Long Transients in Ecology: Theory and Observations

Sergei Petrovskii

Department of Mathematics, University of Leicester, UK

New Mathematical Methods for Complex Systems in Ecology
BIRS, Banff, Canada, July 29 - August 2, 2019

NIMBioS Working Group (2017-19):

Long Transients & Ecological Forecasting

Karen Abbott

Kim Cuddington

Tessa Francis

Gabriel Gellner

Alan Hastings

Ying-Cheng Lai

Andrew Morozov

Sergei Petrovskii

Katherine Scranton

Mary Lou Zeeman

Plan of the talk

- Introduction: what are long transients?
- Basic mechanisms generating long transients (nonspatial systems)
- Relation to tipping points
- A (brief) look at spatial systems
- Conclusions

What is it all about

Transient: lasting for only a short time; temporary

(Cambridge English Dictionary)

Typically, transients are associated with the effect of the initial conditions and disappear relatively fast.

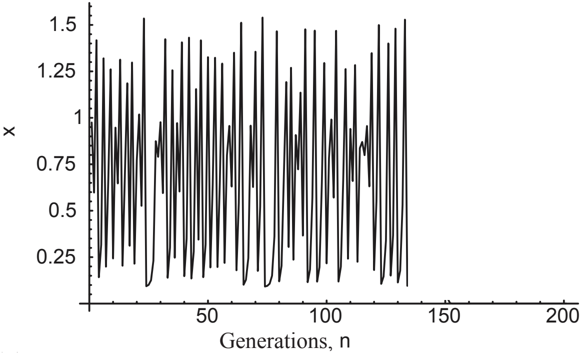
Long-term dynamics are usually associated with the system's attractors.

"Long transient" is apparently an oxymoron??

However...

Examples of long transients in population models

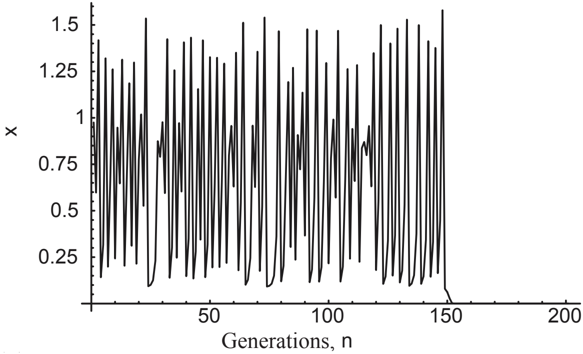
Dynamics of a nonspatial, time-discrete, single-species model:



(from Schreiber, 2003)

Examples of long transients in population models

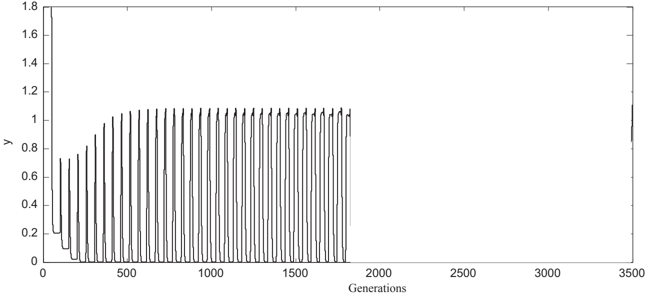
Dynamics of a nonspatial, time-discrete, single-species model:



(from Schreiber, 2003)

Examples of long transients in population models

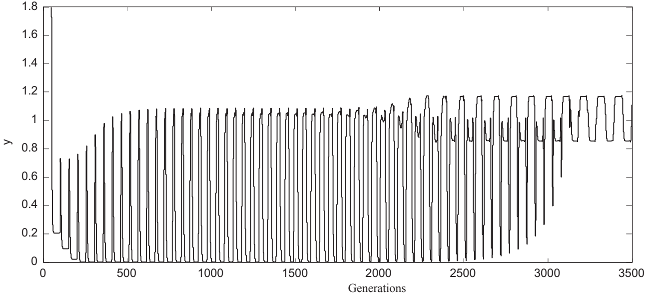
Time-continuous single-species model with time-delay:



(from Morozov et al., 2016)

