



On the structure of attractors for Lotka–Volterra systems

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Heteroclinic cycles

Non-autonomous case

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References

The talk is based on the results of four articles, plus work in progress:

- [AKLS] P. Almaraz, P. Kalita, J.A. Langa, F. Soler-Toscano, Structural stability of invasion graphs for Lotka–Volterra systems, *Journal of Mathematical Biology* vol. 88 (2024), article number 64
- [BKLO] M.C. Bortolan, P. Kalita, J.A. Langa, R. de Oliveira Moura, A theoretical and computational study of heteroclinic cycles in Lotka–Volterra systems, *Journal of Mathematical Biology* vol. 90 (2025), article number 28
- [GKL] J. Garcia-Fuentes, P. Kalita, J.A. Langa, Forwards attractor structures in a planar cooperative non-autonomous Lotka–Volterra system, *Qualitative Theory of Dynamical Systems* vol. 23 (2024), article number 163
- [GKLS] J. Garcia-Fuentes, P. Kalita, J.A. Langa, A. Suarez, Forwards attractors for non-autonomous Lotka–Volterra cooperative systems: a detailed geometrical description, *Discrete and Continuous Dynamical Systems - Series B* vol. 30 (2025), 189–221
- [GKŁ] J. Garcia-Fuentes, P. Kalita, G. Łukaszewicz, Dynamics of the non-autonomous May–Leonard model, in preparation

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Lotka–Volterra system

A system of ODEs:

$$u'_i = u_i \left(b_i + \sum_{j=1}^N a_{ij} u_j \right) \quad \text{for } i \in \{1, \dots, N\},$$

where b are the intrinsic growth rates and $A = (a_{ij})$ is the interaction matrix.

Evolution in the cone $\{u_i \geq 0 \text{ for all } i\}$. Models inter-species interactions in the environment.

The same system in matrix form:

$$u' = \text{diag}(u) (b + Au).$$

The most famous example of such a system is predator–prey

$$A = \begin{pmatrix} 0 & -\beta \\ \delta & 0 \end{pmatrix},$$

$\beta, \delta > 0$: purely imaginary eigenvalues, periodic solutions.

We are interested in the case where A is, in an appropriate sense, [stable](#).

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Mode of stability

A is stable if $\operatorname{Re} \sigma(A) < 0$ — unfortunately, a notion too weak for our purposes.

For every stable matrix A there exists a **symmetric positive definite matrix** P such that $PA + A^T P$ is negative definite.

The matrix A is **Volterra–Lyapunov stable (VL stable)** if there exists a **diagonal positive definite matrix** $H = \operatorname{diag}(h_1, \dots, h_N)$ such that $HA + A^T H$ is negative definite.

- ▶ This is a **proper and essential subclass** of stable matrices.
- ▶ For $N = 2, 3$ easy to check.
- ▶ If the diagonal is negative and A is **strictly** row or column diagonally dominant, then A is VL stable.

From now on: the matrix A of the Lotka–Volterra system is **VL stable**.

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Equilibria

$$u' = \text{diag}(u) (b + Au)$$

Every equilibrium is determined by the set of its **nonzero entries**.

Fix $J \subset \{1, \dots, N\}$:

- ▶ for $i \notin J$ set $u_i = 0$, and solve $A(J)u^* = -b(J)$, where $A(J)$ is the principal submatrix related to the entries in J (VL stability makes every $A(J)$ nonsingular);
- ▶ if all entries of u^* are positive, we obtain an equilibrium, and we call J **admissible** (a **community**); otherwise — reject.

At most 2^N equilibria, one for each J .

Let

$$\overline{C}_+ = \{u \in \mathbb{R}^N : u_i \geq 0 \text{ for all } i\}, \quad C_+ = \text{int } \overline{C}_+.$$

Setting some of the u_i to zero identifies a subsystem on a lower dimensional wall of this cone: $2^N - 1$ systems in total.

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Result of Takeuchi

Y. Takeuchi, Global Dynamical Properties of Lotka-Volterra Systems, World Scientific 1996.

Theorem 3.2.1, Takeuchi

If A is VL stable then for every $b \in \mathbb{R}^N$ there exists a **unique globally asymptotically stable equilibrium** $u^* \in \overline{C}_+$ in the sense that for every $u_0 \in C_+$ the solution $u(t)$ with the initial data u_0 converges to u^* as time tends to infinity.

