j-1}) \right] \phi_j \right\| \]

where the supremum is taken over all partitions \( r = s_0 < \cdots < s_k = t \) and all \( \phi_j \in C_0(\Omega) \), \( \|\phi_j\| \leq 1 \).

\[ \text{Var}(W_0(\sqcup|E), [r, t]) \leq \xi(t) \quad \forall E \in C([0, T], \mathbb{R}^m) \]

There exist \( \gamma, \delta \in (0, 1) \) s.t.

\[ \text{Var}(W_0(\sqcup|E), [r, t]) \leq \gamma, \quad \forall E \in C([0, T], \mathbb{R}^m), 0 \leq t - r \leq \delta. \]
Lipschitz conditions

\[ \| W_0(r, t|E) - W_0(r, t|\tilde{E}) \| \leq \Lambda \int_r^t \| E(s) - \tilde{E}(s) \| ds \]

\[ \| KU_0^*(t, r|E) - KU_0^*(t, r|\tilde{E}) \| \leq \cdots \]

\[ \quad \forall E, \tilde{E} \in \mathcal{E}. \]

Estimates of this type are inherited by \( W \) and \( KU^* \).
O. Diekmann, M. Gyllenberg, and H.R. Thieme: Perturbing evolutionary systems by step responses and cumulative outputs. 
_Diff. Int. Eq._ **8** (1995), 1205-1244