Examples of long transients in population models

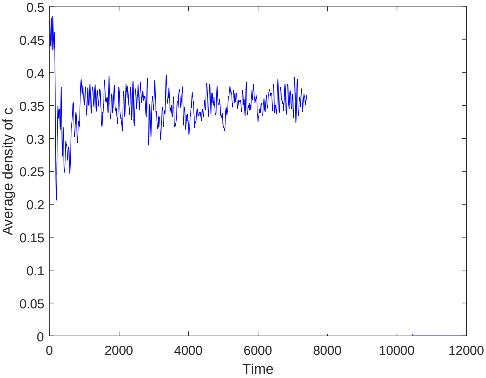
Time-continuous single-species model with time-delay:



(from Morozov et al., 2016)

Examples of long transients in population models

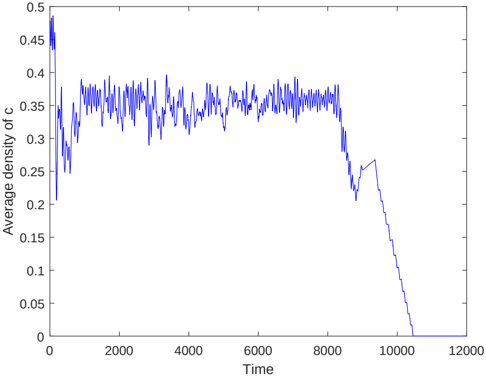
Space-time-continuous, 3-species model (plankton dynamics):



(from Petrovskii et al., 2017)

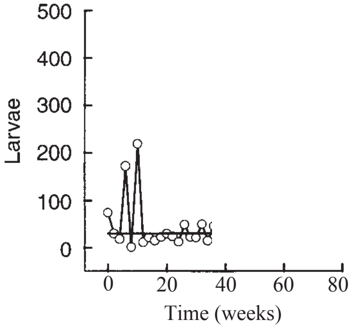
Examples of long transients in population models

Space-time-continuous, 3-species model (plankton dynamics):

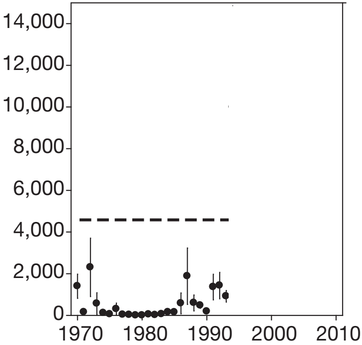


(from Petrovskii et al., 2017)

Empirical examples are abundant too

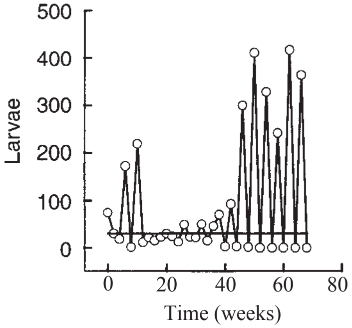


Flour beetle data (lab)
(from Cushing et al., 1998)

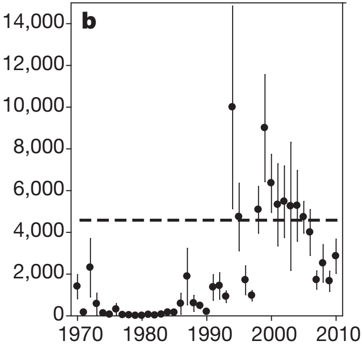


Forage fishes (field)
(from Frank et al., 2011)

Empirical examples are abundant too



Flour beetle data (lab)
(from Cushing et al., 1998)



Forage fishes (field)
(from Frank et al., 2011)

In all above examples, a regime shift occurs

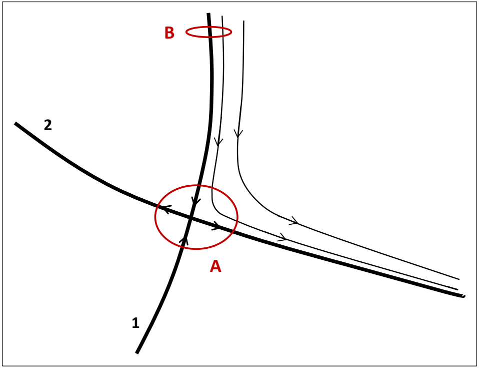
A well-known theory of regime shifts relates it to a tipping point: a bifurcation (e.g. saddle-node) due to a slow change in some system's parameter (environmental conditions) (e.g. Scheffer et al. 2009, 2012; Kuehn 2011; Dakos et al., 2012, 2014)

Interestingly, in all above examples, parameters (environmental conditions) are constant!

How that can be possible?