In particular, if the solution $\bar{u}$ of the system $A\bar{u} = -b$ is positive, then $u^* = \bar{u}$.

True for the full system and for all subsystems.

Proof: by a Lyapunov function (which works only inside the cone, as it tends to infinity on its boundary).

Forward dynamics: always convergence to some equilibrium, called the **GASS** (globally asymptotically stable solution). In particular, all ω -limits are single equilibria.

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Chesson's invasion rates

P. Chesson, Multispecies competition in variable environments, Theoretical Population Biology 45 (1994) 227–276.

Suppose $u^I = (u_1, \dots, u_N)$ is an equilibrium with $u_j > 0 \Leftrightarrow j \in I$, and let $|I| = k$.

Define the invasion rate of this equilibrium by the species $i \notin I$ as

$$r_i(I) = b_i + \sum_{j \in I} a_{ij} u_j, \quad \text{with the convention } r_i(\emptyset) = b_i.$$

The spectrum of the linearized system around this equilibrium is given by

$$\sigma(B) \cup \{r_i(I)\}_{i \notin I},$$

where B is a $k \times k$ matrix and — since A , and hence $A(I)$, is VL stable — $\sigma(B) \subset \{\operatorname{Re} z < 0\}$.

Hence the equilibrium is **hyperbolic** if and only if $r_i(I) \neq 0$ for all $i \notin I$.

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Invasion graph of Hofbauer and Schreiber

J. Hofbauer, S.J. Schreiber, Permanence via invasion graphs: incorporating community assembly into modern coexistence theory, *Journal of Mathematical Biology* vol. 85 (2022) article number 54

Vertices are the equilibria (at most 2^N). Each equilibrium is denoted by the set I of its nonzero entries (species).

The graph contains the edge from I to J (denoted $I \rightarrow J$) if $I \neq J$, $r_i(I) > 0$ for every $i \in J \setminus I$, and $r_i(J) < 0$ for every $i \in I \setminus J$.

Does not have to be a partial order (it may contain cycles).

Result of Hofbauer and Schreiber

Assume that all equilibria are hyperbolic (that is, $r_i(I) \neq 0$ for every I and $i \notin I$).

There exists a heteroclinic connection from I to J



There exists the edge $I \rightarrow J$ in the invasion graph.

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Result of [AKLS]

Main result of [AKLS]

Assume that all equilibria are hyperbolic (that is, $r_i(I) \neq 0$ for every I and $i \notin I$) AND the matrix A is VL stable.

There exists a heteroclinic connection from I to J



There exists the edge $I \rightarrow J$ in the invasion graph.

VL stability alone already gives one implication: every edge of the invasion graph is realized by a heteroclinic connection. If nonhyperbolic equilibria are present, there may exist connections which the graph does not capture.

So, in the hyperbolic case, the invasion graph represents all equilibria and all their heteroclinic connections.

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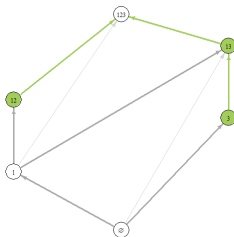
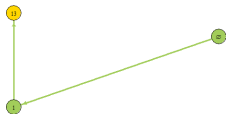
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How can the invasion graph look like?



Two examples of acyclic graphs. Is the system then gradient with respect to the equilibria? Can α -limits be more than singletons?



The last example is the celebrated May–Leonard problem (it contains a cycle). The system is not gradient with respect to the equilibria — and we obtain a graph with a cycle.

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On the global attractor

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Theorem [AKLS]

If the matrix A is VL stable then the system **has a global attractor $\mathcal{A}$** .

Moreover, every edge of the invasion graph is realized by a heteroclinic connection, so the graph always represents a **substructure** of the global attractor: the attractor contains all the equilibria and all their heteroclinic connections.

Question: does the invasion graph represent the **whole** global attractor, and if not, what else may the global attractor contain?



A general result on semigroups

Auxiliary result of [BKLO]

Let $\{\mathcal{T}(t)\}_{t \geq 0}$ have a global attractor $\mathcal{A}$ and let ξ be a bounded global solution of $\mathcal{T}$. Assume also that there exists an isolated equilibrium $e^* \in \alpha(\xi)$, satisfying

if $x \in \mathcal{A}$ and $\mathcal{T}(t)x = e^*$ for some $t > 0$ we have $x = e^*$, (*)

and a point $x \in \alpha(\xi)$, with $x \neq e^*$.

Then there exist nontrivial bounded global solutions ϕ and ψ of $\mathcal{T}$ with

$$\phi(t) \rightarrow e^* \text{ as } t \rightarrow -\infty \quad \text{and} \quad \psi(t) \rightarrow e^* \text{ as } t \rightarrow \infty.$$

Furthermore, $\phi(t), \psi(t) \in \alpha(\xi)$ for all $t \in \mathbb{R}$.

For Lotka–Volterra systems condition (*) is automatic: the system generates a **group**.

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How can an α -limit for Lotka–Volterra look like?

The matrix A is VL stable, and the equilibria are isolated.

- 1 Suppose the α -limit set of some solution in $\mathcal{A}$ contains e^* and another point.
- 2 Then the α -limit contains a global solution $\phi(t) \rightarrow e^*$ as $t \rightarrow -\infty$.
- 3 As the matrix is VL stable, $\phi(t) \rightarrow e_1$ as $t \rightarrow \infty$, where e_1 is an equilibrium in the α -limit.
- 4 But the lemma above implies that there exists another solution in the α -limit, $\phi_1(t) \rightarrow e_1$ as $t \rightarrow -\infty$.
- 5 Repeating this construction, and because the number of equilibria is finite, we obtain a heteroclinic cycle in the α -limit (i.e. a loop of connections).
- 6 So EITHER the α -limit is a single point OR it contains a cycle.

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A posteriori test

So if all equilibria are hyperbolic and there are no cycles in the invasion graph, then each α -limit must be a single equilibrium. The same is always true for ω -limits, by VL stability.

The previous argument on the structure of α -limits leads to the following algorithm.

- I Find all equilibria.
- II Check their hyperbolicity (by calculating the invasion rates).
If at least one is nonhyperbolic, then there is no guarantee that the whole structure of the global attractor will be recovered.
- III Build the invasion graph.
- IV Check if it contains cycles.
- V If there are no cycles, then we have captured the whole structure of the global attractor, which is gradient with respect to the equilibria (the acyclic graph defines a partial order).

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What if cycles DO occur

Then we have only partial knowledge.

More on α -limits

Let ξ be a bounded global solution with $d = \dim \xi$, and assume that $\alpha(\xi)$ is not a singleton. Then the dimension of any equilibrium belonging to $\alpha(\xi)$ is between 1 and $d - 2$.

$\Rightarrow$ In 1-d and in 2-d there can be no cycles.

$\Rightarrow$ In 3-d only equilibria with one nonzero entry can be contained in a nontrivial $\alpha(\xi)$.

$\Rightarrow$ So in 3-d either all α -limits are singletons (and hence all the dynamics is in the invasion graph), or we have the May–Leonard model with a repelling cycle

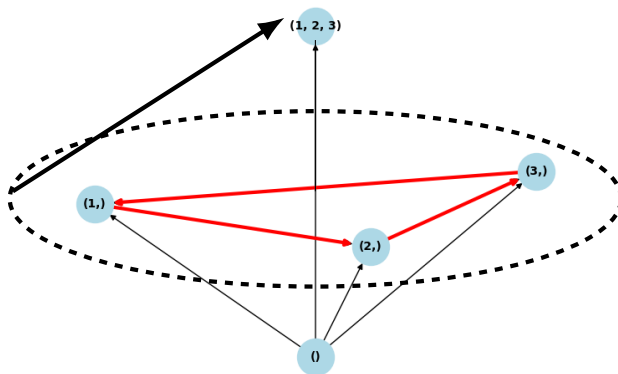
$$A = \begin{pmatrix} -1 & -\beta & -\alpha \\ -\alpha & -1 & -\beta \\ -\beta & -\alpha & -1 \end{pmatrix},$$

with $0 < \alpha < 1 < \beta$ and $\alpha + \beta < 2$, and $b_i = 1$.

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Structure of the attractor: May–Leonard



The only possibility of a “hyperedge” in 3-d: the solutions whose ω -limit is the GASS and whose α -limit is the cycle of one-species equilibria.

Open question: construct an algorithm to find all hyperedges, i.e. unstable manifolds of cycles (or of more complex structures containing cycles).