Overview of the baseline mechanisms

"Crawl-by": transients induced by a **saddle**



Here *A* is the 'small' vicinity of the saddle, *B* the range of appropriate initial conditions

Transients induced by a saddle

Consider a generic population dynamics model:

$$\frac{du_k(t)}{dt} = f_k(\mathbf{u}), \qquad k = 1, \dots, n,$$

where $\mathbf{u} = (u_1, \dots, u_n)$ are the population densities, t is time.

Linearized system in the vicinity of a steady state $\bar{\mathbf{u}}$:

$$\frac{dx_k(t)}{dt} = a_{k1}x_1 + \dots a_{kn}x_n, \qquad k = 1, \dots, n,$$

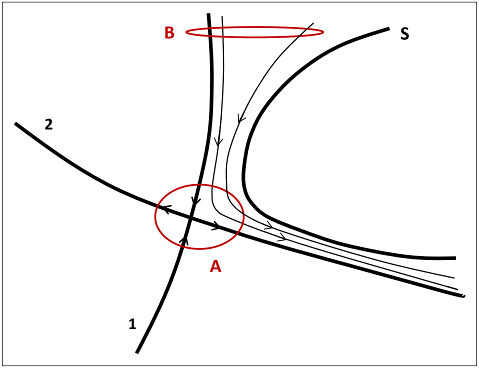
where $x_k(t) = u_k(t) - \bar{u}_k$.

Solution is a linear combination of exponents $e^{\lambda_i t}$. Let λ_1 be the eigenvalue with the largest real part, $\mathrm{Re}\lambda_1 > 0$. The time spent in the vicinity of the (unstable) steady state is estimated as

$$\tau \propto \frac{1}{\mathrm{Re}\lambda_1}.$$

Transients induced by a saddle

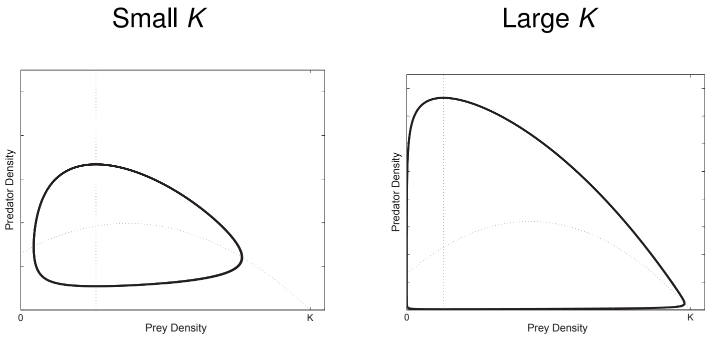
Nonlinear effects can substantially increase the range of appropriate initial conditions:



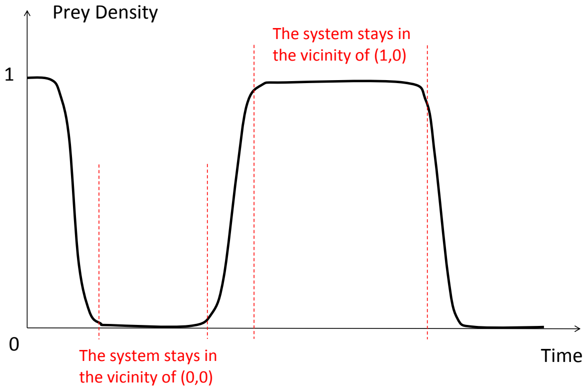
A is the ‘small’ vicinity, *B* the range of appropriate initial conditions, *S* is a separatrix

Example: Rosenzweig–MacArthur model

$$\frac{du(t)}{dt} = \alpha u \left(1 - \frac{u}{K}\right) - \frac{\gamma uv}{u+h}, \qquad \frac{dv(t)}{dt} = \frac{\nu\gamma uv}{u+h} - mv$$



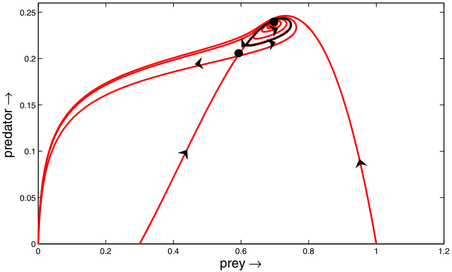
This will result in recurrent long transients:



Generalization 1

A modified prey-predator system can have a saddle point in the interior of the domain (not at the origin), so that the decay to low density is not a necessary property