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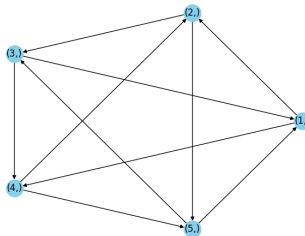
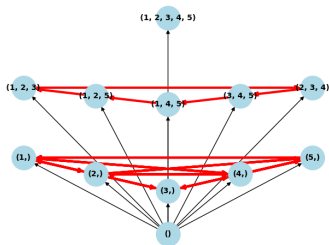
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Cycles in higher dimensions



Rock–Paper–Scissors–Lizard–Spock (5 species): the complete invasion graph (left) and its one-species part (right). Cycles of arbitrary size can occur.

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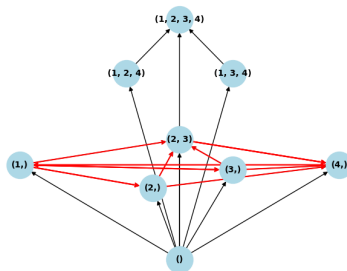
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Cycles between equilibria of different dimensions



A cycle containing equilibria of **different dimensions** (here a double species invasion in a single species environment).

Open question: find sets of data that are backwards attracted to each cycle.

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Diagonally dominant case

We never observed cycles in the diagonally dominant case, but we could not prove this rigorously. Only some partial results.

No cycles of one-species equilibria

If A is either row or column (strictly) diagonally dominant, there are no heteroclinic cycles in 3-d. In general, for a Lotka–Volterra system in any dimension, if A is either row or column diagonally dominant, then there is no cycle involving only single-species equilibria.

Strong diagonal dominance

Assume that $\mathbf{b} = (b_1, \dots, b_N) \in \mathbb{R}^N$ is such that $\min_{i=1, \dots, N} b_i > 0$ and that the matrix $A = (a_{ij})_{i,j=1}^N \in \mathbb{R}^{N \times N}$ is VL stable and

$$\max_{i=1, \dots, N} \sum_{j \neq i} \left| \frac{a_{ij}}{a_{jj}} \right| < \frac{1}{1 + M}, \quad \text{where} \quad M = \frac{\max_{i=1, \dots, N} b_i}{\min_{i=1, \dots, N} b_i}.$$

Then all 2^N communities are admissible (maximal frondosity), there are no cycles, and — if all equilibria are hyperbolic — $I \rightarrow J$ if and only if $I \subsetneq J$.

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Prevalence of cycles

On VL stable matrices

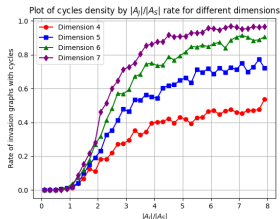
The matrix $A \in \mathbb{R}^{N \times N}$ is VL stable if and only if A can be written in the form

$$A = H(S + J),$$

where $H = \text{diag}(h_i)$, with $h_i > 0$ for $i = 1, \dots, N$, S is a symmetric stable matrix in $\mathbb{R}^{N \times N}$, and J is an antisymmetric matrix in $\mathbb{R}^{N \times N}$. Beware: S and J above are *not* the symmetric and antisymmetric parts of A ,

$$A = A_S + A_J, \quad A_S = \frac{A + A^T}{2}, \quad A_J = \frac{A - A^T}{2}$$

(they coincide only for $H = \text{Id}$). For symmetric A there is a global Lyapunov function and no cycles occur.



$|\cdot|$: sum of absolute values of the entries; 500 random VL stable matrices per rate and dimension.

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A non-autonomous counterpart [GKL], [GKLS]

$$u'_i = u_i \left(a_i(t) - b_{ii}u_i - \sum_{j \neq i} b_{ij}u_j \right), \quad i \in \{1, \dots, n\},$$

with $b_{ii} > 0$ and $b_{ij} < 0$ for $i \neq j$, so that the system is **cooperative**, and with the column diagonal dominance

$$c_j b_{jj} + \sum_{i \neq j} c_i b_{ij} > 0 \quad \text{for } j \in \{1, \dots, n\}, \quad (\text{H})$$

for some positive constants $c_1, \dots, c_n$. In the planar case

$$\begin{cases} u'_1 = u_1(a_1(t) - b_{11}u_1 - b_{12}u_2) \\ u'_2 = u_2(a_2(t) - b_{21}u_1 - b_{22}u_2) \end{cases}$$

and (H) reads $c_1 b_{11} > -c_2 b_{21}$ and $c_2 b_{22} > -c_1 b_{12}$.