Example: strong Allee effect for prey, quadratic mortality for predator

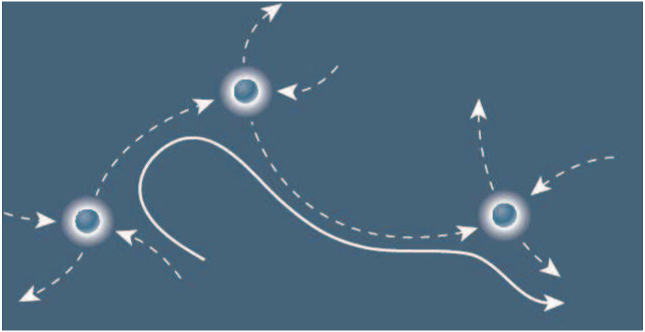


(Sen & Banerjee 2015)

Generalization 2

Saddle-induced transients in a higher-dimensional systems

A case of more complex dynamics: connected saddles:

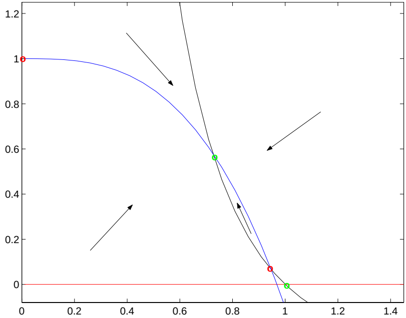


(Ashwin & Timme, 2005)

Ghost attractors

Consider a generic two-species system:

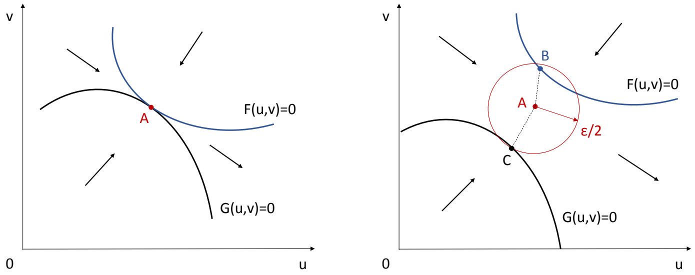
$$\frac{du}{dt} = F(u, v; p), \qquad \frac{dv}{dt} = G(u, v; p)$$



Two-species nonlinear competition model (Hastings et al. 2018)

Ghost attractors

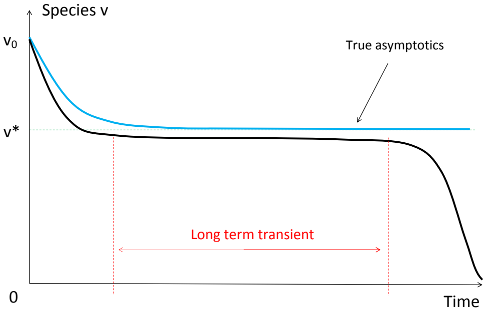
A change in the parameter value can bring the system beyond the saddle-node bifurcation:



However, the local bifurcation does not change the global structure of the phase flow: the system slows down in the vicinity of the pre-bifurcation steady state location

Ghost attractors

The long transient dynamics occur:



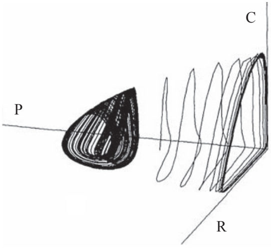
The transient's duration depends on the closeness to the bifurcation:

$$\tau \propto |p - p_c|^{-0.5} .$$

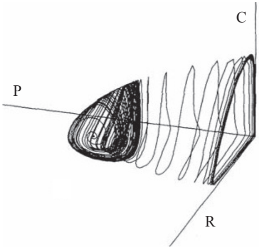
Ghost attractors

A similar mechanism applies to more complicated dynamics, e.g. periodic solutions (limit cycles) and chaos.

Example: long-term chaotic transient (chaotic ghost) in a resource-consumer-predator system(Hastings and Powell 1991; McCann and Yodzis 1994)



Pre-bifurcation: chaotic attractor coexists with a stable limit cycle



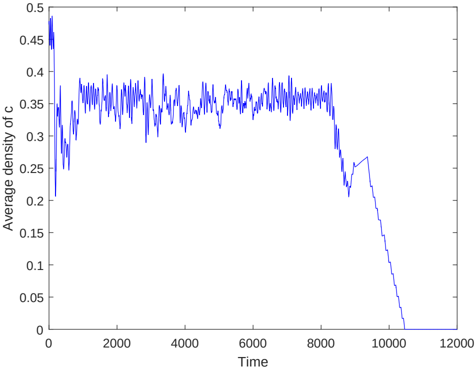
Post-bifurcation: the two basins merge, chaotic attractor disappears