There are no equilibria any more. Their role is played by **complete bounded solutions**, and we describe the **forwards** attractor — not only the pullback one.

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The building block: the logistic equation

$$u' = u(a(t) - bu), \quad b > 0, \quad a \text{ continuous and bounded.}$$

Following Ahmad and Lazer, everything is decided by the **averaged growth rate**:

$$m[a] = \lim_{n \rightarrow \infty} \inf_{t-s \geq n} \frac{1}{t-s} \int_s^t a(\tau) d\tau,$$

$$M[a] = \lim_{n \rightarrow \infty} \sup_{t-s \geq n} \frac{1}{t-s} \int_s^t a(\tau) d\tau.$$

Theorem [GKL]

If $m[a] > 0$ (**permanence**) there exists a **unique complete solution** u^* **bounded away from zero and from infinity**; it attracts, forwards in time, every solution with a positive initial datum.

If $M[a] < 0$ then every nonnegative solution tends to zero:
extinction.

u^* replaces the equilibrium a/b . If a is T -periodic,
 $m[a] = M[a] = [a] = \frac{1}{T} \int_0^T a(\tau) d\tau.$

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Planar case: which solution is globally stable

Assume that a_1, a_2 are periodic, so that $m[a_i] = M[a_i] = [a_i]$. Then the plane of the averaged growth rates decides which **globally stable solution** occurs.

Conditions on $[a_1], [a_2]$	Globally stable solution
$[a_1] > \frac{b_{12}}{b_{22}}[a_2] \ \& \ [a_2] > \frac{b_{21}}{b_{11}}[a_1]$	(u_1^*, u_2^*) — coexistence
$[a_1] > 0 \ \& \ [a_2] < \frac{b_{21}}{b_{11}}[a_1]$	$(\tilde{u}_1, 0)$
$[a_2] > 0 \ \& \ [a_1] < \frac{b_{12}}{b_{22}}[a_2]$	$(0, \tilde{u}_2)$
$[a_1] < 0 \ \& \ [a_2] < 0$	$(0, 0)$ — extinction of both

Note that the cone of coexistence **extends beyond the first quadrant**: cooperation lets a species with a negative averaged growth rate survive. The n -dimensional version is in [GKLS].

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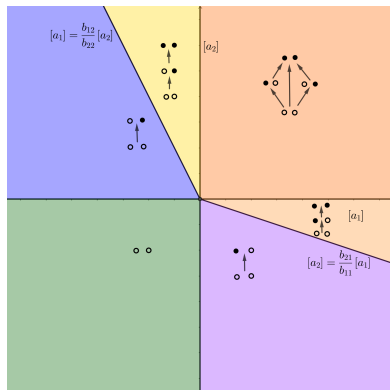
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Structure of the forwards attractor [GKL]



Each node is a complete bounded solution: a **black** dot marks a coordinate which is strictly positive, a **white** one a coordinate identically zero. Arrows are the heteroclinic connections.

The coexistence region splits into **three** subregions according to the signs of $[a_1]$, $[a_2]$: the same globally stable solution, but **different attractor structure**.

Six structures in total.

Open question: the structure on the boundaries between the regions (nonsharp inequalities) — i.e. **non-autonomous attractor bifurcation**.

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Non-autonomous May–Leonard [GKL]

$$\begin{cases} u_1' = u_1(\gamma_1(t) - u_1 - \alpha(t)u_2 - \beta(t)u_3), \\ u_2' = u_2(\gamma_2(t) - u_2 - \beta(t)u_1 - \alpha(t)u_3), \\ u_3' = u_3(\gamma_3(t) - u_3 - \alpha(t)u_1 - \beta(t)u_2), \end{cases}$$

with $0 < \alpha(t) < 1 < \beta(t)$ and $\alpha(t) + \beta(t) < 2$ for every t , and $\gamma_{\min} = \inf_{i,t} \gamma_i(t) > 0$.

Frozen in time this is exactly the VL stable May–Leonard matrix: an interior GASS and a **repelling cycle** of the three axial equilibria.

We assume in addition that, for $i \in \mathbb{Z}_3$ and every $t_0 \in \mathbb{R}$,

$$\int_{t_0}^{\infty} (\gamma_{i+1} - \gamma_i - \gamma_{\min}(\beta - 1)) \, ds = \int_{-\infty}^{t_0} (\gamma_{i+1} - \gamma_i - \gamma_{\min}(\beta - 1)) \, ds = -\infty.$$

For $\gamma_1 \equiv \gamma_2 \equiv \gamma_3$ this only says that $\beta(t) - 1$ accumulates at both ends of time.