Chaotic transients can be particularly long: $\tau \propto \exp\left(k|p - p_c|^{-\gamma}\right) \quad (k, \gamma > 0)$

(Grebogi et al. 1983, 1985)

Ghost attractors

Example of the time-series generated by a chaotic ghost:



(Petrovskii et al., 2017)

Slow-fast systems

Consider

$$\frac{du(t)}{dt} = f(u, v, \epsilon), \qquad \frac{dv(t)}{dt} = \epsilon g(u, v, \epsilon), \qquad \epsilon \ll 1. \tag{1}$$

Introducing a rescaled time $\tau = \epsilon t$, it turns into

$$\epsilon \frac{du(\tau)}{d\tau} = f(u, v, \epsilon), \qquad \frac{dv(\tau)}{d\tau} = g(u, v, \epsilon). \tag{2}$$

In the limit $\epsilon \to 0$, system (1) turns into

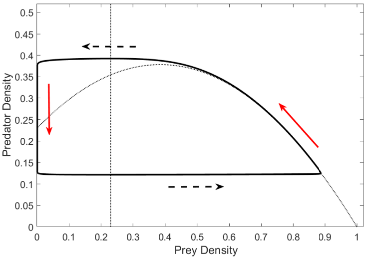
$$\frac{du(t)}{dt} = f(u, v, 0), \qquad \frac{dv(t)}{dt} = 0,$$

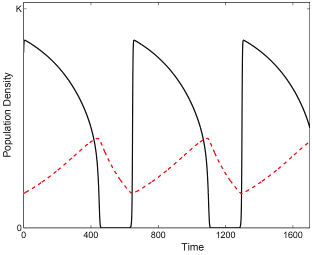
and system (2) turns into

$$0 = f(u, v, 0), \qquad \frac{dv(\tau)}{d\tau} = g(u, v, 0),$$

Slow-fast systems

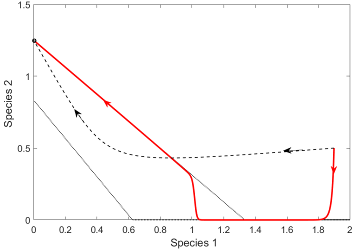
Example 1: periodical dynamics in a prey-predator system ($\epsilon = 0.01$)

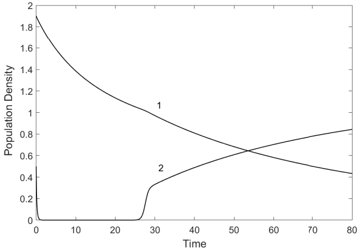




Slow-fast systems

Example 2: aperiodical dynamics in a two-species competition system

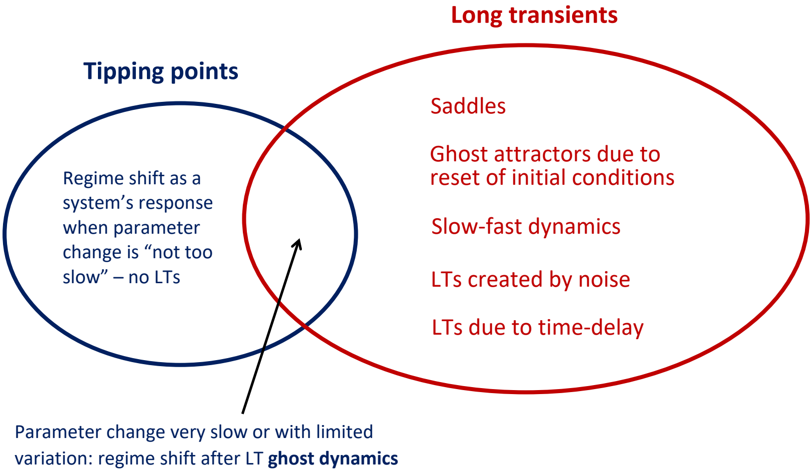




Black (dashed) curve for $\epsilon = 1$, red curve for $\epsilon = 0.002$

Relation between long transients and tipping points

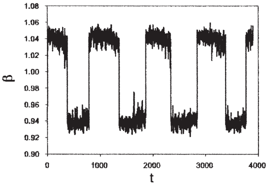
Relation between long transients and tipping points



Long transients in higher dimensional systems

- Effect of time-delay is known to generate long transients but the scaling law is unknown

- Effect of noise - broad and variable. For non-chaotic systems (saddles and ghosts), tends to decrease the transient's life-time but would not normally destroy it. Can create the transient dynamics (e.g. in bistable systems):



- For chaotic transients, noise can increase as well as decrease the transient's life-time (Grebogi et al. 1983; Do and Lai 2004, 2005).