Goal: a **time-dependent heteroclinic cycle** joining the three axial complete solutions u_1^*, u_2^*, u_3^* .

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The tool: carrying simplex via the graph transform

Hirsch: a **carrying simplex** is a compact invariant **unordered** set $\Sigma \subset \overline{C}_+ \setminus \{0\}$ such that every nonzero orbit is asymptotic to an orbit in Σ . We build a **non-autonomous family** $\{\Sigma(t)\}_{t \in \mathbb{R}}$, following the graph transform of Mierczyński and Baigent.

1 A **positively invariant region**

$$D = \{\gamma_{\min} \leq \sum_i u_i \leq 2\gamma_{\max}\} \cap \overline{C}_+.$$

2 **Retrotonicity**: if $u(t) \leq \bar{u}(t)$ then $u(s) \leq \bar{u}(s)$ for $s \leq t$ — the order is preserved *backwards*.

3 Hence $S(t, s)$ maps radial graphs over Δ onto radial graphs, and preserves unorderedness: the **graph transform** $\mathcal{T}(t, s)$.

Starting from the two constant graphs $\Delta_{\gamma_{\min}}$ and $\Delta_{2\gamma_{\max}}$, the pullback iteration is monotone, and the two limits coincide:

$$\Sigma(t) = \text{graph}_{\text{rad}}(f_t) = \lim_{s \rightarrow -\infty} S(t, s) \text{graph}_{\text{rad}}(f_0) = \mathcal{K}(t),$$

the **backward kernel** — the points admitting a complete backward orbit inside D .

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Two species: the connection lives on the simplex

$$\begin{cases} u_1' = u_1(\gamma_1(t) - u_1 - \alpha(t)u_2), \\ u_2' = u_2(\gamma_2(t) - u_2 - \beta(t)u_1). \end{cases}$$

Here $\Sigma(t)$ is a **curve** joining $(u_1^*(t), 0)$ and $(0, u_2^*(t))$.

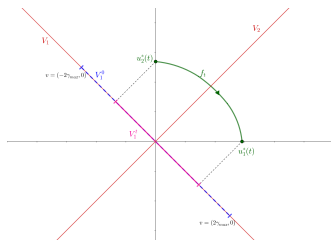
Theorem [GKŁ]

Every complete solution on the relative interior of $\Sigma(t)$ satisfies

$$u(t) \rightarrow (0, u_2^*(t)) \quad (t \rightarrow -\infty),$$

$$u(t) \rightarrow (u_1^*(t), 0) \quad (t \rightarrow +\infty).$$

The proof follows $w = u_2/u_1$: on D we have $\sum_i u_i \geq \gamma_{\min}$, so $(\log w)' \leq \gamma_2 - \gamma_1 - \gamma_{\min}(\beta - 1)$, and the divergence assumption forces $w \rightarrow 0$ forwards and $w \rightarrow \infty$ backwards. The convergence to u_i^* then follows from the logistic equation for $1/u_i$.



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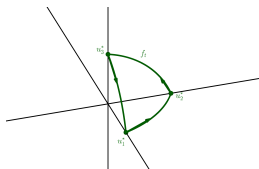
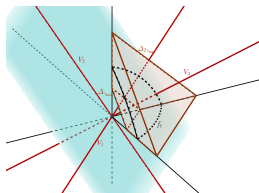
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Three species: the non-autonomous cycle



- ▶ The same construction in 3-d gives a family of **Lipschitz radial graphs** $\Sigma(t)$ over Δ (constant $\sqrt{2}$, from the geometry of the unordered cone).
- ▶ Its **boundary** consists of the three one-dimensional carrying simplices of the two-species subsystems.
- ▶ Each of them is a heteroclinic connection, and together they close up into a **cycle**, $u_1^* \rightarrow u_3^* \rightarrow u_2^* \rightarrow u_1^*$.

To our knowledge the first direct graph-transform construction of a non-autonomous heteroclinic cycle. (For general non-autonomous carrying simplices in the Kolmogorov class see Shen and Wang.)

Open: is the cycle the α -limit of the interior solutions, as in the autonomous case? And what replaces the invasion graph when there are no equilibria?

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Thank you!