- Spatial systems: new types of transients (e.g. related to population waves propagation).

A brief look at the spatial systems

What are the new phenomena brought in by explicit space?

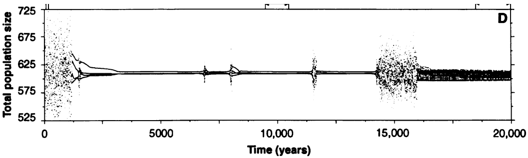
- Pattern formation
- Synchronization / desynchronization & onset of spatiotemporal chaos
- Travelling waves

A brief look at the spatial systems

Consider the space-continuous, time-discrete single-species system:

$$u(x, t+1) = \int_0^L g(x-y)F(u(x,t))dx, \quad F(u) = ue^{r(1-u)}.$$

For distributed random initial conditions, the system's dynamics exhibit a chaotic saddle:



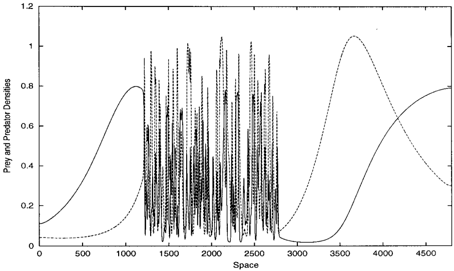
(Hastings and Higgins, 1994)

A brief look at the spatial systems

The above system exhibits long transients in terms of the spatially average values

Knowledge of the spatial population distribution can provide a different angle on long transients

Example: “wave of chaos” in a space-time-continuous prey-predator system:



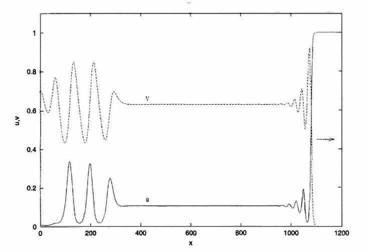
(Petrovskii and Malchow, 2001)

Spread of the chaotic phase over the system can take a very long time, $\tau \propto \frac{L}{c}$.

A brief look at the spatial systems

For compact initial conditions, the system's dynamics usually consists of a succession of population waves

Example: space-time-continuous (diffusion-reaction) prey-predator system, invasion of predator; dynamical stabilization in the wake of the invasion front

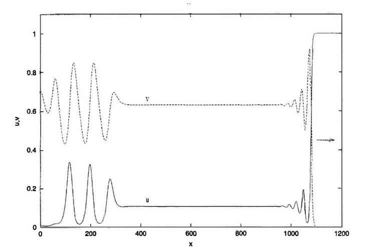


(Petrovskii and Malchow, 2000)

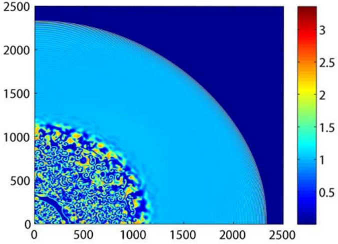
A brief look at the spatial systems

For compact initial conditions, the system's dynamics usually consists of a succession of population waves

Example: space-time-continuous (diffusion-reaction) prey-predator system, invasion of predator; dynamical stabilization in the wake of the invasion front



(Petrovskii and Malchow, 2000)



(Petrovskii et al., 2016)

Conclusions

- Long transients do occur
- The life-time of long transients can be arbitrary long (cf. scaling laws)
- We have identified a few basic mechanisms for the long transients to occur
- Long transients provide an alternative scenario of regime shifts

References

Hastings A, Abbott KC, Cuddington K, Francis T, Gellner G, Lai YC, Morozov A, Petrovskii S, Scranton K, Zeeman ML (2018) Transient phenomena in ecology. *Science* **361**, eaat6412.

Morozov A, Abbott KC, Cuddington K, Francis T, Gellner G, Hastings A, Lai YC, Petrovskii S, Scranton K, Zeeman ML (2019) Long transients in ecology: theory and applications. *Physics of Life Reviews*, under revision.

Thanks for listening